2012

ECOLOGY OF MATING PATTERNS AND SEXUAL SELECTION IN DICKCISSELS BREEDING IN MANAGED PRAIRIE

Bridget Frances Sousa

University of Kentucky, spiza1@gmail.com

Click here to let us know how access to this document benefits you.

Recommended Citation

Sousa, Bridget Frances, "ECOLOGY OF MATING PATTERNS AND SEXUAL SELECTION IN DICKCISSELS BREEDING IN MANAGED PRAIRIE" (2012). Theses and Dissertations--Biology. 17.
https://uknowledge.uky.edu/biology_etds/17

This Doctoral Dissertation is brought to you for free and open access by the Biology at UKnowledge. It has been accepted for inclusion in Theses and Dissertations--Biology by an authorized administrator of UKnowledge. For more information, please contact UKnowledge@lsv.uky.edu.
STUDENT AGREEMENT:

I represent that my thesis or dissertation and abstract are my original work. Proper attribution has been given to all outside sources. I understand that I am solely responsible for obtaining any needed copyright permissions. I have obtained needed written permission statement(s) from the owner(s) of each third-party copyrighted matter to be included in my work, allowing electronic distribution (if such use is not permitted by the fair use doctrine) which will be submitted to UKnowledge as Additional File.

I hereby grant to The University of Kentucky and its agents the irrevocable, non-exclusive, and royalty-free license to archive and make accessible my work in whole or in part in all forms of media, now or hereafter known. I agree that the document mentioned above may be made available immediately for worldwide access unless an embargo applies.

I retain all other ownership rights to the copyright of my work. I also retain the right to use in future works (such as articles or books) all or part of my work. I understand that I am free to register the copyright to my work.

REVIEW, APPROVAL AND ACCEPTANCE

The document mentioned above has been reviewed and accepted by the student’s advisor, on behalf of the advisory committee, and by the Director of Graduate Studies (DGS), on behalf of the program; we verify that this is the final, approved version of the student’s thesis including all changes required by the advisory committee. The undersigned agree to abide by the statements above.

Bridget Frances Sousa, Student
Dr. David Westneat, Major Professor
Dr. Brian Rymond, Director of Graduate Studies
ECOLOGY OF MATING PATTERNS AND
SEXUAL SELECTION IN DICKCISSELS BREEDING IN
MANAGED PRAIRIE

D I S S E R T A T I O N

A dissertation submitted in partial fulfillment of the
requirements for the Doctor of Philosophy in the
College of Arts & Sciences
at the University of Kentucky

By

Bridget Frances Sousa

Lexington, Kentucky

Director: Dr. David F. Westneat, Professor of Biological Sciences

Lexington, Kentucky

2012

copyright © Bridget Frances Sousa 2012
ABSTRACT OF DISSERTATION

ECOLOGY OF MATING PATTERNS AND SEXUAL SELECTION IN DICKCISSELS BREEDING IN MANAGED PRAIRIE

Males of many species have elaborate phenotypes that are absent in females and that are thought to be the result of sexual selection. Sexual selection requires: (i) variance in male mating success, (ii) variation in male phenotype, and (iii) covariation between male mating success and male phenotype. Environmental conditions influence these factors, and management practices that alter environmental conditions have the potential to shape mating patterns and sexual selection. I investigated the hypothesis that the frequency of fire, used to manage tallgrass prairie, affects the mating patterns and process of sexual selection in the organisms breeding in managed prairies.

I studied dickcissels (Spiza americana), a small songbird resident in tallgrass prairie. I first examined mating patterns and sexual selection in dickcissels independent of burning regime. I found variation among males in the number of mates attracted, in the number of offspring sired with each mate, and the offspring sired with the mates of other males. I found a positive association between social mates and siring success, but no evidence for an effect of breeding density or synchronous nesting on mating success. Male dimorphic traits, size, song, and plumage, showed between-individual variation but selection gradients were weak and often fluctuated between the years of study.

I next examined patterns of mating success in plots burned on a variable schedule. I found little evidence that burning influenced either the mean or the variance in social mating success, paternity, or male phenotype. Burning regime also had no influence on sexual selection gradients with the single exception of selection on tarsus length. Temporal variation was more important for patterns of mating success and sexual selection gradients on male traits than was burning regime. The demography of dickcissels in the breeding season suggests, however, that habitat management on a larger scale may be more influential. My findings extend our understanding of sexual selection in birds and the effects of management on the factors required for sexual selection and the magnitude of selection.

KEYWORDS: sexual selection, grassland management, mating patterns, dickcissel, tallgrass prairie
Bridget F. Sousa
Student Signature

Date
ECOLOGY OF MATING PATTERNS AND SEXUAL SELECTION IN DICKCISSELS BREEDING IN MANAGED PRAIRIE

By

Bridget Frances Sousa

__________________________
David Westneat
Director of Dissertation

__________________________
Brian Rymond
Director of Graduate Studies
This dissertation is dedicated to my mother.

You were right, that was a good research idea
ACKNOWLEDGEMENTS

This dissertation is dedicated to my mother, Dr. Sheila Byrne Sousa, whose response to my every childhood question was, “That sounds like a great research project.” She has offered her encouragement and support throughout, sacrificing several months of vacation over the years to assist me as field technician and secretary. I am forever grateful for her many years of technical, field, financial and grammatical support. My father has also provided love and support throughout my education.

I would also like to extend my profound thanks to my brother, Dr. Duncan Sousa, and my dear friend, Lauren Reynolds. They picked me up when I was down, were a constant source of encouragement and perspective, and even assisted me in the field despite a total lack of any reasonable form of compensation.

Dr. David Westneat has been an understanding and insightful advisor. He has helped me develop as a professional and provided valuable guidance in the analysis of non significant data. I have benefited immensely from his expertise and mentoring. Dave’s rock star popularity has led a number of students through his doors. My lab mates have been a constant source of support. We have read each others’ manuscripts, learned from each other and taught each other so much more than statistics and lab techniques. My thanks go out to Sarah Martin Stewart, Dr. Ian Stewart, Dan Wetzel, Kate “Utah” Newman, Dr. Amanda Ensminger, Patricia Hartman, Sanh Kin Diep and Damon Orsetti.

I would also like to thank my committee and outside examiner for their helpful suggestions. Dr. Nicholas McLetchie, Dr. Phil Crowley, Dr. Charles Fox and Dr. John Cox have all been very supportive.
Many people at the Museum of Vertebrate Zoology guided me through my years as an undergraduate. Their aid continued into my graduate career. Thanks to Dr. Eileen Lacey and Dr. Jim Patton for inspiration, education and the invitation to conduct my lab work at the MVZ.

No research endeavor can be accomplished without the mostly invisible army that supports it. I also owe a great deal of thanks to the staff of the Biology Department, particularly Beverly Taulbee, Melissa Justice, Cheryl Edwards, Kelley Salyers and Mike Adams. Missy and Bev have been especially helpful throughout my graduate career and I appreciate their time and efforts. I am also indebted to the faculty and staff at Konza Prairie Biological Station, especially Dr. Brett Sandercock, Barb van Slyke and Tom van Slyke. A number of undergraduates also spent countless hours enduring blood sucking insects, vicious dickcissels, fire, flood and the occasional golf ball sized hail storm. Thank you Wayne Li, Lauren Scopel, Daily Leonhard and Ryan Sheldon for all your hard work and dedication.

Finally, I would like to acknowledge Konza Prairie Biological Station, which is a preserve of The Nature Conservancy managed by the Division of Biology at Kansas State University, and the following sources of funding: the Gertrude Flora Ribble Fund, the Department of Biology, the UK Graduate School, the Animal Behavior Society, and the American Philosophical Society’s Lewis and Clark Fund for Field Research.
# TABLE OF CONTENTS

Acknowledgements ........................................................................................................ iii

List of Tables .................................................................................................................. vii

List of Figures ............................................................................................................... ix

Chapter One: Introduction ............................................................................................ 1

Chapter Two: Sickly singers: a review of song and parasite mediated sexual selection  
Hypotheses of parasite mediated sexual selection ......................................................... 7  
Avian song characteristics ......................................................................................... 13  
Consideration of song in parasite mediated sexual selection ................................... 15  
Future directions ...................................................................................................... 29

Chapter Three: Polygyny and extrapair paternity in dickcissels (*Spiza americana*)  
Introduction ................................................................................................................. 38  
Methods ....................................................................................................................... 40  
Results ......................................................................................................................... 43  
Discussion ..................................................................................................................... 47

Chapter Four: Variance in mating success does not produce strong sexual selection on  
ornaments in a polygynous songbird  
Introduction .................................................................................................................. 54  
Methods ....................................................................................................................... 56  
Results ......................................................................................................................... 59  
Discussion ..................................................................................................................... 62

Chapter Five: Effects of fire management on mating patterns in dickcissels (*Spiza  
americana*)  
Introduction .................................................................................................................. 73  
Methods ....................................................................................................................... 76  
Results ......................................................................................................................... 79  
Discussion ..................................................................................................................... 80

Chapter Six: Sexual selection varies across time in a managed environment  
Introduction .................................................................................................................. 91  
Methods ....................................................................................................................... 95  
Results ......................................................................................................................... 98  
Discussion ..................................................................................................................... 99

Chapter Seven: Conclusions and future directions ..................................................... 112
Appendices
   Appendix 1: Assumptions of Hamilton and Zuk.......................................................116
   Appendix 2: Measures of Song..................................................................................117
   Appendix 3: Design and effectiveness of a novel trap for capturing nesting
songbirds.........................................................................................................................122
   Appendix 4: Matlab code for the calculation of yellow feather coloration..............128
   Appendix 5: Demographic parameters of dickcissels.............................................132

References........................................................................................................................139

Vita...................................................................................................................................165
LIST OF TABLES

Table 2.1: Effects of developmental stress on song complexity and output ..........31
Table 2.2: Results of studies investigating the relationship between testosterone and song complexity ..................................................................................................................32
Table 2.3: The effects of testosterone on song output ........................................33
Table 3.1: Characteristics of microsatellite loci used in dickcissel paternity analysis .51
Table 3.2: Comparison of models explaining nest survival in dickcissels ..................51
Table 4.1: Repeatability of color variables across measurements of individual dickcissel feathers and across averaged measurements for each male ..........67
Table 4.2: Repeatability of dickcissel song variables within recordings and between recordings .................................................................................................................................67
Table 4.3: Mean ± standard deviation, coefficient of variation and sample sizes of male dickcissel traits in 2006 and 2007 .................................................................67
Table 4.4: Correlations among male dickcissel phenotypic traits ................................68
Table 4.5: Means, variances, standardized variances and proportion of total variance of components of male dickcissel reproductive success in each breeding season .........................................................................................................................68
Table 4.6: Estimated directional selection gradients for dickcissels in each breeding season .................................................................................................................................69
Table 4.7: Associations between male traits and harem size, within pair paternity, and extrapair siring success in dickcissels .........................................................................................................................70
Table 5.1: Sample sizes and burn history for the watersheds included in this study ............................................................85
Table 5.2: Variation in harem sizes among burn regimes studied in 2008 and 2009 ....85
Table 5.3: Effect sizes, F statistics and p-values for the analysis of the effects of harem size, shrub cover, year and their interactions on dickcissel paternity .........................................................................................................................86
Table 5.4: Mean and variance in harem sizes across three studies of dickcissels ......86
Table 6.1: Sample sizes and burn history for the sites included in this study...........106
Table 6.2: Pearson correlations among measures of dickcissel male body size .......106
Table 6.3: Relationships between four measures of traits of male dickcissels and each of two components mating success .................................................................107
Table 6.4: Mean and standard deviation of fitness and male traits for the four years of the study .................................................................................................................................108
Table 6.5: Mean, standard deviation and tests of homogeneity of variance in fitness components and male traits across the two burn regimes .......................................109
Table A5.1: Sample sizes and burn history for the sites included in this study.........136
Table A5.2: Proportion of banded dickcissels that returned to breed in the following year.................................136

Table A5.3: Number of females renesting and double brooding...............................................136

Table A5.4: Fates of nests studied from 2006-2009...........................................................................137

Table A5.5: Burn treatment models tested in Program MARK to predict survival rates of dickcissels on Konza in 2008 and 2009.................................137
| Figure 2.1: | Under the original IHH testosterone positively affects sexual signals, but has a negative quantitative effect on the immune response to parasites |
| Figure 2.2: | In Wedekind and Fosldad’s version of the IHH, testosterone mediates tradeoff in the allocation of energy between immunity and ornaments |
| Figure 2.3: | There are two possible pathways by which stress may act on adult song learning in the developmental stress hypothesis |
| Figure 2.4: | Hypothetical trill rate by frequency bandwidth plot |
| Figure 3.1: | Variation across years and sites in the proportion of extrapair young occurring in dickcissel broods |
| Figure 3.2: | Variation across years and sites in the proportion of dickcissel nests containing at least one extrapair chick |
| Figure 3.3: | Scatter plot of the proportion of nearby dickcissel chicks sired thorough extrapair copulations by males with different harem sizes |
| Figure 3.4: | The total number of related dickcissel fledglings sired by males with different harem size |
| Figure 4.1: | I photographed each male dickcissel in a standard upright position with the bill pointed directly at the camera lens |
| Figure 4.2: | Reflectance spectrum of dickcissel yellow breast feathers |
| Figure 4.3: | A typical dickcissel song, with two dick and three cissel phrases |
| Figure 5.1: | In watersheds without shrubs, males perch on tall forbs and grass to monitor their territories |
| Figure 5.2: | False color aerial photograph illustrating shrub cover in dickcissel male territories on an unburned watershed |
| Figure 5.3: | Variance in harem size across the burn treatments studied in 2008 and 2009 |
| Figure 5.4: | Mean ± standard error of dickcissel harem size and within pair paternity for each burn regime in 2008 |
| Figure 5.5: | Standard deviation of forb and small woody shrub cover for all watersheds studied in 2008 |
| Figure 5.6: | Mean and standard error of dickcissel harem size and within pair paternity for each burn regime in 2009 |
| Figure 5.7: | Standard deviation of forb and small woody shrub cover in 2009 |
| Figure 6.1: | Selection gradients ± standard error are plotted for each year and for all years combined |
| Figure 6.2: | Selection gradients ± standard error are plotted for each burn regime |
Figure A2.1: Some basic song vocabulary illustrated on a spectrogram from the
dickcissel. .............................................................................................................119
Figure A2.2: Spectrogram of dickcissel song showing some song output variables.....120
Figure A2.3: Dickcissel spectrogram illustrating song frequency variables ...............121
Figure A3.1: Diagram of the nest trap used to capture female dickcissels and indigo
buntings .............................................................................................................126
Figure A3.2: The nest trap positioned over a “nest” using deployment method one .....127
Figure A3.3: The nest trap deployed using method two .........................................127
Figure A5.1: Dickcissel nesting phenology for each year of the study .................138
Chapter 1

Introduction

Males of many species have elaborate phenotypes that are absent in females. Such dimorphisms are generally thought to be the result of sexual selection (Darwin 1871; Andersson 1994). However, in order for sexual selection to act, three conditions are needed: (i) variance in male mating success (the opportunity for sexual selection), (ii) variation in male phenotype, and (iii) a process creating covariance between male mating success and male phenotype (Andersson 1994).

All three of these conditions have been well studied, but the discovery of widespread extrapair paternity has added complexity to the study of variance in male mating success. The original works describing how variance in mating success might be measured focused on the number of mates a male acquires and number of offspring he produces with those mates (e.g. Wade 1979; Arnold and Wade 1984). More recent work demonstrating male mating outside of social pair bonds adds complexity to measures of variance in mating success (reviewed in Westneat et al. 1990). The opportunity for sexual selection is determined by variance in both within- and extrapair mating success. The interaction between these two forms of mating success can affect the overall opportunity for sexual selection (Webster et al. 1995). In organisms that engage in extrapair mating, total variance in mating success, \( \text{Var}(T) \), can be measured by adding the variance in within-pair mating success, \( \text{Var}(W) \); the variance in extrapair mating success, \( \text{Var}(E) \); and twice the covariance between the two (Webster et al. 1995):

\[
\text{Equation 1: } \text{Var}(T) = \text{Var}(W) + \text{Var}(E) + 2 \text{Cov}(W, E)
\]

An increase in the opportunity for sexual selection will be seen if there is a positive covariance between within- and extrapair mating success, as has been found in several polygynous species (Moller 1992; Hasselquist 1994; Hasselquist et al. 1995b; Hasselquist and Sherman 2001). Nevertheless, one component may contribute to overall variance in mating success more than another. In monogamously mating species, extrapair mating success usually contributes more to variance in mating success than within-pair mating success (Whittingham and Lifjeld 1995; Whittingham and Dunn 2005; Webster et al. 2007; Perlut et al. 2008). It is possible that the same pattern is found in polygynously mating species (Gibbs et al. 1990); however, most studies of polygynous birds have found that social pairing success contributes more to variance in male mating success than extrapair mating success (Webster et al. 1995; Freeman-Gallant 1997; Weatherhead and Boag 1997; Whittingham and Dunn 2005). Whether this pattern holds across all or even most polygynous species is unknown, as few such species have been studied.

Previous research has demonstrated that social mating interacts with extrapair mating in a number of species (reviewed in Hasselquist and Sherman 2001; Vedder et al. 2011). A logical next step is to explore why these relationships exist and the consequences of such relationships for sexual selection. Two interesting factors that can influence components of male mating success are variation in male phenotype and habitat. Male phenotype is frequently an important determinant of male reproductive success (Andersson 1994). In organisms with multiple routes to mating success,
ornaments might play different roles in different mating contexts. In the first half of my dissertation I examine components of male mating success and the association of male ornaments with mating success in each mating context.

One of the central tenets of mating system theory is that environmental factors can influence patterns of mating (Emlen and Oring 1977; Westneat et al. 1990). There is also evidence that environmental conditions can affect the association between ornaments and mating success (e.g. Seehausen et al. 1997). Increasingly, human activities alter the environmental conditions under which animals breed. Nevertheless, few studies have addressed how human alteration of the environment influences vertebrate mating patterns or sexual selection. In the second half of my dissertation, I examine the effects of habitat management practices on mating patterns and sexual selection.

Male phenotype and variation in male mating success

The associations among components of male mating success and male phenotypes may be complex, with a number of factors influencing the nature of these associations. First, the mechanisms linking male traits to reproductive success could lead to a reduction in selection on traits over an evolutionary time scale. Female preferences for particular male traits seem likely to reduce genetic variation and eventually lead to fixation of the phenotype (the paradox of the lek, Kirkpatrick and Ryan 1991). The strength of selection on male traits could therefore depend on the sustainability of mechanisms linking male traits to reproductive success. One way ornaments may be linked to male mating success in an evolutionarily stable manner is if they signal health and vigor. Condition dependent expression of male ornaments could then be used by other males as a signal of competitive ability, much like badges of status (Rohwer 1982; Smith et al. 1988). Such traits could also be used by females seeking to obtain either direct or indirect benefits from their mates (Kirkpatrick and Ryan 1991). For example, there is strong support for the condition dependence of carotenoid ornaments. Hill (2002) found that male house finches with brighter red breasts were better foragers and provided more food to their nestlings than duller males. Furthermore, redder males tended to produce redder sons (Hill 1991). Other male ornaments may also signal a male’s condition. For instance, several male song traits, such as song rate and the proportion of time spent singing, may more accurately reflect a male’s current condition than would plumage traits produced months earlier (Gil and Gahr 2002). Such traits could be used by males to assess potential rivals and by females to assess the suitability of potential mates. In chapter two I review the evidence for some alternative hypotheses regarding the role of song traits in advertising male quality.

Second, the potential for male ornaments to contribute to male reproductive success may vary depending on the association between social and extrapair mating success. Two major hypotheses have been posited describing the link between social and extrapair mating success in polygynous birds (Hasselquist and Sherman 2001). According to the tradeoff hypothesis, males face a number of potential conflicts when pursuing social mates, guarding fertility with those mates, and seeking extrapair fertilizations (Westneat et al. 1990; Hasselquist and Sherman 2001). Such tradeoffs would reduce the variance in male mating success and potentially limit the contribution of male phenotypes to reproductive success. Alternatively, the female choice hypothesis suggests that females bias mating towards the same males in all contexts (Hasselquist and...
Sherma 2001). This would enhance variance in mating success and maximize the potential contribution of male phenotypes to reproductive success. Few studies have examined the associations among social and extrapair mating success in polygynous birds. In chapter three, I test the predictions made by the two hypotheses describing the link between social and extrapair mating success.

Finally, the strength and direction of sexual selection may depend on which traits influence which components of mating success. In polygynous birds, complex associations among traits, social mating success and extrapair mating success could generate complicated patterns of sexual selection (Webster et al. 1995; Jones et al. 2001; Vedder et al. 2011). While a number of studies have investigated the role of male ornaments in determining mating success in monogamous birds, few have investigated the complexities of sexual selection in polygynous birds. In chapter four, I measure sexual selection in a polygynous songbird and examine the associations of male traits with each component of male fitness. I then examine these associations to determine how sexual selection interacts among different components of mating.

Habitat effects on the components of sexual selection

Environmental conditions can influence variance in male mating success (Emlen and Oring 1977; Perlut et al. 2008), variance in male phenotypes (Hill 1993, 2002), and the covariance between the two (e.g. Seehausen et al. 1997). One of the most obvious ways that habitat can affect male mating patterns is by influencing rates of polygyny. A central tenet of mating system theory is that habitat structure and composition affect the distribution of individuals in time and space, which in turn affects patterns of mating within a population (Verner and Willson 1966; Orians 1969; Emlen and Oring 1977). Habitat heterogeneity leads to high variance in territory quality, which favors polygyny. In contrast, homogenous distribution of resources decreases variance in territory quality, favoring monogamy (Emlen and Oring 1977). The idea that variance in male mating success is higher in polygynous than in monogamous mating systems has received mixed theoretical support (Clutton-Brock 1988; Ims 1988; Wiegmans and Nguyen 2006), although interspecific comparisons generally support the idea (Clutton-Brock 1988). Intraspecific studies comparing populations of varying polygyny rates are rare, but there is some support for the idea that variance in mating success increases with heterogeneity in resource distribution (Lindstrom and Seppa 1996). Therefore, the opportunity for sexual selection may increase in heterogeneous habitats that promote polygynous mating. If so, then sexual selection could be stronger in more heterogeneous habitats. Despite a long history of research on mating systems theory, very little research has directly assessed the association between habitat heterogeneity and polygyny.

Another way that habitat may affect mating patterns is via extrapair mating. One way this can occur is through habitat effects on population density (Westneat and Sherman 1997; Griffith et al. 2002). Population densities are expected to increase in areas of high resource availability. Encounter rates between individuals on different territories should also increase in densely populated areas, thereby increasing the opportunity for extrapair mating (Birkhead 1978; Westneat and Sherman 1997). The effects of population density on EPP rates have been frequently tested (reviewed in Griffith et al. 2002), and results support a general trend for a positive effect of population density on EPP rates (Westneat and Sherman 1997). However, the implications of the
relationship between density and EPP for sexual selection itself have not been well studied.

Extra pair mating rates may also depend on the ability of males to effectively guard their mates from other males (Sherman and Morton 1988; Westneat et al. 1990). Effective mate guarding may trade off with territory defense, pursuit of additional mates (either social or extrapair), or foraging activity (Westneat et al. 1990). Habitat structure can influence these tradeoffs by affecting the efficiency and ease with which a male can guard his mate(s) (Sherman and Morton 1988; Westneat and Stewart 2003; Mays and Ritchison 2004). For example, visually occluded habitats may make effective mate guarding more difficult. In yellow-breasted chats (*Icteria virens*), rates of EPP were higher in territories with dense vegetation verses those in open habitats. This difference was attributed to the decreased ability of males to guard their mates in visually occluded habitats (Mays and Ritchison 2004). No other studies have examined whether visual occlusion does indeed increase EPP rates. So while the hypothesis is clearly plausible, its applicability to other systems and habitats is unknown.

In addition to its influence on variance in mating success, ecological conditions can also affect variance in male phenotypes. One way this can occur is through variation in the environmental availability of resources necessary for the production of male ornaments. For instance, Hill (1993, 2002) found that variation in plumage coloration in house finches (*Carpodacus mexicanus*) depended on the environmental availability of carotenoids. Populations in habitats with high carotenoid availability expressed the full range of male coloration, from pale yellow through bright red. In contrast, populations where carotenoids were in poor supply uniformly expressed dull yellow or orange plumage.

While ecological conditions may vary depending on climate and location, human activities also have profound effects on the environment. Habitat destruction is widespread and efforts to mitigate the negative consequences of human activity have grown in response. Habitat management strategies are now required for most of the remaining wildlife habitat in North America. While the effects of management practices on survival and fecundity are well studied, the more subtle influences of management on mating patterns and sexual selection are not frequently the target of research. I examine the above associations between ecological factors and mating patterns in the context of habitat management in chapter five.

Finally, environmental conditions can vary substantially across time and space. Since environmental variation can influence the components of sexual selection, the strength and direction of selection might vary in response to changing conditions. This possibility might help explain some of the inconsistent results of selection studies (e.g. Andersson 1994; Weatherhead and Boag 1995; Gontard-Danek and Moller 1999; Moller et al. 2006; Westneat 2006). Nevertheless, studies of variation in selection gradients in response to changes in environmental conditions are rare, especially in birds. I examine variation in sexual selection across time and management regimes in chapter six.

**Study System**

I studied the ecology of mating patterns and sexual selection in a neotropical migrant bird, the dickcissel (*Spiza americana*). Dickcissels are facultatively polygynous (Zimmerman 1971). While extrapair fertilizations are common in passerine birds
(Westneat et al. 1990; Schlicht et al. 2011), it is not known if dickcissels engage in extrapair copulations.

Dickcissels are sexually dimorphic. Males have a bright yellow breast, black bib, and simple song that are lacking or much reduced in the drabber female. These birds are obligate prairie nesters. They generally nest near the ground in dense grass, forbs, or low woody shrubs, but will occasionally build nests up to 4 m above ground in woody plants (Gross 1968). Zimmerman (1971) showed that dickcissels prefer habitat that is structurally diverse and predominantly forbs rather than grasses or trees, as forbs provide the structure needed to support a nest.

Dickcissels are native to the tallgrass prairie ecosystem and breed in large numbers on the plains of the American Midwest (Temple 2002). Tallgrass prairie is an early successional ecosystem dependent on fire to prevent the incursion of trees and other woody plants. The time between fires (burn interval) affects the structural complexity and composition of prairie vegetation. Short intervals produce simple, grass dominated communities and longer intervals promote a structurally complex mix of grass, forbs, and woody shrubs (Hartnett and Fay 1998). Historically, fires in this ecosystem are thought to have occurred every 2-10 years (Rowe 1969; Hulbert 1973; Wright and Bailey 1982). Current management practices favor annual burns that maximize primary productivity. While the effects of burning on the vegetative composition of grasslands are well studied, the consequences of these treatments for avian mating systems and sexual selection are not known.

Specific Aims

The first half of my dissertation focuses primarily on variance in male mating success and the covariance between male phenotypes and components of male mating success. The second half of my dissertation examines the effects of managed prairie burning on sexual selection and all three of its component factors (variance in mating success, variance in phenotype and covariance between the two).

Strong directional selection on male traits could lead to loss of phenotypic variation and eventual fixation of traits (Borgia 1979b; Kirkpatrick and Ryan 1991). Nevertheless, phenotypic variation generally persists in species with strong sexual selection on male traits. One way variation in traits may persist in the face of strong directional selection is through parasite mediated sexual selection (Hamilton and Zuk 1982). In chapter two I briefly review three main hypotheses of parasite mediated sexual selection: the Hamilton and Zuk hypothesis (Hamilton and Zuk 1982), immunocompetence handicap hypothesis (Folstad and Karter 1992) and developmental stress hypothesis (Nowicki et al. 1998; Nowicki et al. 2002a). I then examine the potential role of song in testing each of these hypotheses. Bird song is a complex trait consisting of multiple components that can be learned or innate, energetically demanding or condition independent, fixed or labile. This complexity makes song a valuable, but largely underutilized trait for testing hypotheses of parasite mediated sexual selection.

For sexual selection to occur, some males must have higher mating success than others. In chapter three, I examine patterns of male mating success. There are two major hypotheses concerning patterns of social and extrapair mating success. The tradeoff hypothesis posits that the pursuit of extrapair mates may come at a cost. Such costs may include a reduction in paternity with existing mates or the inability to attract additional
social mates. In contrast, the female choice hypothesis states that female preference for particular males across all mating contexts leads to a positive correlation among the components of male mating success. Ecological factors, such as density and nest predation, may influence the interactions among different components of male mating success. In chapter three I examine the association between social and extrapair mating in dickcissels and the contribution of density and nest predation to mating patterns.

Sexual selection results from covariation between male traits and mating success. In chapter four I measure sexual selection acting on sexually dimorphic traits of male dickcissels. First, I describe variation in four major categories of male dimorphic traits: body size, black bib size, yellow breast plumage and song. I then examine the associations of these traits with different components of male mating success. Finally, I use the results of these analyses to determine which components of male mating success contribute to sexual selection.

In the second half of my dissertation, I examine the effects of prescribed fire on mating patterns and sexual selection in dickcissels. There are a number of ways that fire regimes on the tallgrass prairie can influence male mating patterns and I test three of these in chapter five. First, habitat heterogeneity increases with the time between fires (Collins and Smith 2006). According to Emlen and Oring (1977), variance in male mating success should increase with increasing habitat heterogeneity. Therefore, variance in male mating success should increase with the interval between burns. Second, burning regimes influence the abundance of several breeding birds (Westemeier and Buhnerkempe 1983; Zimmerman 1997; Powell 2006, 2008). Dickcissel densities increase with frequent burning (Powell 2006). As the density of male dickcissels increase, territory sizes shrink (Zimmerman 1971). These conditions should increase encounter rates between individuals, which may lead to higher extrapair paternity (Westneat et al. 1990). If extrapair mating increases with territory density, then extrapair paternity rates should be highest in frequently burned sites. Finally, visual obstruction, in the form of large woody shrubs, increases with burn interval. Such visual obstruction could interfere with male mate guarding. If so, then extrapair paternity should be higher on sites where infrequent burning has promoted the growth and spread of large woody shrubs.

Environmental conditions can influence all three factors required for sexual selection (see above), yet these conditions can vary substantially across time and space. In chapter six, I examine whether variance in mating success, variance in male phenotype and sexual selection gradients varied across the four years of my study. I also examine whether these factors differed between frequently and infrequently burned prairie.

Chapter seven provides a summary of my findings. I also take the opportunity to explore several broader questions that my work raises and outline some areas of future research that might be informative.
Chapter 2

Sickly singers: a review of song and parasite mediated sexual selection

Since the publication of Hamilton and Zuk's (1982) seminal paper on the role of parasites in avian sexual selection, the study of parasite resistance and sexual signals has been a major focus of behavioral and evolutionary studies. Much of this work has focused on the role of color signals in advertising male resistance to pathogens. A much smaller but growing literature has been investigating the role of avian song in signaling parasite resistance. Song is composed of a multitude of traits with varying developmental and production mechanisms, upon which sexual selection can act. These traits may be learned or innate, continuous or discrete, subject to physiological constraints or not, fixed early in development or flexible throughout life. This complexity makes song both a challenge to work with and incredibly valuable for testing hypotheses of parasite mediated sexual selection. With such a wide variety of characteristics different theories of parasite mediated sexual selection can be tested by examining different song characteristics within the same species.

This review examines the three major hypotheses of parasite mediated sexual selection: the Hamilton and Zuk hypothesis, immunocompetence handicap hypothesis, and developmental stress hypothesis. First, I review the assumptions, predictions and theoretical framework for each of the three hypotheses. Second, I examine avian song, dividing it into several broad components based primarily on the manner in which song has been studied in the past (Read and Weary 1990; Gil and Gahr 2002). Finally, I consider each component of song separately in light of the three hypothesis of parasite mediated sexual selection. The goal here is to determine which traits are best suited to testing each hypothesis, review the literature examining song traits in tests of the three hypotheses, and clarify areas where study is still needed.

HYPOTHESES OF PARASITE MEDIATED SEXUAL SELECTION

Hamilton and Zuk Hypothesis

Female mating preference for males with particular traits seems likely to produce a loss of genetic variation and fixation of the trait, and yet both trait variation and female preference generally persist. This “paradox of the lek” (Kirkpatrick and Ryan 1991) has been a challenge to many researchers studying sexual selection -- how do animals maintain genetic variation and signal honesty in the face of female preference for particular traits (Borgia 1979a)? Hamilton and Zuk (1982) hypothesized that sexual signals could remain honest and avoid fixation if signals reflected the individual’s genetic resistance to parasites\(^1\). Parasite resistance is advertised by traits whose quality is dependent on the health and vigor of the animal. Host-parasite coadaptational cycles generate variation in heritable resistance within host populations and this process maintains genetic variation in parasite resistance. Hamilton and Zuk's assumptions about the relationship between hosts and parasites are outlined in Appendix 1.

\(^1\) The term parasite is used in the broadest sense to include internal and external, unicellular and multicellular organisms.
There are three criteria for a trait to function in parasite mediated sexual selection. First, females must show a preference for the trait. Second, the trait must be condition dependent. Third, parasitic infection must degrade that condition for the trait to reflect genetic resistance. The first criterion is fairly straight-forward; however Hamilton and Zuk do not clearly define "condition" in relation to the latter two criteria. The most common interpretation is that traits are energy dependent. Parasites use up host energy, both directly by using the host to replicate itself, and indirectly by stimulating an immune response. Thus parasitized animals have less energy to devote to the development and maintenance of sexual ornaments than unparasitized animals. Another way of interpreting condition dependence is that the ornaments are dependent on a limited resource that is decreased by parasitism. For example, the bright reds and yellows of avian plumage are created by carotenoids deposited in feathers. These carotenoids are also important in immune defense (reviewed in Moller et al. 2000). Birds obtain carotenoids solely from their food, so carotenoid availability may be limited. Thus parasitized animals must use some of their carotenoids in fighting infection, reducing the amount of carotenoids they have to put into feathers, and resulting in duller plumage ornaments (Moller et al. 2000).

Hamilton and Zuk explicitly state that their hypothesis would be contradicted if either of two scenarios occurred. First, their hypothesis is contradicted if, within a species, females preferred more heavily parasitized males over less heavily parasitized males. This follows directly from the criteria outlined above. Second, their hypothesis would be contradicted if, among species, those with more elaborate sexual traits were least subject to infection by parasites. This prediction stems from two assumptions. First, species subject to wider varieties of parasites or high likelihoods of parasitism should be under greater selective pressure from parasitism. Second, species under stronger selective pressure to escape parasitism should also be under stronger sexual selection to advertise parasite resistance. Strong sexual selection on a phenotype leads to greater elaboration of that phenotype. Thus species subject to large varieties or higher likelihood of parasites should also exhibit the most complex sexual ornaments.

Measuring Resistance

Parasite Load. One of the challenges of testing the Hamilton and Zuk hypothesis is determining how best to measure resistance to parasites. The most obvious way, and the method employed by Hamilton and Zuk, is to measure parasite load in an individual. However, parasite load measures the result of resistance (or lack thereof), not resistance itself, and can be confounded with other variables. For instance, variation in exposure to pathogens, parasite life histories and pathogenicity all lead to variations in parasite loads that are not directly related to an animal's genetic resistance. Furthermore, to truly test the hypothesis, all parasites that are not purely acute in nature would have to be examined, including ectoparasites, viruses, fungi, etc. Unless this is done, any lack of significant results could be explained by a failure to examine the parasites of importance. However, such a task is impractical, as a full examination for internal and external parasites would be onerous and require the sacrifice of a large number of animals.

Immune Response. One alternative to measuring parasite load is to assess the immune response itself. In populations with high parasite pressure, a higher investment in immunity and higher immune response would be expected. Lindstrom and colleagues
tested this relationship in small ground finches on the Galapagos archipelago. They found that ectoparasites and avian pox were more prevalent and/or intense on larger islands. Correspondingly, birds on large islands had higher concentrations of natural antibodies and a faster response to the KLH antigen than birds on small islands. Cell mediated immune response, measured by wing swelling in response to phytohemagglutinin (PHA), was also significantly related to island size, however it varied in the opposite direction, with birds on small islands having the highest PHA response (Lindstrom et al. 2004). This pattern could reflect tradeoffs between different aspects of the immune response. Thus, immune responses may be a way to test the Hamilton and Zuk hypothesis without exhaustive examinations of endo- and ectoparasites. However, the tradeoffs involved necessitate measuring multiple aspects of the immune response.

Within populations, the relationship between immune response and parasite resistance is less clear. Generally, a stronger response is expected to be more effective against parasites. However, if a weaker response is sufficient to clear the infection, then a stronger response wastes resources that could be used elsewhere in the animal. Strong responses can also be detrimental to the health of the animal. If a strong immune response leads to increased tissue damage or an autoimmune response then an intermediate response might be more beneficial to the animal (Strasser et al. 1991; Westneat and Birkhead 1998; Davidson and Diamond 2001). While most researchers focus on the magnitude of immune responses, other characteristics of the immune response might also be important. For instance, the speed of a response might be an important indicator of immune quality (Onodera et al. 2008). Faster recognition of a parasite could lead to a more effective response, and faster, more complete clearance of the parasite (e.g. Koup et al. 1994; Chakrabarti et al. 1995a; Chakrabarti et al. 1995b). Rapid immune responses could also be detrimental, as faster responses may be more prone to misinterpretation of immune signals and result in autoimmunity.

Finally, there are many ways to measure immunocompetence, including immune organ size, counts of immune cells, and the magnitude of immune responses to specific challenges. Nevertheless, such measures assess a specific function of the immune system, not necessarily the quality of the immune response as a whole. The relationship between broader measures of immunity (size of organs or quantity of cells) and the ability to resist infection by parasites is not always straightforward (Luster et al. 1993). Furthermore, the heritability of these traits is also unclear since condition, infection history, and environment, to name a few, all affect the magnitude and speed of the immune response (Bly et al. 1997; Ewenson et al. 2003; Westneat et al. 2004; Garvin et al. 2006; Gleeson 2006). Finally, there is insufficient evidence that any single measure of immunocompetence can adequately index the ability of an individual to resist parasitic infection (Luster et al. 1993; Siva-Jothy 1995). Thus, such measures may be misleading and their reliability has been questioned (Lochmiller 1995; Owen and Clayton 2007). Lochmiller (1995) suggests the three-tiered approach developed by immunotoxicologists as a viable alternative to reliance on any single immune assay (Luster et al. 1992). This approach employs tests of both the innate and humoral immune responses and has been successfully used in studies of wild birds (Lochmiller et al. 1993). While the use of multiple measures does not fully compensate for all of the above shortcomings of immunological assays, it is a good step forward in addressing the pitfalls of measuring
immunocompetence. For a more complete evaluation of specific immune measures, see the recent review of ecological immunity in Functional Ecology (e.g. Baucom and de Roode 2011; Boughton et al. 2011).

The Major Histocompatibility Complex. While measures of immune response avoid the sampling problems inherent in assessing parasite prevalence, the exact attributes that characterize a "good" immune response can be challenging to determine. Examining variation of genes that confer pathogen resistance avoids this and other problems associated with measuring parasite load and immune response. The major histocompatibility complex (MHC) is a set of genes coding for proteins that recognize and bind foreign antigens and initiate the adaptive immune response (Klein 1986). Variation at this locus can confer either resistance or susceptibility to specific pathogens (Apanius et al. 1997; Penn 2002). Failure of the MHC protein to bind a particular pathogen results in failure of the adaptive immune system to respond to the infection. Poor binding affinity should also increase susceptibility, since fewer MHC molecules will bind and present the antigen. This results in less efficient recognition of infected cells by the immune system, causing a slower response time and a decreased activation of the immune response (Accolla et al. 1995; Pandey 2007). If coadaptational cycles between hosts and parasites exist as predicted by Hamilton and Zuk, then this would result in frequency dependent selection on MHC alleles. In species under heavy parasite pressure, one would expect to find strong frequency dependent selection acting on multiple MHC alleles (Bodmer 1972; Slade and McCallum 1992; Penn and Potts 1999). Under these conditions, a large number of alleles is expected to develop as host mutations to detect parasites coevolve with parasite mutations to avoid detection (Apanius et al. 1997). Thus, a greater number of alleles at MHC loci is expected in species experiencing heavy parasitism. Within species, individuals with MHC genotypes that confer resistance to relevant pathogens in the environment are expected to be in better condition and have better ornaments than those with genotypes that do not confer resistance (Hamilton and Zuk 1982).

While Hamilton and Zuk did not originally envision measuring the genes that confer resistance directly, this approach to testing their hypothesis is increasingly feasible and desirable. As an example, von Schantz and colleagues' study of pheasants (Phasianus colchicus) is particularly relevant. In pheasants, spur length is associated with female preference and male condition (von Schantz et al. 1996). Spur length was found to be correlated to specific MHC genotypes and males with these genotypes had higher survival rates. Furthermore, the MHC genotype associated with spur length and survival changed between years, suggesting changes in parasites that altered the effectiveness of specific MHC combinations (von Schantz et al. 1997). However, it is not known whether changes in genotypes reflect changes in parasites or even whether parasite resistance is causally related to spur length. Both are required by the Hamilton and Zuk hypothesis.

Further support for the MHC's role in parasite mediated sexual selection comes from studies of mammals and fish. A study of wild three-spined sticklebacks showed a positive correlation between male breeding coloration and a particular MHC allele, although the function of this allele in parasite resistance was not known (Jager et al. 2007). MHC diversity has also been shown to be important in mate choice, although the evidence is mixed (Edwards and Hedrick 1998; Penn and Potts 1999). Higher MHC
diversity may convey resistance to a broader range of pathogens; however, the importance of optimal versus maximal diversity and whether females choose based on compatibility or simple allele counting is still being debated in the literature, and there are studies supporting each of these alternatives (Landry et al. 2001; Penn 2002; Bernatchez and Landry 2003; Freeman-Gallant et al. 2003). Nevertheless, the MHC is a very promising and somewhat neglected measure of heritable parasite resistance.

In addition to the MHC, other highly variable, immunity-related gene families could be involved in parasite mediated sexual selection. For example, the genes that code for T and B cell receptor regions also play a vital role in parasite recognition. Sequencing of the receptor coding regions of undifferentiated T and B cells will quantify the variation available for creating the binding sites that recognize antigens. Selection for specific alleles and allele combinations here will presumably function like selection for MHC variants.

**Immunocompetence Handicap Hypothesis**

Under the Hamilton and Zuk hypothesis, condition mediates the relationship between heritable resistance and sexual signals. Other mechanisms linking parasite resistance and sexual signals have since been proposed. In 1992 Folstad and Karter proposed that a significant cost of sexual ornamentation is increased susceptibility to parasites. They further posited that this relationship is caused by the dual effects of testosterone on sexual signals and immunity. Specifically, they proposed that testosterone has a positive dose dependent effect on the development and maintenance of secondary sexual characters, but a negative dose dependent effect on immune function. This system is self regulated, so an individual compensates for infection by decreasing testosterone and thus the sexual signal (Folstad and Karter 1992). Therefore, males with the best sexual ornaments will have higher testosterone levels and fewer parasites. They named their hypothesis the immunocompetence handicap hypothesis (IHH).

One way this could work is if testosterone affects variation in quantity but not quality of the immune response (Figure 2.1). Three assumptions about immunity must be made for this scenario to work. First, testosterone must decrease the number of immune cells recruited in response to infection. Second, an increase in the number of recruited immune cells must be beneficial (e.g. result in faster clearance of infection). Finally, this immune response and the effects of resistance genes must be positively associated. If these conditions are met, then one would expect that males with good resistance genes will have a lower parasite load for a given level of testosterone than males with poor resistance genes.

This hypothesis soon came under fire for being evolutionarily unstable. A mutant that uncoupled the effects of testosterone on the immune system (e.g. by eliminating testosterone receptors in the immune system) would be able to have both a high immune response and good ornaments, thus gaining an advantage over other males. In response, a more plausible modification of the Folstad and Karter's original immunocompetence handicap hypothesis was proposed (Wedekind 1992; Wedekind and Folstad 1994). Instead of directly mediating the interaction between the immune system and sexual signals, testosterone mediates a tradeoff in resource allocation to these two functions (Figure 2.2). Males with good resistance genes will have fewer parasites and be in better condition. Males with poor resistance genes will be more susceptible to parasites and
suffer decreased condition due to both an increase in energy needed by the immune system to fight infection and the energy demands of the parasite itself. The former can allocate energy away from immunity to ornaments by increasing testosterone, while the latter must allocate its resources to its immune system by depressing testosterone. Thus, for a given parasite exposure, males with high testosterone levels and good ornaments will be in better condition and have lower immune responses, but a lower parasite load than males with poor resistance genes. This modification to Folstad and Karter’s original hypothesis brings the IHH much closer to the original Hamilton and Zuk hypothesis. Indeed, the IHH may even be viewed as a specific mechanism through which condition dependent parasite mediated sexual selection acts.

**Developmental Stress Hypothesis**

Another mechanism by which parasites may affect sexual signals, especially avian song, is via developmental stress. The brain structures that mediate song learning develop early in life, when birds are most likely to experience physiological stress. Nowicki and colleagues (1998) originally hypothesized that variation in the ability of young animals to deal with nutritional stress early in life leads to variation in their ability to develop the brain structures necessary for song learning. Furthermore, failure to fully develop brain structures cannot be compensated for later in life. Thus the learned aspects of song could serve as an honest signal of male quality, indicating their ability to deal with under-nutrition early in life (Nowicki et al. 1998; Nowicki et al. 2002a). A mechanism describing how birds might vary in their ability to deal with nutritional stress was not proposed. Variation in foraging ability or parental care might account for this, but there are more direct mechanisms by which females may judge heritable foraging and paternal care abilities in males (e.g. carotenoid coloration Hill 1990; Hill 1991). Authors testing this idea also ignore individual variation in stress management skills in favor of comparing the songs of nutritionally stressed versus unstressed individuals. While this research confirms that under-nutrition affects song development, it does not, in fact, test the nutritional stress hypothesis, which maintains that females gain benefits from preferring males who were not stressed during development.

More recently, the nutritional stress hypothesis has been extended to include other stressors, including parasitism. Parasite mediated sexual selection can be incorporated into the developmental stress hypothesis in two ways. In the original scenario, under-nutrition acts as a stress that decreases overall energy reserves and increases susceptibility to parasitism (Figure 2.3, route 1). Indeed, the immunosuppressive effect of stress in general is well known and widely supported in the literature (McEwen et al. 1997; Apanius 1998; Raberg et al. 1998; Marketon and Glaser 2008). These include the effects of nutritional stress, administration of corticosterone, and other forms of stress, such as social and thermal stress. The negative effects of stress hormones include reduced NK cell activity, lymphocyte populations, lymphocyte proliferation, and antibody production (Marketon and Glaser 2008). Nonetheless, this relationship involves a wide range of complex interactions between the nervous and immune systems, and a direct negative effect of stress and stress hormones on immunocompetence is not always observed.

An alternative scenario is that parasitism itself is the stressor which causes under-nutrition (Figure 2.3, route 2). Since parasites use up host resources and induce
energetically costly immune responses, it seems plausible that parasitism could act in this way. In fact, this is exactly what Hamilton and Zuk envisioned, but here restricted to early development. The difference between these two scenarios is essentially whether parasitism causes nutritional stress or nutritional stress results in increased parasitism. It is likely that both occur, so this difference is arguably not important in an evolutionary sense. Males may be able to compensate for lower resistance with higher investment in immunity, but this may come at a cost to investment in other areas, such as song learning (Nowicki et al. 2002a; Moller et al. 2005). Thus learned features of song can provide an honest signal of an individual's genetic resistance to disease, since conditions early in life make young birds particularly susceptible to infection. Females can use learned features of song to assess a male's heritable resistance to disease.

This version of the nutritional stress hypothesis is identical to the Hamilton and Zuk hypothesis in all respects except timing and traits. Under nutritional stress, the effects of parasite infection on song occur in early development (within the first few months to year of life), and affect only the learned components of song.

**AVIAN SONG CHARACTERISTICS**

Bird song is a complex learned trait with multiple characteristics. Each of these song characteristics may be subject to different selection regimes and constraints. To properly address whether bird song can be used to evaluate hypotheses of parasite mediated sexual selection, the different aspects of song must be considered separately. Several authors have examined the properties of and selective forces acting on avian song (e.g. Read and Weary 1992; Gil and Gahr 2002). I will build on their work to create categories of avian song which may be evaluated in light of the above hypotheses. Appendix 2 explains some basic avian song terminology and defines the traits under consideration in this review.

Gil and Gahr (2002) divide song components into three broad categories: repertoire size, performance related traits, and specific song content. Repertoire size refers to the total number of different songs or song elements a bird sings. Variation in repertoire size between individuals is generally attributed to differences in learning ability. Repertoire size has also been linked to the development of specific brain regions, primarily the HVC (*nucleus hyperstriatalis ventrale, pars caudale*), but also, to some extent, the RA (*nucleus robustus archistriatalis*). A study of forty-one oscine birds showed a significant positive correlation between the volume of the HVC and the number of song types in a species' repertoire (Devoogd et al. 1993). Within a species, HVC volume has also positively correlated with repertoire size (Nottebohm et al. 1981; Airey and DeVoogd 2000), however the evidence is somewhat mixed (Leitner and Catchpole 2004). Since these characteristics are strongly linked, they will generally be addressed together under the heading "song complexity." In addition, copy accuracy, song switching, and song sharing will be included in this category, since they are also associated with learning and/or neural development.

Performance related traits are "characteristics of song that can be measured quantitatively irrespective of song content" (Gil and Gahr 2002, pg. 134). These primarily include measures of the amount of song produced, such as song rate, song length, and intersong interval (Appendix 2). Such traits are mainly constrained by
energetic costs. For example, time spent singing directly competes with time spent doing other activities, such as foraging. Gil and Gahr also include amplitude (loudness) in this category; however, I feel that this trait is best considered separately since its constraints may not be as straightforward as those of other performance measures. Those traits that measure the amount of song produced will be referred to as "song output" traits, while those dealing with loudness will be called amplitude traits.

Finally, specific song content includes measures of song sharing between individuals, song dialect, special syllables, and song frequency. Since these traits do not appear to share much in terms of constraints or selective regimes, I will ignore this category and address these traits individually.

Dialect and song sharing are both ways of measuring an individual's similarity to his neighbors, with song sharing working on a smaller scale (more immediate neighbors) than dialect (usually population level). Song sharing is dependent on learning and matching the songs of a neighbor. Because of its dependence on learning, song sharing will be considered a measure of song complexity and discussed there. Dialect is usually a fixed trait determined by the population in which a bird learned his song. There are multiple theories concerning the evolution and selective advantage of song dialects, however dialect is generally not a strong factor in sexual selection (Chilton and Lein 1996; Riebel and Slater 1998), and so will not be further considered.

Song frequency is an important property of avian song. There are several common frequency measures, including highest, lowest, bandwidth, and frequency of greatest amplitude. Body size may limit frequency production, with larger bird species able to produce lower frequencies; however, variation within species has not been much studied (Wallschlager 1980). It is also not known whether frequency traits are inherent or learned, or if they are condition dependent.

Special syllables are defined in relationship to female choice: they are elements of the song that explain most of the variation in male success. This is a rather vague category of traits that are not unified by any particular constraint and could include traits from other categories. I will therefore redefine "special syllables" as a category of song traits which do not appear to fit into any other category, but whose acoustic properties make them particularly difficult to produce. For example, female swamp sparrows (Melospiza georgiana) prefer males that sing fast trills with large frequency bandwidths (Ballentine et al. 2004). Frequency bandwidth trades off with trill speed, such that it is harder to repeat large bandwidths quickly (Westneat et al. 1993). In addition, it has been proposed that some syllables are more difficult to produce than other syllables, and their inclusion in the repertoire advertises high male quality (Catchpole and Slater 2008).

**CONSIDERATION OF SONG IN PARASITE MEDIATED SEXUAL SELECTION**

**Song Complexity**

*Hamilton and Zuk, Developmental Stress*

The first criterion of the Hamilton and Zuk hypothesis is that females exhibit a preference for the trait. By far, the most common measure of song complexity is repertoire size, so I will discuss it first. A number of studies have shown female preference for large repertoires and increased reproductive success in males with larger
repertoires (Mountjoy and Lemon 1991; Catchpole and Slater 1995; Devoogd 2004). Thus, repertoire size meets Hamilton and Zuk's first criterion.

The second criterion required by Hamilton and Zuk is condition dependence of the trait. Repertoire size is not obviously condition dependent. In fact, Lambrechts and Dhondt (1988) hypothesized that large repertoires might actually reduce the condition dependence of song complexity, as switching between song types could reduce syringeal muscle exhaustion. Later authors criticized this hypothesis for not fitting available physiological data that indicate modifications of these muscles and others involved in repetitive tasks (such as the heart and lungs) promote long term repetitive use, as well as data showing that the ventilatory muscles responsible for air flow would be more susceptible to exhaustion than syringeal muscles (Gaunt et al. 1996). I do not know of any evidence that large repertoires are any more costly to sing than smaller repertoires produced at the same rate, nor does it seem like they should be. There may be neural bioenergetic costs to singing more complex songs; however, a review of these did not find evidence for an increased production cost of more complex songs (Gil and Gahr 2002). Therefore repertoire size does not appear to be directly condition dependent, as required by Hamilton and Zuk.

While repertoire size does not appear to be immediately condition dependent, the development of this trait may be condition dependent in the manner envisioned by the developmental stress hypothesis. The brain structures involved in song production develop during a critical period that occurs soon after fledging and lasts a few months (Brenowitz et al. 1997). This timing makes repertoire size an ideal candidate for testing the developmental stress hypothesis. According to this hypothesis, condition during the critical period of song learning should have a positive effect on song learning and repertoire size. Because most authors approach this problem from the perspective of developmental stress, I will assume that their manipulations (decreased food, food unpredictability, and increased brood size) do indeed decrease nestling condition.

Several studies have found that nutritional stress during the nestling phase results in reduced HVC volume, although the effects on other brain regions involved in song are less clear (Buchanan et al. 2004; Spencer et al. 2005; MacDonald et al. 2006). In addition, Nowicki and colleagues (2002b) found that nutritional stress reduced copy accuracy and the amount of time young birds spent in the learning phase of song development. These results appear to indicate that learning is condition dependent in young birds, and should result in smaller repertoire sizes in adults. Nevertheless, this connection is not always supported by direct assessments of adult repertoire size. Of six studies examining the effect of developmental stress on song complexity, three found that it reduced repertoire size while three found no relationship (Table 2.1). Furthermore, work by Gil and colleagues failed to support an effect of developmental stress on brain structure (Gil et al. 2006).

This inconsistency could be caused by the short period of deprivation employed in all studies. Subsequent to fledging, all birds were provided with ad libitum food. Young birds may be able to make up for poor conditions in the nest during the fledgling and juvenile periods. While differences in body mass and size generally persisted through both of these periods, if resources were devoted to song learning and not to compensatory growth, then significant differences in adult song may not be evident. Differences may also be absent if birds are able to adjust their songs after crystallization. For instance,
adult zebra finches (Taeniopygia guttata) have been shown to adjust the fine structure of their songs to match a tutor (Funabiki and Funabiki 2008) and there may be a lag of up to a year and a half between learning and producing new song elements in starlings (Chaiken et al. 1994). Further work is needed to more precisely determine when and to what extent learning and song adjustment may occur in adult birds. Additionally, experiments are needed that continue nutritional stress through the song learning and juvenile periods to remove the possibility of compensatory feeding and resource allocation to learning. This period is arguably the most likely time for young birds to experience nutritional stress, as they must begin relying on their own foraging abilities.

The final criterion of the Hamilton and Zuk and developmental stress hypotheses is that parasitism decreases the condition upon which repertoire size depends. Since repertoire size is not immediately condition dependent, parasitism need only affect condition during the critical phases of song development. Only two studies have directly investigated the effects of disease early in life on song learning. Spencer and colleagues (2005) found that malarial infection in young canaries resulted in reduced HVC size compared to uninfected chicks. In contrast, Bischoff and colleagues (2009) found no effect of hen flea (Ceratophyllus gallinae) exposure during the nestling phase on the number of song types sung by adult great tits (Parus major). Given the paucity of available studies and the differences between the two existing studies in song trait, parasitic agent and species, no conclusions can be drawn here. In addition, any effects of parasitism on song learning will need to be further explored to determine whether those effects are due to heritable resistance to parasites. Furthermore, the effects of early parasitism on condition will also need to be investigated to fully support the connections between parasites and sexual traits laid out by Hamilton and Zuk.

In addition to their three criteria, Hamilton and Zuk also made two predictions concerning the relationship between parasites and the song traits that meet their criteria. Their intraspecific prediction states that a female's preferred mate should have the fewest parasites. If females prefer males with large repertoire sizes, then according to Hamilton and Zuk repertoire size should correlate negatively with parasite load. However, the evidence for this relationship is mixed. Some studies show a negative correlation between parasitism and song complexity, but a similar number show no relationship (Weatherhead et al. 1993; Buchanan et al. 1999; Garamszegi et al. 2005; Spencer et al. 2005). Furthermore, the studies demonstrating a negative correlation compare presence or absence of parasites, while those with no significant correlations measured infection intensity. There are several explanations for these mixed results. First, absence of infection in an individual could be the result of either resistance or lack of exposure to the parasite. If variation in exposure is not uniform and not influenced by any heritable trait, then song complexity will not be a reliable signal of parasite resistance. Second, as discussed above, repertoire size is not immediately condition dependent. If adult parasite loads are not strongly correlated with parasite loads at the time males learn their songs (usually early in life), then repertoire size would not necessarily predict adult parasite load. This disconnect between adult and juvenile parasite loads could come about through changes in the parasite community over time. Finally, if parasitism as an adult is indeed strongly correlated to juvenile parasitism, then the inconsistency could be due to differences in the parasites examined in each study. The studies that showed no correlation examined infection with lice, while the others examined blood parasites.
Feather louse infestations may not have a strong enough effect on condition to influence song learning (Ash 1960; Booth et al. 1993; Potti and Merino 1995). Thus, repertoire size could reliably signal infection, but only for certain parasites. This is not surprising, since the effect of parasites on song occurs via the effect of parasites on condition. So only parasites that have a marked influence on condition will have an effect on song.

There are two ways to examine the relationship between repertoire size and parasite resistance without such problems. One way is to use manipulative experiments. This approach would avoid non-heritable differences in exposure or parasite species that can create misleading or confusing results. Another way to address the above difficulties is to examine the immune response itself. While Hamilton and Zuk stressed trade-offs in resistance to specific parasites, measures of the immune response may provide a link between resistance and condition if that response is energetically costly. Only three studies have examined this relationship. Two show a positive correlation between immune response and repertoire size, but one does not (Spencer et al. 2004; Reid et al. 2005; Pfaff et al. 2007). This provides weak support for the idea that a female preference for repertoire size reflects a preference for large immune responses. However, more tests will be needed before we can definitively state whether repertoire size truly reflects a more robust immune system. Further work will also be needed to determine whether females prefer males with larger immune responses, or even if larger immune responses are more effective at clearing or preventing parasitism.

Finally, Hamilton and Zuk also predicted that among species, parasite prevalence and variety correlates positively with song traits. To date, only two studies have tested this prediction using song: the original Hamilton and Zuk paper, and a later study conducted by Read and Weary (1990). It may seem surprising that so few authors have tested this prediction, but song data are less widely available than plumage brightness data, harder to obtain, and requires a great deal of effort to analyze.

Hamilton and Zuk's (1982) examination of their interspecific prediction was limited to measures of song complexity, using a subjective six point scale of song complexity and variety. This approach may be a bit over simplistic, and because they relied on a single expert to subjectively score each species' song, the method is not repeatable. Furthermore, it is not possible to determine which measures of song complexity were used, or how they were weighted. Read and Weary (1990), on the other hand, used five quantitative measures of song and one summary statistic to measure both song complexity and output (output to be discussed later). Four of these measures assessed song complexity: song repertoire size, syllable repertoire size, a three point scale of song versatility (measuring how often a bird changed what it was singing), and a summary statistic they termed song showiness, which included both measures of repertoire size and song continuity (the proportion of time spent actually producing song in a song bout). Repertoire size correlated with haematozoan prevalence in the predicted direction, but the correlation was not significant. Song showiness was significantly correlated with parasite prevalence, but the correlation was in the opposite direction as that predicted by Hamilton and Zuk. Song versatility was the only measure of song complexity that was significantly correlated with haematozoan prevalence in the predicted direction. This result is puzzling, since song switching does not appear to be condition dependent (discussed above).
While the results of these studies leave the current status of the prediction equivocal, both studies are limited taxonomically and could benefit from including a wider variety of species in their data set. Nearly half of the host species examined in both studies were from the Fringillidae. Read and Weary claim that this taxonomic bias is the cause of Hamilton and Zuk's significant results, as the Fringillids include species with both high parasite prevalence and elaborate songs. While removal of these species renders the correlation nonsignificant, it cannot be ignored that doing so also halves the sample size and reduces the power of the analysis (Read and Weary 1990). Finally, neither analysis includes tropical bird species, which are generally subject to greater intensities and varieties of parasites and so may be more likely to exhibit sexually selected traits that signal parasite resistance. Indeed, Zuk's (1991) analysis of plumage brightness and parasite prevalence in 526 neotropical birds revealed a significant association between brightness and parasite load among species, even after controlling for phylogeny.

Not only are the studies taxonomically limited in terms of host species, but they are also quite limited in the parasite species examined. Hamilton and Zuk point out themselves that the few high correlations they found were more puzzling than the low ones, since only a single subset of blood parasites were examined. A broader examination of parasitism is needed to ensure that non-significant results are not an artifact of incomplete sampling. Such an examination may be impractical, due to the wide variety of parasites that would need to be assessed. A more direct approach to measuring heritable resistance may be needed. Work with MHC genes and measures of immune response may be valuable alternatives in future tests of this prediction.

The discussion of Hamilton and Zuk's interspecific hypothesis reminds us that there are multiple ways to assess song complexity. The extensive attention to song repertoire above reflects this trait's dominance in the literature. Other measures of song complexity are used far less frequently. Nevertheless, I will examine such evidence as there is to determine the suitability of such traits under Hamilton and Zuk.

Copy accuracy is a measure of the accuracy with which a learning bird reproduces the songs of a tutor. Since this trait is a measure of learning, it would best fall under the developmental stress hypothesis, rather the original Hamilton and Zuk hypothesis. No studies have examined this trait's condition dependence or response to parasitism. Since it is a measure of learning, one would expect it to meet these criteria in much the same way repertoire size does. Female preference for copy accuracy has been demonstrated in a study of song sparrows (*Melospiza melodia*). Nowicki and colleagues (2002c) found that female song sparrows solicited more copulations from young males who had high copy accuracy, compared to those with low copy accuracy. Furthermore, females also preferred males with higher proportions of copied versus invented song material (Nowicki et al. 2002c). Thus copy accuracy appears to be a good candidate for testing the developmental stress version of the Hamilton and Zuk hypothesis.

Song sharing is a measure of the similarity of a male's song to that of his immediate neighbor's. This trait differs from dialect in species where males are able to continually learn or alter their songs to match that of a neighbor. Within these species, it appears that song sharing functions primarily in signaling aggression in male-male interactions (Payne 1983; Beecher et al. 2000; Wilson and Vehrencamp 2001). For example, song sparrows react more aggressively to playbacks of songs that matched their
own songs (Sandra 2001). Since this trait does not appear to function in female mate choice, it is not appropriate for testing parasite mediated sexual selection hypotheses.

Song switching, or versatility, measures the frequency with which a male changes the song unit he is singing (element or phrase). Switching rate has been found to increase in the presence of females in several species (e.g. Horn and Falls 1991; Langmore 1997). To the best of my knowledge, no studies have examined whether switching rate varies between males within a species, or whether females prefer males with faster switching rates. It is also unclear whether switching rate is condition dependent. Switching could serve to decrease exhaustion, as in the anti-exhaustion hypothesis; however, this idea does not appear to be supported in the literature (Riebel and Slater 1999). Furthermore, as there does not appear to be any cost of producing more complex songs (discussed above), it does not seem likely that there would be an increased cost of switching songs. Therefore, it does not appear that song switching meets the criteria of Hamilton and Zuk.

**Immunocompetence Handicap Hypothesis**

The first key assumption of the IHH is that testosterone has a negative dose dependent effect on immunity. The evidence for the immunosuppressive effects of testosterone in birds has been recently reviewed (Hasselquist et al., 1999; Muehlenbein and Bribiescas, 2005; but see Roberts et al., 2005). In short, the evidence is mixed, with studies supporting and refuting a negative effect of testosterone on immunity in birds.

The second key assumption of the IHH is that testosterone should have a dose dependent effect on sexual signals. The presence of androgen receptors in the song system indicates this system’s sensitivity to testosterone. However, support for testosterone's effects on avian song is mixed. Early work associated testosterone with the onset of singing. For instance, increased levels of testosterone were associated with the onset of singing behavior at the beginning of the breeding season and males injected with testosterone could be induced to sing in the non-breeding season; additionally, females treated with testosterone developed male-like singing behavior and brain structure (Gurney and Konishi 1980; Catchpole and Slater 2008). A wide range of song traits have since been examined, with more recent work focusing on testosterone's effects on song learning and brain development. Reviews of this work are numerous and detailed (e.g. Bottjer and Johnson 1997; Schlinger 1997; Harding 2004). For the purposes of this review, I will focus broadly on the evidence for testosterone's effects on song complexity, without going into great detail on its interactions with the nervous system. Only the complexity traits that were found to be involved in female choice (repertoire size, copy accuracy, and song switching) will be considered here.

Testosterone might act on repertoire size in two ways. First, testosterone could increase the number of songs within a bird's repertoire that he performs, regardless of repertoire size. At low levels of testosterone, males with either large or small repertoires would appear to sing small repertoires, while at high levels of testosterone, the full repertoire would be produced. Thus, apparent repertoire size would be affected by testosterone, but not necessarily actual repertoire size. This could work through testosterone's effects on aggression and motivation. Most researchers assess repertoire size from either a single recording, or summed over multiple recordings. To see if testosterone has an effect on the proportion of total repertoire sung, both testosterone levels and repertoire size would have to be measured several times in the same bird.
Alternatively, experiments manipulating testosterone levels in captive birds would also be valuable.

The second way in which testosterone could affect repertoire size is by influencing the developmental and learning process. Since any effect of testosterone on song learning and development will also affect learned song traits, the following discussion is also applicable to copy accuracy and repertoire size. Testosterone is vital to the development of song in young birds, and males that are castrated or given testosterone inhibitors do not develop proper adult song (Marler et al. 1988; Sarah W. Bottjer 1992). Many studies have found that the size of brain regions in the avian song system are positively associated with testosterone (Table 2.2). Furthermore, testosterone also appears to increase song learning, neurogenesis, and neuron survival in these regions, although the evidence is somewhat mixed (Rasika et al. 1994; Absil et al. 2003; Strand and Deviche 2007). The effects of varying levels of testosterone are less well known. Research to date has focused on the effects of the presence or absence of this hormone on the songbird brain. The next step will be to determine whether these effects are sensitive to varying levels of testosterone, or whether testosterone simply activates these changes regardless of dose. If testosterone does have a dose dependent effect on song learning and development, then the hormone levels that influence singing must also have measurable effects on immunity.

Despite testosterone's positive effects on HVC volume, and positive associations between HVC volume and repertoire size, no studies were found that showed any correlation between testosterone and repertoire size (Table 2.2). One complication is that plasma steroid levels do not necessarily reflect steroid levels in the brain, which can synthesize its own steroids (Schlinger and London 2006). Since most researchers only measure plasma testosterone, a relationship between song and testosterone might not be detected if there is no relationship between plasma and brain steroid levels. Nevertheless, the lack of clear associations is not so surprising considering the complex relationship between testosterone and avian song learning. Thus, it appears that testosterone is unlikely to have a direct, dose dependent, positive effect on repertoire size.

Studies have also shown that testosterone does not act alone in song learning. Estrogen has been found to maintain song plasticity needed for song learning (Marler et al. 1987). Estrogen is also necessary for birds to learn new songs or alter existing songs. Exposure to testosterone too early in song development causes early crystallization of songs, resulting in simpler songs and smaller repertoires (Korsia and Bottjer 1991). Marler and colleagues (1988) found that castrated males could learn song normally, but that testosterone was necessary to crystallize these songs. Furthermore, estrogen appears to maintain plasticity in song during song learning while testosterone limits the sensitive period during which males learn new songs (Marler et al. 1987; Marler et al. 1988; White et al. 1999). Korsia and Bottjer (1991) found that chronic exposure to testosterone during song development impairs song learning in zebra finches. Furthermore, the effects of testosterone did not appear to be related to dose, but to the time during development that testosterone was administered (Korsia and Bottjer 1991). Thus, it appears that timing of testosterone exposure is critical to song learning, while level of testosterone may not be, and that exposure to estrogen is also vital to song learning.

Finally, song switching is not a learned behavior, so would not be affected by testosterone in the same manner as copy accuracy and song repertoire. Switching rate
could be affected by rises in testosterone during territorial or mating interactions. Contrary to this expectation, switching rate generally decreases in male-male interactions, when testosterone levels normally rise (Horn and Falls 1991; Langmore 1997). Furthermore, the single study that examined switching rate and testosterone levels found no correlation between the two in red winged blackbirds (*Agelaius phoeniceus*, Weatherhead et al. 1993). Therefore, it seems unlikely that switching rate is a good trait for testing the immunocompetence handicap hypothesis.

**Summary**

In sum there is little evidence for a dose dependent, positive effect of testosterone on either immunity or song complexity in birds. Testosterone's effects on the avian song and immune systems are complex and do not readily fit a straight-forward, simple interaction like that proposed by Folstad and Karter. Instead of simple dose dependency, the timing of testosterone exposure has important effects on song. Similar to the developmental stress hypothesis, testosterone's effects on song complexity are generally confined to the relatively short critical periods of song learning and development. As with the developmental stress and Hamilton and Zuk hypotheses, repertoire size and copy accuracy appear to best meet the criteria for testing this hypothesis. Song switching rate and song matching, on the other hand, do not appear to meet the criteria of these hypotheses and would not be useful in testing them.

Much work must still be done to determine whether parasitism and the costs it imposes, either via condition, nutritional stress, or testosterone mediated immunosuppression, have relevant and lasting effects on adult song complexity. Because song complexity does not appear to be immediately condition dependent or reliant on testosterone titers, its applicability to the IHH and classic Hamilton and Zuk hypothesis appears limited. Since song complexity does appear to be condition dependent in the early phases of life, it is particularly well suited to tests of the developmental stress hypothesis. The next step in testing this hypothesis will be to determine whether parasite induced stress during song development has effects on repertoire size and copy accuracy. Additionally, an examination of individual variation in parasite resistance under similar stress conditions will help us determine whether heritable resistance, as opposed to variation in exposure, does indeed affect song complexity.

**Song Output**

*Hamilton and Zuk*

There are a number of ways to measure song output. The most widely used measure is song rate. Measures of song length and the time spent singing are also popular, while measures of intersong intervals are more rarely used. Several studies have illustrated increased mating success in males with faster song rates, longer songs, shorter intersong intervals or lengthy song bouts (Eens et al. 1991; Wasserman and Cigliano 1991; Kempenaers et al. 1997; Chiver et al. 2008). Thus these traits appear to satisfy the first of Hamilton and Zuk's criteria.

Direct evidence for the condition dependence of song output traits is scarce. Experiments have confirmed the condition dependence of song rate in zebra finches (Zann 1996); however, work in other species is lacking. Indirect evidence also supports the condition dependence of song rate. Studies have found that song rate increases with
food availability and decreases in cold weather, presumably because of the increased energetic demands of thermoregulation (Thomas 1999). While evidence is limited, other song output traits are also likely to reflect current condition and infection. Prolonged singing is energetically demanding and competes directly with other activities, such as foraging (Gil and Gahr 2002). In addition, greater song output, whether due to increases in song length or decreases in the intervals between songs, is expected to require more energy than song bouts with less song content. While the energetic demands of producing a single song or additional song length may be low, it is generally agreed that these costs can add up to significant energy expenditures when summed over the total time spent singing (Gil and Gahr 2002). Direct tests are needed to ascertain the level of condition dependence of song output traits, and whether these traits are sufficiently sensitive to condition to test Hamilton and Zuk.

The final criterion of the Hamilton and Zuk hypothesis is that parasitism degrades the condition upon which the trait depends. Reviews of the literature support a general energetic cost of parasitism and immune defense (e.g. Lochmiller and Deerenberg 2000; Viney et al. 2005). Studies have found that wild birds infected with haematozoans are in poorer condition and have less migratory fat than healthy birds (Valkiunas 1993; Merino et al. 2000). In addition, a study of migratory birds found that neotropical birds reaching their breeding grounds in the United States had lower parasite loads than birds sampled on the wintering grounds in Belize, suggesting that birds with higher parasite loads did not survive migration (Booth and Elliott 2002). Further support for the third criterion comes from the results of studies examining correlations between parasitism and song output. Mite loads in barn swallow (Hirundo rustica) nests are negatively correlated with the proportion of time males spent singing, and experiments confirmed this result (Moller 1991). Another study in barn swallows also found an effect of feather louse load on song duration (Garamszegi et al. 2005). Intuitively, this makes sense, since parasites and the immune response both use up host resources. Nevertheless, there are potential pitfalls in this relationship. For example, Gilman and colleagues (2007) found a negative correlation between Plasmodium infection and song rate, but not between Leucocytozoon infection and song rate. They attribute this inconsistency to differences in the pathology of the two parasites: Plasmodium infection reduces aerobic capacity, while Leucocytozoon generally does not. Thus, the likelihood of song output to reveal current parasite resistance will depend on the specific pathology of the parasite.

To avoid this problem, and the difficulties in assessing parasitism in live birds, other authors have looked at the relationship between immune response and song output traits (primarily song rate). Two studies in European starlings found a positive correlation between immune responses to challenge and both song rate and song bout length (Duffy and Ball 2002; Buchanan et al. 2003). Nevertheless, a similar study in zebra finches found no such relationship (Birkhead et al. 1998). Lastly, a study in barn swallows found a negative correlation between song rate and the concentration of white blood cells (Saino et al. 1997). These confusing results are not so surprising given our limited understanding of what constitutes a "good" immune response. As stated in the introduction, high, low or intermediate immune responses could all be construed as "good" given the right conditions. Future studies will need to determine what levels of response are most effective at defending against parasites, whether and at what level circulating immune cells affect resistance to invaders, and how costly this immunity is.
A greater understanding of these issues will help us determine how song traits advertise male parasite resistance. In sum, the evidence appears to support the third criterion of Hamilton and Zuk. Nevertheless, direct tests of this relationship are still needed to determine the exact costs of parasitism and immunity, and whether these costs are sufficient to affect song output traits.

Song output traits appear to fit the three criteria of the Hamilton and Zuk hypothesis. While it is not completely clear how an increase in song complexity would indicate greater health or vigor, an increase in the time spent singing would certainly require more energy and take away from time spent in other activities, such as resting or foraging. No studies have directly tested Hamilton and Zuk's intraspecific prediction in relation to song output traits, nor did Hamilton and Zuk examine song output when they tested their interspecific hypothesis. Read and Weary (1990), on the other hand, included four measures of song output in their interspecific analysis: song rate, intersong interval, song continuity (proportion of time spent making sound in a song bout), and song duration. Only one of these, song continuity, was significantly correlated with parasite prevalence. Contrary to the Hamilton and Zuk's prediction, song continuity was negatively associated with haematozoan prevalence.

While it seems as though song output should be a good indicator of parasitism in birds, it does not appear to support the interspecific prediction. One possible reason is that different measures of output may be of greater interest to females. The proportion of a male’s daily time budget devoted to song may more accurately reflect the amount of energy he devotes to song advertisements. Another possibility is that haematozoa do not alter condition strongly enough to affect song output. Other parasites might have a greater impact on song output than the ones examined by Read and Weary. Finally, it is possible that sick birds were not as likely to be recorded as healthy ones. One immediate effect of acute illness in birds is a decrease in activity (Valkiunas 1993). If sick birds were less likely to sing than healthy ones, and non-singers are not sampled at all, one would not find any effect of parasite prevalence on song output.

**Developmental Stress**

Developmental stress is not expected to affect song output, since song output is not a learned trait. However, if developmental stress (especially stress caused by parasitism) has detrimental effects on learned song traits, it is conceivable that it also hampers an animal's ability to perform other learned tasks, such as foraging. Birds must learn how to recognize, find, handle, and sometimes store and relocate food. Much of this learning will occur just after fledging, at the same time that birds are learning to sing. Males that develop poor foraging skills will be in poor condition throughout their lives. If this is so, then current song output would be a reliable signal of learning ability across contexts, and especially of learning in the context of foraging. A recent study in zebra finches provides some indirect support of this version of the developmental stress hypothesis. Boogert and colleagues (2008) found a significant correlation between total number of song phrase elements males sang and the speed with which they were able to learn a new foraging task. Thus a song feature that is learned early in development appears to signal adult learning ability in other contexts.

This scenario is much like the original Hamilton and Zuk, where parasites have long lasting, debilitating effects, even after clearance of the original infection. To support
the developmental stress version, one would need to document decreased learning and foraging ability in adult birds that were parasitized early in development. Furthermore, there should be long term differences in condition in birds experiencing parasitism during development.

No studies have examined the effects of early parasitism on adult song output, however several have examined the effects of developmental stress on these traits. None of these studies found any effect of developmental stress on song rate, however several found that developmentally stressed birds produced shorter songs, devoted less time to singing, and sang fewer notes per song bout or syllables per motif (Table 2.1). Nevertheless, all of these studies provided adults with *ad libitum* food after the period of stress, so any differences in foraging ability among stressed and unstressed birds would not be evident. Therefore, these studies do not provide a valid test of this version of the developmental stress hypothesis.

If there are no differences in the foraging success of birds fed *ad libitum* food in captivity, why do studies show an effect of stress on several song output traits? It could be that producing longer songs and more notes per song bout presents a greater mental challenge to birds. Birds with generally impaired brain development could have a more difficult time stringing a large number of notes together, or coordinating the complex neural-muscular interactions required for the production of lengthy songs or song bouts. More work will need to be done to determine the costs associated with these song output traits. In addition, future studies will need to examine whether differences in parasite resistance and parasitism during development cause differences in foraging ability in adults. If so, do these differences result in measurable differences in condition and song output that persist throughout the bird's life?

**Immunocompetence Handicap Hypothesis**

Testosterone must have a dose dependent effect on song output in order for this trait to be used to test the IHH. Testosterone's role in initiating singing behavior, either naturally at the beginning of the breeding season, or artificially in females and nonbreeding males, supports its broad role in regulating song output (Catchpole and Slater 2008). However, the IHH requires a closer association of testosterone with song characteristics. A few experimental studies have shown a positive correlation between testosterone and song rate (Hunt et al. 1997; Absil et al. 2003). Nevertheless, the vast majority of studies, both experimental and correlational, find no association between testosterone and song output (Table 2.3). Instead, song output appears to depend more on social cues, photoperiod and individual condition (e.g. Dloniak and Deviche 2001; Boseret et al. 2006; Gleeson 2006; Soma et al. 2006). These traits do not seem to be regulated by testosterone in a manner consistent with the IHH.

**Summary**

The lack of testosterone dependent expression of song output traits prevents them from being useful for testing the IHH. Similarly, they cannot be used to test the classic developmental stress hypothesis because they are not learned traits. However, if parasite induced developmental stress impairs other learned tasks, like foraging, then the effects

---

2 Developmental stressors used are experimentally increased brood size, decreased food supply to provisioning parents, and administration of corticosterone to nestlings.
of parasitism early in life should have lasting effects on condition. Under this scenario, condition dependent song output traits are useful for testing the developmental stress hypothesis. Finally, song output appears to fit well with the criteria set forth by Hamilton and Zuk. However, more work is needed to strengthen the evidence for parasite mediated sexual selection on song output traits. Evidence for the condition dependence of output traits other than song rate is still largely circumstantial. Direct tests of their condition dependence are needed to ensure that these traits meet the second of Hamilton and Zuk's criteria. The same can be said for the third criterion: more work is needed to determine the effects of parasitism and immune defense on condition. The specific pathology of particular parasites should also be considered when testing this aspect of the hypothesis, since some parasites may be more likely to affect condition than others. The next step will be to link the costs of parasites to the condition dependence of song output: do parasites and immunity incur sufficient costs to meaningfully affect song output traits? Finally, a great deal of attention has been focused on song rate, with relatively little attention paid to testing other measures of song output. These measures are expected to act similarly to song rate under Hamilton and Zuk and could be very useful for further testing this hypothesis.

**Amplitude**

Song amplitude is a fairly poorly studied aspect of avian song. To date, only three studies have examined amplitude in relation to female choice. Searcy (1996) found that female red-winged blackbirds gave more copulation solicitation displays in response to louder playbacks. Nevertheless, this preference was very weak compared to preferences found in anurans and insects (Arak 1983; Forrest 1983). In dusky warblers (*Phylloscopus fuscatus*), the proportion of time spent singing above 20% of peak amplitude significantly predicted whether or not a male sired extra-pair offspring (Forstmeier et al. 2002). Finally, female zebra finches preferred higher amplitude songs over lower ones (Ritschard et al. 2010). So while the evidence is very limited, females do appear to prefer males that produce higher amplitude songs.

A study of the metabolic costs of singing in birds found that loud songs were significantly more costly to produce than soft songs, with a 16% increase in oxygen consumption during loud song production in the European starling (Oberweger and Goller 2001). In zebra finches, experimental manipulation of male body condition found that amplitude increased with body condition (Ritschard and Brumm 2012). Nevertheless, a subsequent study in the same species found no association between oxygen consumption and song amplitude (Zollinger et al. 2011). Thus, there is some evidence supporting the second criterion of Hamilton and Zuk. Nevertheless, the condition dependence of producing high amplitude songs has not been directly tested.

No studies have examined the effect of parasites on song amplitude. If amplitude is condition dependent then one would expect parasites to have a negative effect on song amplitude. It appears as though song amplitude may fit the criteria of Hamilton and Zuk, and would be valuable for testing this hypothesis. Nevertheless, much more work still remains to be done to confirm whether it truly meets the three criteria of Hamilton and Zuk.

The applicability of amplitude to testing either the IHH or developmental stress hypothesis is unknown. It seems unlikely that amplitude will meet the necessary criteria
for consideration under these hypotheses. First, it is not known whether or how testosterone might affect song amplitude. It is possible that testosterone induced increases in aggression and motivation to sing would result in louder songs. Nevertheless, few studies have found a significant effect of testosterone on song output or content (Tables 2.2 and 2.3) so it seems unlikely that testosterone would have a direct effect on song amplitude.

Second, amplitude is not a learned trait and so cannot be used to test the original developmental stress hypothesis. Nevertheless, amplitude is correlated with body size in many anurans and insects (Brackenbury 1979; Forrest 1983). Since body size is determined early in development and stress or parasitism during this time can result in stunted growth, it is conceivable that developmental stress might have an effect on the maximum amplitude an adult bird can produce. Researchers testing developmental stress using song amplitude would also need to demonstrate 1) an intraspecific relationship between body size and song amplitude and 2) that differences in song amplitude were sufficient to signal differences in male quality and parasite resistance. Only if these conditions are met will song amplitude be useful for testing the developmental stress hypothesis.

**Frequency**

Female preference for frequency traits has been shown in the sage grouse (*Centrocercus urophasianus*, Gibson and Bradbury 1985). Male frequency characteristics (measured with principal components) were significantly correlated with mating success on the lek. In general higher frequencies were associated with greater copulation success. In contrast, a study of tawny owls (*Strix aluco*) found no correlation between male mating success and highest, lowest, or peak amplitude frequency (Appleby and Redpath 1997). In a recent review, Cardoso (2011) found preferences for lower song frequencies in some species and preferences for higher frequencies in others. Thus, female preference for frequency traits may exist in some species, but not in others and the direction of this preference may vary across species.

There is little evidence for the condition dependence of frequency traits. In great tits (*Parus major*), variation in note frequency within a strophe increased as note frequency increased (Lambrechts 1997). The author suggested that motor constraints make it more difficult to consistently produce notes at high frequencies compared to low frequencies. This result might indicate greater difficulty in producing high frequency songs, with birds in better condition being better able to perform difficult songs. On the other hand, it could also represent a tradeoff between song frequency and consistency similar to that found in trills (see below) rather than conditions dependence per se. The results of other studies do not support the idea of condition dependence of song frequency traits. There was a negative association between peak amplitude frequency and condition in barn swallows (Galeotti et al. 1997). No relationship between condition and highest or lowest frequency of hoots was found in tawny owls (Appleby and Redpath 1997).

In contrast to the inconsistent effects of condition, environmental factors have been found to have strong influences on the frequencies used by male birds. High frequencies degrade faster in occluded habitat, and male white-throated sparrows (*Zonotrichia albicollis*) will sing higher frequency songs in open habitats versus forests (Wasserman 1979; Waas 1988). The frequency of peak amplitude also tends to reflect
habitat variation, with frequencies that attenuate the least receiving the greatest emphasis (Morton 1975; Ryan and Brenowitz 1985). The frequency of ambient noise also differs between habitats (Slabbekoorn 2004). Males will vary the frequency of their songs in different habitats to fit into windows of relatively low noise in the environment. For example, little greenbul (*Andropadus virens*) songs have lower minimum frequencies in rainforests, where there is little low frequency background noise, than in nearby open woodland (Slabbekoorn and Smith 2002). These studies suggest that environmental factors may have more impact on song frequency traits than variation in male quality or condition.

The effects of parasites on condition dependence have been discussed above. Nevertheless, Redpath and colleagues' (2000) study of tawny owls is worth noting as it is the only study to examine the relationship between parasite load and song frequency. They found a significant negative correlation between parasite load and the highest frequency produced by the owl. Nevertheless, there was no relationship between condition and either parasite load or hoot frequency. So it appears that parasites can affect tawny owl frequency traits, but they do not appear to do so via condition.

In order for frequency traits to be useful in tests of the developmental stress hypothesis, they must have a learned component. In their work on rufous collared sparrows (*Zonotrichia capensis*), Handford and Lougheed (1991) suggested that frequency traits primarily reflect learning processes, as opposed to constraints imposed by body size or habitat. Nevertheless, this idea has not been tested, and work exploring the learned nature of frequency traits is needed.

Another possibility is that some frequency traits may rely on body size, which can be impaired by parasitism and stress during development. If so, then frequency traits could honestly signal parasite resistance during development. Support for an effect of body size on song frequency is mixed. Interspecific studies have shown a strong relationship between body size and song frequency, with body size explaining more than half the variation in species differences in song frequency (Wallschlager 1980). The relationship between body size and frequency range within a species is less clear. A study of Darwin's finches (*Geospiza conirostris* and *difficilis*) found that larger individuals produced broader frequency ranges than smaller birds in both species. Nevertheless, larger birds had lower peak amplitude frequencies than smaller birds in *G. conirostris*, but larger *G. difficilis* had higher mean frequencies (Bowman 1979; Bowman 1983). In summer tanagers (*Piranga rubra*), individuals from western populations have larger body sizes, but higher maximum frequencies and larger frequency ranges than individuals in eastern populations (Shy 1983). Despite their inconsistencies, these studies do appear to support an effect of body size on frequency range, with larger birds producing broader frequency ranges.

Testosterone dependency is necessary for frequency traits if they are to be used to test the IHH. Experiments in non-passerine birds showed decreases in song frequency following testosterone treatment (Abs 1983; Beani et al. 1995). Testosterone implants in zebra finches resulted in significantly lower song frequencies (Cynx et al. 2005). The effects of testosterone on frequency persisted for a full year past implantation, long past the time when implants could conceivably alter testosterone levels in males. The authors therefore concluded that testosterone has a organizational, rather than a dose dependent effect on song frequency.
Because testosterone does not appear to affect song frequency in a dose dependent manner, frequency traits are not appropriate for tests of the IHH. It is unclear whether frequency traits are appropriate for tests of either version of the developmental stress hypothesis. Experiments will be needed to determine whether any frequency characteristics are learned or if they are affected by intraspecific variation in body size. Similarly, it is not clear whether song frequency traits meet the criteria of Hamilton and Zuk. Some species appear to have frequency characteristics that meet at least some of these criteria, but others do not. To add to the confusion, parasite load appears to affect frequency in tawny owls, but not via condition. Clearly, basic information on the factors influencing song frequency is needed before we can apply theories of parasite mediated sexual selection to these traits.

**Special syllables**

Special syllables are song traits that do not fit into any of the aforementioned categories, but whose production is particularly difficult. Several measures of song fit into this category, and many are species specific. I will focus this discussion on trills to illustrate the possible role of these traits in testing parasite mediate sexual selection hypotheses.

Trills are vibrated syllables that feature the rapid repetition of particular frequencies or frequency ranges. Frequency is associated with bill movement, such that high frequencies are produced with a wide beak gape, and low frequencies are accompanied by narrowing the gape (Westneat et al. 1993). This reliance of frequency on beak gape creates a performance constraint on frequency bandwidth and trill rate, such that broadband trills are difficult to produce at high rates (Figure 2.4, but see Figure 3 in Podos 1997).

Female preference for trills produced near the upper limit of the regression of trill rate on frequency bandwidth has been illustrated in two species. In canaries (*Serinus canaria*), females performed more sexual displays in response to songs with shorter internote intervals (Vallet et al. 1998). Similarly, swamp sparrow females displayed more in response to songs performed near the upper limit of the species' trill regression (Ballentine et al. 2004).

The condition dependence of trill performance is not known and has not been tested. It is possible that motor constraints or neuromuscular fatigue play a role in how well males perform trills. Nevertheless, if singing songs close to the physical limit is energetically demanding, then trill performance may be condition dependent (Lambrechts 1996).

Special syllables, including trills, are likely learned features, just as any other syllable in a bird's repertoire is learned. The performance of trills, on the other hand, most likely is not. In an experiment on swamp sparrows, young males were able to memorize artificially accelerated trills, but were not able to produce them (Podos 1996). So it is unlikely that trills would be subject to the process proposed by the developmental stress hypothesis.

The effect of testosterone on trill performance is not known and has not been tested. Female canaries treated with testosterone produced male-like trilled songs. Recordings of these songs elicited sexual displays from other females (Vallet et al. 1996). Therefore, it is possible that testosterone affects whether or how often high performance
trills are produced. Whether testosterone can increase a male's performance level is yet to be tested.

Trills may be useful in testing both the Hamilton and Zuk and Immunocompetence Handicap hypotheses. Initial evidence suggests that trill performance meets the necessary criteria for testing these hypotheses. Tests of the condition dependence, and testosterone dose dependency of this trait are needed. If trill performance is reliant on constraints other than condition, the effects of parasites on these constraints should be examined. Other special syllables with performance constraints should be examined in a similar manner to determine their suitability for tests of these hypotheses.

**Future Directions**

The evidence for parasite mediated sexual selection on avian song is mixed. Nevertheless, it is clear that parasitism can affect sexual signals in meaningful ways. The next major step in testing these hypotheses must be to examine variation in condition and song under uniform parasite exposure. All three hypotheses examined here predict heritable differences in the ability of individuals to resist parasitism. Differences in exposure to parasites do not test this prediction. Evaluation of sexual signals under uniform exposure is necessary to determine whether these signals will be valuable advertisements of heritable parasite resistance. This is not a simple task. Nevertheless, molecular tools are available to type individuals at key immune loci. Uniformity of exposure may be difficult to achieve, but injection of pathogens, or exposure to infected vectors (e.g. mosquitoes, biting flies, mites), which would better mimic natural exposure, are examples of ways in which this could be done.

The relatively recent introduction of song analysis software has made it possible to measure a wide range of song properties. Earlier technology limited our ability to collect and analyze song. New sound analysis programs, on the other hand, can measure a seemingly infinite range of song traits. Authors and programmers continue to come up with new and interesting ways to assess avian song. The exploration of novel song traits can lead us in exciting new directions. The concepts presented in this review provide a framework for evaluating new song traits in light of the hypotheses of parasite mediated sexual selection.

Measures of song complexity appear to be well suited to tests of the developmental stress and classic Hamilton and Zuk hypotheses. Initial studies have provided good support for the negative effects of nestling stress on song learning. Nowicki and colleagues (2002a) argue that stress during the nestling phase is sufficient to produce lasting effects on song development. Nevertheless, the most stressful period of a young bird's life will be after fledging, not before. There is a need for studies investigating how song learning and song traits are affected by stress during the fledgling phase. Furthermore, there is a great need for additional studies investigating the effects of disease during this period on song traits. The final step in testing these hypotheses will be to determine whether heritable resistance reduces or eliminates the effects of parasitism on song development, under conditions of equal exposure.

Song output appears to be a good trait for testing the classic Hamilton and Zuk hypothesis. Song output does not appear to support the interspecific prediction of
Hamilton and Zuk's hypothesis; however, an investigation of time budgets and a greater variety of parasites may provide greater insight into the evolution of ornaments that advertise parasite resistance. Direct tests of the effects of parasites on specific output traits, and of the condition dependence of these traits are also needed. While testosterone does not appear to have a dose dependent effect on output traits, little work has been done to determine testosterone's effects on specific output characteristics. Nevertheless, a focus on the classic Hamilton and Zuk hypothesis seems to be a more valuable approach with song output traits.

Likewise, song output traits are not appropriate for testing the classic developmental stress hypothesis because they are not learned. Nevertheless, if parasite induced developmental stress has broader effects on learning, then foraging ability may be impaired in birds parasitized during development. This should have long lasting effects on condition, making song output traits in adults a reliable signal of parasite resistance both developmentally and in the present. This idea has not been tested, and experiments exploring the effects of parasitism on the development of foraging and other learned tasks are warranted, since they may have major effects on success later in life.

Frequency, amplitude and special syllable traits may well be involved in parasite mediated sexual selection, however few researchers have considered them in this light. There is considerable potential for these traits to function in this manner. More work on the development of these traits, their heritability and condition dependence, is needed to determine whether or not they can honestly advertise parasite resistance.
Table 2.1: Effects of developmental stress on song complexity and output.

<table>
<thead>
<tr>
<th>Species</th>
<th>Design*</th>
<th>Effect¥</th>
<th>Independent Variable</th>
<th>Dependent Variable</th>
<th>Citation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Song Complexity</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Great Reed Warbler</td>
<td>C</td>
<td>+</td>
<td>Length of innermost primary</td>
<td>Repertoire size</td>
<td>Nowicki et al. 2000</td>
</tr>
<tr>
<td>Bengalese Finch</td>
<td>C</td>
<td>-</td>
<td>Brood size, body size or sex</td>
<td>Notes/song bout</td>
<td>Soma et al. 2006</td>
</tr>
<tr>
<td>Canary</td>
<td>E</td>
<td>-</td>
<td>Malaria infection</td>
<td>Repertoire size</td>
<td>Spencer et al. 2005a</td>
</tr>
<tr>
<td>Swamp Sparrow</td>
<td>E</td>
<td>0</td>
<td>Food treatment</td>
<td>Repertoire size</td>
<td>Nowicki et al. 2002</td>
</tr>
<tr>
<td>Zebra Finch</td>
<td>E</td>
<td>-</td>
<td>Cort and food treatment</td>
<td>Notes/song bout</td>
<td>Gil et al. 2006</td>
</tr>
<tr>
<td>Zebra Finch</td>
<td>E</td>
<td>+</td>
<td>Cort and food treatment</td>
<td>Notes/song bout</td>
<td>Gil et al. 2008</td>
</tr>
<tr>
<td>Zebra Finch</td>
<td>E</td>
<td>-</td>
<td>Cort and food treatment</td>
<td>Notes/song bout</td>
<td>Gil et al. 2008</td>
</tr>
<tr>
<td>Starling</td>
<td>E</td>
<td>-</td>
<td>Food treatment</td>
<td>Notes/song bout</td>
<td>Buchanan et al. 2003</td>
</tr>
<tr>
<td>Wild Zebra Finch</td>
<td>E</td>
<td>-</td>
<td>Food treatment</td>
<td>Notes/song bout</td>
<td>Zann and Cash 2008</td>
</tr>
<tr>
<td>Song Output</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Zebra Finch</td>
<td>C</td>
<td>-</td>
<td>Ad libitum food, CORT treatment, or food mixed with husks</td>
<td>Song rate</td>
<td>Birkhead et al. 1998</td>
</tr>
<tr>
<td>Zebra Finch</td>
<td>E</td>
<td>0</td>
<td>Ad libitum food, CORT treatment, or food mixed with husks</td>
<td>Song rate</td>
<td>Spencer et al. 2005b</td>
</tr>
<tr>
<td>Zebra Finch</td>
<td>E</td>
<td>0</td>
<td>Ad libitum food, CORT treatment, or food mixed with husks</td>
<td>Song rate</td>
<td>Spencer et al. 2003</td>
</tr>
<tr>
<td>Song Sparrow</td>
<td>E</td>
<td>0</td>
<td>Ad libitum food, CORT treatment, or food mixed with husks</td>
<td>Song rate</td>
<td>Zann and Cash 2008</td>
</tr>
<tr>
<td>Song Sparrow</td>
<td>E</td>
<td>0</td>
<td>Ad libitum food, CORT treatment, or food mixed with husks</td>
<td>Song rate</td>
<td>Zann and Cash 2008</td>
</tr>
<tr>
<td>Song Sparrow</td>
<td>E</td>
<td>0</td>
<td>Ad libitum food, CORT treatment, or food mixed with husks</td>
<td>Song rate</td>
<td>Zann and Cash 2008</td>
</tr>
<tr>
<td>Song Sparrow</td>
<td>E</td>
<td>0</td>
<td>Ad libitum food, CORT treatment, or food mixed with husks</td>
<td>Song rate</td>
<td>Zann and Cash 2008</td>
</tr>
</tbody>
</table>

*Study design: C refers to correlational studies while E refers to experimental studies of the following design: 1) ad libitum 2) Cort treatment, or food mixed with husks 3) small, medium, or large brood size 4) control vs. experimentally infected with malaria 5) ad libitum or food mixed with husks 6) ad libitum or large

¥+ or – refers to the sign of the correlation or the effect of the experimental treatment relative to controls.
<table>
<thead>
<tr>
<th>Species Design</th>
<th>Effect ¥</th>
<th>Song Variable</th>
<th>Citation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brain Features</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>House Finch</td>
<td>E3 + size HVC and RA</td>
<td>Strand and Deviche 2007</td>
<td></td>
</tr>
<tr>
<td>Dark Eyed Junco</td>
<td>C &amp; E3 + volume of HVC and RA</td>
<td>Gulledge and Deviche 1997</td>
<td></td>
</tr>
<tr>
<td>European Starling</td>
<td>E2 + yearling autumnal neurogenesis</td>
<td>Absil et al. 2003</td>
<td></td>
</tr>
<tr>
<td>Female Canary</td>
<td>E2 + recruitment and/or survival of new HVC neurons</td>
<td>Rasika et al. 1994</td>
<td></td>
</tr>
<tr>
<td>Female Canary</td>
<td>E2 + production of new HVC neurons</td>
<td>Rasika et al. 1994</td>
<td></td>
</tr>
<tr>
<td>Rat</td>
<td>E4 + new hippocampal neuron survival</td>
<td>Spritzer and Galea 2007</td>
<td></td>
</tr>
<tr>
<td>House Finch</td>
<td>E3 + HVC neuron survival</td>
<td>Strand and Deviche 2007</td>
<td></td>
</tr>
<tr>
<td>Zebra Finch</td>
<td>E3 + # new HVC neurons</td>
<td>Tran et al. 2007</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Repertoire Size</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Swamp &amp; Song Sparrow</td>
<td>E1 + song crystallization</td>
<td>Marler et al. 1988</td>
<td></td>
</tr>
<tr>
<td>Zebra Finch</td>
<td>E3 + NMDA EPSC, LMAN and RA</td>
<td>Tran et al. 1999</td>
<td></td>
</tr>
<tr>
<td>House Finch</td>
<td>E3 + number of HVC neurons</td>
<td>Tran et al. 1999</td>
<td></td>
</tr>
<tr>
<td>Female Canary</td>
<td>E3 + maturation of new HVC neurons</td>
<td>Tran et al. 1999</td>
<td></td>
</tr>
<tr>
<td>European Starling</td>
<td>E3 + volume of HVC, RA, X, nXIIts</td>
<td>Tran et al. 1999</td>
<td></td>
</tr>
<tr>
<td>House Finch</td>
<td>E3 + volume of HVC and RA</td>
<td>Tran et al. 1999</td>
<td></td>
</tr>
<tr>
<td>Female Canary</td>
<td>E3 + volume of HVC and RA</td>
<td>Tran et al. 1999</td>
<td></td>
</tr>
</tbody>
</table>

Testosterone treatments: 1) castrated vs. intact males, 2) T implant vs. empty implant, 3) castration followed by implant containing either T, T in inhibitor or nothing, 4) sham castrated vs. castrated and implanted with varying levels of T, 5) castration followed by implant containing either T or empty implant, 6) T implant vs. T implant with E2 inhibitor.

¥ + or − refers to the sign of the correlation or the effect of the experimental treatment relative to controls.

Table 2.2: Results of studies investigating the relationship between testosterone and song complexity.
<table>
<thead>
<tr>
<th>Species</th>
<th>Design*</th>
<th>Effect</th>
<th>Song Variable</th>
<th>Citation</th>
</tr>
</thead>
<tbody>
<tr>
<td>European starling</td>
<td>E1</td>
<td>+</td>
<td>song rate</td>
<td>Absil et al. 2003</td>
</tr>
<tr>
<td>barn swallow</td>
<td>C</td>
<td>0</td>
<td>song rate</td>
<td>Galeotti et al.</td>
</tr>
<tr>
<td>blue tit</td>
<td>E1</td>
<td>0</td>
<td>song rate</td>
<td>Kunc et al. 2006</td>
</tr>
<tr>
<td>Gambel's white-crowned sparrow</td>
<td>E2</td>
<td>0</td>
<td>song rate</td>
<td>Meitzen et al. 2007</td>
</tr>
<tr>
<td>dark-eyed junco</td>
<td>E1</td>
<td>+</td>
<td>song rate</td>
<td>Ketterson et al. 1992</td>
</tr>
<tr>
<td>European starling</td>
<td>C</td>
<td>0</td>
<td>song rate</td>
<td>Duffy and Ball 2002</td>
</tr>
<tr>
<td>barn swallow</td>
<td>C</td>
<td>0</td>
<td>song rate</td>
<td>Saino et al. 1997</td>
</tr>
<tr>
<td>canary</td>
<td>E3</td>
<td>0</td>
<td>syllable production rate</td>
<td>Rybak and Gahr 2004</td>
</tr>
<tr>
<td>European starling</td>
<td>C</td>
<td>0</td>
<td>song bout length</td>
<td>Buchanan et al. 2003</td>
</tr>
<tr>
<td>canary</td>
<td>E3</td>
<td>0</td>
<td>mean song length</td>
<td>Rybak and Gahr 2004</td>
</tr>
<tr>
<td>European starling</td>
<td>C</td>
<td>0</td>
<td>song bout length</td>
<td>Duffy and Ball 2002</td>
</tr>
<tr>
<td>blue tit</td>
<td>E1</td>
<td>0</td>
<td>mean strophe length</td>
<td>Kunc et al. 2006</td>
</tr>
<tr>
<td>canary</td>
<td>E3</td>
<td>+</td>
<td>phrase length</td>
<td>Rybak and Gahr 2004</td>
</tr>
<tr>
<td>barn swallow</td>
<td>C</td>
<td>+</td>
<td>rattle length</td>
<td>Galeotti et al. 1997</td>
</tr>
<tr>
<td>barn swallow</td>
<td>C</td>
<td>0</td>
<td># songs/bout</td>
<td>Saino et al. 1997</td>
</tr>
<tr>
<td>barn swallow</td>
<td>C</td>
<td>0</td>
<td>syllables/bout</td>
<td>Saino et al. 1997</td>
</tr>
<tr>
<td>barn swallow</td>
<td>C</td>
<td>0</td>
<td># impulses in rattle</td>
<td>Saino et al. 1997</td>
</tr>
<tr>
<td>Japanese quail</td>
<td>C</td>
<td>0</td>
<td>onset of crowing</td>
<td>Chiba and Hosokawa 2006</td>
</tr>
<tr>
<td>Lapland longspur</td>
<td>C</td>
<td>0</td>
<td>likelihood of singing</td>
<td>Hunt et al. 2006</td>
</tr>
<tr>
<td>blue tit</td>
<td>E1</td>
<td>0</td>
<td>onset of song relative to sunrise</td>
<td>Kunc et al. 2006</td>
</tr>
<tr>
<td>blue tit</td>
<td>E1</td>
<td>0</td>
<td>mean interstrophe interval</td>
<td>Kunc et al. 2006</td>
</tr>
<tr>
<td>blue tit</td>
<td>E1</td>
<td>0</td>
<td>mean song length</td>
<td>Kunc et al. 2006</td>
</tr>
<tr>
<td>barn swallow</td>
<td>C</td>
<td>0</td>
<td># songs/bout</td>
<td>Saino et al. 1997</td>
</tr>
<tr>
<td>barn swallow</td>
<td>C</td>
<td>0</td>
<td>syllables/bout</td>
<td>Saino et al. 1997</td>
</tr>
<tr>
<td>barn swallow</td>
<td>C</td>
<td>0</td>
<td># impulses in rattle</td>
<td>Saino et al. 1997</td>
</tr>
<tr>
<td>barn swallow</td>
<td>C</td>
<td>0</td>
<td># songs/bout</td>
<td>Saino et al. 1997</td>
</tr>
<tr>
<td>barn swallow</td>
<td>C</td>
<td>0</td>
<td>syllables/bout</td>
<td>Saino et al. 1997</td>
</tr>
<tr>
<td>barn swallow</td>
<td>C</td>
<td>0</td>
<td># impulses in rattle</td>
<td>Saino et al. 1997</td>
</tr>
</tbody>
</table>

*Testosterone treatments: 1) castrated vs. intact males, 2) systemic T implant with cerebral infusion of either control or androgen and estrogen receptor antagonist, 3) T implant with vs. without E2 inhibitor, 4) control vs. injections with: T, E2, DHT, or no hormone 5) no implant vs. implant with no, low or high T.
Figure 2.1: Under the original IHH hypothesis, testosterone positively affects sexual signals, but has a negative quantitative effect on the immune response to parasites. Males with high genetic resistance will have a higher quality immune response and therefore fewer parasites. These males can afford to have high levels of testosterone, good sexual signals, and a quantitatively low immune response. Males with poor genetic resistance will be more susceptible to parasites and thus must invest more in qualitative immune responses by lowering testosterone levels, resulting in poor sexual signals. Arrows represent expected correlations between boxed variables.
Figure 2.2: In Wedekind and Folstad's version of the IHH, testosterone mediates tradeoff in the allocation of energy between immunity and ornaments. Males with good resistance genes will have fewer parasites and thus be in better condition. Lower parasite loads will also decrease the energetic demands of the immune system. Extra energy can then be shunted to the development of sexual signals by increasing testosterone levels. Arrows represent expected correlations between boxed variables.
Figure 2.3: There are two possible pathways by which stress may act on adult song learning in the developmental stress hypothesis. Under the first scenario (path 1, dashed lines), stress decreases condition, which increases the susceptibility of an individual to parasitism. Increased parasitism further decreases condition, resulting in poor learning and low quality adult songs. High genetic resistance to parasite prevents or decreases stress induced parasitism, so males with high resistance can still develop high quality adult songs.

Under the second scenario (path 2, solid line), parasites themselves act as the stressor. Low genetic resistance results in higher parasite loads, which have a negative effect on condition. Low genetic resistance results in higher stress levels, which decreases learning ability and results in lower quality adult songs. Males with high genetic resistance have low parasite loads, and are thus in better condition, have high learning ability, and high quality adult songs.
Figure 2.4: Hypothetical trill rate by frequency bandwidth plot. Lower plot shows the upper-bound regression for the hypothetical species.
Chapter 3

Patterns of social and extrapair mating in a polygynous songbird, the dickcissel
*(Spiza americana)*

In facultatively polygynous species, males appear to gain reproductive benefits by
pairing with multiple females simultaneously. However, this is not necessarily true in
species where extrapair paternity (EPP) is common. Two hypotheses have been posited
describing the relationship between social and extrapair mating success: the tradeoff
hypothesis and the female choice hypothesis (Hasselquist and Sherman 2001).
According to the tradeoff hypothesis polygynous males may face a number of tradeoffs
between social mating success, mate guarding, and the pursuit of extrapair copulations
(EPCs, Arak 1984; Westneat et al. 1990). The pursuit of additional social or extrapair
mates will reduce the amount of time males may spend in other activities, such as
guarding existing mates or defending nests (Hasselquist and Bensch 1991; Dunn and
Robertson 1993; Westneat 1994). Some evidence has been found in support of such
tradeoffs. In red-winged blackbirds (*Agelaius phoeniceus*), for instance, females whose
fertile periods coincided with the settlement of a new female on the same territory were
more likely to have extrapair offspring than other polygynously-mated females. This
result suggests that males were unable to simultaneously attract new mates and maximize
paternity with existing mates (Westneat 1993). Similarly, polygynously mated male tree
swallows (*Tachycineta bicolor*) were twice as likely to be cuckolded than monogamous
swallows (Dunn and Robertson 1993).

In contrast, the female choice hypothesis posits that females bias matings toward
certain males in both mating contexts. In this scenario, extrapair copulations should be
less common among polygynously mated females since they are already mated to males
they perceive as high quality. In contrast, monogamously mated females should be more
likely to engage in EPCs with males they consider superior to their social mate. For
example, polygynous male blue tits (*Parus caeruleus*) spent less time guarding their
mates than monogamous males, but still achieved a similar level of paternity. Even after
polygynous males were removed, copulation attempts by neighboring males largely
failed due to lack of female cooperation (Kempenaers et al. 1995). This suggests that
female choice of social and extrapair partners drives patterns of male mating success in
blue tits. Meta-analysis of interspecific variation in EPP rates lends further support to
this idea, with polygynous species generally exhibiting lower rates of EPP than
monogamous ones (Hasselquist and Sherman 2001).

One would predict a similar covariation between within pair and extrapair success
if male competitiveness, rather than female choice, drives social and genetic mating
patterns. Males that achieve polygyny may be inherently better at attracting and guarding
mates (e.g. Kempenaers et al. 1995) or may defend more attractive territories (Verner and
Willson 1966; Vaclav et al. 2003). Superior fighting ability could make such males
successful at both guarding paternity in their own nests and gaining paternity in other
males’ nests. For example, larger male red-winged blackbirds were more successful in
gaining both social and extrapair mating success (Weatherhead and Boag 1995). In
contrast, female red-winged blackbirds were not able to mate with higher quality males
through extrapair behavior, nor was female involvement in EPC repeatable among years.
These results suggest that male competiveness, not female choice, is driving patterns of mating in the Ontario population of red-winged blackbirds studied by Weatherhead and colleagues.

Both the tradeoff and female choice/male competitiveness hypotheses make distinct predictions. Specifically, the tradeoff hypothesis predicts that: 1) monogamous males are cuckolded less often than polygynous males, 2) among polygynous males, paternity decreases as the overlap in fertile periods within a harem increases, 3) monogamous males are more successful at siring extrapair young, and 4) unmated males should be more successful at attracting newly arrived females to their territories; indeed, females may settle with mated males only when there are no unmated males remaining. In contrast, the female choice/male competitiveness hypothesis predicts that: 1) monogamous males are cuckolded more frequently than polygynous males, 2) paternity is not affected by overlap in female fertile periods within harems, 3) polygynous males are more successful at siring extrapair young than monogamous males, and 4) mated males are more successful at attracting recently arrived females than unmated males.

Socioecological factors, such as breeding density, could also influence the association between social and extrapair mating. Increased breeding density should increase encounter rates between females and males (Birkhead 1978). One would then expect that mate guarding would become more difficult as density increases (Moller and Birkhead 1993). Thus increased breeding density could exaggerate tradeoffs between social and extrapair mating. High breeding densities should also exaggerate the effects of female choice and male competitiveness on social and extrapair mating patterns. If females drive extrapair mating, then increased proximity to potential extrapair mates could facilitate extrapair mating among females seeking such opportunities (i.e. monogamous females). If male competitiveness drives extrapair mating, then increased proximity could also facilitate a competitive male’s attempts to gain extrapair copulations with his neighbor’s females.

Natural selection might also play a role in determining whether polygynous males achieve greater realized reproductive success than monogamous males, particularly in species with high nest predation. Males of many species act as anti-predator sentinels and actively defend nests from predators (e.g. Yasukawa et al. 1992). Vigilance and nest defense may compete with other activities used to attract or guard mates. If so, then nest survival may decline with increasing social mating success. Indeed, evidence for tradeoffs between mating success and nest survival has been found in polygynous species. In red-winged blackbirds nest survival declined with increased harem size (Weatherhead and Robertson 1977; Lenington 1980). Polygynous male great reed warblers (Acrocephalus arundinaceus) defended their nests less vigorously than monogamous males (Trnka and Prokop 2010). Nevertheless, the latter result could be a consequence of decreased predation pressure on the territories of polygynous males (Hansson et al. 2000). A male’s ability to gain and defend a high quality territory may increase both his social mating success and the survival of nests on his territory. Female choice should also favor males that defend territories with low predation pressure, leading to a positive association between male social mating success and nest survival.

I tested the predictions of the tradeoff and female choice/male competitiveness hypotheses in a population of dickcissels (Spiza americana) breeding in northeastern Kansas. Dickcissels exhibit resource defense polygyny, with males defending territories
that contain both nesting and foraging areas (Zimmerman 1966; Fretwell 1986). Social mating in this species includes simultaneous nesting of multiple females, partial overlap of nesting activity, sequential monogamy, and true monogamy. About half of all male dickcissels mate polygynously, with harem sizes varying from two to five females (Zimmerman 1971; 1982). Unlike most male songbirds, male dickcissels do not normally feed their offspring, although they do provide paternal care in the form of nest and fledgling defense (Temple 2002). Lack of male parental care suggests that males devote much of their time to attracting mates, either through polygyny or pursuing extrapair copulations. Although no data is available on extrapair copulations or EPP in this species, even monogamous males provide little care, making it likely that some males pursue them. The prevalence of polygyny and variation in harem size in dickcissels led me to test some of the alternative hypotheses about the relationship between social and genetic mating success. Specifically, I tested 1) the four predictions of each hypothesis, 2) the effect of density on extrapair paternity, 3) the effect of density on the association between harem size and paternity, and 4) the relationship between male mating success and nest survival.

Methods
Field Site and General Methods
I studied dickcissels at the Konza Prairie Biological Station (KPBS) located in Riley and Geary Counties, Kansas (approx. 39°05'N and 96°35'W) in 2006 and 2007. The KPBS is a 3,487 ha area of native tallgrass prairie managed by periodic burning. In 2006 I followed birds inhabiting an unburned watershed (R20A) in the southwestern corner of KPBS. In 2007 the adjacent, biennially burned watershed (2A) was added to the study area. Burning did not occur on either site during this study.

I captured males on their territories using mist nets combined with song playback and, occasionally, a male model. I banded all birds with a U. S. Geological Survey aluminum band and also banded adults with a unique combination of three plastic color bands. My assistants and I located nests primarily by observing female behavior. We then checked nests every three days until the nests either fledged or failed. I assumed a nest had been depredated if it was empty before chicks were old enough to fledge (~8-9 days old). I assumed nestlings had fledged based on the behavior of the parents, since female dickcissels continue to feed fledglings and both parents actively defend them in the vicinity of the nest for an extended period of time (Gross 1968; Temple 2002). Females were trapped at the nest during the nestling phase using a cylindrical nest trap (Sousa and Stewart 2011). Nestlings were banded when at least three days old. Social fathers were assigned to nests based on a combination of active nest defense, pairing behavior with female, and/or location of the nest within a male’s territory (determined from GPS coordinates, see below).

My assistants and I censused the study area weekly to determine the arrival and departure dates of each male. I assumed that males were present on the site until the day before the census after they were last seen. The length of each male’s territory tenure was calculated as the number of weeks a male was present on the study site. The mating status of each male at the beginning of each week was determined retrospectively using the first egg dates of nests occurring within the male’s territory.
I calculated the first egg date for each nest in the study site, assuming one egg laid per day. For nests that were found after the clutch had been completed and survived to the nestling phase, I calculated first egg date from nestling age, assuming a 12 day incubation period. For nests found after the clutch was completed, but depredated before hatching, the first egg date was calculated by assuming that the nest was six days old at the midpoint date of nest checks. I also assumed that the female’s fertilizable period began five days prior to the day the first egg was laid and continued until the day the penultimate egg was laid (Westneat 1993).

**Density Estimate**

The locations of each male were recorded during censuses and focal watches with a Garmin GPSmap 76 or 60Cx handheld unit. Territorial boundaries were determined by recording the GPS coordinates of perches used during 1-hour focal watches, and by flushing males after the watch. One to three focal watches were conducted per male, depending on the length of a male’s tenure on the study site. GPS points were imported into ArcGIS 9.3 for analysis. Minimum convex polygons (MCP; Mohr 1947) were constructed for each male from nest, focal, and census points using the Geospatial Modeling Environment (GME, Beyer 2010). Only nests assigned to males using behavioral data were used when constructing MCPs. The central point of each male’s territory was calculated as its center of gravity (weighted by density of points). Territory size and center points were calculated using the GME. I then calculated an observation-area curve relating the number of GPS points collected to territory size to determine whether sufficient points were collected to accurately determine territory size (Odum and Kuenzler 1955). This curve failed to reach an asymptote, indicating that an insufficient number of points had been collected to accurately measure territory size. I therefore used the center points instead of territorial boundaries to calculate distances to neighbors and other density measures.

I calculated breeding density for each nest as the number of territorial center points within 150m of the nest. A distance of 150m was chosen because it is approximately twice the average distance between a nest and the territorial center point of its nearest neighbor (BF Sousa, unpublished data). I estimated breeding density for a given nest in the week in which the nest was initiated. Census data were used to determine which males were present in a given week.

**Apparent Reproductive Success**

Social mating success in polygynous species can be estimated in a number of ways. One of the most common methods is to measure harem size, which is the maximum number of females simultaneously nesting within a particular male’s territory. Because this measure misses some of the variation in male mating success, I also measured the average number of nests per week for each male. These two values were strongly positively associated (Pearson r = 0.83, p < 0.0001, N = 80). I therefore estimated each male’s social mating success using harem size, since this measure is less likely to be confounded by predation and other stochastic events.

The apparent reproductive success of males with different harem sizes was assessed in two steps. First, I determined the number of nestlings for which a male was the social father, then tallied the subset of these nestlings that were genetically sampled.
This measure was used to compare apparent and genetic reproductive success. Second, I used the total number of fledglings a male produced on his territory as the best measure of his apparent reproductive success.

Paternity Analysis

I defined paternity as the proportion of a social father’s sampled young that he sired. Small blood samples (~50uL) were collected from all adults and nestlings and stored in Queen’s Lysis Buffer (Seutin et al. 1991). Eggs that failed to hatch were collected and examined for contents. No living embryos were found, but partially developed embryos were sometimes present. Dead nestlings were also found at some active and abandoned nests. These nestlings and inviable embryos were collected and stored in 95% ethanol.

DNA was extracted from blood and tissue samples using a 5M NaCl extraction solution (Laird et al. 1991). A phenol-chloroform solution was used to extract DNA from samples with yields less than 5 ng/μL (Chomczynski and Sacchi 2006). 10-20 ng of the extracted samples were amplified in a total reaction volume of 10 μL consisting of 0.2 mM each dNTP, 0.2 μM fluorescently labeled forward primer, 0.2 μM reverse primer, 1X Taq buffer (1.5 mM MgCl, 10 mM Tris-HCl, 50 mM KCl) and 0.35 units Taq polymerase. Amplification was performed in a thermal cycler with the following cycling regime: 94°C for 4 min followed by 35 cycles of 94°C for 30 sec, TA (Table 3.1) for 30 sec, 72°C for 45 seconds and a final cycle of 72°C for 10 min. Amplification for locus Lsw 5 was carried out with the following slight modifications to this procedure: 0.2 μM M13-tagged forward primer, 0.6 μM reverse primer, and the addition of 0.2 μM of fluorescently labeled M13(-21); cycling was carried out as in Schuelke (2000). After amplification 1 μL of PCR product was mixed with 8.8 μL of formamide and 0.2 μL GeneScan LIZ 500 size standard and genotyped in an ABI 3730 capillary sequencer. Genotypes were visualized and scored using GeneMapper 4.0. A small number of samples was genotyped using untagged primers and silver staining (as in Stewart et al. 2010). Genotypes obtained from silver staining were compared to those obtained using the capillary sequencer to ensure comparable results. Exclusion of genotypes obtained from silver staining did not change the results of paternity analysis.

Individuals were genotyped at 6 or 7 microsatellite loci originally developed in other bird species (Table 3.1). Because variability was low at locus VeCr 2, it was not used for all 2007 samples. Cervus 3.0 was used to test for null alleles, deviations from Hardy-Weinberg equilibrium, and to assign paternity to extrapair young (Kalinowski et al. 2007). There was no evidence of null alleles among any of the loci used, nor were there any significant deviations from Hardy-Weinberg equilibrium. Nestlings were considered extrapair if their genotypes did not match their presumed father’s genotype at two or more of the loci typed, since single locus mismatches could be due to mutation.

Cervus weights the probability that a given male sired a chick by allele frequency. To minimize erroneous paternity assignments, multiple criteria were used to assign sires to extrapair chicks. A male was determined to be the sire of an extrapair chick if he was assigned by Cervus with 95% confidence, had a positive trio LOD score (indicating he is more likely to be the sire than a male randomly drawn from the same population), mismatched the chick’s genotype at no more than one locus, and was present at the research site in the week the nest was initiated. I conducted the paternity analysis in three
nested stages. First, the pool of candidate sires for each nest was restricted to the males defending territories directly adjacent to the territorial male. If no sire was assigned at 95% confidence in the first stage, I added all males within 150 m of the focal nest to the pool of candidate sires. If this did not identify a sire, the pool of potential sires was then extended to all males present on the field site during the female’s fertilizable period.

**Nest Survival Analysis**

Predictions regarding variation in nest survival were tested by examining support for a set of candidate nest survival models. First, preliminary models were constructed in Program MARK (White and Burnham 1999) to determine whether nest age, time in season, nesting stage, or year affected nesting success. Model fit was assessed using the Akaike Information Criterion adjusted for finite sample sizes (AICc, Hurvich and Tsai 1989). The terms of the best preliminary model were included in all subsequent models testing the effects of variables related to polygyny on nest survival. A likelihood ratio test was conducted to determine whether these variables contributed significantly to daily nest survival rates.

**Statistical Analyses**

For analyses of male reproductive success all nests within a male’s territory were pooled to obtain overall measures of social and extrapair mating success. Because some males occurred on the study site in both years of the study, male identity was included as a random factor in analyses of reproductive success and patterns of paternity. When these analyses were conducted on binomial variables (e.g., paternity), a generalized linear mixed model (GLMM, Proc GLIMMIX) with a logit link was used. I used a Poisson distribution and log link (GLMM, Proc GLIMMIX) when analyzing harem size. All other measures of reproductive success (e.g. number of chicks fledged) were assumed to be normally distributed and analyzed using a mixed model (Proc Mixed).

Patterns of parentage among nests were also analyzed using a GLMM. Since the probability of extrapair paternity is unlikely to be constant across broods, variance in EPP is likely to be overdispersed in a manner similar to the structure of variance in brood sex ratios (e.g. Krackow and Tkadlec 2001). Therefore, the default restriction of $\phi = 1$ was lifted and a residual variance parameter was estimated for events by trials tests of extrapair paternity. Male identity was included as a random factor to control for possible non-independence of EPP among broods of the same male, both within and between years. The effects of year and site on the incidence of extrapair paternity were assessed using a mixed model that included the random effect of social male identity. Site effects were only assessed for 2007 since only one site was studied in 2006.

Means are reported ± standard deviation and effect sizes are reported ± standard error. All analyses were conducted in SAS 9.2 (SAS Institute 1989), and tests were considered significant at $\alpha = 0.05$.

**Results**

In total, 96 male, 74 female, 175 nestling, and 3 fledgling dickcissels were banded in the course of this study. In 2006, 45 males defended territories on the study site, 38 of which were captured and banded. In 2007, 62 males defended territories in the study area, 48 of which were banded. Of the banded males in 2007, 16 had been marked.
the previous year (42% return rate). I found and monitored a total of 200 nests across the two years of this study.

**Polygyny and Apparent Success**

Polygyny was common in both years of the study. Thirty-seven percent of territorial males were polygynous and harem size peaked at five females, with an average of 1.28 ± 1.03 females. Harem size tended to be smaller in 2006 than in 2007, but not significantly so (Wilcoxon Rank Sum = 1315.5, p = 0.07, 2006: $\bar{x} = 1.1 \pm 0.2, N = 37$; 2007: $\bar{x} = 1.5 \pm 0.2, N = 43$). There was no significant difference in harem size between the two study sites in 2007 (Wilcoxon Rank Sum = 448.5, p = 0.42, R20A: $\bar{x} = 1.7 \pm 0.3$, N = 19; 2007: $\bar{x} = 1.3 \pm 0.1$, N = 24).

Harem size was positively associated with territory tenure (GLMM effect = 0.11 ± 0.03, $F_{1.78} = 11.47$, p = 0.001); however, male identity could not be included as a random factor in this analysis because the variance components were estimated to be zero. Thus, this test violated the assumption that observations were independent. I therefore repeated the analysis with only one record per male and obtained similar results (GLMM, effect = 0.09 ± 0.03, $F_{1.68} = 7.48$, p = 0.008).

The number of young sampled per male was positively associated with both harem size and year (LMM harem size, 2.07 ± 0.36, $F_{1.60} = 33.84$, p < 0.0001; year, 2.20 ± 0.36, $F_{1.60} = 12.17$, p = 0.001). The total number of fledglings each male produced on his territory was highly correlated with harem size, but not with year (LMM harem size, 1.41 ± 0.20, $F_{1.77} = 51.66$, p < 0.0001; year, 0.52 ± 0.40, $F_{1.77} = 1.72$, p = 0.19).

**Female Settlement**

In order to determine whether females settled preferentially with mated males, I calculated the proportion of nests initiated in the territories of already mated males versus unmated males each week of 2006 (9 weeks) and 2007 (12 weeks). For each week, I first calculated the fraction of males present on the study site that were already paired. I then calculated the expected number of polygynous nests started each week as the product of this proportion and the number of nests initiated in that week. There was no evidence that females settled non-randomly with respect to male mating status (2006: $X^2 = 5.49$, p = 0.79, df = 9; 2007: $X^2 = 8.70$, p = 0.73, df = 12).

**Paternity Analysis**

At least one nestling was sired by an EPF in 48 of 92 broods (52%), accounting for 84 of 218 chicks (39%). This excludes a single nestling in 2007 that amplified at fewer than four loci and two fledglings in 2006 whose social father could not be reliably determined. It includes 48 nestlings for which the female was not sampled but were typed at a sufficient number of loci to assess paternity. Extrapair sires were assigned to 57 chicks (68%). Over a third of extrapair young (38%) were assigned to a male from a bordering territory. Of the 27 unassigned offspring, 20 came from nests where a male in a neighboring territory was not sampled and all had at least one unsampled male within two territories. The distance from a nest containing an extrapair chick and the territory of its sire ranged from 35.5m to 760.1m (mean = 192.8 ± 169.1 m).

In 22 broods, all of the chicks were sired by an extrapair male. This includes nine nests containing a single nestling, and eight with two nestlings. These broods were re-
examined to determine whether there had been a mistake when assigning the social male. In all 22 cases, the nests were located within the assigned social male’s territory and blood sample labels matched the field notes taken at the time of capture. Erroneous assignment of a chick as extrapair can also result if the social male was replaced after a previous observation. However, during two years of study, only two cases of mate switching were observed. Both occurred between males on adjacent territories where the nest was located near the territory border. In both cases, a switch occurred when one male took over part of the territory of an adjacent male that contained the nest. In one case DNA was collected from the brood, and the DNA analysis showed that the new social mate did not sire any of the chicks, and the original mate shared paternity with a third, unidentified male.

In four broods, the extrapair chicks were sired by more than one male, as indicated by three paternal alleles at multiple loci. One of these broods occurred in 2006 and was likely the result of the transitory tenure of several immigrating males. Rapid territorial changeover in the area made it impossible to assign a social mate with any confidence; however, none of the three potential social mates matched any of the three offspring of this nest, nor were there any unsampled males on adjacent territories. Four of the seven loci typed produced three paternal alleles per brood, indicating that at least two males likely contributed paternity. Each chick was assigned to a different banded male from neighboring territories. In 2007 three cases of multiple extrapair paternity were observed. In two cases the social father shared paternity with two extrapair males. In the remaining brood, the social male sired none of the brood, an adjacent male sired two chicks, and the remaining chick could not be assigned a sire.

Neither year nor site had a significant effect on the proportion of a brood that was sired through EPFs (Figure 3.1; year, F$_{1,88} = 0.24$, p = 0.62; site, F$_{1,20.2} = 2.67$, p = 0.12). The proportion of nests containing at least one extrapair chick was not different between years (Figure 3.2, F$_{1,88} = 0.67$, p = 0.42). The effect of site on the proportion of nests containing extrapair young could not be estimated when social male identity was included in the model (variance for this parameter was estimated as zero). Therefore, this term was removed from the model and a logistic regression showed that the proportion of nests with extrapair young was significantly higher in watershed 2a than in R20a (Figure 3.2, Wald X$^2 = 6.53$, p = 0.01).

**Polygyny and Paternity**

Paternity (the proportion of a social father’s sampled young that he sired) tended to be higher among males with larger harem sizes (effect = 0.34 ± 0.18, F$_{1,17.8} = 3.58$, p = 0.07). There was no evidence that polygynous males lost paternity when two or more of the females on his territory had overlapping fertile periods (effect = 0.20 ± 0.42, F$_{1,59} = 0.22$, p = 0.64). Females that paired with already mated males were no more likely to produce extrapair young than females that settled with unmated males (effect = -0.02 ± 0.46, F$_{1,73.2} < 0.01$, p = 0.96). In contrast, a male achieved higher paternity in the nests of females that experienced overlapping nesting activity (i.e. when a female was polygynously mated at any point in her nesting cycle; effect = 0.84 ± 0.35, F$_{1,24.8} = 4.36$, p = 0.05).

The number of offspring a male gained through extrapair mating was positively associated with his harem size when using the full dataset (Figure 3.3; Mixed model:...
effect = 0.32 ± 0.14, $F_{1,70.8} = 5.11, p = 0.03$). However, extrapair mating success may be underestimated for males defending territories on the border of the study site. To account for differences in sampling, I defined a male’s opportunity to sire extrapair offspring as the number of genotyped nestlings within 150 m of the center of each male’s territory center (excluding nests within the male’s own territory). This excluded any nestlings sired before or after a male was resident on the study site. I then tallied the proportion of these chicks sired by the focal male. This measure was also significantly positively associated with harem size (Mixed model: effect = 0.52 ± 0.24, $F_{1,72.9} = 4.62, p = 0.03$). This association appears to be driven by males with no social mates, who were also unsuccessful at gaining EPP. When unmated males are removed from the analysis, siring success does not significantly increase with harem size (Mixed model: effect = 0.24 ± 0.26, $F_{1,43.8} = 0.87, p = 0.36$).

A male’s total reproductive success (total number of fledglings including both within pair and extrapair young) also increased with his harem size (Figure 3.4; Mixed model: effect = 4.21 ± 0.19, $F_{1,78} = 41.69, p < 0.0001$). This remained significant when males with no social mating success were excluded from the analysis. Males gained 1.4 ± 0.3 fledglings per additional female (Mixed model, $F_{1,61} = 25.02, p < 0.0001$). Polygynous males were also more likely to fledge at least one related chick than monogamous males (Mixed model effect = 1.63 ± 0.53, $F_{1,61} = 9.43, p = 0.003$).

### Polygyny and Nest Survival

Nest abandonment was rare in both years of the study (8 of 218 nests). However, nest depredation rates were generally high and stable across years and sites at around 64%. In 2006, 23% of nests fledged at least one chick, while 31% of nests fledged in 2007. Since depredation rates were stable across years, higher fledging rates in 2007 were due to a decrease in the number of nest failures resulting from severe weather, poor construction or abandonment. The best fitting base model of nest survival included age, age$^2$, stage and year, but not time of season (Table 3.2). This model was substantially better at explaining variation in daily nest survival (DSR) than the null model of constant DSR ($\Delta AIC = 28.28$). The addition of a female’s pairing status (monogamous vs. polygynous) on the day of clutch initiation did not improve the fit of the nest survival model. Similarly, whether a female’s nesting attempt temporally overlapped that of one or more of the other females on the territory did not improve the model’s fit. In contrast, the addition of the male’s peak harem size did significantly improve the model, with harem size having a positive effect on nest survival ($X^2 = 5.17, p = 0.02$).

### Density and Polygyny

Breeding density did not significantly influence extrapair mating. The proportion of within pair young (WPY) in a nest was not influenced by the number of males within 150 m of the nest in the week of nest initiation (effect = -0.05 ± 0.07, $F_{1,77.5} = 0.51, p = 0.51$). This remained true when nests within 150 m of the border of the study site were excluded from the analysis (effect = -0.08 ± 0.09, $F_{1,59.6} = 0.74, p = 0.39$).

Breeding density could enhance the association between extrapair and social mating success. I tested this idea using a model relating paternity in each nest to breeding density, the number of other females on the territory with nesting activity concurrent with the focal nest, and the interaction of the two. There was no main effect
of breeding density on the proportion of WPY in a brood (effect = -0.004 ± 0.09, F_{1,78.9} = 0.00, p = 0.97). Likewise, the proportion of WPY in a brood was not influenced by the interaction term (effect = -0.09 ± 0.11, F_{1,80.4} = 0.73, p = 0.40). This did not change when nests within 150 m of the border of the study site were excluded from the analysis (density effect = -0.005 ± 0.11, F_{1,54.9} = 0.00, p = 0.96; interaction effect = -0.16 ± 0.14, F_{1,60.5} = 1.31, p = 0.26).

Discussion

The relationships between social and genetic mating in dickcissels generally conform to the predictions made by the female choice/male competitiveness hypothesis, although the fit of the data to the predictions was not always strong. First, a male’s within pair siring success tended to increase, albeit non-significantly, with harem size. Second, there was no evidence of tradeoffs since extrapair young were not more common when a male’s mates had overlapping fertile periods. Instead, paternity was higher in nests where at least a portion of nesting activity overlapped that of another female on the same territory. Additionally, females that settled with mated males had no more extrapair young than did females that settled either monogamously or as primary females. Third, extrapair siring success increased with harem size, and this relationship was stronger when biased sampling was taken into account. Fourth, there was no evidence that male mating status influenced female settlement decisions. Such evidence, taken as a whole, lends some support to the idea that polygynous males are successful in both mating contexts and apparently experience few tradeoffs between them.

There are several mechanisms that could produce this pattern of mating success. One possibility is that certain males are more competitive and thus better able to obtain and defend a high quality territory. The ability to hold a high quality territory could enhance both social and extrapair mating success. For example, being able to defend a territory with abundant food could increase the number of social mates a male attracts (Verner and Willson 1966), decrease the number of extraterritorial forays those mates need to make (Vaclav et al. 2003), and could even attract neighboring females to the territory for foraging bouts and thereby increase opportunities for EPCs (Gray 1998). Previous studies provide mixed support for this idea in dickcissels. Harmeson (1974) found significantly more arthropods in the territories of polygynous versus monogamous male dickcissels, but this was true in only one of three sampling periods. Finck (1983) and Zimmerman (1966) found no differences in arthropod densities between monogamous and bigamous dickcissel territories. Nevertheless, these results do not entirely rule out the possibility that food availability is an important factor in male mating success. Finck (1983) found that males supplemented with food increased the amount of time they spent in activities related to female attraction (e.g. singing). Furthermore, conditions on the tallgrass prairie can vary substantially across years (Knapp et al. 1998b), and arthropod abundance may be more important in some years than in others. It is also possible that some other aspect of territory quality is an important factor in male mating success. For instance vegetation height, density and composition have repeatedly been linked to both nest site selection and nest survival in this species (Hughes et al. 1999a; Dechant et al. 2003; Westneat 2006; Berkeley et al. 2007; Frey et al. 2008). While it is not clear how these factors could influence extrapair mating success, there is
some support for their positive effect on social mating success (Zimmerman 1966; Finck 1983).

Another possibility is that, rather than attracting females to the territory itself, male behaviors that favor the acquisition of attractive territories also contribute to obtaining EPCs off the territory. For example, territorial disputes between neighboring dickcissels can involve chases and direct fighting. Males that excel in such contests could also be more successful in chasing extrapair females and eluding or fighting their mates. Male dominance has been associated with male mating success, but this is often attributed to female preference for dominant males rather than male competitive ability (Otter et al. 1998; Woodcock et al. 2005). Experience could also be an important factor in both social and extrapair mating success. Indeed, a number of studies have found that older, more experienced birds have higher reproductive success (e.g. Nol and Smith 1987; Weatherhead and Boag 1995; Poesel et al. 2006). The effects of age on male mating success have not been examined in dickcissels, and low return rates between years make the effects of experience difficult to assess in this species.

If females control mating, then female choice could result in the same males being successful in all mating contexts (Weatherhead and Robertson 1979; Hasselquist and Sherman 2001; Westneat and Stewart 2003). Females will seek to pair socially with preferred males and resist copulation attempts by other males. When females are unable to settle with their preferred mate, they may still pursue extrapair copulations with that male. In dickcissels, there is little evidence that females prefer particular male traits. Neither body size, bib size, nor the amount of time males spend singing led to higher social mating success (Finck 1983; Finck 1984), but their impact on extrapair success, either in increasing within pair paternity or affecting extrapair siring success, has not been assessed in this species. Bright colors and song traits have frequently been implicated as a target of female choice in other species (reviewed in: Hill 2006; Catchpole and Slater 2008), and male dickcissels have a bright yellow breast and use a simple song in mate attraction and territory defense. The effect of these traits on mating success has not been examined in dickcissels. So while evidence for female choice of male traits is lacking, it is possible females are attending to traits that have not yet been assessed in dickcissels. Thus female choice for male plumage and song traits could be an important factor in shaping mating patterns.

Socioecological factors might also contribute to the mating patterns observed in this study. Most notably, breeding synchrony and density are frequently cited explanations for patterns of extrapair mating success (Birkhead 1979; Stutchbury and Morton 1995; Westneat and Sherman 1997; Thusius et al. 2001; Griffith et al. 2002). High nest mortality during incubation and the presence of unsampled males (whose nests were not monitored) precluded an analysis of site-wide breeding synchrony in this population. Nevertheless, within a male’s harem, within pair paternity was positively associated with synchrony. Since high synchrony among a male’s social mates should make mate guarding more difficult, this result suggests that female choice drives patterns of paternity in harems.

The proximity of conspecifics could also exaggerate patterns of male mating success by increasing encounter rates between potential extrapair mates. Nevertheless, a male’s paternity was not influenced by the interaction between social mating success and breeding density. While this result is not consistent with the tradeoff hypothesis, density
independence is consistent with the predictions of the choice/competitiveness hypothesis. Under the choice/competitiveness hypothesis, females will seek copulations only with preferred males, regardless of the number of other males in the immediate area. Similarly, competitive males may establish their dominance early in the season, leading to fewer attempts by neighbors to cuckold such males regardless of proximity.

Finally, the reproductive success of polygynous males could be negatively influenced by natural selection. For instance, the fledging success of nests declined with harem size in red winged blackbirds (Weatherhead and Robertson 1977; Lenington 1980). In contrast, polygynous male dickcissels maintained high realized reproductive success in the face of high nest depredation rates. In fact, the only significant contribution to the base model of nest survival was a male’s peak harem size. The presence of other nesting females on the territory and mating status of the female at clutch initiation did not significantly affect nest survival. Thus nest survival is most likely influenced by the male or his territory, not by the benefits of nesting near other females.

There are several ways a positive association between harem size and nest survival could come about. First, polygynous males could increase nest survival within their harems if they are more vigilant or defend nests more vigorously than monogamous males. For instance, there is a positive association between harem size and the intensity of male nest defense in red-winged blackbirds (Knight and Temple 1988). Second, polygynous males could defend territories with lower predation pressure, as observed in great reed warblers (Hansson et al. 2000). It is unknown whether there is an association between mating success and nest defense in dickcissels, and data were not available to evaluate this relationship in the current study. Likewise, there is no direct evidence for decreased predation pressure on the territories of polygynous males. Nevertheless, indirect evidence suggests that polygynous males may indeed defend territories with fewer predators. The most common predators of dickcissel nests are snakes (Klug et al. 2010d). Klug (2010c) found that snake predation of grassland bird nests on KPBS was lower in areas with greater vegetation height. This may explain why lowland sites, where vegetation is taller and denser, are usually the first to be settled by arriving males (Zimmerman 1971; Frey et al. 2008). There is also widespread evidence that the vegetative composition near a nest contributes to nest survival (Zimmerman 1982; Hughes et al. 1999a; Berkeley et al. 2007; Klug et al. 2010c). Thus it is possible that increased nest survival in the territories of polygynous males is a function of territory quality and male competitiveness.

Socioecological factors may also contribute to the surprisingly high rates of EPP I observed in Kansas dickcissels. More than half of the broods sampled contained at least one extrapair offspring and 40.8% of all chicks were the result of extrapair fertilizations. Dickcissels are thus one of the most promiscuous avian species studied to date. This is particularly surprising since polygynous species have lower rates of EPP (11%) than monogamous species (23% EPP, Hasselquist and Sherman 2001; Griffith et al. 2002). Both breeding synchrony and density have been associated with high rates of EPP in other species (Birkhead 1979; Westneat et al. 1990; Stutchbury and Morton 1995; Griffith et al. 2002; Stewart et al. 2010). Nonetheless, these factors do not appear to contribute to EPP rates in dickcissels. High predation rates, low female site fidelity, and the female’s proclivity to move large distances between breeding attempts (Walk et al.
2004) would likely lead to low levels of breeding synchrony throughout the breeding season. Thus synchrony is an unlikely explanation for high levels of EPP in dickcissels. Likewise, I found no main effect of breeding density on paternity within nests. This is somewhat surprising since over a third of extrapair young were sired by males on neighboring territories. While density has contributed to extrapair paternity rates in a number of other studies, there is little support for a consistent, positive effect of density on EPP (reviewed by Westneat and Sherman 1997). Indeed, more recent reviews demonstrate that neither synchrony nor density have as strong an effect on EPP rates as originally envisioned (Griffith et al. 2002; Westneat and Stewart 2003).

There are several other possible reasons why EPP rates were unexpectedly high in dickcissels. First, the lack of male provisioning means that males are released from this time constraint on their pursuit of EPP (Werren et al. 1980; Westneat et al. 1990; Westneat and Sherman 1993; Gowaty 1996; Wright 1998). It also means that males cannot further decrease provisioning in response to female infidelity, freeing females from this cost of extrapair mating (Westneat and Sherman 1993; Mulder et al. 1994; Arnold and Owens 2002; Griffith et al. 2002). Second, females dickcissels are known to foray off territory to forage (Zimmerman 1966). Such forays would increase the likelihood that females will encounter extrapair males. Further study is needed to determine whether females actively seek extrapair copulations when foraying off territory and to determine whether males also engage in extrapair copulation attempts off territory.

Higher than average rates of extrapair paternity, combined with a positive association between social and extrapair mating suggest that sexual selection plays an active and important role in shaping mating patterns in this species. One possible concern with these results is that biased sampling could contribute to the patterns of mating success I observed. Polygynous males defended territories longer than other males. Simply by being on the study site longer, polygynous males increase the number of opportunities they have to sire extrapair young (more nearby nest starts) and the probability that at least one of these offspring will survive to sampling. Nonetheless, the positive association between extrapair and within pair mating success remained significant when sampling effort was controlled for. None of the three possible explanations above (territory quality, male competitiveness, and female choice) are mutually exclusive. It is possible that all three contribute to creating a positive association among polygyny, paternity, and extrapair siring success. For example, females could prefer male traits that confer an advantage in territorial acquisition and defense. While the results of this study cannot distinguish among these mechanisms, there is some evidence that all three occur and may interact to produce the patterns observed. Data on the characteristics of successful males, as well as the ecological factors contributing to patterns of EPP are needed to elucidate the causes of high levels of EPP in a polygynous population with high variance in male mating success.
### Table 3.1. Characteristics of microsatellite loci used in dickcissel paternity analysis

<table>
<thead>
<tr>
<th>Locus</th>
<th>k</th>
<th>T&lt;sub&gt;A&lt;/sub&gt;</th>
<th>N</th>
<th>H&lt;sub&gt;O&lt;/sub&gt;</th>
<th>H&lt;sub&gt;E&lt;/sub&gt;</th>
<th>P&lt;sub&gt;1&lt;/sub&gt;</th>
<th>P&lt;sub&gt;2&lt;/sub&gt;</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dp 16</td>
<td>14</td>
<td>55</td>
<td>215</td>
<td>0.69</td>
<td>0.71</td>
<td>0.32</td>
<td>0.51</td>
<td>(Dawson et al. 1997)</td>
</tr>
<tr>
<td>Mcy 4</td>
<td>18</td>
<td>43</td>
<td>214</td>
<td>0.86</td>
<td>0.86</td>
<td>0.55</td>
<td>0.71</td>
<td>(Double et al. 1997)</td>
</tr>
<tr>
<td>Lei 160</td>
<td>10</td>
<td>51</td>
<td>214</td>
<td>0.81</td>
<td>0.84</td>
<td>0.50</td>
<td>0.67</td>
<td>(Gibbs et al. 1997)</td>
</tr>
<tr>
<td>Emb 112</td>
<td>25</td>
<td>55</td>
<td>214</td>
<td>0.87</td>
<td>0.88</td>
<td>0.61</td>
<td>0.76</td>
<td>(Mayer et al. 2008)</td>
</tr>
<tr>
<td>Lsw 5</td>
<td>10</td>
<td>55</td>
<td>208</td>
<td>0.69</td>
<td>0.69</td>
<td>0.29</td>
<td>0.47</td>
<td>(Gibbs et al. 1999)</td>
</tr>
<tr>
<td>Hofi 5</td>
<td>23</td>
<td>55</td>
<td>197</td>
<td>0.92</td>
<td>0.93</td>
<td>0.75</td>
<td>0.85</td>
<td>(Polakova et al. 2007)</td>
</tr>
<tr>
<td>VeCr 2</td>
<td>5</td>
<td>55</td>
<td>146</td>
<td>0.67</td>
<td>0.68</td>
<td>0.24</td>
<td>0.39</td>
<td>(Stenzler et al. 2004)</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td></td>
<td>0.992</td>
<td>0.9995</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

k = number of alleles, N = number of adults genotyped, T<sub>A</sub> = annealing temperature (ºC), H<sub>O</sub> = observed heterozygosity, H<sub>E</sub> = expected heterozygosity, P<sub>1</sub> = exclusion probability of first parent, P<sub>2</sub> = exclusion probability of second parent

### Table 3.2. Comparison of models explaining nest survival in dickcissels, with null model at top, base model second, and three models adding measures of the number and timing of within-territory female nesting.

<table>
<thead>
<tr>
<th>Model</th>
<th>K</th>
<th>AICc</th>
<th>ΔAIC</th>
<th>w&lt;sub&gt;i&lt;/sub&gt;</th>
<th>β</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>constant DSR</td>
<td>1</td>
<td>469.93</td>
<td>31.43</td>
<td>0.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B&lt;sub&gt;0&lt;/sub&gt; + age + age&lt;sup&gt;2&lt;/sup&gt; + stage + year</td>
<td>5</td>
<td>441.65</td>
<td>3.15</td>
<td>0.13</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B&lt;sub&gt;0&lt;/sub&gt; + age + age&lt;sup&gt;2&lt;/sup&gt; + stage + year + harem&lt;sup&gt;1&lt;/sup&gt;</td>
<td>6</td>
<td>438.50</td>
<td>0.00</td>
<td>0.62</td>
<td>0.26</td>
<td>0.12</td>
</tr>
<tr>
<td>B&lt;sub&gt;0&lt;/sub&gt; + age + age&lt;sup&gt;2&lt;/sup&gt; + stage + year + pair&lt;sup&gt;2&lt;/sup&gt;</td>
<td>6</td>
<td>441.67</td>
<td>3.17</td>
<td>0.13</td>
<td>0.32</td>
<td>0.23</td>
</tr>
<tr>
<td>B&lt;sub&gt;0&lt;/sub&gt; + age + age&lt;sup&gt;2&lt;/sup&gt; + stage + year + overlap&lt;sup&gt;3&lt;/sup&gt;</td>
<td>6</td>
<td>441.72</td>
<td>3.22</td>
<td>0.13</td>
<td>0.30</td>
<td>0.22</td>
</tr>
</tbody>
</table>

The number of parameters (K), Akaike Information Criterion (AICc), delta AIC, and Akaike’s weight (w<sub>i</sub>) are reported for each model. Effect size (β) and standard error are reported polygyny variables.

1Harem is maximum number of simultaneously nesting females.

2Monogamous or polygynous on day clutch was initiated.

3Whether nesting activity overlapped that of any other female on the territory.
Figure 3.1. Variation across years and sites in the proportion of extrapair young occurring in dickcissel broods. Means are plotted ± standard error. Means for site are calculated for 2007 only. Statistical analysis revealed no differences once random effects were controlled for.

![Figure 3.1](image1)

Figure 3.2. Variation across years and sites in the proportion of dickcissel nests containing at least one extrapair chick. Means are plotted ± standard error. Means for site are calculated for 2007 only. Asterisk indicates p < 0.05.

![Figure 3.2](image2)
Figure 3.3. Scatter plot of the proportion of nearby dickcissel chicks sired through extrapair copulations by males with different harem sizes.

Figure 3.4. The total number of related dickcissel fledglings (both within pair and extrapair) sired by males with different harem sizes. Point size indicates number of coincident values.
Chapter 4

Variance in mating success does not produce strong sexual selection on ornaments in a polygynous songbird

The sexually dimorphic ornaments and songs of birds are generally thought to be the result of sexual selection (Darwin 1871; Andersson 1994). According to this theory, males with the most extravagant ornaments (e.g. brightest plumage, most elaborate song) should have the highest reproductive success (Darwin 1871; Zahavi 1975; Hamilton and Zuk 1982; Kodric-Brown and Brown 1984). Wade (1979) showed that the strength of this relationship is influenced by the amount of variation in reproductive success in a population, with greater skew in mating success promoting stronger sexual selection. For some time, social mating was thought to be the primary source of variation in reproductive success (Bateman 1948; Emlen and Oring 1977). However, variation in social mating success could not fully explain patterns of sexual selection (Griffith et al. 2002; Westneat and Stewart 2003). The discovery of extrapair paternity in birds revealed that a male's social mating success is not always a good indicator of his true reproductive success (Griffith et al. 2002). This is especially true in passerines, where extrapair paternity is common and can account for a significant portion of a male's reproductive output (e.g. Dolan et al. 2007; Webster et al. 2007; reviewed in Griffith et al. 2002). Thus, the traditional view that variation in sexual dimorphism among avian species can be largely attributed to social mating patterns is no longer justified.

Extrapair mating in monogamous birds can contribute substantially to variation in reproductive success. In yellow warblers (Dendroica petechia) for instance, extrapair mating increased variance in male reproductive success 13-fold (Yezerinac et al. 1995). Indeed, any deviation from strict monogamy is likely to increase variation in male mating success, since social mating success is likely to be fairly uniform in monogamous systems (Jones et al. 2001; Lawler 2009). Thus some have argued that extrapair matings create the primary source of selection favoring the exaggeration of dimorphic plumage ornaments in monogamous songbirds (Moller and Birkhead 1994; Owens and Hartley 1998).

While the contribution of extrapair mating to sexual selection is relatively straightforward in monogamous birds, it is less clear how extrapair mating affects sexual selection in polygynous species. Sexual selection may be strengthened or weakened in polygynous species depending on 1) the patterns of association between social and genetic mating success and 2) the patterns of association between male traits and reproductive success within each mating context. Unlike monogamous mating systems, extrapair mating does not necessarily increase variation in reproductive success in polygynous systems (Webster et al. 1995; Jones et al. 2001). Indeed, a negative association between social and extrapair mating will decrease variation in male mating success in polygynous systems (Jones et al. 2001; Pedersen et al. 2006; Inoue-Muraiyama et al. 2011). It is also not clear whether selection acts primarily through social or extrapair mating in polygynous species (most recently reviewed in Schlicht et al. 2011). In some species, tradeoffs between polygynous mating and within pair paternity resulted in monogamous males siring more related offspring than polygynous males (e.g. Dunn and Robertson 1993; Poirier et al. 2004). In other species, polygynous males had higher
Patterns of association within mating contexts can also influence sexual selection in polygynous species. Sexual selection will be strongest if it is consistent across mating contexts. Opposing selection in different mating contexts should weaken sexual selection (Candolin 2003). In addition, the specific mating context in which selection acts and the contribution of that portion of mating success to overall reproductive success will also influence the strength of sexual selection. For instance, strong selection for male size through extrapair mating success will not result in strong overall sexual selection if extrapair mating contributes little to overall variance in reproductive success.

Few studies have estimated sexual selection in polygynous songbirds. Even fewer have investigated patterns of mating success and sexual selection acting across different mating contexts. In fact, I am aware of only one such study. Westneat’s (2006) study of red-winged blackbirds (Agelaius phoeniceus) used path analysis and experimental manipulation to examine patterns of sexual selection across different mating contexts. Despite positive association between social and extrapair mating success, Westneat found no evidence of sexual selection acting in any mating context. Indeed, a review of associations between male secondary sexual traits and mating success in birds found significantly smaller effect sizes in polygynous species compared to both lek and monogamously mating species (Gontard-Danek and Moller 1999). Nevertheless, this review included only one study of a polygynous species that also assessed paternity, so it is not certain whether this pattern remains true when extrapair mating is accounted for. If extrapair paternity contributes little to total variance in reproductive success (Hasselquist and Sherman 2001), then sexual selection may indeed be weaker in polygynous species. Such a conclusion is premature, however, given the paucity of studies examining actual mating success and sexual selection in polygynous species. Clearly more studies are needed to determine how selection acts on traits in polygynous species, and what patterns of selection are created by interactions among the various mating contexts.

I investigated patterns of male mating success in relation to male phenotype in a facultatively polygynous, sexually dimorphic songbird, the dickcissel (Spiza americana). Males differ from females in four major phenotypic traits. First, male dickcissels are 10-20% larger than females (Temple 2002). Second, males have a black bib that they display in aggressive interactions (Schartz and Zimmerman 1971). Third, dickcissel males have a bright yellow breast that is much paler in the drabber female. Finally, dickcissels are named for the simple song males use to attract mates and defend territories (Temple 2002). I therefore focused my study on sexual selection acting on these four traits.

Previous work found high variance in male mating success, as well as a positive association between within pair and extrapair mating success in this species (chapter 3). In addition, males do not normally provide any care for their offspring (Temple 2002). These conditions should promote strong sexual selection in this species. The focus of this study was twofold: first, to determine whether sexual selection is acting on male traits in a polygynous species with high variance in male mating success and, second, to determine whether selection on male traits is consistent across mating contexts.
Methods

General Methods

I captured male and female dickcissels with mist nets and banded each with a unique combination of three plastic color bands and a U. S. Geological Survey aluminum band. Blood samples were collected from all adults and nestlings for paternity analysis. My assistants and I checked nests every three days until they either fledged or failed. Social fathers actively defended nests, engaged in pairing behavior with the female, and/or defended the territory in which the nest was located. I genotyped all adults and young at six to seven variable microsatellite loci. Chicks were considered extrapair if they mismatched the putative father at two or more loci. Only males present in the week the nest was initiated were considered a potential sire of that nest’s extrapair offspring. Sires were assigned to extrapair young using Cervus 3.0 (Kalinowski et al. 2007). A male was considered the sire if he: was assigned by Cervus with 95% confidence, had a positive LOD score (indicating he is more likely to be the sire than a male randomly drawn from the same population), and mismatched the chick’s genotype at no more than one locus. Details of the paternity analysis are presented in chapter 3.

Male Traits

Male Size. Upon capture, I measured tarsus length, natural wing chord, bill length and bill depth for all adults. Since none of these measures were strongly correlated ($|r| < 0.25$), they could not be combined using principal components. Wing chord can vary across the season due to wear on the outer primaries and bill size and shape are presumably constrained by their role in feeding. Tarsus length, on the other hand, is a skeletal feature that should not vary once a bird reaches adulthood. Because of these considerations, I subsequently used tarsus length to represent male body size.

Black bib. I used ImageJ (Abramoff et al. 2004) to calculate the total area of black breast coloration from digital photographs taken in the field. Each male was held in a standard upright position by grasping the upper legs, tail and wing tips between forefingers and thumb (Figure 4.1). I then photographed the male against a background with both a size and black color standard.

Yellow breast. Upon capture, I collected two feathers from the breast of each male in 2006, while four feathers were collected in 2007. I quantified plumage coloration using a USB2000 spectrometer and pulsed xenon light source (PX-2; Ocean Optics, Dunedin, FL, USA). The probe was mounted in a metal sheath that excluded light from the measurement area and held the probe perpendicular to the feather at a distance of 6mm. Reflectance spectra were standardized to a Spectralon® light standard (Labsphere, Inc., North Sutton, NH) and flat black background. I stacked feathers one atop the other and took a reading from the yellow portion of the feather. Because different numbers of feathers were collected in the two years of the study, the methods for measuring feather coloration varied slightly between years. In both years, five readings were taken for each male. In 2006, three measurements were taken, then the feathers were rearranged and two more measures were taken. The probe was lifted off the feathers between each reading. In 2007, the stack of feathers was rearranged into a unique order after each measure. The stacking method used in 2006 was also used for 10 males in 2007.
measurements obtained in this manner were then compared to measurements from the same 10 males obtained using the 2007 feather stacking method. This was done in order to determine whether the two stacking methods yielded similar results.

I restricted the spectral analysis to wavelengths between 300 and 700 nm, since this likely represents the visual range of passerines (Jacobs 1981; Cuthill et al. 2000). Figure 4.2 illustrates the ranges over which ultraviolet (UV) and yellow coloration were evaluated. I measured UV coloration from 300 nm to the point at which the reflectance curve reached its first nadir (point A in Figure 4.2). I measured yellow coloration from point B (the second nadir in the reflectance spectrum) to 700 nm. Mean brightness was calculated for the UV, yellow, and full visual range as the sum of the percent reflectance over each range, divided by the number of values summed. In order to calculate UV hue, I fit a quadratic function to the UV curve, then defined UV hue as the wavelength at which this function reached its maximum. I measured yellow hue as the wavelength at which the slope of the yellow curve was greatest (Figure 4.2, Montgomerie 2006). The slope of the reflectance curve was calculated over all 1.7 nm intervals (5 reflectance measurements) within the yellow range. Yellow hue was then calculated as the wavelength corresponding to the reflectance value at the midpoint of the interval with the greatest change in reflectance. All spectral analyses were performed in Matlab 7 (code presented in Appendix 4). The color variables described above were measured separately for each of the five readings taken from each male’s feathers. These five measures were then averaged to obtain a single measure of each color variable for each male.

**Song.** My assistants and I recorded the songs of all banded, territorial males between dawn and 14:00 hours CST using a Sony TCM-5000EV cassette recorder and Sennheiser long shotgun microphone (me67). An effort was made to obtain at least two recordings per male and ~25 songs per recording. I digitized and analyzed all song recordings using Raven 1.3 song analysis software.

Dickcissels sing a simple song comprised of two repeated phrases: a short “dick” and a longer “cissel” containing three distinct elements (Figure 4.3). I quantified variation in song quality from the clearest recording of each male (i.e. least amount of freeway, wind, and non-focal bird noise). Specific song characteristics were measured from 5 contiguous songs in each recording: number of “dick” phrases, number of “cissel” phrases, frequency range, center frequency of the c1 bridge and c3 tail, song length, and intersong interval. In males that did not have a c1 bridge, the center frequency of the entire c1 syllable was recorded. I used the mean of the 5 measurements in analyses of song variation.

**Variance in Reproductive Success**

Variance in reproductive success was calculated from the number of young genotyped. I estimated each male’s total reproductive success as the total number of sampled young that a male sired, including both within and extrapair young. Apparent reproductive success was estimated as the number of young typed in each male’s territory. In organisms that engage in extra-pair mating, total variance in mating success, Var(T), can be measured by adding the variance in within-pair mating success, Var(W); the variance in extra-pair mating success, Var(E); and twice the covariance between the two (Webster et al. 1995):
Partitioning variance in this manner enables an examination of the relative contribution of different sources of variation in male mating success to the overall variance. I calculated the standardized variances ($I_s$) for apparent and each component of realized reproductive success as the variance divided by the squared mean reproductive success for each term (Crow 1958; Arnold and Wade 1984). Standardized covariance was estimated as the covariance divided by the product of the square roots of the variances of the terms. Measures of apparent reproductive success assume that no extrapair paternity exists (all chicks produced on a male’s territory are sired by that male) and are based on the number of genotyped offspring.

**Repeatability**

The intraclass correlation, or repeatability of each male trait except bib size and body size was calculated using one-way ANOVA with individual identity as the grouping variable (Lessells and Boag 1987). I calculated repeatabilities for song variables in two ways. First, I determined the repeatability of each song variable within a song recording using one recording for each male present in 2007. Song traits that were significantly repeatable within a recording were then assessed for repeatability across recordings for a subset of 11 males.

Because two different feather stacking methods were used, I calculated the repeatability of color traits separately for each method. In both cases, an additional five measurements (total 10 measurements per bird) were obtained from the feathers of each of ten males from whom four feathers were collected. This was done first with the full set of four feathers using the methods employed in 2007, then the feathers were split into two groups of two feathers each and measurements were then taken on each group using the 2006 methods. I assessed measurement error at two levels. First I calculated repeatability for the full set of ten measurements for each bird using an ANOVA with male identity as the independent variable. Next, I split the ten measurements taken for each bird into two sets of five. The average of each set of five measurements was taken, since this average is the value that would be used in data analysis. I then determined the repeatability of these measures with the two average values per male as the dependent variable and male identity as the independent variable. Finally, I compared the repeatability of color traits separately for each method using Pearson correlation.

**Statistical Analysis**

For each male present on the study site for one or more weeks, I calculated the following variables: the number of weeks the male was present on the study site (tenure), the maximum number of simultaneously breeding females on his territory (harem size), the total number of sampled young sired (realized reproductive success), the number of sampled within-pair young sired (paternity), the number of young within 150 m of his territory center sampled during his tenure on the site (opportunity for extrapair fertilizations), and the number of those nearby young he sired (extrapair siring success).
I analyzed paternity and extrapair siring success using the events by trials syntax of Proc Glimmix in SAS, with male identity as a random factor and a logit link. A residual variance parameter was estimated for these tests to account for any overdispersion of EPP among broods (e.g. Krackow and Tkadlec 2001). Harem size was not normally distributed, therefore I assessed the association of harem size with male traits using Proc Glimmix with a Poisson distribution and log link. Each male is included in the analysis separately for each year he defended a territory on the study site. While this approach violates the assumption of independence for observations, the number of returning males was small. Furthermore, I believe this approach better reflects an evolutionary perspective, where each male contributes equally to selection in every year he breeds and males breeding in multiple years are more likely to have an impact on selection.

I estimated directional selection within each breeding season using a multiple linear regression of relative realized reproductive success (\(w_i/\overline{w}\)), with mean fitness calculated within each season, on male traits standardized to \(x = 0\) and \(\sigma = 1\). While realized reproductive success was not normally distributed, this is not necessary for the estimation of selection gradients (Arnold and Wade 1984). Sample sizes were not sufficient for estimating stabilizing (or disruptive) selection gradients for the number of traits under consideration (Lande and Arnold 1983).

All analyses were conducted in SAS 9.2 (SAS Institute 1989). All values are reported as means ± standard deviation and statistical effect sizes are reported ± standard error.

Results

Trait Variation

Recapture of dickcissels was rare. Thus, the repeatability of bib size and tarsus could not be assessed since multiple measures of these traits could not be taken. All measurements of yellow feather coloration using the 2006 methods were significantly repeatable, both across individual measurements (Table 4.1) and across averaged measurements (\(r_{IC} > 0.46, p < 0.01\)). Measurements taken using the 2007 methods were also significantly repeatable at both levels of analysis (Table 4.1). The three reflectance measurements were significantly correlated (\(p < 0.0001\); total reflectance x UV reflectance: \(r = 0.79\), total reflectance x yellow reflectance: \(r = 0.94\), and UV reflectance x yellow reflectance: \(r = 0.53\)); therefore, only total reflectance was used in subsequent analyses. Likewise, yellow and UV hue were significantly correlated (\(r = -0.82, p < 0.0001\)), so a single measure of hue was calculated as the difference between the two measures. The methods used in 2006 produced similar hue measurements to those obtained in 2007 (Pearson \(r = 0.99, p < 0.0001\)). Measurements of total reflection, on the other hand, were not comparable between methods (Pearson \(r = 0.32, p = 0.37\)). Thus, between-year comparisons of total reflectance values or selection on total reflectance were not conducted.

All song variables were significantly repeatable across songs within a song recording; however, several were not repeatable between recordings (Table 4.2). Specifically, the number of cissel syllables, frequency range and intersong interval were not consistent between recordings. The number of cissels sung was largely invariant in the population as a whole, so occasional inconsistencies within males created greater
variation within males than existed between males (negative repeatability). Measures of frequency bandwidth were strongly affected by suboptimal recording conditions, such as high winds and traffic noise. In contrast, the high frequency c1 bridge and low frequency c3 tail were significantly repeatable within and between recordings and unaffected by environmental noise. The difference between these two measures was therefore used to estimate frequency range in male dickcissels (called simply “frequency range”, hereafter). Finally, intersong interval was repeatable within a song bout, but varied widely depending on time of day, day in season, and behavioral interactions with other birds. This variation made it impossible to accurately estimate song rate or intersong interval for an individual from song recordings. Finally, the number of dick syllables was significantly associated with song length (r = 0.27, p = 0.02). Given this association and limits in sample sizes this variable was also dropped.

In total, six traits were considered in the analyses of selection and reproductive success: tarsus length, total area of black throat markings, total reflectance and hue of yellow breast feathers, song frequency range, and song length. These traits differed in the amount of variation exhibited by males (Table 4.3). Total area of black had the highest coefficient of variation and tarsus varied the least, with yellow plumage and song traits in between. None of these traits were significantly correlated (Table 4.4).

In 2007 I assessed male age using tail and wing morphology (Pyle 1997). Only black breast markings varied with age, with after second year males (ASY) having more black (127.7 ± 48.5 mm$^3$) than second year (SY) males (86.0 ± 33.5 mm$^3$; t = -2.54, p = 0.02, N = 43). None of the five other male phenotypic traits differed between the two age groups (p ≥ 0.30).

**Male Reproductive Success**

Because extrapair paternity is common in dickcissels, male reproductive success may be divided into within and extrapair components. These components may be further divided into a suite of variance and covariance terms (Webster et al. 1995); however, survival to sampling was so low in dickcissels, these terms could not be accurately estimated. I examined variance in reproductive success separately in each year. Variance was high in both years, but the opportunity for sexual selection was substantially higher in 2007 than in 2006 (Table 4.5). In contrast, the intensity of sexual selection ($I_s$, Crow 1958) was 2.07 in 2006, nearly twice that of 2007. Extrapair mating in this population increased the intensity of sexual selection in both years, but the magnitude of this increase varied between years. In 2006, $I_s$ was 3.9 times the standardized variance in apparent reproductive success ($I_{s,app}$). In 2007, extrapair paternity resulted in a 1.5-fold increase in $I_s$ over $I_{s,app}$. Despite these differences, the relative contributions of within pair and extrapair reproductive success to the total variance were similar in both years. Within pair reproductive success accounted for approximately 60% of the total variance in reproductive success, while extrapair mating activity accounted for only ~20%. Covariance between the two forms of reproductive success was positive and accounted for another ~20% of the variance in reproductive success.
Sexual Selection

Directional selection on male size and color was not consistent between years with the exception of yellow feather hue (Table 4.6). Selection on hue was consistently negative, indicating that males with higher UV hues and lower yellow hues had higher reproductive success in both years. Selection on hue differed in strength in the two years, with the selection gradient in 2006 twice as strong as that in 2007. Sexual selection on frequency range was consistently negative, with males singing low bandwidth songs gaining higher relative reproductive success. Positive selection on song length was observed in both years. Overall, evidence for selection on male traits was poor, with standard errors exceeding the estimated selection gradient in most cases (Table 4.6).

The relationship between male traits and reproductive success might be different in different mating contexts. I analyzed whether a male’s traits influenced his ability to attract social mates, maintain paternity with those mates, and sire extrapair young. Harem size was not different between SY and ASY males ($F_{1,43} = 0.20, p = 0.66$). Harem size was also not significantly associated with tarsus length, black coloration, hue or song traits (Table 4.7). A number of males, mostly bachelors, were not included in the previous model because measures could not be obtained for all six traits. This was primarily due to failure to collect song recordings from males with short tenures on a territory. I therefore repeated the analysis excluding the two song variables. The results of this analysis were quite similar (Table 4.7).

A male’s ability to sire young, either within pair or extrapair, was not significantly associated with his size, coloration or song (Table 4.7). Extrapair sires did tend to have smaller frequency ranges ($4602.1 ± 54.1$) than the males they cuckolded ($4752.5 ± 55.2$; paired $t = 1.98, p = 0.06, N = 18$), but did not significantly differ in any other respect. Events by trials logistic regression also showed no age difference in siring success, either on or off a male’s territory (WPY: $X^2 = 0.83, p = 0.36, N_{SY} = 6, N_{ASY} = 28$; EPY sired: $X^2 = 0.001, p = 0.97, N_{SY} = 9, N_{ASY} = 33$).

A male’s mating success may be influenced by how early he arrives at the breeding grounds (e.g. Reudink et al. 2009b) and the amount of time he is able to maintain a territory (e.g. Westneat 2006). Indeed, dickcissel males that arrived earlier had significantly longer territory tenures ($Kendall’s \tau = -0.55, p < 0.0001$). To determine the independent effects of tenure and arrival date, both variables were included in the models examining their effects on male reproductive success. Harem size was positively associated with territory tenure, but not arrival week (Mixed model tenure effect: $0.15 ± 0.05, F_{1,77} = 9.45, p = 0.003$ and arrival effect: $0.08 ± 0.07, F_{1,77} = 1.45, p = 0.23$). Paternity of chicks sired on a male’s territory was not associated with either tenure or arrival week (GLMM, tenure effect: $0.01 ± 0.11, F_{1,50} = 0.01, p = 0.92$; arrival effect: $-0.08 ± 0.16, F_{1,50} = 0.26, p = 0.61$). Likewise, a male’s success at siring extrapair young was not influenced by his tenure or time of arrival on the study site (GLMM, tenure effect: $0.05 ± 0.10, F_{1,74} = 0.26, p = 0.61$; arrival effect: $-0.16 ± 0.16, F_{1,74} = 1.00, p = 0.32$).

Male traits might indirectly influence a male’s mating success if they have an effect on his ability to maintain a territory. I therefore examined whether size, plumage color or song predicted a male’s tenure or arrival on the study site. Tenure was not normally distributed; however, the distribution of the residuals of the general linear model relating tenure to the six male traits was not different from normal (Kolmogorov-
Smirnov $D = 0.10$, $p > 0.15$). The model did not show any association between territory tenure and any of the six male traits examined (Table 4.7).

Arrival date also deviated from a normal distribution, and the residuals of the linear model did as well, so I used rank correlation (Kendall’s tau) to assess the associations of arrival date with male traits. Males with higher yellow feather hues arrived significantly earlier ($\tau = -0.29, p = 0.0008$), but arrival date was not associated with any other male trait (tarsus $\tau = -0.04, p = 0.65$; bib $\tau = 0.04, p = 0.63$; total reflectance $\tau = 0.07, p = 0.40$; frequency range $\tau = 0.15, p = 0.11$; song length $\tau = -0.12, p = 0.16$).

**Discussion**

Despite high variance in both reproductive success and male phenotypes, I found no evidence for sexual selection in dickcissels. Sexual selection was weak overall and inconsistent between years, with standard errors overlapping zero in at least one year for nearly all traits examined. An analysis of the components of mating success likewise did not produce any clear trends in male mating success. Indeed, male traits did not significantly contribute to male success in any context. These results support the general trend of relatively weak sexual selection in polygynous species (Hasselquist and Sherman 2001). It is possible that extrapair paternity, natural selection, random processes and annual fluctuations in selective pressures all serve to weaken sexual selection in this species.

**Components of Reproductive Success**

The opportunity for sexual selection in dickcissels is high compared to that found in other North American migratory passerines, which ranged from 0.46 in hooded warblers (*Wilsonia citrina*) to 1.02 in great reed warblers (*Acrocephalus arundinaceus*, Albrecht et al. 2007). In contrast, the contribution of EPP to Is is comparatively small despite relatively high levels of EPP in dickcissels. This study adds to growing evidence that extrapair paternity contributes relatively little to variance in male reproductive success in polygynous species. For instance, a study of savannah sparrows (*Passerculus sandwichensis*) found that extrapair mating increased the opportunity for sexual selection less than two-fold (Freeman-Gallant et al. 2005). Such results are common in the literature (e.g. Westneat 1993; Hasselquist et al. 1995a; Weatherhead and Boag 1997; Freeman-Gallant et al. 2005). Indeed, Freeman-Gallant and colleagues (2005) found that extrapair paternity resulted in a more than 2-fold increase in the opportunity for sexual selection in only a single study. In contrast, extrapair paternity in monogamous species commonly results in substantial increases in the opportunity for sexual selection (Freeman-Gallant et al. 2005). In light of such findings, it is perhaps not surprising that selection via EPP in polygynous species is often weak.

Extrapair mating could be relatively unimportant for a number of reasons. First, if there are tradeoffs between social and extrapair mating success, then the occurrence of EPP will decrease variance in male mating success in polygynous species. Indeed, tradeoffs have been found for a number of polygynous species (Hasselquist and Sherman 2001; Vedder et al. 2011). Nevertheless, there is no evidence of such tradeoffs in dickcissels (chapter 3). Instead, social and extrapair mating success are positively associated.
Second, differences in the number of mates a male attracts may swamp any contribution from other sources of variation in reproductive success. For instance, in red-winged blackbirds, differences among males in number of social mates accounted for 41.7% of the variance in male mating success, while total variance in extrapair mating success accounted for only 9.7% (Webster et al. 1995). A similar partitioning of total variance in reproductive success was not possible in dickcissels, since high brown-headed cowbird (Molothrus ater) parasitism and low survival of offspring to sampling would overestimate the contribution of female fecundity (number of young typed per female) to total variance. Nevertheless, extrapair mating success accounted for less than 20% of the variance in reproductive success in dickcissels, while within pair mating success accounted for ~60%. Furthermore, a male’s ability to sire the offspring of his social mate(s) was positively associated with his ability to attract multiple social mates. This positive association increased the difference in reproductive success achieved by polygynous versus monogamous males. Thus, among dickcissels, a male’s ability to sire young with his own mates was more important than his ability to sire young with other male’s mates.

Finally, the spatial scale at which extrapair mating occurs could decrease the contribution of extrapair paternity on sexual selection (Pedersen et al. 2006). Most extrapair mating occurred locally, with EP sires located predominantly within two territories of the male they cuckolded (chapter 3). This pattern would prevent any single male, or even a small number of males, from monopolizing extrapair siring success in the local population. While males may face a number of constraints on the distance they may travel from their territory (lost within pair paternity, increased territory incursions from neighbors, etc., Westneat et al. 1990), it is not clear why females do not pursue extrapair copulations from more distant males. Females might be reluctant to venture far from their nesting territory if they face increased harassment from non-mates (Birkhead and Moller 1992; Mennill et al. 2004) or if they suffer greater predation risk in unfamiliar areas (Westneat et al. 1990). It has also been suggested that females may prefer to mate with more familiar males (Slagsvold and Lifjeld 1997; Slagsvold et al. 2001). These explanations do not seem to fit female dickcissel behavior, however, since females will frequently travel long distances between breeding attempts (Walk et al. 2004) and rarely renest with the same male or even nearby males (pers. obs.). Another possibility is that fertile females may be subject to physical aggression from their mates if absent from the territory for extended periods of time (e.g. Barash 1976; Valera et al. 2003); however, this idea has not been tested in dickcissels.

The present study examined reproductive success over a relatively short time frame (2 years). It is possible that the contribution of extrapair paternity to total fitness variation is stronger in some years than in other (Say et al. 2001; Twiss et al. 2007). Indeed, both the mean and variance in reproductive success were strikingly different between the two years of the study. In 2007, reproductive success was more than twice as high on average with nearly five times the variance as 2006. Despite these fluctuations, the relative contribution of within pair and extrapair mating to overall reproductive success was nearly identical in the two years of the study. Such consistency lends confidence to the conclusion that extrapair mating contributes little to overall fitness variation in this species.
Male Traits and Fitness

Overall, male traits did not predict male fitness or fitness components. Sexual selection was generally weak. Additionally, I found no evidence for significant associations between male fitness components and male traits. These results support a number of other studies suggesting relatively weak sexual selection in polygynous songbirds (e.g. Gontard-Danek and Møller 1999; Westneat 2006; Reudink et al. 2009a; Vedder et al. 2011). There are a number of factors that could have contributed to the weak selection observed in this and other studies, including: alternative mating strategies, incorrect identification of traits under selection, strong natural selection, random processes, and temporal fluctuations in selection. First, alternative mating tactics might reduce the intensity of sexual selection. This could occur if different traits are used in different mating contexts, reducing the contribution of any single trait to a male’s total fitness. Opposing selection on traits would also result in balancing selection or weak directional selection. My study did not find evidence of opposing selection, either through correlations among traits or through selection occurring in different mating contexts. Westneat (2006) also found no evidence for opposing selection across mating contexts in red-winged blackbirds. Indeed, only one avian study has found evidence for opposing selection across mating contexts (Delhey et al. 2003), but most studies have not even tested for it.

Second, my study may have missed selection occurring though some unmeasured trait. For instance, some other aspect of male song, such as amplitude or song rate could be important to male fitness (e.g. Eens et al. 1991; Searcy 1996; Kempenaers 1997; Forstmeier 2002). This might explain why males sing songs, but does not explain what characteristic(s) of black throats or yellow breasts are under selection. Studies in other birds provide some ideas. For instance, the darkness of black feathers might advertise male access to nutrients and thus foraging ability (Poston et al. 2005; McGraw 2006). So while my results do not preclude selection from occurring in dickcissels, it does leave unanswered the question of why males sing songs, have black throats, and produce yellow breasts.

Another possibility is that sexual selection in this system is swamped by natural selection. For instance, yellow hue predicts arrival time on the breeding grounds, which is positively associated with territory tenure. Social mating success was greater in males with longer territory tenures. Nevertheless, there was no evidence for selection on yellow coloration in males. It is possible that the benefits of early arrival are countered by extremely high rates of brown-headed cowbird parasitism early in the season. Parasitism in this population of dickcissels (both rate and intensity) was highest early in the breeding season and decreased with time in the breeding season (Rivers et al. 2010). Indeed, the majority of nests initiated in May and June were parasitized by cowbirds (81%, n = 89), and multiple parasitism occurred in most cases (62%). Such parasitism decreases dickcissel hatching and fledging success (Jensen and Cully 2005). Some early breeders reared cowbirds exclusively. Thus, the advantages to males of early arrival may be diminished by the negative impacts of heavy cowbird parasitism.

In addition to cowbird parasitism, dickcissels experience high levels of predation throughout the breeding season. Two thirds of all nests (64%) were lost to predators, but this loss was not related to time in season (chapter 3) or nest density (Zimmerman 1984). If there is a cost to assessing males or male territories (Alatalo et al. 1988; Real 1990),
and such evaluation provides little or no benefit in terms of increased probability of nest survival, then there may be little advantage to females for preferring particular males. If there is a cost to choosiness, but little benefit, then female preferences for male traits are expected to decline (Andrew 1987).

Natural selection could also lead females to prefer males that defend safer territories. Nest survival in dickcissels has been associated with the vegetative characteristics of the nesting site and surrounding area (Hughes et al. 1999b). If high quality males defend territories with such desirable vegetative characteristics, then females choosing to nest in such territories should accrue a survival benefit. Nest survival was found to increase with a male’s harem size (chapter 3). So certain males may indeed defend safer territories, but it is not clear whether a male’s traits contribute to his ability to defend nests from predators or whether they are associated with his ability to obtain a safer territory.

Random processes could also weaken or even overwhelm selection acting on male traits (Schlicht et al. 2011). This is especially relevant if a male’s traits influence his fitness indirectly. For instance, the effect of yellow hue is separated from fitness by at least three steps (hue → arrival week → tenure → social mating success → paternity). Stochasticity in each of these associations will weaken the effect of hue on subsequent variables. Female choice for male territories, rather than male traits, would also add a degree of separation between traits and male fitness. It may therefore require particularly large sample sizes to detect an indirect effect of male traits on fitness.

Finally, fluctuations in both the target and magnitude of sexual selection could drastically reduce, or even eliminate sexual selection on phenotypic traits (Merila et al. 2001; Chaine and Lyon 2008). Indeed, changes in the direction of selection on dickcissel traits occurred in half of the traits examined. Fluctuations in magnitude were also noted (e.g. there was a five-fold decrease in selection on song length between years), although standard errors were large. Differences in sexual selection across years or populations have also been observed in other species. For instance, Weatherhead and Boag (1995) found a positive association between male size and mating success in red winged blackbirds, but Westneat (2006) did not. Similarly, some studies of great reed warblers found an association between a male’s song repertoire size and his reproductive success (Catchpole 1986; Leisler et al. 1995; Hasselquist 1998), but a subsequent study by Forstmeier and Leisler (2004) found no evidence of such a relationship. Such inconsistency in sexual selection across populations or years has also been found in lark buntings (Chaine and Lyon 2008) and house sparrows (Anderson 2006). Indeed, changes in the strength and target of sexual selection may be common and would reduce the overall strength of sexual selection. Nevertheless, few researchers have tested for significant differences in selection across breeding seasons or populations.

Contrary to earlier theories, sexual selection may be less intense in polygynous species than in monogamous ones (Hasselquist and Sherman 2001). Indeed, polygyny and EPP appear to have a complex and variable relationship across species (Vedder et al. 2011). Despite little evidence for strong sexual selection, sexual dimorphism persists in a number of polygynous species. It is possible that strong sexual selection is not necessary to maintain sexual dimorphism (Price 1984; Hedrick and Temeles 1989). Instead a lack of selection against dimorphism may be sufficient to explain the persistence of sexually dimorphic male ornaments (Westneat 2006). However, this scenario leaves the origin of
sexual dimorphism unexplained. It may be that sexual dimorphism in dickcissels is the ghost of selection past, as may have occurred in red-winged blackbirds (Westneat 2006). This hypothesis is difficult to evaluate in dickcissels, since Spiza is a monotypic genus with no close relatives and the evolutionary history of the Cardinalinae is not well understood (Tamplin et al. 1993; Carling and Brumfield 2008). A closer examination of how sexual selection varies among different populations and across time is necessary to understand how sexually dimorphic traits are maintained in the face of weak or fluctuating sexual selection.
Table 4.1: Repeatability ($r_{IC}$) of color variables across measurements of individual dickcissel feathers and across averaged measurements for each male. All p-values are < 0.0001 unless otherwise indicated.

<table>
<thead>
<tr>
<th>Color Trait</th>
<th>Individual Feather</th>
<th>Male Average</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$r_{IC}$ 2006</td>
<td>$r_{IC}$ 2007</td>
</tr>
<tr>
<td>UV Reflectance</td>
<td>0.53</td>
<td>0.50</td>
</tr>
<tr>
<td>Yellow Reflectance</td>
<td>0.42</td>
<td>0.50</td>
</tr>
<tr>
<td>Total Reflectance</td>
<td>0.43</td>
<td>0.51</td>
</tr>
<tr>
<td>UV Hue</td>
<td>0.92</td>
<td>0.80</td>
</tr>
<tr>
<td>Yellow Hue</td>
<td>0.39</td>
<td>0.42</td>
</tr>
<tr>
<td>Hue</td>
<td>0.85</td>
<td>0.85</td>
</tr>
</tbody>
</table>

*p < 0.001, † p = 0.009

Table 4.2: Repeatability ($r_{IC}$) of dickcissel song variables within recordings (N = 36 males), and between recordings (N = 10 males).

<table>
<thead>
<tr>
<th>Song Trait</th>
<th>Within Recording</th>
<th>Within Season</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$r_{IC}$</td>
<td>p</td>
</tr>
<tr>
<td>Number Dick</td>
<td>0.58</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Number Cissel</td>
<td>0.35</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Frequency Bandwidth</td>
<td>0.79</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>C1 Bridge Frequency</td>
<td>0.87</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>C3 Tail Frequency</td>
<td>0.84</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Song Length</td>
<td>0.61</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Intersong Interval</td>
<td>0.41</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Table 4.3: Mean ± standard deviation, coefficient of variation and sample sizes of male dickcissel traits in 2006 and 2007.

<table>
<thead>
<tr>
<th>Trait</th>
<th>2006</th>
<th>2007</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>mean ± SD</td>
<td>CV</td>
</tr>
<tr>
<td>Tarsus (mm)</td>
<td>23.3 ± 0.6</td>
<td>0.03</td>
</tr>
<tr>
<td>Total Black (mm³)</td>
<td>109.3 ± 58.1</td>
<td>0.53</td>
</tr>
<tr>
<td>Total Reflectance</td>
<td>18.2 ± 2.2</td>
<td>0.12</td>
</tr>
<tr>
<td>Hue (nm)</td>
<td>128.8 ± 6.2</td>
<td>0.05</td>
</tr>
<tr>
<td>Frequency Range (kHz)</td>
<td>4692 ± 305</td>
<td>0.06</td>
</tr>
<tr>
<td>Song Length (s)</td>
<td>1.45 ± 0.25</td>
<td>0.17</td>
</tr>
</tbody>
</table>
Table 4.4: Correlations among male dickcissel phenotypic traits. Pearson correlation coefficients of are presented above their corresponding p-values.

<table>
<thead>
<tr>
<th></th>
<th>Tarsus</th>
<th>Total Black</th>
<th>Total Reflectance</th>
<th>Hue</th>
<th>Frequency Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total Black</td>
<td>-0.17</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(0.16)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total Reflectance</td>
<td>-0.19</td>
<td>0.02</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(0.12)</td>
<td>(0.90)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hue</td>
<td>-0.21</td>
<td>0.11</td>
<td>0.06</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(0.09)</td>
<td>(0.40)</td>
<td>(0.63)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Frequency Range</td>
<td>0.04</td>
<td>-0.21</td>
<td>-0.25</td>
<td>-0.02</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(0.80)</td>
<td>(0.15)</td>
<td>(0.09)</td>
<td>(0.92)</td>
<td></td>
</tr>
<tr>
<td>Song Length</td>
<td>0.01</td>
<td>0.09</td>
<td>-0.14</td>
<td>-0.11</td>
<td>-0.11</td>
</tr>
<tr>
<td></td>
<td>(0.94)</td>
<td>(0.53)</td>
<td>(0.31)</td>
<td>(0.44)</td>
<td>(0.45)</td>
</tr>
</tbody>
</table>

Table 4.5. Means, variances, standardized variances ($I_s$, variance divided by mean squared or covariance divided by the square root of the product of the component variances) and proportion of total variance of components of male dickcissel reproductive success in each breeding season.

<table>
<thead>
<tr>
<th>Component</th>
<th>Mean</th>
<th>Variance</th>
<th>$I_s$</th>
<th>Proportion of Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>2006</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Within Pair</td>
<td>0.81</td>
<td>1.55</td>
<td>2.35</td>
<td>0.59</td>
</tr>
<tr>
<td>Extrapair</td>
<td>0.41</td>
<td>0.58</td>
<td>3.54</td>
<td>0.22</td>
</tr>
<tr>
<td>Cov(within pair, extrapair)</td>
<td>0.49</td>
<td>0.26</td>
<td>0.19</td>
<td></td>
</tr>
<tr>
<td>Residual</td>
<td>0.00</td>
<td></td>
<td></td>
<td>0.00</td>
</tr>
<tr>
<td>Total</td>
<td>1.13</td>
<td>2.62</td>
<td>2.07</td>
<td></td>
</tr>
<tr>
<td>2007</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Within Pair</td>
<td>2.35</td>
<td>8.00</td>
<td>1.45</td>
<td>0.64</td>
</tr>
<tr>
<td>Extrapair</td>
<td>1.00</td>
<td>2.36</td>
<td>2.36</td>
<td>0.19</td>
</tr>
<tr>
<td>Cov(within pair, extrapair)</td>
<td>2.13</td>
<td>0.25</td>
<td>0.17</td>
<td></td>
</tr>
<tr>
<td>Residual</td>
<td>0.01</td>
<td></td>
<td></td>
<td>0.00</td>
</tr>
<tr>
<td>Total</td>
<td>3.35</td>
<td>12.50</td>
<td>1.12</td>
<td></td>
</tr>
</tbody>
</table>

68
Table 4.6. Estimated directional selection gradients (β ± SE) for dickcissels in each breeding season. Gradients are partial standardized regression coefficients from a multiple regression of relative realized reproductive success on standardized male traits in each breeding season.

<table>
<thead>
<tr>
<th>Trait</th>
<th>2006 β</th>
<th>2006 SE</th>
<th>2007 β</th>
<th>2007 SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tarsus</td>
<td>-0.23</td>
<td>0.50</td>
<td>0.16</td>
<td>0.37</td>
</tr>
<tr>
<td>Black</td>
<td>0.74</td>
<td>0.49</td>
<td>-0.15</td>
<td>0.23</td>
</tr>
<tr>
<td>Total Reflectance</td>
<td>0.14</td>
<td>0.48</td>
<td>-0.42</td>
<td>0.33</td>
</tr>
<tr>
<td>Hue</td>
<td>-0.34</td>
<td>0.52</td>
<td>-0.17</td>
<td>0.31</td>
</tr>
<tr>
<td>Frequency Range</td>
<td>-0.53</td>
<td>0.41</td>
<td>-0.41</td>
<td>0.29</td>
</tr>
<tr>
<td>Song Length</td>
<td>0.52</td>
<td>0.38</td>
<td>0.10</td>
<td>0.30</td>
</tr>
</tbody>
</table>
Table 4.7. Associations between male traits and harem size, within pair paternity (proportion of typed young sired), and extrapair siring success (proportion of nearby typed young sired) in dickcissels. The first two columns present effect sizes and F-values from the multiple regressions of harem size on the six traits and tenure on the six traits, respectively. Italicized values in the first column are the results of the model excluding male song traits from the analysis. The third column presents effect sizes and F-values from the multiple regression of paternity on the six traits using the events by trials syntax in Proc GLIMMIX. Lastly, the final column presents effect sizes and F-values from the multiple regression of extrapair siring success on the six traits, using the events by trials syntax in Proc GLIMMIX. Sample sizes are as follows: Harem size, N = 49; Tenure, N = 49; Paternity, N = 33; EP siring, N = 48.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Harem Size</th>
<th>Tenure</th>
<th>Paternity</th>
<th>Extrapair Success</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tarsus</td>
<td>1.21</td>
<td>0.43</td>
<td>0.03</td>
<td>-0.03</td>
</tr>
<tr>
<td>Black</td>
<td>1.02</td>
<td>0.24</td>
<td>0.002</td>
<td>-0.002</td>
</tr>
<tr>
<td>Total Reflectance</td>
<td>1.25</td>
<td>2.00</td>
<td>0.039</td>
<td>0.10</td>
</tr>
<tr>
<td>Hue</td>
<td>0.12</td>
<td>0.24</td>
<td>0.007</td>
<td>0.11</td>
</tr>
<tr>
<td>Frequency Range</td>
<td>1.26</td>
<td>0.0005</td>
<td>-0.001</td>
<td>-0.003</td>
</tr>
<tr>
<td>Song Length</td>
<td>2.54</td>
<td>0.85</td>
<td>1.33</td>
<td>1.25</td>
</tr>
</tbody>
</table>

† 0.06 < p < 0.10
Figure 4.1. I photographed each male dickcissel in a standard upright position with the bill pointed directly at the camera lens. The background of each photograph included a size standard (horizontal and vertical lines, length in mm), black standard (black boxes), and a post-it note with the male’s full band number, color band combination, capture site, and capture date.

Figure 4.2. Reflectance spectrum of dickcissel yellow breast feathers. UV measurements were made from 300 nm to point A (shaded box), yellow from point B to 700 nm (open box), and yellow hue was determined from the slope indicated by C.
Figure 4.3. A typical dickcissel song, with two "dick" and three "cissel" phrases. The "cissel" phrase contained three distinct elements, beginning with a high frequency buzz (c1), followed by a bridge (B), bisected by a bridge (B'), followed by a mid frequency series of notes (c2), and ending with a low frequency tail (c3).
Effects of fire management on mating patterns in dickcissels (*Spiza americana*)

A central tenet of mating system theory is that habitat structure and composition affect the distribution of individuals in time and space, which in turn affect patterns of mating within a population (Emlen and Oring 1977; Westneat et al. 1990). Environmental conditions are increasingly influenced by human activity, creating the potential for such activities to alter the mating patterns of animals breeding in altered environments. For instance, human pollution and agricultural practices have caused eutrophication and increased turbidity in African Rift Valley lakes (Smith 2003). The resulting decrease in visibility has interfered with female mate choice, causing a relaxation of sexual selection and breakdown in reproductive isolation that could threaten cichlid species diversity (Seehausen et al. 1997). In birds, forest fragmentation from logging and urban development has led to a change in the mating system of capercaillie grouse (*Tetrao urogallus*). Ims and colleagues (Ims et al. 1993) found that males in unfragmented forests competed for mates in leks, while males in fragmented forests performed solitary displays on individual territories. Such effects could have far-reaching ecological and evolutionary implications (Trivers 1972; Emlen and Oring 1977; Davies 1985; Andersson 1994; Johnson and Burley 1998; Perlut et al. 2008).

While the negative effects of habitat destruction are well known, a common response to such negative impacts is to use management techniques to restore or maintain habitat. It is becoming more apparent that these practices can also affect the reproduction and viability of target species in more subtle, but no less important ways. For example, a number of prairie fragments are maintained by frequent mowing, which prevents the establishment of trees. Mowing in agricultural fields increased breeding synchrony in savanna sparrows (*Passerculus sandwichensis*) leading to much higher variance in realized reproductive success in hayed fields (Perlut et al. 2008). Such a drastic change in mating patterns could alter evolutionary processes in savannah sparrows. Indeed, a number of management practices have the potential to alter mating system and mate choice dynamics. Despite the ever increasing role of management in conserving species and their habitats, little research has addressed the effects of this management on mating patterns.

One of the most heavily impacted and intensively managed ecosystems in North America is the tallgrass prairie. An estimated 88 to 99% of the tallgrass prairie has been lost, primarily to agricultural development (Vickery et al. 2000). What remains of this early successional ecosystem must be intensively managed to prevent its transition to woodland habitat. Historically, frequent fires helped maintain prairie habitat (Knapp et al. 1998b; Vickery 2000). The time between fires (burn interval) affects the structural complexity and composition of prairie vegetation, with short intervals producing simple, grass dominated structures and longer intervals promoting a structurally complex mix of grass, forbs, and woody shrubs (Hartnett and Fay 1998; Collins and Smith 2006).

Historically, fires are thought to have occurred every 2-10 years (Rowe 1969; Hulbert 1973; Wright and Bailey 1982). Current management practices favor the extremes, with cattle ranchers conducting annual burns that maximize primary productivity (Patten et al. 2006; With et al. 2008) while most other lands, such as exurban developments, remain...
permanently unburned. While it is known that annual burns decrease the abundance of certain grassland birds, the effects of burn interval on the reproduction and mating system of these birds are unknown.

I investigated the effects of fire, as used to manage tallgrass prairie, on the mating system of an obligate grassland breeding bird, the dickcissel (*Spiza americana*). Dickcissels are an abundant avian denizen of tallgrass prairie. Males defend territories and attract mates with songs sung from tall perches. Females generally nest near the ground in dense grass, forbs, or low woody shrubs, but will occasionally build nests up to 4 m above ground in woody plants (Gross 1968). Dickcissels require two key features in their breeding grounds: a nesting site and song perches from which males advertise and defend territories. Zimmerman (1971) showed that dickcissels prefer habitat that is structurally diverse and predominantly forbs rather than grasses or trees, as the former provides the structure needed to support a nest. Because dickcissels are facultatively polygynous (Zimmerman 1971) and exhibit extrapair mating (chapter 3) they are ideal for testing hypotheses concerning the effects of management techniques on mating patterns.

There are several ways in which burn management could influence dickcissel mating patterns. First, burning could affect variance in harem size by altering the distribution of resources within an area, as predicted by mating systems theory (Verner and Willson 1966; Orians 1969; Emlen and Oring 1977). Emlen and Oring (1977) hypothesized that the distribution of resources in a habitat influences the ability of males to monopolize mates. Variance in social mating success would be highest in areas where resources are heterogeneously distributed. Many studies have examined the effects of ecology on polygyny in birds, with varying results (reviewed in: Slagsvold and Lifjeld 1994; Searcy and Yasukawa 1995; Ligon 1999). Despite such a wealth of research, few studies have examined the association between variance in harem size and habitat heterogeneity. Some have tested associations between harem size and mean territorial quality. For instance, Orians (1972) found that harem sizes of red winged blackbirds within individual marshes were positively associated with the mean insect productivity of the marsh, but he did not determine whether territories on more productive marshes were also more heterogeneous in their insect productivity. Similarly, studies of dickcissels have demonstrated an association between the reproductive success of both sexes and characteristics of the male’s territory (e.g. vegetation volume, Zimmerman 1971). While these studies show differing rates and levels of polygyny across habitats, habitat heterogeneity was never quantified (Zimmerman 1971; Zimmerman 1982). Indeed, I have found no study of avian polygyny that has specifically compared variance in harem size within habitats to measures of habitat heterogeneity. This is rather surprising, since heterogeneity in resource distribution is supposedly one of the driving factors in the evolution and maintenance of polygyny.

Managed burning influences heterogeneity in the tallgrass prairie in predictable ways. Heterogeneity in tallgrass prairie plant and invertebrate communities is highest on infrequently burned sites and lowest on frequently burned sites (Collins and Smith 2006). Long term ecological research at the Konza Prairie Biological Station (Konza, hereafter) indicates that patterns of species richness, heterogeneity, and community structure are primarily the result of long term burn regimes, not individual fire events (Gibson 1988; Knapp et al. 1998a; Knapp et al. 1998b; Collins 2000; Veen et al. 2008). Thus, variance
in harem size should be highest in sites with long burn intervals, regardless of specific burn history.

Burning could also influence patterns of extrapair mating through its effects on factors known to influence extrapair mating. For example, Birkhead (1978) hypothesized that increased breeding density should increase extrapair paternity (EPP), assuming that increased density results in increased proximity between females and thereby increases encounter rates. Several studies have shown that the abundance of breeding birds in a habitat is influenced by burning regimes (Westemeier and Buhnerkempe 1983; Zimmerman 1997; Powell 2008; but see Powell 2006). Long term abundance data from replicated burn treatments show that dickcissel abundance increases with the frequency of fire (Powell 2006). Furthermore, Zimmerman (1971) showed that dickcissel territory sizes shrink as male density increases. These conditions should increase encounter rates between individuals, increasing the chances of EPC as density increases (Birkhead 1978; Birkhead and Biggins 1987; Westneat et al. 1990). Thus, EPP rates should be highest in watersheds with short burn intervals and decline with increasing time between burns.

Another way habitat may affect patterns of extrapair mating is by influencing the ability of males to effectively guard their mates. Effective mate guarding may include preventing territorial intrusions from neighboring males seeking EPC, preventing females from foraging off territory in search of EPCs, or both (Birkhead 1979; Sherman and Morton 1988; Lifjeld et al. 1994). Such activities may trade off with other demands, such as foraging and pursuit of additional social or extrapair mates (Westneat et al. 1990; Westneat and Stewart 2003). Habitat structure can influence these tradeoffs by affecting the efficiency with which a male can guard his mate(s) (Westneat and Stewart 2003; Mays and Ritchison 2004). For example, mate guarding may be more difficult in visually occluded habitats. In yellow-breasted chats (*Icteria virens*), rates of EPP were higher in territories with dense vegetation verses those in open habitats. This difference was attributed to the decreased ability of males to guard their mates in visually occluded habitats (Mays and Ritchison 2004). This hypothesis has not yet been tested in any other system.

In tallgrass prairie, visual occludedness increases with the incursion of large woody shrubs. The abundance and density of these woody plants increases with the time between burns. At low densities, isolated shrub islands could enhance male mate guarding by providing tall perches from which males may monitor their territories for intruding males or foraging females. As shrub density increases, however, the benefit of tall perches is eliminated by the presence of other shrubs islands that obscure portions of the territory (Figure 5.1). Thus, EPP rates should positively covary with shrub density. Furthermore, if visual occludedness negatively affects mate guarding efficiency, then its impact may be greater for males with multiple mates nesting simultaneously. Unlike monogamous males, polygynous males must balance guarding fertile mates with defense of existing nests (Alatalo et al. 1987; Hasselquist and Bensch 1991). The conflict between these two demands may be exaggerated in occluded habitats, where it is more difficult to do either activity and it is unlikely that males can do both simultaneously. Thus, the relationship between polygyny and paternity may be different in habitats with large shrubs, compared to those without these plants.
Methods

Study Population

I studied dickcissels at the Konza Prairie Biological Station in 2008 and 2009. Konza is a long-term ecological research facility with a thirty year history of replicated burn treatments conducted at the watershed level. This facility encompasses 3,487 hectares of native tallgrass prairie in northeastern Kansas (39°05' N, 96°35' W). A detailed description of the effects of burning on the Konza’s vegetative communities of can be found in Knapp et al. (1998b).

I monitored dickcissel reproductive success in nine ungrazed watersheds within Konza’s boundaries (Table 5.1). These sites represent the full range of variation in burning interval available at the station. Most watersheds were maintained at the same burn interval throughout Konza’s history. Two watersheds, R20a and R1a were part of a reversal experiment, wherein their burn interval was reversed beginning in 2000. Thus R1a was not burned until 2000, at which time annual burning was implemented and R20a was burned annually until 2000, at which time prescribed burning ceased on this site. In addition, an unplanned burned occurred on R20a early in May of 2008. I monitored eight watersheds in 2008: two each burned at 2, 4 and ≥10 year intervals, one burned annually, and one reversal site (R20a). The 10 and 20 year burn regimes were both treated as “unburned.” I attempted to capture ~10 male dickcissels in each watershed as males began arriving on the breeding site. My assistant and I then monitored the reproductive success of these males throughout the breeding season. I censused the banded males in each site approximately once every week. My assistant and I conducted a full census of all males defending territories on each watershed once during a two week period in late June/early July.

In 2009, I monitored three watersheds with different burn histories: one annually burned, one unburned, and one reversal site (R1a). R1a’s unique burning history has produced a watershed with the large woody vegetation (and relatively high visual obstruction) typical of unburned watersheds, but high primary productivity and dense grasses and forbs typical of annually burned sites. My field assistants and I attempted to capture all males breeding on these watersheds. We fully censused all banded and unbanded males occurring on the three sites approximately once per week.

In both years, my assistants and I captured males on their territories using mist nets placed adjacent to a song playback and male model. We then monitored each male to determine the number of females he attracted and the number, contents and success of nests built on his territory (see below). We captured females on nests using a cylindrical nest net (Sousa and Stewart 2011) when nestlings were at least three days old. Each adult was banded with a unique combination of three plastic color bands and one USGS aluminum band and each nestling received a single USGS band. We collected a small blood sample from every bird to use in paternity analysis.

The first egg date of each nest was determined from hatching or laying date, assuming a 12 day incubation period. When these dates were not known, the first egg date was determined by assuming the nest was midway through incubation when it was depredated. I considered a nest active from the first egg date to the day before the last nest check. These dates were then used to determine each male’s harem size, where harem size is defined as the maximum number of females simultaneously nesting in a given male’s territory.
I genotyped all adults and nestlings at six variable microsatellite loci (Chapter 3). Each nestling’s parentage was determined by comparing its genotype to that of the female trapped at the nest and the male defending the territory in which the nest was located. Nestlings were considered extrapair if their genotype mismatched the putative father’s at two or more loci. Extrapair sires could not be assigned in 2008, since only a subset of the population breeding in a watershed was sampled. In 2009, I assigned sires to extrapair offspring using Cervus 3.0 (Kalinowski et al. 2007). A male was considered the sire of an extrapair chick if he was identified by Cervus with 95% confidence, had a positive trio LOD score (indicating a better match to the chick than would be obtained at random), and mismatched the chick’s genotype at no more than one locus. Since watershed 20c is adjacent to 1d, I included as a putative extrapair sire any male present in either watershed in the week a given nest was initiated. R1a is located ~3.5 km west of the other two watersheds, so only males breeding in R1a were considered as putative sires for extrapair young from that site.

Habitat Heterogeneity
I established latitudinal transects in each watershed to estimate heterogeneity across different burn regimes. Distance between transects and between sampling points along each transect was varied between watersheds, but remained constant within watersheds such that ~30 evenly spaced points were sampled per watershed. I placed transects 103 to 190m apart, with the first transect randomly placed 50 to 150m from the northern border of each watershed. I rolled a 10-sided die and added 10 to this number to determine the distance from the latitudinal edge of the watershed to place the first sampling point along each transect. Subsequent points were then evenly spaced 50-80m along each transect. This was done to obtain approximately equal sampling among watersheds while providing full coverage of the watershed’s topology. All vegetation measures were taken between 19 May and 12 June.

Zimmerman noted that females settle according to the availability of suitable nesting sites (Zimmerman 1966, 1982). Dickcissels nest primarily in forbs and small woody shrubs (Blankespoor 1970; Temple 2002), and in dogwood shrubs where available (pers obs.). I therefore estimated cover and height for four categories of vegetation: grasses, forbs, small woody plants, and large woody plants occurring within 3 m of each sampling point. Small woody shrubs were primarily leadplant (Amorpha canescens), New Jersey tea (Ceanothus americanus), buckbrush (Ceanothus cuneatus), and smooth sumac (Rhus glabra). Large woody plants were primarily dogwood (Cornus drummondii), red cedar (Juniperus virginiana) and honey locust (Gleditsia triacanthos). I also measured the maximum height of a plant class, excluding outliers. In some cases, more than one layer of forbs with at least 5% cover was noted. In these cases, I recorded the height of each layer and used the average of these values to represent forb height for the given point. I estimated percent canopy cover for each of the four plant classes using a modified Braun-Blanquet (1932) cover-abundance scale with 1 = less than 25% cover, 2 = 25-50%, 3 = 50-75%, and 4 = greater than 75% cover. Because dickcissels prefer to nest in forbs and small woody shrubs and nesting success is positively associated with forb cover (Klug et al. 2010c), I estimated heterogeneity in two ways: the standard deviation of forb cover and the standard deviation of small woody shrub cover.
**Breeding Density**

In 2008, my assistant and I censused the number of territorial males breeding in each of the eight monitored watersheds between 19 Jun and 2 July, the peak of the breeding season. This number was used as an estimate of peak male density in each watershed. In 2009, my assistant and I censused each watershed once every 10 days, on average. GPS coordinates of males were recorded at each census and male territories were mapped in both years by recording the perches of flushed males. All GPS points were obtained using a Garmin GPSmap 76 or 60Cx. These points were combined with the locations of male nests in ArcGIS 9.3. I then used the Geospatial Modeling Environment (GME, Beyer 2010) to calculate minimum convex polygons (MCP; Mohr 1947) for each male. The GME was also used to calculate the center of gravity (weighted by density of points) of each male territory. I estimated the density of breeding males in proximity to a fertile female as the number of male territory center points within 150 m of a nest in the week the nest was initiated. This distance is approximately twice the width of the average male territory. I calculated the peak density of males breeding in a given watershed (dickcissels per hectare) by dividing the maximum number of males in a territory (from censuses in 2009, estimated in 2008) by the area of that watershed. Watershed area was obtained from Konza spatial data, downloaded from http://www.konza.ksu.edu/KNZ/pages/data/GISdata.aspx.

**Visual Obstruction**

Large woody shrubs, primarily dogwood and red cedar, readily invade infrequently burned prairie (Bragg and Hulbert 1976). These shrubs create visual barriers within territories that potentially limit the ability of males to monitor the movements of mates and neighboring males. I measured the cover of large woody shrubs within male territories using orthorectified false color composite aerial photographs acquired as digital ortho-quarter quadrangles obtained from the National Agriculture Imagery Program. Since shrub cover was unlikely to exhibit any detectable change over a single year, the image taken September 2008 was used for both 2008 and 2009. Large woody shrubs were readily visible as dark patches on a brighter background of herbaceous cover (Figure 5.2). I drew a polygon around each shrub island using the Editor tool in ArcGIS. Red cedars were marked with a point and assigned an area of 1 m², which was typical for their size. The total area of shrubs occurring in each male territory, as well as the size of each male’s territory was calculated in ArcGIS. I then used these data to determine the proportion of each male’s territory covered by large woody shrubs.

**Statistics**

I included watershed as a random factor in analyses of burn regime effects. When analyses were conducted on binomial variables (e.g., paternity), a generalized linear mixed model (GLMM, Proc GLIMMIX) with a logit link was used. Harem size was not normally distributed; I therefore analyzed the effects of burn regime on harem size using a GLMM (Proc GLIMMIX) with a log link and Poisson distribution. Variance in harem size was also underdispersed, so the default restriction of $\phi = 1$ was lifted and a residual variance parameter was estimated.

Patterns of parentage among nests were also analyzed using a GLMM. Since the probability of extrapair paternity is unlikely to be constant across broods, variance in EPP
is likely to be overdispersed in a manner similar to the structure of variance in brood sex ratios (e.g. Krackow and Tkadlec 2001). A residual variance parameter was therefore estimated for events by trials tests of paternity (events = number of within pair young, trials = number of young genotyped on a male’s territory).

Patterns of reproductive success by burn regime were examined using a mixed model with watershed included as a random effect. When variables were symmetrically distributed (e.g. forb cover), Levene’s test was used to assess equality of variance (Levene 1960). When the dependent variable had a skewed distribution (e.g. harem size), equality of variance was assessed using the Brown-Forsythe test for equal variance, which is robust to deviations from the normal distribution (Brown and Forsythe 1974).

Means and effect sizes are reported ± standard error. All analyses were conducted in SAS 9.2 (SAS Institute 1989), and tests were considered significant at \( \alpha = 0.05 \).

Results

Polygyny and Heterogeneity

Polygyny was common in all watersheds studied in both 2008 and 2009 (Table 5.2, mean = 1.36 ± 0.11 and 1.71 ± 0.14 respectively). Harem size did not vary significantly among watersheds in 2008 (GLMM F\(_{7,73} = 0.73\), p = 0.64), nor was there significant variation in harem size among burn regimes (Table 5.2, GLMM F\(_{3,65} = 0.75\), p = 0.53). Harem size in 2009 varied significantly among the three watersheds studied (Table 5.2, GLMM F\(_{2,49} = 3.63\), p = 0.03).

Variance in harem size was not different among burn regimes in 2008 (Brown-Forsythe F\(_{3,65} = 1.16\), p = 0.33, Figure 5.3), nor did mean harem size differ by burn regime (F\(_{3,65} = 0.75\), p = 0.53, Figure 5.4). Variance in forb and small woody shrub cover was significantly different among watersheds, with variance in cover generally increasing with burn interval (forbs, Levene’s F\(_{3,227} = 9.80\), p < 0.0001; woody shrubs Levene’s F\(_{3,243} = 6.06\), p = 0.0005, Figure 5.5). Patterns of variance were less clear when examined at the watershed level. Variation in forb cover was significantly different among watersheds (Levene’s F\(_{6,224} = 3.49\), p = 0.003), as was variation in small shrub cover (Levene’s F\(_{6,240} = 3.07\), p = 0.007). Watersheds within the same burn regime tended to have similar levels of variance with the exception of the 4-year burns (Figure 5.5). The more recently burned of these two watersheds showed much greater variance in forb and shrub cover.

In 2009, variance in harem size was also not different among watersheds (Brown-Forsythe F\(_{2,49} = 0.08\), p = 0.93, Figure 5.3) but mean harem size differed significantly among the watersheds (F\(_{2,49} = 3.63\), p = 0.03, Figure 5.6). Harem sizes were highest in the annually burned watershed and lowest in the unburned watershed. Variance in the cover of forbs and small woody shrubs was not different among the sites studied in 2009 (forbs, Levene’s F\(_{2,77} = 1.74\), p = 0.18; small shrubs Levene’s F\(_{2,78} = 0.51\), p = 0.60, Figure 5.7).

I determined the standard deviation of forb cover, small shrub cover, and harem size for each site in both years. Standard deviation in forb cover was not significantly correlated with the standard deviation in small shrub cover (R = 0.48, p = 0.16, N = 10), so their effects on harem size variability were assessed separately. The standard deviation of harem size was not significantly related to the standard deviation of forb
cover ($\beta = -0.25 \pm 0.25$, $F_{1,8} = 0.97$, $p = 0.35$, $r^2 = 0.11$). Similarly, the standard deviation of harem size was not associated with the standard deviation of small woody shrub cover ($\beta = -0.29 \pm 0.31$, $F_{1,8} = 1.17$, $p = 0.31$, $r^2 = 0.11$).

**EPP and Burn Management**

The proportion of sampled young a male sired on his territory (paternity hereafter) was not different among the burn regimes examined in 2008 ($F_{3,29} = 0.89$, $p = 0.46$, Figure 5.4). Paternity was significantly different among the three sites studied in 2009 ($F_{2,33} = 4.45$, $p = 0.02$, Figure 5.6).

**Male Density and EPP** – Weekly censuses in 2009 confirmed that male density peaked in each watershed in late June to early July. Thus, measures of male density taken during this time period in 2008 are likely to be a good reflection of peak density in each watershed. Peak male density varied significantly across burning regimes and generally increased with burn regime, although this relationship is complex in watersheds with 2 or 4-year burn cycles (Mixed model effect: annual = 0.18 ± 0.04, biennial = 0.08 ± 0.03, quadrennial = 0.14 ± 0.03, $F_{3,81} = 8.80$, $p < 0.0001$).

Contrary to my earlier prediction, paternity was significantly higher in watersheds with high peak male density (Mixed model effect: 4.50 ± 1.48, $F_{1,68.8} = 9.30$, $p = 0.003$). Indeed, local density did not appear to affect paternity. In 2009, the proportion of young a social father sired in a given nest was not related to the number of males within 150 m of that nest (Mixed model effect: -0.008 ± 0.15, $F_{1,61.7} < 0.00$, $p = 0.96$). Thus, it does not appear that an increase in the number of nearby males results in an increase in extrapair paternity in dickcissels.

**Visual Obstruction and EPP** – Large shrub islands were present in 3 watersheds in 2008: one 4-year burn and both unburned sites. In 2009, large shrub islands were present in both the unburned watershed and the reversal treatment (unburned until 2001, then annually burned). Rates of extrapair paternity were not higher on watersheds with shrubs compared to those without shrubs (Mixed model effect: -0.22 ± 0.56, $F_{1,6,5} = 0.16$, $p = 0.70$). Paternity on individual territories was also not associated with the density of large shrubs on the territory either linearly or quadratically (Mixed model effects, shrub = -1.01 ± 6.50, $F_{1,66.8} = 0.02$, $p = 0.88$; shrub*shrub = 9.75 ± 21.48, $F_{1,56.7} = 0.21$, $p = 0.65$).

While shrub density did not directly affect extrapair paternity rates, it is possible that visual obstruction could influence the interaction between paternity and harem size. I tested this prediction by examining the effects of harem size, shrub density within male territories, year, and their two-way interactions on paternity. If shrub density does indeed influence the relationship between polygyny and paternity, then the interaction term of harem size*percent shrub cover should be significantly negative. This interaction was not significant (Table 5.3), indicating that shrub cover did not affect paternity differently in males with different harem sizes.

**Discussion**

Differences in the fire management of prairie fragments on Konza did not produce differences in dickcissel mating patterns as predicted by theory on the ecology of mating systems. Heterogeneity in harem sizes and rates of extrapair paternity were not
significantly related to habitat heterogeneity and shrub density, respectively. While extrapair paternity was associated with male density, the association was in the opposite direction to the one predicted. Furthermore, mean harem sizes were not different among watersheds in 2008, but varied significantly in 2009. This last result suggests that if burn regimes influence dickcissel mating patterns, they do so in complex ways.

Variance in harem size did not appear to be affected by watershed-level heterogeneity, whether heterogeneity was based on burn history or on the availability of common nesting substrates (forbs and small woody shrubs). It is possible that differences in territory quality within sites were not sufficient to produce large differences in mating success. This does not seem to be the case, however, since variance in harem size was not zero and males within a watershed attracted harems ranging from one to four females.

Most studies of the ecology of polygyny have focused on the effects of heterogeneity on a local scale (e.g. Harmeson 1974; Pleszczynska 1978; Wittenberger 1980; Lightbody and Weatherhead 1988; Moskwik and O’Connell 2006, but see reviews by Searcy and Yasukawa 1995, Ligon 1999, and Shuster and Wade 2003). These studies implicitly assume that females evaluate potential mates on a local level. However, Emlen and Oring (1977) did not specify the spatial scale over which habitat heterogeneity should affect mating patterns. It is nonetheless clear that they and a few subsequent researchers have considered this effect at multiple spatial scales. For instance, Orians (1972) found that mean harem size in different marshes was associated with the average resource availability in that marsh. To my knowledge, no author has examined whether differences in resource heterogeneity across populations influences variance in harem size, as originally predicted by Emlen and Oring and others (Verner and Willson 1966; Orians 1969; Emlen and Oring 1977).

It can be difficult to determine whether females of a species truly evaluate breeding situations at a local scale. Nonetheless, this is unlikely to be the case in dickcissels, where females frequently move more than 10 km between nesting attempts (Walk et al. 2004). If female dickcissels are assessing nesting situations on a broader spatial scale, then measures of habitat heterogeneity should also be taken on a larger scale. For instance, heterogeneity in harem size on Konza, which has a mosaic of different burning and grazing regimes, may be higher than heterogeneity on other, similarly sized areas that experience only a single burning and grazing regime. I tested this idea by comparing variance in harem size on Konza to that presented in previously published studies conducted near Konza. I found no differences (Brown-Forsythe F_{1,302} = 0.07, p = 0.79; Konza SD = 1.00, Zimmerman SD = 0.88, Table 5.4). However, since I was unable to directly measure heterogeneity among sites, I cannot rule out the possibility that heterogeneity in resources important to female dickcissels is similar on Konza and the nearby sites where dickcissels have been studied. Thus, I conclude that a better understanding of the scale at which female birds compare mating situations, coupled with measures of habitat heterogeneity at that scale are needed to properly test Emlen and Oring’s prediction.

While variance in harem size was not different among watersheds, mean harem sizes did vary significantly in one year of the study. In 2009, harem sizes were highest in the annual burn, where primary productivity and grasshopper abundance are typically highest. Indeed, a number of studies have found an association between harem size and resource abundance, both within and between populations (e.g. Zimmerman 1966; Orians
1972; Wittenberger 1980; Zimmerman 1982). In the current study, patterns of variation in mean harem size among watersheds in the two years of the study further supports this idea. The breeding season of 2008 was characterized by record rainfall and high primary productivity, with grasses reaching eight feet in height by August (Sousa, unpublished data). Such favorable growing conditions may have reduced differences in resource abundance among the different burn regimes in 2008. In contrast, 2009 was relatively cool and dry (NASS 2010), with grasses remaining under five feet in height in August and grasshoppers suffering a 45% decline in abundance from the previous year (Anthony Joern and Angela Laws, pers comm). These conditions likely exaggerated differences between watersheds in 2009. While resource abundance clearly influences the number of breeding females a territory can support, it cannot explain differences in harem sizes among males in the absence of significant heterogeneity in the distribution of these resources.

I also found unusual patterns in the effects of ecology on extrapair paternity. For example, I found that extrapair paternity was significantly lower in watersheds with more territorial males per hectare. This result is unusual compared to nearly all other studies of density and EPP (Westneat and Sherman 1997). One possible way this could occur is if females on smaller territories are more easily guarded than those on larger ones. Males may more readily detect intruders and track female movements on smaller territories. Alternatively, breeding density may have different effects depending on how it is measured. For instance, Stewart and colleagues (2010) found a positive effect of the number of birds breeding within a given area on extrapair paternity, but no effect of the proximity of these neighbors on EPP rates. I found similar inconsistencies among different measures of density in dickcissels. Peak breeding density was negatively associated with EPP, but the number of males within 150 m of the nest did not influence EPP. A possible explanation for this pattern is if female forays off territory drive EPP and females are more likely to foray in poor quality habitats. If a female can acquire the food and other resources necessary for reproduction within her mate’s territory, then she may spend less time off territory and have a lower probability of encountering potential extrapair mates. Thus, the probability of encountering extrapair mates would actually be lower in high density, high resource watersheds.

While it is unclear what resources represent high quality habitat to dickcissels, the number of fledglings produced per male increased significantly with peak watershed density (Mixed model effect: \(2.63 \pm 1.04, F_{1,125} = 6.47, p = 0.01\)). In addition, plant primary productivity and grasshopper densities increase with burning frequency and are highest in the two summers following burning (Knapp et al. 1998a; Joern 2004). Peak dickcissel territory density varied significantly by burn frequency, with densities highest in annual burns and lowest in unburned watersheds. Watersheds with 2 or 4-year burn cycles had intermediate densities, but biennially burned sites had lower densities on average than quadrennially burned sites. This pattern was likely caused by an interaction of burn interval with time since burning in these watersheds (Powell 2008). Long term data indicate that dickcissels are most abundant in watersheds one year post burn, when vegetation density is sufficient to support and conceal nests (Powell 2006). Thus peak dickcissel territory density tends to follow the same patterns as grasshopper density and primary productivity. All these relationships support the idea that high breeding density areas are also high quality habitats where females may not need to travel off territory to
acquire food or other resources. An association between peak breeding density and habitat quality could lead to lower encounter rates with extrapair males and hence lower extrapair paternity on densely settled sites.

Additional support for this scenario comes from patterns of paternity and polygyny observed across the three years of the study for which weather and grasshopper abundance data were available. In 2007, paternity tended to increase with harem size (chapter 3). In 2008, no significant relationship between paternity and harem size was found, although the relationship was still positive (effect: 0.44 ± 0.27, F_{1,31} = 2.68, p = 0.11). In both of these years, rainfall was above average (NASS 2008, 2009). In 2009, temperatures were below average (NASS 2010) and grasshopper abundance declined 35-45% from 2007 and 2008 levels (Anthony Joern and Angela Laws, pers comm). In 2009, paternity decreased significantly with increased harem size (effect: -0.47 ± 0.22, F_{1,35} = 4.61, p = 0.04). One way this pattern could come about is through increased extra-territorial forays by females sharing limited territorial resources with the male’s other mates. For instance, Westneat (1994) showed that the availability of food on red-winged blackbird territories significantly decreased the time males spent off territory and tended to decrease the time that females spent off territory. Males with food supplements on their territories also had significantly higher paternity in their nests than unsupplemented males (Westneat 1994). Both female and male dickcissels will foray off territory (pers. obs., Zimmerman 1966; Finck 1983). These forays likely have several functions, including searching for new territories (pers. obs., Finck 1983) and for extrapair mates (pers. obs.). Nevertheless, their frequency and distance could also be affected by food availability on the territory. Indeed, Zimmerman (1966) observed females foraging off territory. Thus, female movements off territory in search of food could contribute to extrapair fertilizations in dickcissels.

Male birds typically attempt to guard their fertile mates to prevent them from engaging in extrapair copulations (Westneat et al. 1990). Female attempts to solicit EPC and male attempts to gain EPC on another male’s territory may be difficult in open habitats, where such forays are readily observable. Attempts by males to prevent EPC could be thwarted by the presence of dense vegetation within territories (Mays and Ritchison 2004). Nevertheless, this does not appear to be the case in dickcissels. The density of large woody shrubs within male territories did not have any effect on the territorial male’s paternity. One possible reason such visual barriers did not affect EPP is if female choice, rather than male mate guarding, controls fertilization. For instance, polygynous male blue tits (Parus caeruleus) guarded their mates less vigorously than monogamous males, but did not suffer higher paternity loss (Kempenaers et al. 1995). Since female dickcissels may pair polygynously, they may be more likely to pair socially with a male they also prefer for copulation. Such females would be unlikely to pursue extrapair copulations or submit to attempts by non-preferred males to mate, regardless of the presence of visual barriers. Indeed, the female choice/male competitiveness hypothesis appears to be a better explanation for patterns of polygyny and extrapair mating in dickcissels than tradeoff hypotheses (chapter 3). Another reason visual barriers might not influence paternity is if extrapair copulations occur off territory. If females actively seek extrapair mates, or if females must foray off territory for resources, then male mate guarding would have to take place off territory in order to be effective. This sort of off territory mate guarding is prevented by male-male aggression. Nevertheless,
males have been observed intruding onto territories with fertile females, so clearly some extrapair mating may occur on a female’s home territory. Thus, the inability of males to guard their mates off territory cannot fully explain the lack of association between EPP and visual obstruction.

Interestingly, shrub density did not significantly interact with patterns of male mating success. If monogamous females are more likely to seek extrapair copulations, then increased visual barriers within territories should promote such activities. For instance, Mays (2004) observed some male yellow breasted chats herding their mates back onto the territory when those mates attempted to leave. In visually obstructed areas, females should be better able to avoid detection by their mates when attempting to leave the territory in search of extrapair mates. It is possible that monogamous males are simply poor mate guarders or that female attempts to gain EPP are not affected by male attempts to mate guard, regardless of the male’s mating status. Alternatively, the polygyny threshold hypothesis predicts that monogamous males defend territories with fewer resources than polygynous males (Emlen and Oring 1977). If this is so, then monogamously mated females may need to obtain resources off the territory more frequently than polygynous females even though monogamous females do not share territorial resources with other females. If monogamous females are more likely to engage in extraterritorial forays than polygynous females, and extraterritorial forays increase the chances of EPC, then monogamous females will be more likely to have extrapair young regardless of the density of visual barriers in a territory.

Dickcissel mating patterns appear to respond to burn management in complex ways. While patterns of productivity, species richness, and heterogeneity in plants and grasshoppers are driven primarily by long term burn regimes (Knapp et al. 1998a; Joern 2004), this does not appear to be the case in dickcissels. Instead, dickcissel mating patterns appear to be the result of an interaction between long term burning patterns, short term fire history (i.e. the number of years since burning), and yearly variation in climatic conditions. For instance, harem size did not vary significantly among watersheds in 2008, when primary productivity was high and resources were abundant. In contrast, harem size was significantly higher in the annually burned watershed in 2009 when poor growing conditions likely exaggerated differences between watersheds. Thus differences in mating patterns among burning regimes may be stronger in years with poor growing conditions and weaker in year with good growing conditions. Clearly longer term studies on a broader spatial scale are needed to tease apart the relationships among mating patterns, long and short term management history and yearly climatic variation.

© Bridget F. Sousa 2012
Table 5.1. Sample sizes and burn history for the watersheds included in this study. Years postburn is presented for the year a watershed was included in the study and is number of years since the last fire occurred. Burn intervals of reversal sites (name starting with “R”) are presented as the burn interval before 2000 followed by the burn interval initiated in 2000.

<table>
<thead>
<tr>
<th>Name</th>
<th>Burn Interval</th>
<th>Years Postburn</th>
<th>Territories Studied in Each Year</th>
</tr>
</thead>
<tbody>
<tr>
<td>R20a</td>
<td>1, 20</td>
<td>0</td>
<td>12</td>
</tr>
<tr>
<td>2a</td>
<td>2</td>
<td>0</td>
<td>10</td>
</tr>
<tr>
<td>2d</td>
<td>2</td>
<td>1</td>
<td>13</td>
</tr>
<tr>
<td>4f</td>
<td>4</td>
<td>1</td>
<td>10</td>
</tr>
<tr>
<td>4b</td>
<td>4</td>
<td>3</td>
<td>10</td>
</tr>
<tr>
<td>10a</td>
<td>10</td>
<td>7</td>
<td>3</td>
</tr>
<tr>
<td>20c</td>
<td>20 &gt;15</td>
<td>14</td>
<td>15</td>
</tr>
<tr>
<td>1d</td>
<td>1</td>
<td>0</td>
<td>9</td>
</tr>
<tr>
<td>R1a</td>
<td>20, 1</td>
<td>0</td>
<td>19</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>81</td>
<td>50</td>
</tr>
</tbody>
</table>

Table 5.2. Variation in dickcissel harem sizes among burn regimes studied in 2008 and 2009.

<table>
<thead>
<tr>
<th>Burn Regime</th>
<th>Mean</th>
<th>SE</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>2008</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>annual</td>
<td>1.67</td>
<td>0.33</td>
<td>0-3</td>
</tr>
<tr>
<td>biennial</td>
<td>1.26</td>
<td>0.17</td>
<td>0-4</td>
</tr>
<tr>
<td>quadrennial</td>
<td>1.40</td>
<td>0.23</td>
<td>0-3</td>
</tr>
<tr>
<td>unburned</td>
<td>1.12</td>
<td>0.22</td>
<td>0-3</td>
</tr>
<tr>
<td>reversal</td>
<td>1.58</td>
<td>0.34</td>
<td>0-4</td>
</tr>
<tr>
<td>2009</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>annual</td>
<td>2.22</td>
<td>0.24</td>
<td>1-4</td>
</tr>
<tr>
<td>unburned</td>
<td>1.33</td>
<td>0.29</td>
<td>0-4</td>
</tr>
<tr>
<td>reversal</td>
<td>1.53</td>
<td>0.19</td>
<td>0-3</td>
</tr>
<tr>
<td>Total</td>
<td>1.50</td>
<td>0.09</td>
<td>0-4</td>
</tr>
</tbody>
</table>
Table 5.3. Effect sizes, F statistics and p-values for the analysis of the effects of harem size, shrub cover, year and their interactions on dickcissel paternity (number of sampled young a male sired on his territory); N = 70 males. Shrub Cover is the proportion of a male’s territory covered by large woody shrubs.

<table>
<thead>
<tr>
<th>Effect ± SE</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Harem Size</td>
<td>-0.49 ± 0.28</td>
<td>&lt;0.00</td>
</tr>
<tr>
<td>Shrub Cover</td>
<td>-2.89 ± 7.56</td>
<td>0.54</td>
</tr>
<tr>
<td>Year</td>
<td>-2.55 ± 0.97</td>
<td>6.89</td>
</tr>
<tr>
<td>Harem Size * Shrub Cover</td>
<td>2.22 ± 2.53</td>
<td>0.77</td>
</tr>
<tr>
<td>Harem Size * Year</td>
<td>1.00 ± 0.37</td>
<td>7.47</td>
</tr>
<tr>
<td>Year * Shrub Cover</td>
<td>-4.49 ± 4.80</td>
<td>0.87</td>
</tr>
</tbody>
</table>

Table 5.4. Mean and variance in harem sizes across three studies of dickcissels. Konza refers to data from this study.

<table>
<thead>
<tr>
<th>Study</th>
<th>Mean</th>
<th>Variance</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zimmerman (1966)</td>
<td>1.52</td>
<td>0.81</td>
<td>23</td>
</tr>
<tr>
<td>Zimmerman (1982)</td>
<td>1.73</td>
<td>0.77</td>
<td>147</td>
</tr>
<tr>
<td>Konza (2008)</td>
<td>1.35</td>
<td>0.93</td>
<td>81</td>
</tr>
<tr>
<td>Konza (2009)</td>
<td>1.70</td>
<td>1.06</td>
<td>53</td>
</tr>
</tbody>
</table>
Figure 5.1. In watersheds without shrubs, males perch on tall forbs and grass to monitor their territories (panel 1). At low shrub densities (panel 2), shrubs may enhance the ability of males to guard their mates and territories from intruding males by providing tall perches. As shrub densities (panel 3), shrubs may enhance the ability of males to guard their mates and territories. At higher densities, shrub islands are visual barriers that may interfere with a male's ability to guard his territory.
Figure 5.2. False color aerial photograph (red, green and near infrared bands) illustrating shrub cover in dickcissel territories on an unburned watershed (20c). Male territories are outlined in blue. Shrub islands appear as darker areas (e.g. solid arrows) while red cedars appear as black spots (e.g. dashed arrows) against the lighter background of live and dead standing herbaceous cover.

Figure 5.3. Variance in dickcissel harem size across the burn treatments studied in 2008 (solid bars) and 2009 (hatched bars).
Figure 5.4. Mean ± standard error of dickcissel harem size (solid bars) and within pair paternity (hatched bars) for each burn regime in 2008. Within pair paternity is the proportion of sampled young a male sired on his territory.

Figure 5.5. Standard deviation (SD) of forb and small woody shrub cover for all watersheds studied in 2008. SD of forbs in the annual burn was zero in 2008.
Figure 5.6. Mean and standard error of dickcissel harem size (solid bars) and within pair paternity (hatched bars) for each burn regime in 2009. Within pair paternity is the proportion of the young genotyped on a male’s territory that he sired.

Figure 5.7. Standard deviation of forb and small woody shrub cover in 2009.
Sexual selection varies across time in a managed environment

Sexually dimorphic male traits such as song and colorful plumage are generally thought to arise and persist through sexual selection (Darwin 1871; Lande 1980; Andersson 1994). However, studies seeking a link between sexually dimorphic traits and reproductive success frequently discover only weak or inconsistent relationships. For instance, male size was associated with male reproductive success in one population of red-winged blackbirds (Agelaius phoeniceus, Weatherhead and Boag 1995), but not in another (Westneat 2006). In barn swallows (Hirundo rustica), sexual selection on tail length was generally positive across years, but varied in intensity among populations (Moller et al. 2006). Variation in sexual selection has also been documented within populations. Chaine and Lyon (2008) found strong sexual selection in lark buntings (Calamospiza melanocorys), but the target and intensity of this selection differed from year to year. For instance, sexual selection on male black body plumage was significantly positive in 2000, but significantly negative in 2003. Chaine and Lyon also documented intense sexual selection on male beak size in 1999, weak selection in 2002 and no selection on beak size in any other year. Indeed, contradictory evidence for sexual selection is fairly common in the literature (Andersson 1994; Gontard-Danek and Moller 1999). Despite such inconsistencies, few studies have specifically addressed whether sexual selection varies temporally or spatially within a species.

One issue is that defining sexual selection has not been straightforward. Sexual selection is the correlation between a trait and reproductive success. Andersson (1994) summarized the traditional definition of sexual selection as: “differences in reproductive success, caused by competition over mates, and related to the expression of the trait.” However, the definition of sexual selection and its proper role and application in evolutionary research has been a topic of some recent debate (e.g. Kavanagh 2006; Carranza 2009; Clutton-Brock 2010; Roughgarden and Akcay 2010; Shuker 2010; but see Roughgarden and Ackay 2010 and replies). I chose to focus on the traditional definition of sexual selection. While some authors raise valid concerns over this definition (e.g. Carranza 2009; Roughgarden and Akcay 2010), it has several advantages, including fairly broad support in the literature and a long history of empirical application that are both lacking for other, more controversial, definitions of sexual selection.

The debates concerning the definition of sexual selection have also raised some important issues regarding the measurement of selection (most recently in Klug et al. 2010a; Krakauer et al. 2011). A number of indices have been suggested; two of the most commonly employed are the selection gradient (Lande and Arnold 1983) and the opportunity for sexual selection (Crow 1958; Wade 1979; Wade and Arnold 1980). The selection gradient is the slope of the linear regression of relative fitness on standardized trait values. Measuring selection in this manner implicitly assumes a causal relationship between the trait and some process that affects fitness. The opportunity for sexual selection (OSS) is the standardized variance in reproductive or mating success for a population. Unlike the selection gradient, it does not measure selection on a specific trait, but measures the theoretical upper limit of sexual selection in a given population (Crow 1958; Wade 1979; Arnold and Wade 1984; Jones 2009).
OSS can include random variation in fitness not associated with sexually selective processes (Koenig and Albano 1986), it can give both qualitatively and quantitatively different results from selection gradients (Klug et al. 2010a). Indeed, selection gradients are generally less sensitive to random variation in reproductive success (Hubbell and Johnson 1987; Klug et al. 2010a; Fitze and Galliard 2011). A recent study demonstrated that both measures of selection can vary significantly depending on the pool of individuals studied and the component of reproductive success measured; however, selection gradients were far more consistent in all contexts than the OSS (Fitze and Galliard 2011). Thus, for comparisons of sexual selection across time and space, the selection gradient may be the best index to employ.

On the other hand, the OSS may be useful in explaining why sexual selection does or does not vary. Sexual selection requires variation in mating success. If variation in fitness fluctuates temporally or spatially, then the strength of the selection gradient may also vary. Theory has long held that variation in fitness can be influenced by environmental variation. For instance, the polygyny threshold hypothesis posits that resource distribution affects variance in the number of social mates a male attracts (Emlen and Oring 1977). Resource distribution can fluctuate substantially across years with changes in rainfall, temperature, and myriad other factors. In addition to natural variation in breeding conditions, anthropogenic activities can also influence variation in fitness. Recent studies have shown that agricultural practices can have strong effects on breeding birds. In one example, haying in agricultural fields increased breeding synchrony and thereby altered variance in extrapair mating success in Savannah Sparrows (Passerculus sandwichensis). The resulting increase in the variance in mating success has the potential to increase sexual selection in savannah sparrows breeding in hayed agricultural fields (Perlut et al. 2008). While the exact cause of changes in the OSS may not always be apparent, testing whether the OSS varies may provide valuable insight into what sorts of factors may be causing patterns of variation (or lack thereof) in sexual selection.

Phenotypic variance is also necessary for sexual selection. Like the OSS, phenotypic variance can fluctuate across time or space and such fluctuations could influence sexual selection. For instance, variation in plumage coloration in house finches (Carpodacus mexicanus) is influenced by the environmental availability of carotenoids (Hill 1993, 2002). Indeed, standardizing carotenoid access among captive male house finches essentially eliminated variation in male coloration (Hill 2002). It is conceivable that carotenoid availability could also differ across years in response to changing weather patterns and plant productivity, creating temporal fluctuations in trait variance and potentially, sexual selection. Indeed, condition dependent traits may be particularly susceptible to fluctuations because their expression is tied to resource availability. Another way that phenotypic variance can differ temporally is if natural selection varies across years. For instance, in years with particularly low winter temperatures, smaller males may suffer higher mortality than larger males (e.g. Johnston and Fleischer 1981), leading to lower variance in male size in the following breeding season. Some traits, however, may be less likely to exhibit differences in variation over time. For instance, melanin based plumage patches are thought to be condition independent badges of status in many species of birds (Rohwer 1975; Smith et al. 1988; McGraw 2008; Santos et al. 2011). Since these badges are replaced each year and the size of the new badge is
theoretically dependent on the social environment of each male (Smith et al. 1988), variation in these types of traits is unlikely to change much over time unless they are linked to overwinter survival. Variation in badges of status may vary spatially if males with larger badges prefer particular patches and exclude smaller badged males from these areas. A decrease in the variance of a phenotypic trait, either in a particular year or site, will alter the potential strength of selection on that trait in much the same way a change in the OSS can influence sexual selection. As in variance in mating success, the exact cause of patterns of phenotypic variation across time or space may not be immediately evident, but evidence for differences in trait variance among years or habitats may indicate likely causes for patterns of sexual selection.

Finally, mating success is not a single component of fitness, especially in birds. Many male birds gain fitness through both social pairings and extrapair matings. The number of social mates, extrapair mates, and the proportion of each mate’s offspring a male sires all contribute to a male’s total fitness. Thus several different measures of fitness may be used to calculate selection gradients (e.g. Wade 1979; but see Fitze and Galliard 2011). Which measure used depends on both the question being asked and on the practical limitations of the species being examined. For instance, lifetime reproductive success is most appropriate for predicting the expected change in population mean trait values due to sexual selection. This measure is less informative when considering whether selection varies spatially or temporally, especially in species that breed over multiple years and in several sites. Instead, total reproductive success within a single breeding season would be of greater utility when examining variation in sexual selection. Within-season reproductive success can be further divided into different components, such as social mating success, within-pair siring success, and extrapair siring success (Webster et al. 1995). This approach is particularly useful because sexual selection can act differently through different components of reproductive success. For instance, males with UV shifted crown hues had higher within-pair siring success in blue tits (Parus caeruleus), but males with blue shifted crown hues had higher extrapair siring success (Delhey et al. 2003).

I studied temporal and spatial variation in sexual selection in dickcissels (Spiza americana) breeding in tallgrass prairie. Several aspects of this species make it a good candidate for examining variation in sexual selection. First, patterns of mating indicate that the opportunity for sexual selection is high in dickcissels. Harem size was positively associated with both within pair paternity and extrapair siring success. Variation in harem sizes and within-pair paternity accounted for the majority of the variance in reproductive success (~60%) while extrapair siring accounted for an additional ~20% of variance (chapter 4). In addition to high variance in male mating success, dickcissels also have moderate sexually dimorphism and show little paternal involvement in offspring. These attributes suggest that sexual selection should be strong in this species.

Second, there is some indication that selection may vary temporally in this species. Previous research found that a male’s bib size predicted his social mating success (Finck 1983), but a subsequent study found no association between bib size and mating success (chapter 4). Indeed, sexual selection gradients for three of six sexually dimorphic traits changed direction across two years of study (chapter 4). Selection gradients also varied in magnitude, and in one case a 5-fold decrease in the magnitude of sexual selection was observed between years (chapter 4). Although significance tests
were not conducted, these results nevertheless suggest that variation in selection may indeed occur in this species.

Third, dickcissels breed in an early successional habitat that is by definition dynamic. Precipitation on the tallgrass prairie can range from extreme flooding in one year to extreme drought in the next, producing annual fluctuations in breeding conditions (Borchert 1950; Hayden 1998). In addition, the tallgrass prairie ecosystem is reliant on intensive fire management to prevent the invasion of large woody plants. The frequency of fire has substantial effects on the heterogeneity and species composition of prairie communities (Knapp et al. 1998b). Variation in fire frequency produces a patchwork of successional stages across the landscape. These patches can vary substantially in the availability of both food and suitable nesting sites (Zimmerman 1982; Knapp et al. 1998b; Joern 2004). Such spatial variation in available breeding resources could produce spatial variation in sexual selection.

Finally, a study of the effects of management strategies on sexual selection in a declining population of native birds is particularly relevant. Grassland birds are declining faster than any other group of North American avifauna, and dickcissels are no exception to this trend (Sauer et al. 1995). Management practices can have profound effects on the fates of species reliant on managed lands (Crandall et al. 2000; Kinnison and Hairston Jr 2007). Thus it is important to examine whether management practices influence sexual selection in these populations.

Some predictions can be made a priori regarding sexual selection in dickcissels. First, if sexual selection is maintaining sexual dimorphisms in dickcissels, then there should be significant sexual selection on traits. Specifically, male dickcissels are larger than females, have a bright yellow breast and black bib that are much reduced in the drabber female, and sing a simple song to defend territories and attract mates (Temple 2002). Thus sexual selection for these traits should be evident.

Second, the expression of some traits is dependent on the condition of the animal at the time the trait is produced. For instance, carotenoid-based plumage ornaments are replaced each year, and their quality has been linked to male condition and access to carotenoid containing food during molt in numerous passerine species (Hill 1991, 1992, 2002; Hill and McGraw 2006). Food availability is likely to vary annually. In years when resources are plentiful, most males should be able to fully express condition dependent ornaments, leading to a decrease in phenotypic variance in such traits and a corresponding decrease in sexual selection. In years when resources are scarce, variance in the expression of condition dependent traits is likely to be high, so sexual selection on such traits may also increase in these years. Thus, sexual selection on condition dependent plumage traits should vary temporally.

Third, a number of studies have suggested that body size and melanin ornaments serve primarily in male-male competition (Rohwer 1975, 1977; Smith et al. 1988; Andersson 1994; Jawor and Breitwisch 2003). Dickcissels prefer to breed in frequently burned sites, and are more abundant in these sites than infrequently burned patches (Zimmerman 1997; Reinking 2005; Powell 2006). Thus, male-male competition should be more intense in frequently burned sites, leading to stronger selection on traits associated with male-male competition in these sites.

Finally, bird song is a complex trait with multiple components that may be under sexual selection (Gil and Gahr 2002). It has been suggested that song frequency traits
could be an honest signal of body size and thus function in male-male competition (Ryan and Brenowitz 1985; Gil and Gahr 2002). If so, then sexual selection on song frequency traits should vary spatially in the same manner as male body size.

**Methods**

*Study Population*

I studied dickcissels at the Konza Prairie Biological Station (Konza) from 2006 to 2009. Konza is a long-term ecological research facility encompassing 3,487 hectares of native tallgrass prairie. Konza has a thirty year history of replicated burn treatments conducted at the watershed level. I studied eight ungrazed watersheds within Konza (Table 6.1). In 2008 and 2009 I categorized each of the watersheds examined as either frequently or infrequently burned. Frequently burned watersheds were burned either once every year or every two years. Infrequently burned sites were burned no more than once every 4 years. I chose this range because large woody plants generally do not occur in sites burned at 2-year or shorter intervals, while sites burned at 4-year or greater intervals support moderate to high densities of such plants, primarily roughleaf dogwood (*Cornus drummondii*) and red cedar (*Juniperus virginiana*).

Most watersheds were maintained at the same burn interval throughout Konza’s history. One watersheds, R20A, was part of a reversal experiment, wherein its burn interval was reversed beginning in 2000. Thus R20A was annually burned until 2000, at which time burning ceased. In addition, an unplanned burned occurred on R20A in 2008. Because of this unusual burn history, I excluded this watershed from the analysis of sexual selection across burn regime. Data from 2006 and 2007 were also excluded from the habitat analysis because there was insufficient variation in burn history in these years. Analyses of yearly variation in sexual selection included all watersheds from 2006-2009.

I captured male and female dickcissels using mist nets (see chap 2 for details). Each adult was banded with a U.S. Geological Survey aluminum band and a unique combination of plastic color bands. Blood samples were collected from all adults at capture and from nestlings at ~3 days of age.

*Male Traits*

I studied four sexually dimorphic male traits: body size, black bib size, yellow breast coloration, and song. Each of these traits can be described by multiple measurements. For example, yellow coloration can be described by: total reflectance, yellow reflectance, UV reflectance, yellow hue, UV hue, yellow chroma, and UV chroma (Hill and McGraw 2006). Since sample sizes were limited, not all components of each trait could be included in the analysis of sexual selection. Because the justification for inclusion differed for each trait, I discuss the criteria used to choose each trait component below.

*Body and Bib Size* – Measures of tarsus length, natural wing chord, bill length and bill depth were not all correlated, which precluded the use of principal components to represent body size (Table 6.2). I therefore used tarsus length to represent male body size since it is considered a good estimate of male skeletal body size (Senar and Pascual 1997). Digital photographs of male dickcissels were taken against a size standard. Each male was photographed in an upright position with bill pointed towards the camera lens.
I then used ImageJ (Abramoff et al. 2004) to calculate the total area of black markings on the throat and breast of each male.

Yellow Breast – I collected 2 yellow breast feathers from males at the time of capture in 2006. In subsequent years, I collected 4 feathers from each male. Spectral reflectance was measured from these feathers using a USB2000 spectrometer and pulsed xenon light source (PX-2; Ocean Optics, Dunedin, FL, USA). Reflectance was measured over the full passerine visual spectrum of 300 to 700 nm (Jacobs 1981; Cuthill et al. 2000). I measured three components of yellow feather coloration: total reflectance, UV hue and yellow hue. Total reflectance was calculated as the sum of all reflectance values between 300 and 700 nm divided by the total number of measurements taken in this range (Montgomerie 2006). I defined UV hue as the wavelength of peak reflectance in the UV range (300 - 400 nm) and yellow hue as the wavelength at the inflection point of the curve in the yellow range (475 - 525 nm, Montgomerie 2006). Because UV and yellow hue were negatively correlated ($r = -0.82$, $p < 0.0001$), a composite measure of hue was calculated as the difference between yellow and UV hue, which will be referred to as hue hereafter. The change in the number of feathers collected after 2006 produced different measures of total reflectance, but did not affect measures of hue (chapter 4). Details of color measurements and analysis are presented in chapter 4.

I calculated the repeatability of each component of yellow coloration as the proportion of total trait variance due to individual identity (Lessells and Boag 1987). Total reflectance was less repeatable than hue (reflectance: $r = 0.87$, $p < 0.0001$ and hue: $r = 0.96$, $p < 0.0001$). Therefore, hue was used in subsequent analyses.

Song – My assistants and I recorded male songs between dawn and 14:00 hours CST using a Sony TCM-5000EV cassette recorder and Sennheiser long shotgun microphone (me67). I then digitized the recordings using Raven 1.3 song analysis software. Dickcissels sing a simple song consisting of two repeated phrases: a “dick” component consisting of a single note, and a “cissel” consisting of three elements (c1, c2, and c3, see chapter 4 for details). I measured seven components of male songs: number of dick phrases, number of cissel phrases, frequency range, center frequency of the c1 bridge and c3 tail, song length, and intersong interval. Each component was measured from 5 songs within a single recording and the average of these measures was used for further analysis. The most repeatable component of male song was frequency range (chapter 4), so all subsequent analyses focused on this measure.

Reproductive Success

I assigned social fathers to nests through a combination of active nest defense, courting behavior with the female, and nest location within the territory. All birds were genotyped at six variable microsatellite loci. I compared each nestling’s genotype to the genotypes of the male and female associated with the nest and considered nestlings extrapair if they mismatched the putative father at more than one locus. Extrapair sires could be assigned to a majority of chicks in only two of the four years of this study. Furthermore, social mating success accounted for the majority of the variance in reproductive success (chapter 4). I therefore focused on sexual selection acting through social pairing success and within-pair paternity (paternity hereafter).
Measurements of Sexual Selection

Within each breeding season, trait values were standardized to $\bar{x} = 0$ and $\sigma = 1$ and relative fitness was calculated by dividing each male’s fitness by mean fitness. I calculated selection gradients as the slope of the linear regression of standardized trait values on relative fitness. Fitness was estimated by two parameters: harem size and paternity. I defined harem size as the maximum number of simultaneously nesting females mated to a male (the minimum number of social mates) and paternity as the proportion of genotyped young produced on a territory sired by the defending male.

Relative fitness was not normally distributed, nor did transformation of the underlying fitness variables improve the fit of a normal model to the data. While normality is not necessary for the estimation of selection gradients (Lande and Arnold 1983), non-normality may seriously affect the estimation of standard errors and bias significance tests associated with selection gradients (Mitchell-Olds and Shaw 1987). Thus, an analysis of the effects of year and burn frequency on selection gradients per se was not appropriate. Instead, I assessed variation in trait-fitness relationships among years and burn regimes. I modeled effects on harem size using a model with a Poisson distribution and log link (Proc GENMOD in SAS). Harem size was underdispersed, so models were adjusted to include a dispersion parameter that corrected for underdispersion. Variation in sexual selection via paternity was tested using a model of paternity in which the dependent variable had the events by trials syntax (events = number of offspring sired by the resident male; trials = number of young genotyped on each male’s territory), a binomial distribution and logit link in Proc GENMOD. Paternity was overdispersed, so a correction factor based on the Pearson Chi square was added to the model (McCullagh and Nelder 1990).

I used separate models to evaluate the effects of year and the effects of burn frequency on sexual selection gradients. Previous analyses showed no significant correlation among male traits (chapter 4) and samples sizes were limited, so I evaluated each trait independently. The interaction term of year by trait value was used to test whether selection gradients differed significantly among years. Because no specific patterns of change in selection were expected among years, year was treated as a class variable. I calculated the main effect of each trait on fitness over all 4 years using the above models.

Analyses of the effects of burning on sexual selection were restricted to data from 2008 and 2009 when there was sufficient variation in burning regimes. As in the analysis of year effects, each trait was evaluated in a separate model. Models included the fixed effects of trait, year and burn frequency, and the interaction term of trait by burn frequency. I used the interaction term to test whether selection gradients differed significantly between burn treatments.

Variation in Phenotype and Fitness

I determined whether variance in each trait differed among years or among burn regimes using Levene’s test (Levene 1960). I tested for heteroscedacity of reproductive success across years and burn regimes by focusing on variation in harem size and paternity. Because fitness was not normally distributed, I used the Brown-Forsythe test (Brown and Forsythe 1974) to determine whether variance in harem size or paternity differed among years or burn regimes. The Brown-Forsythe test uses departures from the
median, rather than the mean to test for homogeneity of variances among groups. This methodology makes the Brown-Forsythe test more robust to departures from normality than Levene’s test, both for skewed (harem size) and for heavy tailed (paternity) data (Brown and Forsythe 1974). Both Levene’s and Brown-Forsythe tests for homogeneity of variances were conducted using Proc ANOVA with HOVTEST syntax. Variance tests for paternity used the proportion of young a male sired. All analyses were conducted in SAS 9.2 (SAS Institute 1989).

Results
Selection Gradients
I found no significant main effect of any trait on either harem size or paternity (Table 6.3). Sexual selection gradients appeared to vary in both direction and magnitude across the years of the study (Figure 6.1). In all cases the selection gradient for all years was near zero and nonsignificant.

Variation in Sexual Selection
Sexual selection on tarsus length, bib size, or yellow brightness via harem size did not vary significantly among years (Figure 6.1). Selection on song frequency range via harem size did vary significantly among years of the study ($F_{3,124} = 8.97, p = 0.03$). Indeed the selection gradients for song frequency range declined steadily across the four years, such that selection was moderately positive in 2006, near zero in 2007 and 2008, and strongly negative in 2009 (Figure 6.1).

Sexual selection on song frequency range via paternity also varied significantly by year ($F_{3,76} = 7.92, p = 0.048$). The pattern of change among years was similar to that observed for harem size, with the notable exception of 2009. In this year positive selection on frequency range was observed, which is opposite to selection on frequency range via harem size in the same year (Figure 6.1). Sexual selection on bib size via paternity also tended to vary among years, but not significantly so ($F_{3,106} = 6.37, p = 0.09$). Selection on tarsus length and yellow brightness via paternity did not vary significantly among years (Figure 6.1).

Burning regime had little effect on sexual selection through either harem size or paternity (Figure 6.2). Only selection on tarsus length was significantly influenced by burning through differences in harem size ($F_{1,91} = 4.84, p = 0.03$). There was also a tendency for sexual selection on bib size via paternity to vary across burn regimes, although this was not significant ($F_{1,50} = 2.85, p = 0.09$). In both cases, selection was negative in frequently burned sites, but positive in unburned sites. I did not find any significant difference in sexual selection on frequency range between the two burn regimes (Figure 6.2). Frequency range was also not significantly associated with male size (Pearson $r = 0.01, p = 0.88, N = 134$), so it is possible that this trait is not related to male-male competition in the manner envisioned by Gil and Gahr (2002).

Variance in Fitness
Variation in the opportunity for sexual selection is one possible cause for variation in sexual selection. I found no difference in the variance in harem size across years (Table 6.4, Brown-Forsythe $F_{3,184} = 0.83, p = 0.48$); however, previous research showed that mean harem size was not constant across years (chapters 3 and 5). I
therefore standardized harem size within each year (harem size divided by the mean for that year) and tested for homogeneity of variance. The standardized variance in harem size showed significant heterogeneity of variance across years (Brown-Forsythe $F_{3,184} = 2.79, p = 0.04$). Variance in paternity did not differ significantly across years (Table 6.4, Brown-Forsythe $F_{3,111} = 0.69, p = 0.56$). Because there was no indication that mean paternity varied across years (chapters 3 and 5), I did not conduct any post hoc tests of variance in paternity.

The two measures of fitness did not show significant heterogeneity of variance across burn regimes ($p >> 0.05$, Table 6.5). Earlier tests indicated no effect of burning regime on mean harem size or paternity (chapter 5), so post hoc standardization of variances was not warranted.

**Variance in Phenotype**

None of the four traits examined showed significant heteroscedacity across years or across burn regimes (Tables 6.4 and 6.5). However, song frequency range did have a non-significant tendency toward heterogeneity in variance across years ($F_{3,130} = 2.46, p = 0.07$). This could have been influenced by differences in mean frequency range across years (ANOVA $F_{3,130} = 2.40, p = 0.07$), so I standardized frequency range across years by mean centering measures within each year. Standardized frequency range showed significant temporal heteroscedacity ($F_{3,130} = 2.73, p = 0.046$).

**Discussion**

I did not find any evidence for significant sexual selection on the four sexually dimorphic traits examined in dickcissels. An examination of selection gradients in each year shows that selection was never consistently positive or negative for any trait (Figure 6.1). Further, selection gradients were frequently near zero, with error bars overlapping zero in at least two of the four years examined for all traits in all fitness contexts examined. This was unexpected, since dickcissels exhibit a number of characteristics suggestive of active sexual selection (e.g. high OSS, sexual dimorphism, no paternal care). There are a number of possible explanations for these results. First, opposing selection across time, space or mating contexts could diminish or even eliminate net sexual selection on a trait. Second, conditions on the wintering grounds could contribute to weak sexual selection. A third possibility is that the manner in which I measured sexual selection failed to detect selection acting on male traits.

A particularly intriguing possibility is that variation in selection gradients across years or burn regimes could diminish or even eliminate net sexual selection. Indeed, I found evidence that selection gradients varied both temporally and spatially. The cause of this variation was not clear. In the latter half of this discussion, I will explore four major factors that might contribute to variation in sexual selection, including: mechanisms linking trait expression to mating success, heteroscedacity of fitness and phenotype, correlational selection and management practices occurring off Konza.

**Sexual Selection Gradients**

Sexual selection was weak across both mating contexts and in all years with only a few exceptions (e.g. song frequency range in 2009). There are several factors that could have contributed to the overall weak sexual selection observed in this study. First,
opposing selection in different years, habitats or mating contexts could result in weak net sexual selection. Second, there is some evidence that conditions on the wintering grounds contribute to variation in mating success on the breeding grounds (e.g. Reudink et al. 2009). If so, then it is possible that extensive human alteration of dickcissel wintering grounds could further weaken sexual selection on the breeding grounds. Finally, the manner in which I measured sexual selection could have missed significant sexual selection acting through extrapair paternity, pre-settlement processes, or non-linear selection (Klug et al. 2010b).

Opposing selective forces may have contributed to the weak sexual selection observed in dickcissels. In those cases where sexual selection appeared non-zero in a given year, such selection was counterbalanced by contrasting patterns of selection in alternate years or mating contexts. For instance, positive selection on song frequency range was observed in some years and negative selection occurred in others. In 2009, selection on song frequency range also differed across mating contexts, with positive selection occurring through paternity, but negative selection occurring through harem size. Selection gradients also tended to oppose each other across burning regimes. Selection on both tarsus (via harem size) and bib size (via paternity) was positive in unburned prairie, but negative in frequently burned prairie. Such patterns of opposing selection across time, mating contexts and habitats could weaken or even eliminate net direction sexual selection on a trait (Delhey et al. 2003).

Another possibility is that conditions on the wintering grounds influence sexual selection on the breeding grounds. For instance, American redstarts (Setophaga ruticilla) wintering in high quality habitats achieved higher reproductive success, both through polygyny and paternity, than males wintering in poor quality habitats (Reudink et al. 2009b). In the case of dickcissels, the opposite may be happening: homogenization of the wintering grounds through agriculture could weaken sexual selection. Much of the grasslands in the dickcissel’s native wintering grounds have been converted to cereal crops, which now constitute the majority of the dickcissel’s winter diet (Basili 1997; Basili and Temple 1999b). Reliance on an irrigated, fertilized, super-abundant grain crop may reduce the signaling value of carotenoid plumage traits by reducing competition for food and carotenoids. A decoupling of the trait and its signaling function could explain both a lack of sexual selection and of variation in selection on yellow plumage ornaments. Since male dickcissels are difficult to recapture and keep in captivity, it may be difficult to test this idea. Alternatively, ornaments that signal foraging ability may be of limited value in a species where males do not provision young. Unless foraging ability has a strong heritable component, there may be few benefits to females of preferring mates with yellower plumage.

Finally, the manner in which I measured sexual selection could influence selection estimates in several ways. These methods could also influence the results of the analysis of variation in sexual selection and mating success, so the implications for those analyses are also discussed here. First, it is possible that limiting my analysis of selection and variance in fitness to harem size and paternity missed selection acting through extrapair siring success. Nonetheless, previous research indicated that extrapair siring success is unlikely to contribute much to sexual selection or to variation in selection in this species. Extrapair siring accounted for ~20% of the variation in male mating success and was positively associated with variation in social mating success (chapters 3 and 4),
which would suggest that it would contribute little to variation in sexual selection. Furthermore, most extrapair young were sired by nearby males (within 150m of nest, chapter 3) and reciprocal cuckoldry was common (Sousa, unpublished data). These patterns suggest extrapair siring success does not play a strong role in sexual selection in this species.

Second, both selection gradients and variance in components of fitness may be sensitive to the pool of individuals from which these measures are estimated. My focus on post settlement sexual selection may miss selection acting on male traits via territory acquisition (Klug et al. 2010b). Earlier research indicated that territory tenure, which partially captures the effects of territory acquisition, influenced mating success, but was not associated with any male trait (chapter 4). Nonetheless, males that did not attempt to defend territories or were quickly excluded could not be included in the analysis, so I cannot reject the possibility that sexual selection occurs through territory acquisition. Fitze and Galliard (2011) found that selection gradients were generally robust to changes in the pool of individuals measured, but the OSS was sensitive to such changes. Estimates of post settlement fitness may miss important variation in the number of males able to acquire territories in different years (e.g. Kvarnemo and Ahnesjo 1996). Indeed, annual changes in the density of territories within particular plots suggest that in some years more males are able to acquire territories than in others. Such variation could contribute to patterns of change in fitness variance that might better explain patterns of sexual selection.

Third, my focus on directional selection might have missed significant non-linear selection acting on traits. For instance stabilizing sexual selection results when females prefer intermediate levels of male traits (e.g. Wollerman 1998; Brooks et al. 2005), or mate assortatively according to quality (e.g. Kempenaers 1994; Andersson et al. 1998). Such processes could occur in dickcissels as well, however sample sizes were insufficient to test this possibility (Lande and Arnold 1983) and no other studies of dickcissels have investigated non-linear selective processes. While non-linear selection might maintain dimorphisms in dickcissels, they cannot explain the origin of such traits. Thus, the lack of current direction selection in dickcissels suggests that selective processes have changed in the evolutionary history of these birds.

Another concern regarding these results is whether sample sizes were sufficient to detect meaningful differences in selection or variance among groups of breeding birds. Sample sizes were modest in each year and in each burning regime. In addition, selection gradients were generally small for all traits in all years. Gontard-Danek and Moller’s (1999) meta-analysis of sexual selection studies found an average effect size of 0.30. All cumulative selection gradients were lower than this average and most of the selection gradients in each year were also smaller than this value. Because selection gradients were small, the change in selection in each year likewise tended to be small. This is especially true in the examination of differences between burn regimes. Since only two years had sufficient variation in burn regime to be included in the analysis, sample sizes were necessarily smaller. Thus, the results should be interpreted with caution, since only moderate to large fluctuations in either selection, fitness variance or phenotypic variance are likely to be detected. Despite these limitations, significant fluctuations in selection were observed across years and burn regimes, and significant heteroscedacity in both harem size and phenotype were observed across years.
Variation in Sexual Selection

Sexual selection on male traits varied significantly across time and burn regimes. Indeed, selection gradients varied significantly for two of the four traits examined and tended to vary for a third trait. There are a number of possible explanations for this variation. First, the development or function of particular traits predicts specific patterns of variation. Nonetheless, variation in selection for male traits did not conform to the predictions made in the introduction. Second, it has been suggested that heteroscedacity in fitness components or male phenotypes could result in variation in sexual selection (Emlen and Oring 1977; Hill 2002). While I detected significant heteroscedacity for harem size across years, patterns of variation in harem size did not match patterns of variation in selection gradients. Neither fitness components nor male phenotypes exhibited significant spatial heteroscedacity. Thus, differences in the variance in mating success or phenotype could not explain changes in selection gradients. Third, selection on correlated traits could produce different patterns of variation in selection. Finally, a large number of factors off the study site could produce the patterns of variation observed on Konza. If so, then sexual selection may be occurring on a broader spatial scale that the one I examined.

Predictions of Trait Variation – Variation in sexual selection did not conform to predictions made from the development and function of particular male traits. I predicted that condition dependent traits would vary temporally, since food availability is subject to temporal variation. Sexual selection on yellow breast coloration did not conform to this prediction. Indeed, yellow hue was the only trait that did not exhibit temporal or spatial variation. Dickcissels molt into their yellow plumage ornaments on the wintering grounds. These wintering grounds have been converted to grain crops (Basili and Temple 1999a), so agricultural practices on the wintering grounds could affect the availability of carotenoids and subsequent expression of yellow plumage. More detailed studies of dickcissel dietary preferences and carotenoid availability on the wintering grounds are needed to determine the extent to which sexual selection on yellow plumage coloration is likely to vary.

I also predicted that traits involved in male-male competition would vary spatially, since competition would be greater in preferred breeding sites and weaker in secondary breeding sites. This prediction was also not supported by the data. Selection on song frequency range did not vary spatially. However, frequency range was not associated with male size, and so may not be involved in male-male competition, as previously predicted. Selection on tarsus length was significantly stronger in the less preferred unburned sites. Selection gradients for bib size also tended to differ between the two burn sizes, but this difference was one of direction rather than magnitude. Sexual selection on bib size was positive in unburned sites and negative on frequently burned sites. Thus sexual selection on both bib size and tarsus length was the opposite of that predicted. It is possible that territory quality within frequently burned sites is less variable than in unburned sites. Indeed, variance in forb and small shrub cover tended to be higher in unburned sites (chapter 5). Thus, competition for high quality territories may actually be stronger within unburned sites, leading to the observed patterns of selection on tarsus length and bib size. Another way selection on traits used in male-male competition could differ between burn regimes is if the manner in which territories are acquired in these sites differ. For instance, returning residents may have an advantage...
over new arrivals in acquiring territories (e.g. Stamps 1987; Deverill et al. 1999). This could lead to decreased sexual selection on traits associated with male-male competition. In contrast, selection on traits important in territory acquisition may be stronger in areas where return rates are low. Return rates were lower in less frequently burned sites (appendix 5). Thus, differences in selection on traits important in male-male competition may be driven by differences in site fidelity among burn regimes.

**Heteroscedacity of Fitness and Phenotype** – A second reason sexual selection might vary is if there is significant heteroscedacity in the components necessary for sexual selection, i.e. reproductive success and male phenotype. Nevertheless, patterns of variance in reproductive success and phenotype could not fully explain the observed variation in sexual selection. First, heteroscedacity in reproductive success contributed little to variation in sexual selection. Indeed, I found significant temporal variation in fitness variance for only one component of fitness (harem size), and no significant spatial heteroscedacity in either harem size or paternity. Second, patterns of heteroscedacity of fitness components did not match patterns of variation in sexual selection on traits. For example, selection on frequency range was strongest in 2006 and 2009, and near zero in the intervening years. In contrast, variance in harem size was fairly similar from 2007 through 2009, and strongest in 2006. So while variation in the OSS might help explain why selection in 2006 differed from the other years, it does not explain why selection on frequency range was stronger in 2009. It is also somewhat surprising that none of the other three traits showed stronger selection in 2006 compared to other years.

There are several ways in which a high OSS may not be realized in selection gradients. Klug and colleagues (2010a) discuss a number of these possibilities. First, a high OSS will not be realized if mating occurs at random. Clearly this is not the case in dickcissels. Previous research has demonstrated skewed mating in dickcissels, with some males attracting multiple females and others attracting none (Harmeson 1974; Zimmerman 1982; Finck 1983). Furthermore, the same males are successful in all mating contexts (chapter 3). Second, high variance in fitness will not lead to strong sexual selection if there is insufficient variation in phenotype. This is unlikely since traits were chosen specifically because they were variable (chapter 4). Third, females may evaluate only a small portion of the population before choosing a mate. This ‘best of N’ strategy results in selection gradients that are not well predicted by the OSS when N is not large (Klug et al. 2010a). It is doubtful that female dickcissels evaluate the traits of all potential mates. It is therefore possible that this strategy creates variance in male mating success that is unrelated to male traits.

As in the analysis of fitness variance, patterns of phenotypic variance could not explain differences in selection among years or burn regimes. I found no evidence for spatial heterogeneity in phenotype. Indeed, trait variance was quite similar between burn regimes for three of the four traits examined. Significant temporal heterogeneity in phenotype was observed in song frequency range only. While this was also the only trait that showed significant temporal variation in selection, patterns of trait variance among years did not match patterns of selection. Similarly, temporal patterns of phenotypic variance in bib size also did not match patterns of sexual selection on bib size. Thus, differences in phenotypic variance cannot explain the patterns of sexual selection in this species.
Higher variance in phenotype is often assumed to predict stronger selection. As in the examination of fitness variance, this might not always be the case. Phenotypic variance is required, but alone is not sufficient for sexual selection. If there is a breakdown in the mechanisms linking traits and fitness, then sexual selection will be weakened or even eliminated. This has been observed in cichlid fish, where eutrophication of the Great Rift Lakes prevents females from evaluating male coloration (Seehausen et al. 1997). In dickcissels, agricultural practices on both the breeding and wintering grounds could cause a disassociation between male traits and fitness. For instance, large males may gain high quality territories only to have those territories mowed in the middle of the breeding season. Genetic manipulation and selective breeding of grain crops could also produce patches of carotenoid rich rice or sorghum that dickcissels are unable to distinguish from carotenoid poor varieties of these crops. This scenario would create variation in male plumage traits that is unrelated to foraging ability or competition for high quality food.

**Correlational Selection** – A third reason that selection for the traits examined might vary is if these traits are correlated with another, unexamined trait for which selection varies. Correlational selection could account for some of the directional variation in sexual selection. Chaine and Lyon (2008) found that the target of selection varied across years in response to varying environmental conditions. Correlation selection, combined with variation in the target of selection, could produce the directional changes I observed in dickcissels. For instance, positive selection on song frequency range was observed in 2006. The switch to negative selection on frequency range in 2009 (via harem size) could arise if song frequency range was negatively associated with another trait under strong positive selection in this year. There was no evidence of this among the four measured traits. There were no significant correlations among these traits (chapter 3) and none of the changes in the direction of selection in any given trait were matched to changes in the direction of selection in another trait. Thus, sexual selection may be acting on another, unmeasured trait that is correlated with those I examined, but what that might be is unclear. Body size, plumage, and song are the main characters that differ between males and females, and any other dimensions to these characters that I measured showed lower repeatability, making them even less likely to be correlated with those I did measure. One remaining possibility is the traits I measured were correlated with a behavioral trait such as aggressiveness or tendency to foray, or sperm attributes such as sperm number or swimming speed that may be under sexual selection.

**External Factors** – A fourth possibility is that factors off Konza influence sexual selection on dickcissels on Konza. The striking variability in the patterns of selection across years lends support to this idea. It is certainly possible to come up with a story for each significant pattern, but no single explanation can account for all the observed patterns of selection for the traits examined. Konza is a small island of native prairie amidst an ocean of corn, alfalfa, and cattle pasture. Agricultural practices off Konza could easily alter the selective patterns observed on Konza. For instance, haying on adjacent fields could produce a surge of immigrants onto the site. These resettling females may relax their selection criteria because they are under intense pressure to quickly attempt another brood. The number and proximity of hayed fields, and thus displaced females, is likely to vary each year depending on agricultural markets and crop conditions.
External factors could also influence variation in sexual selection among burn regimes. Selection on tarsus length and bib size were both variable across burn regimes, although the fitness contexts differed. In both cases, positive selection was observed in unburned plots. One way selection on traits used in male-male competition could differ between burn regimes is if the manner in which territories are acquired in these sites differ. Breeding started later in infrequently burned plots (appendix 5). Furthermore, competition for territories in unburned sites is less likely to be confounded by advantages to returning residents (see above). If haying and heavy grazing off site displace high quality males, competition for territories in unburned prairie may be strong. This could lead to stronger sexual selection on traits used in male-male competition on infrequently burned sites.

The possibility that conditions off Konza influence sexual selection on Konza indicate that a broader scale approach to sexual selection is warranted in dickcissels and possibly other species too. Dickcissels are especially mobile, even for birds. Females often move large distances between breeding attempts and males have relatively low site fidelity (Fretwell 1972; Walk et al. 2004; Fletcher et al. 2006). Such mobility could lead to multiple levels of selection (Heisler and Damuth 1987; Goodnight et al. 1992). For instance, the best breeding grounds may be settled by the most competitive males (e.g. the largest), while less competitive males may settle in poorer breeding habitats. This would result in low phenotypic variation within sites, but high phenotypic variation across sites. Female choice might then act within habitats, either on the same trait or on different traits than those selected for by male competition over territories. If selection occurs on multiple spatial scales within a broad landscape, then comparisons among relatively small burn plots may not capture the full effects of habitat variation on sexual selection. For instance, Svensson and Sinervo (2004) found variation in selection gradients for egg size in side blotched lizards (Uta stansburiana) depending on the spatial scale at which selection was measured. Similarly, sexual selection on male leg size and weight in a in golden orb-weaving spiders (Nephila plumipes) varied significantly between two sites, and in some instances was the opposite of that estimated for the population as a whole (Kasumovic et al. 2008). Thus patterns of selection may differ depending on the scale at which selection is measured. Given the propensity of male and female dickcissels to disperse long distances, the study of sexual selection in this species may benefit from a hierarchical approach (Heisler and Damuth 1987; Goodnight et al. 1992).

Conclusions

Dickcissels join a growing number of species with complex patterns of sexual selection on sexually dimorphic traits. A number of other studies have demonstrated that sexual selection can vary across years (lark bunting, Chaine and Lyon 2008), across populations (house sparrow, Anderson 2006), or possibly across the evolutionary history of a species (red winged blackbird, Westneat 2006). In the case of dickcissels, it is possible that human impacts on the environment have made a mess of selective processes. The challenge now is to untangle all of the different factors, both natural and anthropogenic, affecting sexual selection.

© Bridget F. Sousa 2012
Table 6.1. Sample sizes (number of males) and burn history for the sites included in this study. Burn interval for R20A (the reversal site) is presented as the burn interval pre-2000 followed by the burn interval initiated in 2000.

<table>
<thead>
<tr>
<th>Site</th>
<th>Burn Interval</th>
<th>Years included</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>2006</td>
</tr>
<tr>
<td>R20A</td>
<td>1, 20</td>
<td>37</td>
</tr>
<tr>
<td>2A</td>
<td>2</td>
<td>–</td>
</tr>
<tr>
<td>2D</td>
<td>2</td>
<td>–</td>
</tr>
<tr>
<td>4F</td>
<td>4</td>
<td>–</td>
</tr>
<tr>
<td>4B</td>
<td>4</td>
<td>–</td>
</tr>
<tr>
<td>10A</td>
<td>10</td>
<td>–</td>
</tr>
<tr>
<td>20C</td>
<td>20</td>
<td>–</td>
</tr>
<tr>
<td>1D</td>
<td>1</td>
<td>–</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td></td>
<td><strong>37</strong></td>
</tr>
</tbody>
</table>

Table 6.2. Pearson correlations among measures of dickcissel male body size. Pearson correlation coefficients are presented in the upper right diagonal and p-values are italicized in the lower left diagonal.

<table>
<thead>
<tr>
<th></th>
<th>Tarsus</th>
<th>Wing</th>
<th>Bill Depth</th>
<th>Bill Length</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tarsus</td>
<td>0.21</td>
<td>0.08</td>
<td>0.12</td>
<td></td>
</tr>
<tr>
<td>Wing</td>
<td>0.002</td>
<td>0.12</td>
<td>-0.03</td>
<td></td>
</tr>
<tr>
<td>Bill Depth</td>
<td>0.24</td>
<td>0.09</td>
<td>0.21</td>
<td></td>
</tr>
<tr>
<td>Bill Length</td>
<td>0.09</td>
<td>0.71</td>
<td>0.003</td>
<td></td>
</tr>
</tbody>
</table>
Table 6.3. Relationships between four measures of traits of male dickcissels and each of two components of mating success. Effect sizes ± SE, Wald X² and p-values are from a generalized linear model including trait value, year, and their interaction.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Paternity</th>
<th>Harem Size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tarsus</td>
<td>0.05 ± 0.13</td>
<td>0.05 ± 0.13</td>
</tr>
<tr>
<td>Bib Size</td>
<td>-0.11 ± 0.32</td>
<td>0.04 ± 0.11</td>
</tr>
<tr>
<td>Frequency Range</td>
<td>-0.33 ± 0.12</td>
<td>0.47 ± 0.29</td>
</tr>
<tr>
<td>Hue</td>
<td>0.47 ± 0.42</td>
<td>0.66 ± 0.33</td>
</tr>
<tr>
<td>Hu</td>
<td>0.08 ± 0.24</td>
<td>0.04 ± 0.40</td>
</tr>
<tr>
<td>Frequency Range</td>
<td>0.12 ± 1.02</td>
<td>0.11 ± 0.33</td>
</tr>
<tr>
<td>Tarsus</td>
<td>0.95 ± 1.11</td>
<td>0.80 ± 1.18</td>
</tr>
<tr>
<td>Paternity</td>
<td>0.12 ± 0.49</td>
<td>0.11 ± 0.24</td>
</tr>
<tr>
<td>Harem Size</td>
<td>0.12 ± 0.13</td>
<td>0.11 ± 0.09</td>
</tr>
</tbody>
</table>

Effect df = SE X² p df effect ± SE X² p df
Table 6.4. Mean ($\bar{x}$) and standard deviation ($\sigma$) for fitness and male traits for the four years of the study. The test statistic, degrees of freedom and p-value for tests of homogeneity of variance are also presented. I mean centered harem size and frequency range within each year for *post hoc* analysis. Therefore the standard deviation and test statistics for these standardized scores are presented parenthetically after the $\sigma$ for non-standardized values.

<table>
<thead>
<tr>
<th>Fitness Component</th>
<th>$\bar{x}$</th>
<th>$\sigma$</th>
<th>F</th>
<th>p</th>
<th>df</th>
</tr>
</thead>
<tbody>
<tr>
<td>Harem Size</td>
<td>2006</td>
<td>1.11</td>
<td>1.10  (0.99)</td>
<td>0.83 (2.73)</td>
<td>0.48 (0.04)</td>
</tr>
<tr>
<td></td>
<td>2007</td>
<td>1.47</td>
<td>0.93  (0.64)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2008</td>
<td>1.48</td>
<td>0.97  (0.61)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2009</td>
<td>1.87</td>
<td>1.15  (0.61)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Paternity</td>
<td>2006</td>
<td>0.50</td>
<td>0.37</td>
<td>0.69</td>
<td>0.56</td>
</tr>
<tr>
<td></td>
<td>2007</td>
<td>0.65</td>
<td>0.35</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2008</td>
<td>0.60</td>
<td>0.40</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2009</td>
<td>0.70</td>
<td>0.32</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tarsus (mm)</td>
<td>2006</td>
<td>23.3</td>
<td>0.60</td>
<td>0.42</td>
<td>0.74</td>
</tr>
<tr>
<td></td>
<td>2007</td>
<td>23.1</td>
<td>0.73</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2008</td>
<td>23.1</td>
<td>0.62</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2009</td>
<td>23.2</td>
<td>0.64</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bib Size (mm$^2$)</td>
<td>2006</td>
<td>110.6</td>
<td>57.8</td>
<td>1.52</td>
<td>0.21</td>
</tr>
<tr>
<td></td>
<td>2007</td>
<td>118.9</td>
<td>48.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2008</td>
<td>110.9</td>
<td>45.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2009</td>
<td>95.5</td>
<td>37.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hue (nm)</td>
<td>2006</td>
<td>128.8</td>
<td>6.2</td>
<td>0.28</td>
<td>0.84</td>
</tr>
<tr>
<td></td>
<td>2007</td>
<td>130.1</td>
<td>6.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2008</td>
<td>130.5</td>
<td>6.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2009</td>
<td>128.4</td>
<td>7.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Frequency Range (hz)</td>
<td>2006</td>
<td>4691.8</td>
<td>304.9 (0.07)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2007</td>
<td>4708.3</td>
<td>378.9 (0.08)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2008</td>
<td>4852.8</td>
<td>343.3 (0.07)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2009</td>
<td>4616.8</td>
<td>573.6 (0.12)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 6.5. Mean (\(\bar{x}\)), standard deviation (\(\sigma\)), and tests of homogeneity of variance in fitness components and male traits across the two burn regimes: frequently burned (burned) and burned no more than once in four years (unburned).

<table>
<thead>
<tr>
<th>Fitness Component</th>
<th>(\bar{x})</th>
<th>(\sigma)</th>
<th>F</th>
<th>p</th>
<th>df</th>
</tr>
</thead>
<tbody>
<tr>
<td>Harem Size</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>burned</td>
<td>1.75</td>
<td>0.96</td>
<td>0.02</td>
<td>0.89</td>
<td>1,94</td>
</tr>
<tr>
<td>unburned</td>
<td>1.44</td>
<td>1.07</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Paternity</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>burned</td>
<td>0.64</td>
<td>0.35</td>
<td>0.92</td>
<td>0.34</td>
<td>1,53</td>
</tr>
<tr>
<td>unburned</td>
<td>0.60</td>
<td>0.40</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tarsus (mm)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>burned</td>
<td>23.1</td>
<td>0.63</td>
<td>0.01</td>
<td>0.92</td>
<td>1,119</td>
</tr>
<tr>
<td>unburned</td>
<td>23.2</td>
<td>0.63</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bib Size (mm(^2))</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>burned</td>
<td>108.0</td>
<td>42.9</td>
<td>0.01</td>
<td>0.91</td>
<td>1,118</td>
</tr>
<tr>
<td>unburned</td>
<td>105.3</td>
<td>43.6</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hue (nm)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>burned</td>
<td>128.2</td>
<td>6.6</td>
<td>0.08</td>
<td>0.78</td>
<td>1,96</td>
</tr>
<tr>
<td>unburned</td>
<td>131.8</td>
<td>7.0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Frequency Range (hz)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>burned</td>
<td>4804.3</td>
<td>555.0</td>
<td>2.41</td>
<td>0.13</td>
<td>1,65</td>
</tr>
<tr>
<td>unburned</td>
<td>4796.8</td>
<td>345.0</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 6.1: Selection gradients ($\beta$) ± standard error (SE) are plotted for each year (black circles) and for all years combined (gray diamonds). $\beta$ is the slope of the linear regression of relative reproductive success on standardized trait values. Left panels show $\beta$ ± SE for traits via social mating success. Right panels show $\beta$ ± SE for traits via within pair paternity. Wald $X^2$ and p-values are from the generalized linear model including trait value, year, and their interaction.
Figure 6.2: Selection gradients ($\beta$) ± standard error are plotted for each burn regime. Panels on the left show selection gradients for traits via social mating success. Panels on the right show $\beta$ ± SE for traits via within pair paternity. Wald $X^2$ and p-values are from the generalized linear model including trait value, year, burn regime, and the interaction of trait and burn regime (trait * burn).
Chapter 7

Conclusions and Future Directions

Sexual dimorphism is generally thought to be the result of and maintained by sexual selection (Darwin 1871; Andersson 1994). Three conditions must be met for selection to act on male phenotypes. There must be (i) variance in male phenotype, (ii) variance in male mating success, and (iii) a process creating covariance between male traits and mating success (Andersson 1994). In organisms with extrapair fertilizations, total variance in male mating success includes variance in social mating success, extrapair mating success, and twice the covariance between the two. My research showed that extrapair paternity was common in dickcissels, and that patterns of social and extrapair mating success were positively associated. I also found significantly repeatable variation in four sexually dimorphic male ornaments (body size, bib size, yellow plumage and song). Despite conditions suggesting strong, active sexual selection in this species, sexual selection was weak and inconsistent in both magnitude and direction. This remained true across all four years of my study. Furthermore, differences in management across sites had little effect on mating patterns or sexual selection in this species. Nevertheless, environmental conditions clearly have some influence on selection, as evidenced by significant temporal variation in selection gradients.

Several themes emerged from my analysis of dickcissel mating patterns and sexual selection. First, patterns of male and female settlement could lead to multilevel sexual selection. Second, the spatial scale across which dickcissels assess potential partners may be larger than previously considered in the literature. If so, then sexual selection and the ecology of mate choice must be considered at a much larger scale than normally examined. Third, agricultural practices on both the breeding and wintering grounds could disrupt the mechanisms linking male traits with reproductive success.

Hierarchical Sexual Selection

The results of my research indicate that sexual dimorphism in dickcissels is not maintained by moderate or strong directional selection, despite widespread predictions to this effect (Lande 1980; Andersson 1994). One way dimorphism may be maintained is if sexual selection acts at multiple hierarchical levels. Hierarchical selection extends the analysis of sexual selection to multiple levels of structured populations (Heisler and Damuth 1987; Goodnight et al. 1992). This approach can detect patterns of selection that are not evident when a single selection gradient is measured for all individuals. For instance, studies of side-blotched lizards (*Uta stansburiana*) found weak stabilizing selection for egg size for the population as a whole (Sinervo et al. 1992; Svensson and Sinervo 2000), but an analysis of selection at the local (neighborhood) level revealed strong directional selection that varied among neighborhoods. This variation may be important in maintaining genetic variation in fitness-related traits in this population (Svensson and Sinervo 2004).

A similar hierarchical approach may be useful in explaining the maintenance of dimorphic traits in dickcissels. Males arrive first on the breeding grounds and compete for territories. Females arrive after males and settle on male territories to breed (Temple 2002). Male competition for territories in high quality breeding sites could lead to the
assortment of males among habitats, with highly competitive males settling in the best habitats and less competitive males settling in marginal habitats or failing to gain territories altogether. If male ornaments are associated with competitive ability and territory acquisition, then groups of males in high quality habitat will have better ornaments than groups of males in low quality habitat. Greater female settlement and productivity in high quality habitat would then lead to selection for male ornaments associated with territory acquisition in these habitats.

This hierarchical approach to sexual selection has been applied primarily in the plant and insect systems; however, this approach would also be valuable in avian systems. It is particularly relevant in highly fragmented habitats like the tallgrass prairie. While my study did not find differences in male phenotypes among burn regimes, the study area was relatively small and restricted to ungrazed native prairie. Differences among burn regimes within native prairie may be smaller than differences between native prairie and other potential breeding areas. Patches of native prairie, fallow fields, hay fields and heavily grazed pasture all vary in their suitability for nesting birds. Zimmerman (1982) showed that dickcissels settled fallow fields earlier and more densely than native prairie. Polygyny was also higher in fallow fields than in prairie. An examination of male traits in each of these habitats would provide valuable insight into the mechanisms maintaining sexual dimorphism in dickcissels. This approach may also prove useful in studies of other sexually dimorphic species for which little or no sexual selection has been detected (e.g. red-winged blackbirds, Westneat 2006).

The Scale of Mating Decisions

An emerging theme from my research is importance of scale in assessing mating patterns and sexual selection. The spatial scale over which dickcissels choose their mates has important implications for a number of aspects of the study of avian mating patterns, including social mating patterns, sexual selection and the influence of management practices on selection and mating patterns.

In most studies of avian mating there is an implicit assumption that females settling within a study area choose their social mates from among the territorial males within that area. This might not be true for female dickcissels, which have low site fidelity (Appendix 5) and frequently move long distances between nesting attempts (Walk et al. 2004). Instead, females might assess potential breeding sites and social mates on a much larger spatial scale than typically considered. If so, then it is perhaps not surprising that selection gradients for male social mating success were weak and variable. Such results would be expected if only a portion of potential mates were compared.

Tracking the movements of females will help determine the scale at which females compare mates. While some attempts have been made using radio tracking, they rely on capturing females that have already arrived on the breeding grounds and do not track females that leave the local population (e.g. Bensch and Hasselquist 1992). It is not clear that females arriving in a breeding population have not already assessed and rejected males in another population. This possibility calls for the use of tracking devices that can be detected at greater distances or that report detailed location data remotely (e.g. GPS tracking of albatross and whales). Unfortunately the size of such devices limits their
utility. Nevertheless, such studies are plausible for larger birds and could provide valuable insight into mate choice and sexual selection in birds.

Another consequence of broad scale social mate evaluation is that the potential effects of habitat on mating patterns must be evaluated across a much larger area than typically considered. Emlen and Oring (1977) hypothesized that polygyny would be more common in heterogeneous habitats than in homogenous habitats. They did not, however, specify the spatial scale over which habitat heterogeneity would influence polygyny. Most authors implicitly assumed that heterogeneity has a local effect. Indeed, a number of studies have found that polygynous males defended territories with more resources than monogamous males within a population (e.g. Verner 1964; Willson 1966; Zimmerman 1966; Searcy and Yasukawa 1995, but see Wittenberger 1976). Nevertheless, comparisons of territory quality between populations are rare and measurements of resource heterogeneity even rarer. Indeed, I can find no other study that measured variance in resource availability across different habitats. Thus, Emlen and Oring’s prediction that areas with greater variance in resource distribution should lead to greater variance in reproductive success is untested above the local level. Clearly a broader scale approach is warranted, especially in mobile species with the potential to evaluate nesting sites across broad spatial scales.

Agriculture and Mechanisms of Sexual Selection

The tallgrass prairie has experienced extreme changes over the past century. High cattle stocking rates and frequent haying could result in more frequent movements and lower site fidelity among both female and male dickcissels. Indeed, male return rates were much lower in frequently mowed alfalfa fields (Igl 1992) than in undisturbed fields (Zimmerman and Finck 1989). Several authors have observed marked increases in female and male dickcissel densities on undisturbed patches that coincided with local haying (Taber 1947; Schartz and Zimmerman 1971; Igl 1992). Moreover, breeding dickcissels may be displaced multiple times, since fields are hayed up to four times over the course of the breeding season (Igl 1992). Thus, current agricultural practices probably displace breeding dickcissels far more frequently that historic grazing and fire (Rowe 1969; Hulbert 1973; Wright and Bailey 1982; Knapp et al. 1998b). This could have interesting effects on sexual selection, both for males and for females.

Among females, displacement from agricultural activity could contribute to large scales of social mate evaluation or in a relaxation of female choice criteria. The former is expected when females are displaced early in the season. The latter may occur any time females are displaced from their breeding site. A relaxation of female choice after displacement could help explain the weak and variable sexual selection I detected in dickcissels. A comparison of selection gradients before and after haying in the region would help address whether this is indeed occurring. In order to fully address whether selection is influenced by agricultural activities in the above manner, detailed data on the timing of local and regional haying activity would be required. In addition, tracking displaced females would be necessary to determine the effects of displacement on female choice; however, such efforts may be difficult given the long distances females frequently travel after a failed nesting attempt (Walk et al. 2004).

Among males, agricultural practices could weaken sexual selection occurring through male-male competition. Competition for high quality territories early in the
breeding season is one mechanism that could produce an association between male traits and reproductive success (Darwin 1871; Rohwer 1977). Indeed, a number of studies have demonstrated positive associations among male arrival date, territory quality and male ornaments (Howard 1974; Rohwer 1982; Warner and Schultz 1992; Andersson 1994; Hasselquist 1998; Santos et al. 2011). Displacement of males by agricultural practices could disrupt such a relationship. High quality males may be forced to settle unoccupied, lower quality territories or to compete with resident males for occupied, high quality territories. Residents may have an advantage in territorial disputes (Stamps 1987; Deverill et al. 1999), so the association between male quality and territorial quality may weaken or even break down altogether after widespread haying.

Agricultural development on the dickcissels’ wintering grounds could also disrupt the mechanisms linking male ornaments to mating success. Dickcissels winter primarily in the grasslands of Venezuela. Within the past hundred years, much of these grasslands have been converted to cereal grain crops. Agricultural development has changed both the diet of wintering dickcissels and the size of their aggregations (Basili and Temple 1999a). Cereal grains now constitute more than 75% of the dickcissels’ winter diet (Basili and Temple 1999a). This change in diet could disrupt mechanisms linking male quality and ornaments (chapter 6). Agricultural development has also led dickcissels to form larger aggregations and concentrate into a much more limited geographic region than they did historically (Levey and Stiles 1992; Basili and Temple 1999a). This change in flock size could alter social interactions among males. Since social interactions are thought to influence the development and utility of badges of status (Rohwer 1975, 1977), recent changes in flock dynamics could alter sexual selection on badges of status.

Final Conclusions

My research has shown that sexual selection can be influenced by ecological factors. These factors can be stochastic in nature (e.g. weather patterns) or largely controlled by human agricultural and management decisions. In highly mobile organisms, the effects of ecological variables on mating patterns and sexual selection may not be apparent on the spatial scales normally examined by researchers. Indeed, the very practices we wish to evaluate may increase the distances organisms move over the course of the breeding season. A larger spatial scale of analysis will be necessary to tease apart the short and long term effects of management practices on mating patterns and sexual selection. The integration of local scale mating decisions with landscape level habitat selection and movement patterns will be necessary to fully understand mating and selection.
Appendix 1

Assumptions of Hamilton and Zuk

Hamilton and Zuk make four key assumptions about the nature of the relationships between hosts and parasites. First, coadaptational cycles must exist between hosts and parasites. These cycles must be long enough to allow hosts to develop resistance to the parasite, but not so long that variation in host resistance declines to near fixation of a particular resistance allele. Extremely short cycles would also render choice for resistance genes impossible, as parasites would evolve ways to escape host defenses before genes that confer resistance could benefit a female's offspring. Cycles of the appropriate periodicity, however, ensure a continual source of variation in fitness among different resistance genotypes.

Second, the effects of the pathogen on the host must be non-lethal and debilitating, but persist in chronic form in survivors. If the pathogen is highly lethal, then sexual signals are not needed to discriminate between resistant (living) and susceptible (dead) animals. The chronic persistence of the disease or its effects is necessary to maintain the signal's honesty after acute infection; if an animal recovers completely, then it no longer honestly signals its genetic resistance to disease. However, it is not necessary for the parasite itself to persist in the animal if its effects on the animal are long lasting.

Third, exposure to the parasite must be fairly uniform. Resistant animals are indistinguishable from those that were never exposed to the parasite. Unless behaviors that avoid exposure are heritable (and may thus be broadly accepted as resistance genes, albeit by a different mechanism of resistance), exposure must be widespread and uniform for this system to work.

Fourth, disease resistance must be heritable. Hamilton and Zuk envisioned a large class of genes that confer resistance or susceptibility to parasites. The genes of the major histocompatibility complex (MHC) fit this assumption. MHC genes are known to confer resistance to particular pathogens. Furthermore, tradeoffs in resistance to particular pathogens or pathogen strains is known to tradeoff with susceptibility to others, setting the scene for cycles of the type outlined above (Apanius et al. 1997).

These assumptions are generally ignored in the literature. Indeed, there is a need for studies that investigate in greater detail the cyclic relationship between parasites and their hosts and the specific effects of parasites on host life history. However, for the purpose of this review, I will assume that these conditions do exist.
Appendix 2

Measures of Song

Basic Song Vocabulary (Figure A2.1)

note/element: The simplest individual, contiguous sound produced in song.
syllable: A group of elements repeated together in a regular pattern.
phrase/motif/strophe: A sequence of syllables repeatedly occurring in song. The word "song" is also used in this context.
song bout: A continuous period of singing, separated from other song bouts by non-singing behavior.

HVC (nucleus hyperstriatalis ventrale, pars caudale, high(er) vocal center, or HVc)*1: codes for motor unit sequences, such as syllables, highly involved in song learning and production.

RA (nucleus robustus archistriatalis)*2: codes for subsyllable components, probably connects the forebrain with motor areas involved in singing, involved in song learning and production.

Song Complexity

repertoire size: The total number of unique syllables or songs sung by an individual bird. The use of syllables versus songs to calculate repertoire size is species specific. For instance, some bird species have only one song type, with varying numbers of syllables.
copy accuracy: How similar a learning bird's song is to his tutor.
song sharing: A measure of the similarity of a bird's songs or song syllables to those of a neighboring bird. Also measured as the proportion of a bird's repertoire that it shares with a neighbor.
song switching/versatility: The frequency with which a male changes the song, syllable, or phrase he is singing (whichever is the repeated unit). Some males may repeat a phrase many times before switching to another, while others switch phrases frequently.

Song Output (Figure A2.2)

song rate§: The number of songs a bird sings per unit time.
percent time singing: The total amount of time a bird spends singing (versus other activities, such as resting or foraging), summed over a period of observation. Usually used in time budgets and behavioral studies.
song length§: Length of a song measured in seconds or milliseconds.
intersong interval§: The amount of time between the end of one song and the beginning of the next.
number of elements per song§: The average number of elements produced per song. Can also be measured for the number of syllables or phrases per song, number of elements per syllable, etc.
**Amplitude**

amplitude: The loudness of a song, measured in decibels.

percentage peak performance\(^2\): Generally used as a measure of the amount of time a bird spends producing song at high amplitudes. Calculated from the Raven Song Analysis Software's "band limited energy detector," which can be used to detect areas in a song spectrogram that are above a user specified percentage (usually 20%) of the highest amplitude produced by an individual bird.

**Frequency (Figure A2.3)**

high frequency: The highest frequency measured. Measured either for an entire repertoire or separately for different elements or phrases.

low frequency: The highest frequency measured. Measured either for an entire repertoire or separately for different elements or phrases.

frequency bandwidth: The frequency range of a bird's song (high frequency – low frequency).

frequency of peak amplitude/power: The frequency of the loudest sound a bird produces in its song.

**Special Syllables**

trill rate/frequency bandwidth: Frequency bandwidth trades off with trill rate, such that large bandwidths are harder to produce quickly.

special syllables: The inclusion of particular syllables in a repertoire that are inherently difficult to produce.

* Nomenclature for this nucleus has changed over the years, as more information about it became available. Newer nomenclature proposed that the abbreviation 'HVC' be kept, as it was already widely in use. See Margoliash et al. 1994 or Brenowitz et al. 1997 for a discussion of HVC nomenclature.

§ These measures are also commonly computed for notes, syllables, and phrases. The definition remains the same, but the variable "song" is replaced with one of the other components of song. For example, element rate is the number of elements sung per unit time.

1. Gil and Gahr 2002
2. Forstmeier et al. 2002
Figure A2.1. Some basic song vocabulary illustrated above on a spectrogram from the dickcissel (Spiza americana).
Figure A2.2: Spectrogram of dickcissel song showing some song output variables.
Figure A2.3: Dickcissel spectrogram illustrating song frequency variables
Appendix 3

Design and effectiveness of a novel trap for capturing nesting songbirds
Bridget F. Sousa and Sarah L. M. Stewart

Capturing songbirds at their nests is an essential part of many behavioral studies, but can be time-consuming and disruptive to both birds and their nest sites. Traps have been designed to capture some species of waterfowl, shorebirds, and cavity-nesting species at their nests (e.g. Coulter 1958; Dietz et al. 1994; Friedman et al. 2008), but few have been designed to capture songbirds at open-cup nests. Potter traps have been modified to capture tree-nesting songbirds (Putnam 1949; Stutchbury et al. 2007), but they can be too heavy to capture birds with cup nests attached to herbaceous vegetation or saplings. In addition, many species of songbirds use a variety of nest substrates, and Potter traps and larger wire-cage traps designed to enclose nests and the surrounding vegetation (e.g. Newbrey and Reed 2008) are difficult to quickly modify for use with such species.

Placing mist nets around a nest (e.g., in a V formation; sensu Martin 1969) is an alternative to cage traps. However, setting up and checking mist nets may result in trampled vegetation near nests, potentially increasing predation risk either by making nests more accessible or by providing cues concerning nest locations to predators (Bowen et al. 1976). Using mist nets is also time consuming, can be difficult in dense vegetation, and may be impractical in windy habitats such as grasslands.

Traps constructed from mist-net material would be light in weight and less disruptive to surrounding vegetation. For example, Nolan (1961) described a horizontally oriented hoop net, similar to a butterfly net, for capturing nesting birds in early successional habitats. However, Nolan’s (1961) hoop net must be monitored at close range, cannot be used for ground-nesting birds, and relies on target birds flushing in a specific direction to be successful. Swanson and Rappole (1994) found that multiple capture attempts were frequently required because birds often failed to flush in the direction of the net.

We had limited success capturing nesting dickcissels (Spiza americana) using mist nets set in a V formation. Nets were highly visible in the open grassland habitat where dickcissels nested, a problem exacerbated by frequent windy conditions. Moreover, setting up nets left 6-m-long swaths of trampled vegetation near nests. Because of these difficulties, we designed a cylindrical mist-net trap for capturing female dickcissels that were feeding nestlings. We subsequently used the trap to capture female indigo buntings (Passerina cyanea) that were also feeding nestlings. Our nest trap is simple to construct and can be adapted to capture birds at nests in herbaceous vegetation, shrubs, and saplings.

Methods
Trap materials and construction

Our trap had four components: a hoop, three stakes, a section of mist net, and three twist ties. We constructed the trap using a 48-cm-diameter metal hoop obtained from a craft store (Hobby Lobby, sku#181537). Quilting hoops and tomato cages are widely available alternatives. We used three threaded rods (1 m x 6.5 mm) as stakes to
support the hoop. Two pieces of netting were cut from a mist net: a circular piece 4 cm wider than the diameter of the hoop and a rectangular piece three trammels high (~2.0 m) and 30 cm longer than the circumference of the hoop (~1.8 m long). We removed trammel lines from all but the bottom of the rectangular piece of netting.

We attached the circular piece of net to the hoop to form the top of the trap. The rectangular piece of net was then sewn to the hoop and the open edges stitched together to produce a cylinder. We then threaded two trammel lines through the net at ~50% and 75% of the height of the cylinder to create trammels for the modified net (Figure A3.1). All knots were secured with a small drop of glue. We sometimes used a drawstring slide to adjust tension on the trammel lines. When not in use, the net was folded into the hoop and stored and transported in a pillowcase.

**Trap deployment**

We deployed our trap using one of two methods, depending on nest height and substrate. For nests < 1 m above ground in grasses, forbs, or small shrubs, we placed three stakes equidistant around the nest. We then secured the rim of the hoop to the stakes using twist ties, and loosely draped the cylinder of netting around the outside of the stakes so it enclosed the nest, nest substrate, and some of the surrounding vegetation. The bottom of the net was positioned as close to the ground as the vegetation would allow (usually 5–20 cm from the ground). Depending on the nest substrate and the behavior of targeted females, we sometimes raised the netting to encourage the bird to enter the nest from below (Figure A3.2). We generally positioned the trap so that the top was at least 10 cm above the nest, and the bottom was at least 3 cm below the nest’s rim.

For nests higher than 1 m and in shrubs, tall forbs, or tree saplings, we used a second method of deployment. For most of these nests, we could attach the hoop directly to forbs or woody vegetation around each nest. When this was not possible, we used mist-net poles (1.8 m) as stakes. Longer poles could also be used for nests >1.7 m above ground. When a nest substrate was too large to fit inside the nest trap, we were often able to isolate a few branches that supported the nest from the rest of the plant and enclosed them within the nest trap, taking care not to damage the plant. Because females nesting above 1 m were often reluctant to approach their nests from below, we created a gap in the mist netting at nest height by taking the bottom of the net directly below the nest, pulling it up to nest height, and securing the gathered netting to any available anchor with twist ties (Figure A3.3). Females entered these altered traps most readily when a natural perch near the trap entrance allowed them to land before approaching the nest. Netting at the bottom of the trap was sometimes gathered together below nests and secured with twist ties to prevent females from escaping through the bottom of the trap. We typically did this when a nest was >1.5 m above ground and when vegetation in the bottom third of the net was sparse, allowing females to easily fly out through the bottom.

Females were captured inside the nest trap when they attempted to leave nests and were caught in the netting. Most birds were captured in the netting at or slightly above nest height. Entangled birds were gently secured in hand before lifting the netting to disentangle them from the inside.
Capturing Dickcissels

We studied dickcissels from May through September, 2006 to 2009 at the Konza Prairie Biological Station near Manhattan, Kansas. Most nests were in small, shrub-like leadplants (Amorpha canescens) and New Jersey tea (Ceanothus americanus). Grasses, forbs, tree saplings, and large shrubs (primarily dogwood, Cornus drummondii) were also common nesting substrates. Nests varied in height from 5 to 155 cm ($\bar{x} = 30 \pm 25$ [SD] cm) above ground, and nesting substrates ranged from 15 to 254 cm ($\bar{x} = 79 \pm 38$ cm) in height.

All capture attempts were made during the latter part of the nestling period (4-12 days post hatching) to minimize chances of nest abandonment. Deployment method one was used unless nests were more than 1 m above ground or were in large shrubs or saplings.

Deployment of the nest trap took 2 to 5 min, depending on the complexity of the nest substrate and surrounding vegetation. The trap was positioned over nests when females were absent, then monitored from a distance of ~50 to 100 m with binoculars. Because of the open habitat, we were able to observe female dickcissels returning to the vicinity of nests, but vegetation sometimes obscured their entry into the trap. In these cases, cues used to indicate that a female had entered the trap included movement of vegetation within the trap or no sightings of a female that had been observed approaching a nest for >5 min. Once a female entered the trap, we walked to within ~10 m, then ran toward the nest to flush the female into the net.

Once we captured a female, the trap was removed. Removal took ≤1 min.

Trapping was attempted from ~1 hr before dawn until 20:00, with most attempts between 05:30 and 14:00. The duration of trap deployment varied, but was usually 20 to 60 min. We generally continued trapping attempts as long as a female continued to attempt to enter the nest trap (≤15 min between attempts). However, attempts were terminated when females showed no indication that they would return to the nest or when temperatures became too hot (~35°C) to safely trap birds.

Capturing Indigo Buntings

Indigo buntings (~15 g) were studied from May to August, 2010 at the Miller-Welch Central Kentucky Wildlife Management Area in Madison County, Kentucky. We used the nest trap at nests in a variety of tree saplings, e.g., sweet gum (Liquidambar sp.) and dogwood, and forbs, e.g., goldenrod (Solidago sp.) and ragweed (Ambrosia artemisiifolia). Nest height ranged from 53 to 90 cm ($\bar{x} = 70.5 \pm 10.9$ cm) above ground and the height of nest substrates ranged from 92 to 250 cm ($\bar{x} = 163 \pm 38$ cm).

Female indigo buntings would not approach nests when we were nearby so we could not observe them returning to nests after trap deployment. Therefore, we attempted to capture females during a 5-min period immediately after trap deployment and then, if unsuccessful, during an ~10-min period after nestlings were removed from a nest to be banded. If the female had still not been captured, we returned nestlings to the nest checked it every 5-min until the female was either captured or the trapping attempt was abandoned after 60 min. At the end of each period or with each nest check, we quickly walked toward the trap in an attempt to flush females into the netting.
Results
Most attempts (167 of 196, or 85%) to capture female dickcissels were successful. Attempts failed primarily because females would not approach the trap (N = 28, or 14.3%). Five of 167 females (3.0%) deserted nests after being trapped, all later in the breeding season (after 21 July). Two nests (1%) were predated by snakes during a trapping attempt. No females or nestlings were injured during trapping attempts.

We attempted to catch 15 female indigo buntings with the nest trap and captured nine (60%). Before 10 July 2010, only one of four attempts was successful, probably because we used deployment method one. We subsequently switched to method two and our success rate was 73% (8 of 11 females).

Female buntings were captured during all three trapping periods described previously, with one captured during the first phase, two during the second phase, and six during the last phase (i.e., after each brood had been returned to its nest). Only one female indigo bunting abandoned her nest after being captured, and this occurred near the end of the breeding season (mid-August). No nests were predated and no buntings were injured during trapping attempts.

Discussion
We captured 85% of targeted female dickcissels and 60% of targeted indigo buntings. Our success rate for indigo buntings improved to 73% using deployment method two. These success rates are comparable those reported previously. Using Nolan’s (1961) hoop net, Swanson and Rappole (1994) captured 76 to 82% of targeted white-winged doves (Zenaida macroura). Using a cage trap they designed, Newbrey and Reed (2008) captured 83% of targeted female yellow-headed blackbirds (Xanthocephalus xanthocephalus).

Few female dickcissels and indigo buntings abandoned nests after being captured in our nest trap. Similarly, only 3% of female red-winged blackbirds (Agelaius phoeniceus) abandoned nests after being trapped with Potter traps (D. Westneat, unpubl. data) and 3% of white-winged doves abandoned nests after being captured in Nolan’s hoop net (Swanson and Rappole 1994). All nest desertions in our study occurred late in the breeding season. Late season nests are often less successful due to seasonal decreases in food supply and increased energetic demands on adults imposed by the onset of molt (Siikamaki 1998). Such factors may increase the likelihood of brood abandonment after disturbance.

We did not attempt to catch females during incubation due to the possibility of nest abandonment, and would advise other investigators to avoid trapping during incubation unless prior experience or data indicate that this is not a potential problem (e.g., yellow-headed blackbirds; Newbrey and Reed 2008). Because we found that female dickcissels and indigo buntings may abandon nests after trapping attempts late in the breeding season, investigators should also consider time within the breeding season before attempting to trap females at nests.

Our nest trap is lightweight, versatile enough for use in a variety of grassland and shrub habitats, and easily carried and deployed in the field. In addition, we believe our trap design could be modified to capture larger birds by increasing the size of the hoop and the mesh size of the netting. For species where both males and females provision nestlings, our trap would likely also be effective for capturing males at nests.
Figure A3.1. Diagram of the nest trap used to capture female dickcissels and indigo buntings, with trammels and hoop labeled.
Figure A3.2. The nest trap positioned over a “nest” using deployment method one, with the optional opening at the bottom right.

Figure A3.3. The nest trap deployed using method two. Twist ties are used to make an opening near a perch at nest height and to secure the net under the nest.
Appendix 4

Matlab Coding for Spectral Analyses of Yellow Feathers

% This file uses my own definitions of yellow and UV based on where curves
% start and end. Other color programs use the definitions for colors given
% by physics and Geoff Hill's 'Bird Coloration'. Color vision in birds is
% assumed to be 300-700nm.

variables = {'Tot Reflectance', 'UV Reflectance', 'UV Hue', 'peakUV', ...
'Yellow Reflectance', 'Yellow Hue'};
% creates a cell array with each title in a different cell--only way to get
% Matlab to export title in one cell instead of one letter per cell

column_names = {'1'; '2'; '3'; '4'; '5'; 'ave'};
ndata = xlsread...
(C:\Documents and
Settings\bs\Desktop\BS\Data_Analysis\AnalyzedColor\2006color\all_birds\93349_PXPB 
_female'); % gets data from an excel spreadsheet
[r, c] = size(ndata);
ndata(ndata<0)=0; % replaces all negative numbers in the matrix with

%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
% Total brightness, range = visual range of birds
Tot = find(ndata(:,1) > 300 & ndata(:,1) < 700);
t = numel(Tot);
TR = cumsum(ndata(Tot,:));
TR = TR(t,2:c); % report this number if DFW doesn't like the divide by number of
measures thing
TotR = TR./t; % take average of reflectance value
aveT = sum(TotR)/5; % takes average repeated measures
TotR = [TotR, aveT]; % makes vector of measures and their average

%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%%
% UV brightness
% find minimum from 425 to 475, use that number to define the end point of
% the UV curve

LowPt = find(ndata(:,1) > 425 & ndata(:,1) < 475); % finds data around area where UV
min occurs in all spectrograms
UVbright = zeros(1,5);
UV_AveBright = zeros(1,5);

for j = 2:6; % does UV 1 column at a time
    [umin, I] = min(ndata(LowPt, j)); % finds the minimum value within the above range in
each of the 5 measurements
    stuff = LowPt(I); % gets index for the minimum value (index relevant to ndata)
    stuff2 = ndata(stuff, 1); % gets wavelength at which min occur
uv = find(ndata(:,1) > 300 & ndata(:,1) < stuff2); %gets indexes for data in relevant range for UV
    u = numel(uv); %# elements in UV range
    sumUV = cumsum(ndata(uv,j)); %cumulative sum of column of interest in UV range
    k = j-1;
    UV_bright(k) = sumUV(u);
    UV_AveBright(k) = sumUV(u)/u;
end
UVbright_AVE = sum(UVbright)/5; %takes average
UV_AveBrightave = sum(UV_AveBright)/5; %takes average
UVbright = [UVbright, UVbright_AVE]; %sticks average at end of UV brightness matrix
-- uncorrected total UV brightness
UV_AveBright = [UV_AveBright, UV_AveBrightave]; %total UV brightness divided by number of measures taken

%--------------------------------------------------------------------------
%  UV hue, curve fit
UV_WL = zeros(1,5);
peakUV = zeros(1,5);
for j = 2:6;
    yWL = ndata(uv,j); %does each column of reflection values one at a time
    xWL = ndata(uv,1); %defines lambda values of UV range as x variable
    pWL = polyfit(xWL,yWL,2); %fits a binomial curve to above x and y variables
    qWL = polyder(pWL); %takes derivative of above polynomial
    UVmaxWL = roots(qWL); %finds lambda at 0 (max of binomial curve)
    UVmax = polyval(pWL,UVmaxWL); %finds value of reflectance at lambda using the equation for the line (not the actual data)
    k = j-1;
    UV_WL(k) = UVmaxWL; %records value at corresponding column in reporting matrix
    peakUV(k) = UVmax;
end
aveUV_WL = sum(UV_WL)/5; %takes average of measured max UV wavelengths
UV_WL = [UV_WL, aveUV_WL]; %appends ave. just calculated to end of reporting matrix
AVEpeakUV = sum(peakUV)/5;
peakUV = [peakUV, AVEpeakUV];
%--------------------------------------------------------------------------
%Yellow Brightness
%find minimum from 475 to 525 and use that to define start point of yellow
%curve.  Also use that point for start of algorithm to find the inflection
%point for yellow hue.
LowPt = find(ndata(:,1) > 475 & ndata(:,1) < 525); %finds data around area where Yellow min occurs in all spectrograms
Ymin = zeros(1,5);
Yel_bright = zeros(1,5);
Yel_AveBright = zeros(1,5);
for j = 2:6; % does Yel 1 column at a time
    [ymin,I] = min(ndata(LowPt,j)); %finds the minimum value within the above range in each of the 5 measurements
    stuff = LowPt(I); %gets index for the minimum value (index relevant to ndata)
    stuff2 = ndata(stuff,1); % gets wavelength at which min occur
    yel = find(ndata(:,1) > stuff2 & ndata(:,1) < 700); %gets indexes for data in relevant range for Yel
    y = numel(yel); %# elements in Yel range
    sumYel = cumsum(ndata(yel,j)); %cumulative sum of column of interest in Yel range
    k = j-1;
    Yel_bright(k) = sumYel(y);
    Yel_AveBright(k) = sumYel(y)/y;
    Ymin(k) = stuff2;  %creates vector of wavelengths at which min occurs for use in yellow hue measure
end

Yel_bright_AVE = sum(Yel_bright)/5;
Yel_AveBrightave = sum(Yel_AveBright)/5;
Yel_bright = [Yel_bright, Yel_bright_AVE]; %uncorrected
Yel_AveBright = [Yel_AveBright, Yel_AveBrightave];  %corrected for number of samples done

%--------------------------------------------------------------------------------------------------------------------------
%Yellow Hue
%calculates the slope of the line iteratively over 5 data points, with %overlapping ranges of points; then calculates the wavelength at which max %slope occurs (uses point at middle of range used to calculate slope. %Chose 5 because it is odd # (midpoint easy) and large enough %to avoid some of the random weirdness of the data, but small enough to %give decent precision.
%using Ymin from yellow brightness for min
%hue_y = zeros(1,5);
for j = 2:6;
    k = j-1;
    count = 0;
    yel = find(ndata(:,1) > Ymin(k) & ndata(:,1) < 600);
    a = numel(yel);
    yell = ndata(yel,:);
    b = a/5;
    b = round(b);
    b = b + 1; %the number of slope calculations will perform below
a = a-4; % prevents matrix from trying to calculate slope outside of yellow range (the
bb = aa+4 will push it past otherwise)
for aa = 1:5:a;
    count = count+1; % keeps track of which iteration of the loop I'm on -- used in
indexing slope reporting (where to put slope calculated in the array)
    x1 = yell(aa,1);  % wavelength at lower bound
    bb = aa+4;
    x2 = yell(bb,1);  % wavelength at higher bound
    dx = x2-x1;  % delta x (run)
    y1 = yell(aa,j);  % reflectance at lower bound
    y2 = yell(bb,j);  % reflectance at upper bound
    dy = y2-y1;  % delta y (rise)
    slope(count) = dy/dx;  % slope of line for given range this iteration
    cc = aa+2;  % midpoint on 10 wavelengths at which find slope
    huey(count) = yell(cc,1);  % wavelength at which slope occurs
end
[slopes, I] = max(slope);  % find max of slope vector
hue_y = huey(I);  % find wavelength at which max slope occurs and put it in the
vector
end
ave_huey = sum(hue_y)/5;
hue_y = [hue_y, ave_huey];

% Report Data to excel
result = [TotR; UV_AveBright; UV_WL; peakUV; Yel_AveBright; hue_y];
results = result';
summary = results(6,:);
summary = [93349, summary];
% write in column names for summary sheet by hand
xlsxwrite('C:\Documents and
Settings\bs\Desktop\BS\Data_Analysis\AnalyzedColor\2006my_chroma', results,
'93349', 'B2');
xlsxwrite('C:\Documents and
Settings\bs\Desktop\BS\Data_Analysis\AnalyzedColor\2006my_chroma', variables,
'93349', 'B1');
xlsxwrite('C:\Documents and
Settings\bs\Desktop\BS\Data_Analysis\AnalyzedColor\2006my_chroma', column_names,
'93349', 'A2');
xlsxwrite('C:\Documents and
Settings\bs\Desktop\BS\Data_Analysis\AnalyzedColor\2006my_chroma', summary,
'summary', 'A100');
% be sure to change name in: summary, all xlsxwrites
% also change "A2" in last xlsxwrite to next number to create a summary sheet.
% be sure to "clear all" between runs!
Appendix 5

Dickcissel demographic data

Introduction

Dickcissels are frequently a target of studies assessing the effects of grassland management on avian reproductive success (McCoy et al. 1999; Walk and Warner 2000; Dechant et al. 2003; Shochat et al. 2005; Churchwell et al. 2008; Sandercock et al. 2008). Despite such popularity, a number of basic demographic parameters are either unknown or poorly characterized for this species (Walk et al. 2004; Fletcher et al. 2006). In this appendix, I present demographic data obtained from a four-year study of marked individuals.

Methods

Field Site and General Methods

I studied dickcissels at the Konza Prairie Biological Station (hereafter “Konza”) located in Riley and Geary Counties, Kansas (approx. 39°05’N and 96°35’W) from 2006 to 2009. The KPBS is a 3,487 ha area of native tallgrass prairie with replicated variation in burn interval at the watershed level. I monitored dickcissel reproductive success in nine ungrazed watersheds within Konza (Table A5.1). These sites represent the full range of variation in burning interval available on Konza. Most watersheds were maintained at the same burn interval throughout Konza’s history. Two watersheds, R20a and R1a were part of a reversal experiment, wherein their burn interval was reversed beginning in 2000. Thus R1a was not burned until 2000, at which time annual burning was implemented and vice versa for R20a. In addition, an unplanned burned occurred on R20a in 2008.

I attempted to capture all males defending territories in each watershed included in the study in 2006, 2007 and 2009. In 2008, a subset of the males breeding in each watershed was captured, with an effort made to capture ~10 males per watershed. I trapped males on their territories using a mist net combined with a song playback and, occasionally, a male model. Upon capture, males were banded with a USGS aluminum band and a unique combination of three colored plastic bands. My assistants and I then monitored the reproductive success of banded males throughout the breeding season. We censused the banded males in each site approximately once each week. In all years but 2008, unbanded males were also noted in censuses.

My assistants and I located nests primarily by observing female behavior and occasionally by searching likely nesting locations. We then checked nests every three days until the nests either fledged or failed. If a nest was empty before chicks were old enough to fledge (~8-9 days old), I assumed it had been depredated. When chicks were old enough to fledge, I used parental behavior to determine whether the nest had fledged. Female dickcissels continue to feed fledglings and both parents actively defend the young in the vicinity of the nest for an extended period of time (Gross 1968; Temple 2002), so these activities were assumed to indicate that a nest had successfully fledged. I trapped females trapped at the nest during the nestling phase using a cylindrical nest trap (Sousa and Stewart 2011) and banded females in the same manner as males. Nestlings were banded with a single USGS aluminum band when at least three days old. Social fathers

132
were assigned to nests based on a combination of active nest defense, pairing behavior with female, and/or location of the nest within a male’s territory. I calculated the first egg date of each nest from by backdating from hatching date or laying rates, assuming a 12 day incubation period and one egg laid per day. When these dates were not known, the first egg date was determined by assuming the nest was six days old at the midpoint date of nest checks. For nests found after the clutch was completed, but depredated before hatching, the first egg date was calculated by assuming that the nest was six days old at the midpoint date of nest checks.

I examined whether burning regime influenced nest initiation using data collected in 2008 and 2009. Since females do not remain site faithful during the breeding season, I used the first egg date of the first nest initiated in each male’s territory to compare nest initiation across burn regimes. I included year as a fixed effect in the model examining the effects of burn regime on nest initiation date.

Dickcissels are the primary host of brown-headed cowbirds (*Molothus ater*) in Kansas (Rivers et al. 2010). Cowbirds frequently remove host eggs from the nests they parasitize. I therefore calculated dickcissel clutch sizes from unparasitized and parasitized nests separately. Since cowbirds can also negatively influence hatching success of host eggs (Hoover 2003; Jensen et al. 2005), I calculated brood sizes and hatching success rates separately for parasitized and unparasitized nests. Hatching success in the latter case was calculated from the dickcissel eggs present for the full incubation period.

**Nest Survival Analysis**

I examined the effect of burn regimes and year on nest survival using data from 2008 and 2009. Differences in nest survival were tested by examining support for a set of candidate nest survival models. First, preliminary models were constructed in Program MARK (White and Burnham 1999) to determine whether nest age, time in season, nesting stage, or year affected nesting success. Model fit was assessed using the Akaike Information Criterion adjusted for finite sample sizes (*AICc*, Hurvich and Tsai 1989). The terms of the best preliminary model were included in all subsequent models testing the effects burn interval on nest survival. A likelihood ratio test was conducted to determine whether these variables contributed significantly to daily nest survival rates.

**Statistics**

Means are presented ± standard error. Tests of the effects of burn regime on demographic variables were conducted in using a general linear model including the effects of year and burn regimes as class variables (PROC GLM). All statistical tests were conducted in SAS.

**Results**

Over the four years of this study I banded 224 male and 179 female and 395 nestling dickcissels. I also found and monitored a total of 499 nests.

**Return Rates.** Dickcissels did not frequently return to the same breeding grounds in subsequent years. The proportion of males returning each year varied to some degree (Table A5.2). Over the four years of the study, male return rates were 33%. The
probability that a male returned the following breeding season was positively affected by his harem size (logistic regression effect = 0.90 ± 0.37, $X^2 = 6.00, p = 0.01$), but was not influenced by the proportion of nests fledged on his territory (logistic regression effect = -1.72 ± 1.15, $X^2 = 2.23, p = 0.13$). Female return rates were low, with only 15.5% returning to breed in subsequent years. Females that successfully fledged young were no more likely to return the following year than unsuccessful females (logistic regression effect = 0.03 ± 0.15, $X^2 = 0.04, p = 0.85$).

Fledglings rarely returned to the site from which they fledged. I banded 325 nestlings that survived to fledge. Only two of these fledglings returned to the study site in subsequent years: one male and one female. Both birds were fledged by the same male. The female fledged in 2006 and the male in 2008. The returning female attempted two nests in 2007 which were depredated during incubation. The returning male unsuccessfully attempted to defend form a territory in his first year, but returned the following year and was observed defending a territory on the watershed from which he fledged.

Dickcissel return rates may be influenced by burn management. In 2008 I banded and monitored 11 males in an annually burned watershed and 15 males in an unburned watershed. In the following year, 8 (72%) of the males banded in the annually burned watershed returned to breed in that site. In contrast, 7 males (44%) banded in the unburned watershed returned the following year. Female return rates were also higher in the annually burned site. Five of eight females (63%) banded in 2008 returned to nest in the annually burned watershed. Only two of six females (33%) banded in the unburned watershed returned to nest there in 2009.

Nests

I found and monitored 532 nests over the four years of this study. Full data was not available for all nests (e.g. some nests were found soon after depredation), so sample sizes vary among analyses. In all years, nesting began in late May and peaked in June and July (Figure A5.1). In the two years with the highest rainfall (2007 and 2008) nest initiation continued into late August, while no nests were initiated in August in 2006 and 2009. Nesting began earliest in annually burned sites and latest in unburned sites. Sites burned at 2 and 4-year intervals had similar, intermediate initiation dates (GLM effect: annual = -20.3 ± 4.4, biennial = -13.5 ± 5.1, quadrennial = -12.8 ± 5.4, $F_{3,78} = 5.13, p = 0.03$).

**Fecundity and Natality.** Most dickcissel nests were parasitized by cowbirds (65.5%). Unparasitized females laid 1 to 6 eggs, with a mean of 3.34 ± 0.07 eggs per nest (N = 165 nests). Brood sizes for unparasitized nests ranged from 1 to 6 chicks (mean = 2.72 ± 0.10, N = 105). In contrast, parasitized females incubated an average of 2.20 ± 0.06 dickcissel eggs (N = 322). Broods in parasitized nests averaged 1.01 ± 0.06 host chicks (N = 327). Host hatching success was significantly lower in parasitized nests (mean unparasitized = 0.80 ± 0.02, parasitized = 0.73 ± 0.02, $t_{292} = 1.83, p = 0.03$).

Unparasitized nests fledged an average of 2.91 ± 0.14 dickcissel chicks. Parasitized nests fledged 1.53 ± 0.10 dickcissel chicks on average. Fledging rates for nests that hatched at least one chick were not different for parasitized and unparasitized nests (mean unparasitized = 0.95 ± 0.02, parasitized = 0.94 ± 0.02, $t_{139} = 0.34, p = 0.73$).
Renesting and Double Brooding. Females did not frequently renest, with 13.7% of banded females initiating another nest at Konza (Table A5.3). It takes a female dickcissel a minimum of 22 days to build a nest and incubate, hatch and fledge her young (Temple 2002). In most years, few nests were initiated after August 15. It is therefore unlikely that a female can be double brooded if she initiated her first nest after July 1. I therefore calculated two measures of double brooding rates: the proportion of all nesting females that fledged a brood and the proportion of females that fledged young before July 1. A total of 108 females fledged young in the four years of this study. Of these, 16 laid a subsequent nest (14.8%) and 9 of those nests fledged. Less than half of the females that fledged nests initiated those nests before July 1. Double brooding rates were thus 30.2% (16 of 53 females) when only females with sufficient time to raise a second brood were included in the analysis.

Nest Survival

Most nests that failed to fledge young were depredated. Other causes of nest failure, such as abandonment and structural failure, accounted for less than 6% of all nest failures (Table A5.4). The best preliminary model (basic model hereafter) of nest survival in both years included nest age, a quadratic nest age term, nesting stage, and an age * stage interaction term. In 2008, the addition of burn treatment, site, and/or burn frequency did not improve the fit of the model (Table A5.5). However, support for the model including burn frequency was not statistically different from the basic model ($X^2 = 0.34, p = 0.56$), although there was substantially more support for the basic model. In 2009, survival was not different amongst the three burn treatments (Table A5.5). Thus there was little support for an effect of burn management on nest survival in either year.

The addition of year to the basic model significantly improved the fit of the model ($X^2 = 4.49, p = 0.03$); nests were twice as likely to survive to fledging in 2009 compared to 2008 (Table A5.5). The addition of fire frequency to the model including year did not improve the model’s fit, nor was there a significant interaction between year and fire ($\beta = -0.107, CI = -0.852, 0.638$).

Burn regime did not improve the fit of the base model in either 2008 or 2009 (Table A5.5).
Table A5.1. Sample sizes (number of banded males) and burn interval and specific burn history for the sites included in this study. Burn intervals for reversal sites (“R” prefix) are presented as the burn interval pre-2000 followed by the burn interval initiated in 2000. The most recent year of burning is listed for each watershed under “Burn History.”

<table>
<thead>
<tr>
<th>Site</th>
<th>Burn Interval</th>
<th>Burn History</th>
<th>Years included</th>
</tr>
</thead>
<tbody>
<tr>
<td>R20A</td>
<td>1, 20</td>
<td>2008</td>
<td>37 20 12</td>
</tr>
<tr>
<td>R1A</td>
<td>20, 1</td>
<td>all</td>
<td>19</td>
</tr>
<tr>
<td>2A</td>
<td>2</td>
<td>2008</td>
<td>26 10</td>
</tr>
<tr>
<td>2D</td>
<td>2</td>
<td>2007</td>
<td>13</td>
</tr>
<tr>
<td>4F</td>
<td>4</td>
<td>2007</td>
<td>10</td>
</tr>
<tr>
<td>4B</td>
<td>4</td>
<td>2005</td>
<td>10</td>
</tr>
<tr>
<td>10A</td>
<td>10</td>
<td>1997</td>
<td>3</td>
</tr>
<tr>
<td>20C</td>
<td>20</td>
<td>1991</td>
<td>14 13</td>
</tr>
<tr>
<td>1D</td>
<td>1</td>
<td>all</td>
<td>9 18</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>37 46 81 50</td>
<td></td>
</tr>
</tbody>
</table>

Table A5.2. Proportion of banded dickcissels that returned to breed in the following year. Sample sizes for each interval are included in parentheses.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Males</td>
<td>0.298</td>
<td>0.382</td>
<td>0.296</td>
<td>0.330</td>
</tr>
<tr>
<td></td>
<td>(57)</td>
<td>(55)</td>
<td>(27)</td>
<td>(139)</td>
</tr>
<tr>
<td>Females</td>
<td>0.207</td>
<td>0.173</td>
<td>0.119</td>
<td>0.155</td>
</tr>
<tr>
<td></td>
<td>(29)</td>
<td>(52)</td>
<td>(67)</td>
<td>(148)</td>
</tr>
<tr>
<td>Fledglings</td>
<td>0.003</td>
<td>0.00</td>
<td>0.002</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>(36)</td>
<td>(93)</td>
<td>(48)</td>
<td>(177)</td>
</tr>
</tbody>
</table>

Table A5.3. Number of females renesting and double brooding. Double brooded females are those that initiated a nest after successfully fledging a nest earlier in the breeding season. Numbers in parentheses are the number of females who successfully fledged a subsequent brood. Banded Females is the total number of banded females nesting in that year. Banded Early refers to females banded before July 1.

<table>
<thead>
<tr>
<th></th>
<th>2006</th>
<th>2007</th>
<th>2008</th>
<th>2009</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Banded Females</td>
<td>29</td>
<td>51</td>
<td>68</td>
<td>34</td>
<td>182</td>
</tr>
<tr>
<td>Fledged Early</td>
<td>7</td>
<td>16</td>
<td>13</td>
<td>17</td>
<td>53</td>
</tr>
<tr>
<td>Renested</td>
<td>3</td>
<td>12</td>
<td>6</td>
<td>4</td>
<td>25</td>
</tr>
<tr>
<td>Double Brooded</td>
<td>1 (1)</td>
<td>9 (4)</td>
<td>3 (3)</td>
<td>3 (1)</td>
<td>16 (9)</td>
</tr>
</tbody>
</table>
Table A5.4. Fates of dickcissel nests studied from 2006-2009. Nests in the “Other” category failed due to poor construction or high winds. Four nests were destroyed by hail in a severe storm early in 2008.

<table>
<thead>
<tr>
<th>Fate</th>
<th>N</th>
<th>Percent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fledged</td>
<td>167</td>
<td>31.6</td>
</tr>
<tr>
<td>Depredated</td>
<td>331</td>
<td>62.6</td>
</tr>
<tr>
<td>Abandoned</td>
<td>19</td>
<td>3.6</td>
</tr>
<tr>
<td>Other</td>
<td>8</td>
<td>1.5</td>
</tr>
<tr>
<td>Hail</td>
<td>4</td>
<td>0.8</td>
</tr>
</tbody>
</table>

Table A5.5. Burn treatment models tested in Program MARK to predict survival rates of dickcissels on Konza in 2008 and 2009. In both years, the basic model includes the following parameters: age, age², stage, stage*age. AICc is the Akaike Information Criterion corrected for finite sample sizes, wi is the Akaike weight which represents the relative support for each model, K is the number of parameters in the model, and P(fledge) is the probability that a given nest will survive the full 21-day nesting cycle to fledge.

<table>
<thead>
<tr>
<th>Model</th>
<th>K</th>
<th>Deviance</th>
<th>AICc</th>
<th>wi</th>
<th>P(fledge)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>2008</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Constant DSR</td>
<td>1</td>
<td>371.1</td>
<td>373.1</td>
<td>0.000</td>
<td>0.218</td>
</tr>
<tr>
<td>Basic</td>
<td>5</td>
<td>346.8</td>
<td>356.8</td>
<td>0.642</td>
<td>0.152</td>
</tr>
<tr>
<td>Basic + Burn Frequency</td>
<td>6</td>
<td>346.4</td>
<td>358.5</td>
<td>0.277</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.174</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.060</td>
</tr>
<tr>
<td>Basic + Burn Interval</td>
<td>8</td>
<td>345.0</td>
<td>361.2</td>
<td>0.074</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.220</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.145</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.100</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.186</td>
</tr>
<tr>
<td><strong>2009</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Constant DSR</td>
<td>1</td>
<td>428.2</td>
<td>430.2</td>
<td>0.001</td>
<td>0.294</td>
</tr>
<tr>
<td>Basic</td>
<td>5</td>
<td>406.5</td>
<td>416.5</td>
<td>0.831</td>
<td>0.253</td>
</tr>
<tr>
<td>Basic + Site</td>
<td>7</td>
<td>405.6</td>
<td>419.7</td>
<td>0.168</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.223</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.259</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.308</td>
</tr>
</tbody>
</table>
Figure A5.1: Dickcissel nesting phenology for each year of the study. Plots are frequency distributions of nests based on date of first egg in 5-day increments.
References

Beyer HL (2010) Geospatial Modelling Environment. In, 0.3.3 Beta edn. Spatial Ecology LLC
Blankespoor GW (1970) The significance of nest and nest site microclimate for the dickcissel, Spiza americana. In, vol PhD. Kansas State University, Manhattan, KS


Cynx J, Bean NJ, Rossman I (2005) Testosterone implants alter the frequency range of zebra finch songs. Hormones and Behavior 47:446-451

Darwin C (1871) The Descent of Man and Selection in Relation to Sex. Murray, London


Dawson RJG, Gibbs HL, Hobson KA, Yezierinae SM (1997) Isolation of microsatellite DNA markers from a passerine bird, Dendroica petechia (the yellow warbler), and their use in population studies. Heredity 79:506-514


Finck EJ (1983) Male behavior, territory quality and female choice in the dickcissel (Spiza americana). In: Division of Biology, vol Ph.D. Kansas State University Manhattan


Gibbs HL, Tabak LM, Hobson K (1999) Characterization of microsatellite DNA loci for a neotropical migrant songbird, the Swainson's thrush (*Catharus ustulatus*). Molecular Ecology 8:1551-1552
Gulledge CC, Deviche P (1997) Androgen control of vocal control region volumes in a wild migratory songbird (Junco hyemalis) is region and possibly age dependent. Journal of Neurobiology 32:391-402


Ims RA, Rolstad Jr, Wegge P (1993) Predicting space use responses to habitat fragmentation: can voles Microtus oceonomus serve as an experimental model system (EMS) for capercaillie grouse Tetrao urogallus in boreal forest? Biological Conservation 63:261-268


Jensen WE, Cully JF (2005) Geographic variation in brown-headed cowbird (Molothrus ater) parasitism on Dickcissels (Spiza americana) in great plains tallgrass prairie. Auk 122:648-660


Correlates of Fitness in the Dark-Eyed Junco (Junco-Hyemalis). American Naturalist 140:980-999


152


Mohr CO (1947) Table of equivalent populations of north american small mammals. American Midland Naturalist 37:223-249


Nowicki S, Searcy WA, Peters S (2002a) Brain development, song learning and mate choice in birds: a review and experimental test of the "nutritional stress hypothesis". Journal of Comparative Physiology a-Neuroethology Sensory Neural and Behavioral Physiology 188:1003-1014
Onodera T, Poe JC, Tedder TF, Tsubata T (2008) CD22 regulates time course of both B cell division and antibody response. The Journal of Immunology 180:907-913


Rasika S, Nottebohm F, Alvarezbuylla A (1994) Testosterone increases the recruitment and/or survival of new high vocal center neurons in adult female canaries. Proceedings of the National Academy of Sciences of the United States of America 91:7854-7858


Senar JC, Pascual J (1997) Keel and tarsus length may provide a good predictor of avian body size. Ardea 85:269-274


Spencer KA, Buchanan KL, Goldsmith AR, Catchpole CK (2003) Song as an honest signal of developmental stress in the zebra finch (Taeniopygia guttata). Hormones and Behavior 44:132-139


Wasserman FE (1979) Relationship between habitat and song in the white-throated sparrow. Condor 81:424-426
Weatherhead PJ (1999) Sequential mating patterns suggest extra-pair mating is not part of a mixed reproductive strategy by female red-winged blackbirds. Proceedings of the Royal Society of London. Series B: Biological Sciences 266:1027-1031
Westneat DF (1994) To Guard Mates or Go Forage: Conflicting Demands Affect the Paternity of Male Red-Winged Blackbirds. The American Naturalist 144:343-354
With KA, King AW, Jensen WE (2008) remaining large grasslands may not be sufficient to prevent grassland bird declines. Biological Conservation 141:3152-3167
Vita

Bridget Frances Sousa

EDUCATION

PROFESSIONAL POSITIONS HELD
2010-2012: Graduate teaching assistant, University of Kentucky
   Ornithology
   Principles of Integrative Biology I
   Principles of Integrative Biology II
2011-2012: Grader, University of Kentucky
   Introduction to Biology 102
   Introduction to Biology 103
2003-2005: Laboratory Technician, Evolutionary Genetics Lab, Museum of Vertebrate Zoology, University of California at Berkeley. Supervisors: Dr. Eileen Lacey and Dr. Jim Patton.
2001: Biological Field Assistant, Rocky Mountain Biological Laboratory.
2000: Biological Field Assistant, University of California at Santa Cruz.
1999: Curatorial Assistant, Museum of Vertebrate Zoology, University of California at Berkeley.

RESEARCH GRANTS
2009: Dissertation Enhancement Award. University of Kentucky. $3000
2008: Animal Behavior Society. $1000
2006: Lewis and Clark Fund for Field Research. American Philosophical Society. $4000
2005-2011: Graduate School and Department of Biology Flora G. Ribble Fund, University of Kentucky. Multiple competitive and non-competitive awards totaling $10,912

FELLOWSHIPS, SCHOLARSHIPS AND AWARDS
Flora G. Ribble Fellowship. University of Kentucky. Fall 2009
Presidential Fellowship. University of Kentucky. Fall 2008 – Spring 2009
Multi-year Fellowship. University of Kentucky. Fall 2005 - Spring 2008
Honorable Mention, NSF Graduate Research Fellowship
Honorable Mention, Cooper Ornithological Society Mewaldt-King Student Research Award
University of California, Berkeley Chancellor’s Scholarship (4-year)
Robert C. Byrd Scholarship (4-year)
AWARDS AND HONORS

- Western Section of the Wildlife Society Travel Award
- American Ornithologists Union Travel Award
- Honorable Mention, NSF Graduate Research Fellowship
- Honorable Mention, Cooper Ornithological Society Mewaldt-King Student Research Award
- Phi Beta Kappa Member
- High distinction in general scholarship, University of California, Berkeley.
- University of California, Berkeley Chancellor’s Scholarship (4-year)
- Robert C. Byrd Scholarship (4-year)

PUBLICATIONS


