

FACTORS AFFECTING BREEDING PERFORMANCE IN MERLINS (*Falco columbarius*): TACTICS, ROLES AND RESPONSES OF TWO SEXES

A Thesis Submitted to the College of
Graduate Studies and Research
in Partial Fulfillment of the Requirements for the
Degree of Doctor of Philosophy
in the Department of Veterinary Anatomy
University of Saskatchewan
Saskatoon

by

Richard Henry Maclaren Espie

© Copyright Richard H. M. Espie, 1999. All Rights Reserved



**National Library
of Canada**

**Acquisitions and
Bibliographic Services**

**395 Wellington Street
Ottawa ON K1A 0N4
Canada**

**Bibliothèque nationale
du Canada**

**Acquisitions et
services bibliographiques**

**395, rue Wellington
Ottawa ON K1A 0N4
Canada**

Your file Votre référence

Our file Notre référence

The author has granted a non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

0-612-63864-2

Canada

PERMISSION TO USE

In presenting this thesis in partial fulfilment of the requirements for a Doctor of Philosophy degree from the University of Saskatchewan, I agree that the libraries of this University may make it freely available for inspection. I further agree that permission for copying this thesis in any manner, in whole or in part, for scholarly purposes may be granted by the professor who supervised my thesis work or, in their absence, by the Head of the Department of Veterinary Anatomy or the Dean of the Western College of Veterinary Medicine. It is understood that any copying, publication or use of this thesis or parts thereof for financial gain shall not be allowed without my written permission. It is also understood that due recognition shall be given to me and to the University of Saskatchewan in any scholarly use which may be made of any material in my thesis.

Requests for permission to copy or to make other use of material in this thesis in whole or in part should be addressed to:

Head of the Department of Veterinary Anatomy

Western College of Veterinary Medicine

University of Saskatchewan

52 Campus Drive,

Saskatoon, Saskatchewan

S7N 5B4

ABSTRACT

Most ecological studies examining breeding performance in natural populations of vertebrates last less than the lifetimes of the longest lived individuals. This results in inherent weaknesses in any measure of the variation of breeding performance among individuals. In this study I used long-term data of Merlins (*Falco columbarius*) nesting in Saskatoon, Saskatchewan in order to examine individual differences in breeding performance.

Beginning in 1985 and ending in 1997 breeding Merlins were live-trapped during the nestling period (June to early July) using mist nets and a Great Horned Owl (*Bubo virginianus*) as a lure. Reproductive data were derived from 378 captures of 129 individual females and 101 individual males. Chick hatch date, brood size, lifetime reproductive success (LRS), and recruitment of offspring provided estimates of breeding performance and were used to evaluate the effects of parent age, body size, mate choice, territory quality, bird quality and body condition.

Among females, improvements in breeding performance in relation to age were mostly due to the selection of superior breeders, and thus, supported the differential mortality hypothesis. For males, however, improvements occurred mostly within individuals early in life suggesting that they improved breeding performance by gaining experience in skills related to reproduction (i.e., nest defense, hunting, courtship). In both sexes, longevity influenced LRS and recruitment. Past mid-life, birds of both sexes with reduced brood size were more likely to survive to breed again whereas

just the opposite was true for Merlins before mid-life.

For both sexes, body size appeared to influence breeding performance only among yearling birds. For yearling females, bigger birds tended to be better performers and were more likely to survive to breed again. Among yearling males, smaller birds had larger broods, but, larger males were more likely to survive to breed again. In adult Merlins, body size had little influence on breeding performance in either sex; however, the trends between body size and brood size in the two sexes were different from each other suggesting increased fecundity by smaller males and larger females.

Mate choice of male body size by females was almost repeatable and suggests that individual females tended to choose the same size mates in subsequent breeding attempts. However, choice of male size was not related to the size of the female. There was no repeatability of female choice for body condition of male mates, nor male choice of female mates' body size or condition. There was no support for the compatibility hypothesis and among mated pairs, only large female body size improved breeding performance. There was no apparent effect of body condition on breeding performance among mated pairs. Body size showed high heritability between parents and male offspring. Body condition exhibited low heritability between parents and male offspring.

I found little evidence of the influence of territory quality on any of the measures of breeding performance for female Merlins. Even so, when females switched territories they tended to go to ones of higher quality.

Females in poorer body condition tended to have earlier chick hatch dates and higher LRS than ones in better condition. Hatch date was repeatable for the same females occupying different nest places, but, was not repeatable for the same nest places occupied by different females. Among males, birds surviving past each age category occupied higher quality territories than those that did not survive. In addition, LRS was positively correlated with territory quality in males, but, this was mostly due to the heavy influence of the poorest quality territories. Like females, when males switched territories they tended to go to ones of higher quality. Male body condition was not related to breeding performance nor survival. Hatch date was not repeatable for the same males occupying different nest places.

These findings suggest that considerable differences exist between the Merlin sexes in terms of how the different factors studied impact breeding performance in this species. Furthermore, this study illustrates that despite heavy contributions by both sexes to the breeding attempt, their different responsibilities during breeding can strongly influence the effect of the factors studied.

ACKNOWLEDGMENTS

I am grateful to the many funding agencies without whose support over the years, this research would not have occurred. Funding was provided by the Natural Sciences and Engineering Research Council of Canada through an operating grant to Paul James and Lynn Oliphant. I also thank the University of Saskatchewan for providing me with a Graduate Scholarship, the Canadian Wildlife Federation and Saskatchewan Wildlife Federation for scholarships, and the Western College of Veterinary Medicine Wildlife Health Fund for financial support.

I am thankful that both Bob Clark and Joe Schmutz agreed to reside on my committee as it always made for enjoyable and interesting meetings (at least for me) and I'm sure the direction and quality of the thesis would not have been the same without them.

I am grateful to the people in the Department of Veterinary Anatomy for their support and for providing me with a place to work and I will really miss the friendly atmosphere that was so apparent there.

Thanks also go to my fellow graduate students in both the Department and at the Western College of Veterinary Medicine who helped to make my time spent there so enjoyable.

I acknowledge the many people who have participated in this long-term study and without their hard work and dedication none of this would have been possible. In particular, I must single out two individuals; Ian Warkentin and Navjot Sodhi. I thank Ian for all of the hard work and tedium that he must have endured in trapping during the "early" years and for

developing the computer data set that I relied upon so heavily. I am extremely grateful to Navjot for his insightful and exhaustive work on the foraging ecology of Merlins as it was his research that allowed me to draw many of my conclusions.

I am extremely indebted to Paul James for convincing me way back when, that I should consider doing work on Merlins. Without his initial input it is doubtful I would have ever considered working on Merlins. Although his name is not listed in an "official" supervisory role, I'm quite sure he is well aware of the importance he has played in helping bring my Merlin research to this stage.

I am very grateful that Lynn Oliphant agreed to take on one final graduate student. Without his guidance and suggestions many of my ideas probably would never have come to fruition. Lynn has a rare combination of traits not found often among graduate student supervisors; to stand up for you when no one else will and in the next breath smash your best theories when they make absolutely no sense. This latter quality often led to huge arguments, with much shouting and gesticulating on both our parts (much to the dismay of Department onlookers). On rare occasions I believe I even actually won. Lynn has definitely changed the way I look at the world and I know I am much better off for having convinced him to take me on as a graduate student. Have a happy retirement Lynn!!!

Finally, I thank my wife to be, Tracy Fisher, for encouragement and support throughout.

TABLE OF CONTENTS

	Page
PERMISSION TO USE	i
ABSTRACT	ii
ACKNOWLEDGMENTS	v
TABLE OF CONTENTS	vii
LIST OF TABLES	ix
LIST OF FIGURES	x
1. INTRODUCTION	1
2. METHODS	4
2.1 Study Area	4
2.2 Study Species	4
2.3 Nest Searches	5
2.4 Identification and Capture of Individuals	5
2.5 Measurement of Breeding Performance	6
3. AGE DEPENDENT BREEDING PERFORMANCE	9
3.1 Abstract	9
3.2 Introduction	10
3.3 Methods	13
3.3.1 Determination of Ages	13
3.3.2 Analyses and Hypothesis Testing	14
3.4 Results	19
3.5 Discussion	27
3.5.1 Between-individual Trends	29
3.5.2 Within-individual Trends	31
3.5.3 LRS and Recruitment	32
4. SELECTION PRESSURES ACTING ON BODY SIZE	35
4.1 Abstract	35
4.2 Introduction	35
4.3 Methods	38
4.3.1 Analysis of Body Size	38
4.3.2 Effects of Body Size on Breeding Performance	40
4.4 Results	41
4.4.1 Body Size, Age and Selective Mortality	41
4.4.2 Influence of Body Size on Breeding Performance	46
4.5 Discussion	53
4.5.1 Body Size, Age and Selective Mortality	53
4.5.2 Influence of Body Size on Breeding Performance	53
5. MATE CHOICE FOR BODY SIZE AND CONDITION AND ITS INFLUENCE ON BREEDING PERFORMANCE	59
5.1 Abstract	59
5.2 Introduction	60
5.3 Methods	62
5.3.1 Quantification of Body Condition and Body Size	62

	5.3.2 Analyses	63
	5.4 Results	64
	5.5 Discussion	66
6.	INFLUENCE OF TERRITORY QUALITY, BIRD QUALITY AND BODY CONDITION ON BREEDING PERFORMANCE	76
	6.1 Abstract	76
	6.2 Introduction	77
	6.3 Methods	79
	6.3.1 Quantification of Territory Quality	79
	6.3.2 Quantification of Body Condition	80
	6.3.3 Analyses	81
	6.4 Results	86
	6.5 Discussion	99
	6.5.1 Influence of Territory Quality on Breeding Performance	102
	6.5.2 Influence of Bird Condition and Quality on Breeding Performance	107
7.	CONCLUSIONS	112
8.	LITERATURE CITED	118

LIST OF TABLES

TABLE	Page
3.1 Recruits produced and expected by different age Merlins.	28
4.1 Repeatability of Merlin morphometric measures.	42
4.2 Morphometric variable loadings on PC1 axis for male and female Merlins.	43
4.3 Mean wing chord of adult Merlins that produced at least one versus no recruits.	52
5.1 Effects of male and female body condition on breeding performance.	67
5.2 Effects of male and female body size on breeding performance.	68
6.1 Recruits produced and expected by Merlins on different quality territories.	94
6.2 Body condition of Merlins that produced at least one recruit and those that produced no recruits.	101

LIST OF FIGURES

FIGURE	Page
3.1 Age distributions of breeding Merlins in Saskatoon.	20
3.2 Scatter diagram of chick hatch date and parent ages.	21
3.3 Mean chick hatch dates for Merlins surviving and not surviving past different age classes.	23
3.4 Mean brood sizes for Merlins surviving and not surviving past different age classes.	25
3.5 Scatter diagram of longevity and LRS in Merlins.	26
4.1 Mean wing chord for Merlins surviving and not surviving past different age classes.	45
4.2 Mean wing chord and brood sizes of yearling Merlins in Saskatoon.	47
4.3 Mean wing chord and brood sizes of adult Merlins in Saskatoon.	48
4.4 Scatter diagram of parent wing chord and chick hatch date for yearling Merlins.	49
4.5 Scatter diagram of parent wing chord and chick hatch date for adult Merlins.	50
4.6 Scatter diagram of wing chord and LRS for adult Merlins.	51
5.1 Scatter diagram of female wing chord and mean mates' wing chord.	65
5.2 Lifetime reproductive success and mean hatch date for different size female Merlins.	69
5.3 Scatter diagram of mid-parent body condition and male offspring body condition in Merlins.	70
5.4 Scatter diagram of mid-parent wing chord and male offspring wing chord in Merlins.	71
6.1 Mean quality of territory for Merlins surviving and not surviving past different age classes.	88

6.2	Mean body condition scores for Merlins occupying different quality territories.	89
6.3	Mean chick hatch dates for breeding Merlins occupying different quality territories.	91
6.4	Mean brood sizes for Merlins occupying different quality territories.	92
6.5	Scatter diagram of mean quality of territory occupied and LRS in Merlins.	93
6.6	Mean body condition scores for Merlins surviving and not surviving past different age classes.	95
6.7	Mean chick hatch dates for Merlins of different body condition breeding in Saskatoon.	97
6.8	Mean brood sizes for Merlins of different body condition breeding in Saskatoon.	98
6.9	Scatter diagram of a bird mean body condition and LRS for Merlins breeding in Saskatoon.	100

1. INTRODUCTION

Most studies of breeding performance in animals have concentrated on factors influencing the number of young produced in individual attempts or particular years (Clutton-Brock 1988). These studies can all be described as cross-sectional, in that they involve the collection of data at a particular point in time and mostly for different and unknown individuals. A much more powerful way of examining breeding performance is through long-term (i.e., longitudinal) studies of marked individuals because they allow one to compare the breeding performance of the same individuals at different stages (i.e., different ages, nest places, mates, etc). From these studies, it also is possible to determine lifetime reproductive success (LRS; i.e., the number of offspring produced by an individual over its lifetime, *sensu* Newton 1989). Studies which incorporate LRS have several advantages over traditional cross-sectional studies. The most obvious is that they combine two key measures of individual performance (survival and success in breeding events) into one measure of performance (Clutton-Brock 1988, Newton 1989). Secondly, LRS allows one to more accurately assess the full extent of individual variation in performance and longitudinal (i.e., lifetime) measures of performance are less susceptible to short term changes in environment or individuals than are cross-sectional measures.

For this thesis I was interested in several factors that may impact breeding performance in male and female Merlins (*Falco columbarius*). Namely, how do variables such as parent age, body size, mate choice, habitat quality, bird quality, and body condition, influence breeding performance measures such as the number of young produced in an individual's lifetime or within a given breeding season, the hatch date of one's chicks and ultimately whether or not those chicks are "recruited" and become part of the breeding population. These questions are important for any understanding of population ecology, life history strategies and evolution (Stearns 1992). In order to address these important questions one requires an extensive long term data set. Long term study of a population of Merlins breeding in Saskatoon, Saskatchewan, Canada enabled me to examine differences in individual breeding performance in this species in relation to the factors discussed above. I settled on the above measures (both the "dependent" and "independent" ones) for study mostly because I thought they were important to the general ecology and life history strategy of Merlins and partly due to characteristics of the long-term data set and the study area.

The following paragraph provides a brief synopsis of the structure of the thesis. In Chapter 2 I provide the reader with a general description of the methods employed and the collection of data during the long-term study of Merlins in Saskatoon. Chapter 3 focusses on the influence of age on breeding performance in Merlins. More specifically I attempt to determine how much of

the age related changes in breeding performance arise due to changes between individuals (differential mortality hypothesis) compared to within individuals (restraint and constraint hypotheses). In Chapter 4, I examine whether body size influences mortality and breeding performance in Merlins and I test whether there is any evidence to support the sexual selection hypothesis for body size in Merlins. In Chapter 5, I determine whether mate choice for body size and condition is repeatable in males and females and whether mate choice for these characters influences breeding performance. In addition, I also test the compatibility hypothesis and calculate the heritability of body size and body condition between parents and male offspring. Chapter 6 centers on the effects of habitat quality, bird quality and body condition and in it I attempt to isolate the potentially confounding effects of "territory" and "bird". In Chapters 3-6, in addition to testing the specific hypotheses presented there, I had two goals that I wanted to achieve. My first and primary goal was to determine the effect of each factor on breeding performance in male and female Merlins. My second goal was then to relate my findings to the general ecology of Merlins and to compare my findings to other species and pertinent literature on the subject in order to attempt some generalizations. Finally in Chapter 7, I speculate on which factors of those studied are the most important regulators of breeding performance in the Saskatoon Merlin population.

2. METHODS

2.1 STUDY AREA

The study area comprised the city of Saskatoon, Saskatchewan, Canada (52°07'N, 106°38'W), which is located at the northern edge of the Great Plains of North America. The city is approximately 12200 ha in size and is bisected by the south Saskatchewan river (Warkentin and James 1988). Most nesting by Merlins occurred in residential areas and parks and the vegetation in these areas consisted mostly of introduced species, including: American elm (*Ulmus americana*), Manitoba maple (*Acer negundo*), balsalm poplar (*Populus balsimifera*) and weeping birch (*Betula pendula*). White spruce (*Picea glauca*) and blue spruce (*Picea pungens*) were the dominant conifers in the residential areas (Warkentin and James 1988).

2.2 STUDY SPECIES

Merlins in Saskatoon belong to the sub-species known as Richardson's Merlin (*Falco columbarius richardsonii*). Adult males are smaller than females and possess a blue-grey dorsal plumage which is noticeably different from the brown colouration of females and juvenile males (Temple 1972). Pairs establish themselves on territories from February to March in the Saskatoon study area (Sodhi et al. 1993). Females lay eggs from late April to late May

and only one clutch is produced per season (Sodhi et al. 1992). Merlins in Saskatoon show a marked preference for breeding in old American Crow (*Corvus brachyrhynchos*) nests in the numerous spruce trees (*Picea* spp.) that have been planted in residential areas (Warkentin and James 1988). An abundance of House Sparrows (*Passer domesticus*) serves as the primary prey species for Merlins in Saskatoon (Sodhi and Oliphant 1993).

Migration begins in early August (Sodhi et al. 1993) but, more recently some Merlins have been observed wintering at the northern limit of the Great Plains (James et al. 1987).

2.3 NEST SEARCHES

Every year since 1971 nest searches were conducted each spring by visiting sites previously used by Merlins and by systematically searching new areas for signs of activity. Searches were initiated in early April and conducted until mid- to late-May. A tape of Merlin vocalizations was often used to elicit a response and to check sites for occupancy (James et al. 1989). Efforts to find all nesting pairs in the city each year were supplemented by reports of birds from interested members of the public.

2.4 IDENTIFICATION AND CAPTURE OF INDIVIDUALS

Since 1971 nestling Merlins were banded with a United States Fish and Wildlife Service (USFWS) aluminum leg bands (Oliphant and Haug 1985). From 1982 onwards year specific, anodized aluminum colour bands were also placed on the leg opposite the the USFWS band (James et al. 1989).

Beginning in 1985 and ending in 1997 breeding Merlins were live-trapped during the nestling period (June to early July) using mist nets and a Great Horned Owl (*Bubo virginianus*) as a lure. Attempts were also made to catch breeding birds with a dho-ghaza net modified from the design of Clark (1981) using a House Sparrow as a lure. All unmarked individuals were marked with a USFWS band at the time of capture. To reduce the possibility of including birds still alive at the end of the study, any birds captured in 1996 or 1997 were excluded in these data analyses and the calculations of LRS. A few individuals breeding near the end of the study period may have evaded capture; however, this group was probably very small based on the level of capture success (Lieske et al. 1997), and the fact that I allowed two additional years for recapture. On average 57.2% of males and 84.5% of females were captured in each year (Lieske et al. 1997). Therefore, the reported values must be considered estimates.

2.5 MEASUREMENT OF BREEDING PERFORMANCE

Reproductive data were derived from 378 captures of 129 individual females and 101 individual males. I measured four parameters to assess changes of breeding performance with age in Merlins: (1) Brood size--the number of chicks (at the time of banding) produced by an individual male or female in each year it was captured. (2) Hatch date--calculated by backdating from the age of the chicks at the time of banding. Ages were determined by comparison with an unpublished ageing scheme developed for Merlins from

captive rearing studies and observations of wild birds. (3) Lifetime Reproductive Success--the total number of fledglings produced over an individual's lifetime (Newton 1989a). (4) Recruits produced--the number of offspring produced by individuals breeding in the study area that survived and bred within the study area and were captured in some subsequent year. Any measure of recruitment is of course affected by natal dispersal. For this Merlin population natal fidelity is relatively high (compared to other raptors) and 10.4% of males and 4.1% of females returned to breed in a subsequent year (Lieske 1997).

An ideal measure of LRS would require data from complete life cycles. Because of post-natal dispersal in many species (including most birds), these data are difficult to obtain (Barrowclough and Rockwell 1993). It has been reasoned, therefore, that lifetime production of fledglings may provide a reasonable approximation in most circumstances (Newton 1989). Even so, the number of young resulting from extra-pair fertilizations could bias estimates of LRS (Weatherhead and Boag 1997). In this population of Merlins, although the behaviour of extra-pair copulations have been observed (Sodhi 1991), DNA fingerprinting has revealed no cases of extra-pair fertilizations ($n = 20$ broods; Warkentin et al. 1994). Breeding dispersal (i.e., movement between birds' successive breeding attempts) is quite low in this population and the density of nesting Merlins is much lower outside the city than within (Sodhi et al. 1992). Females in Saskatoon moved an average (\pm one SD) of 2.3 ± 1.83 km, while

males moved just (\pm one SD) of 1.1 ± 0.90 km between successive breeding attempts (James et al. 1989). I allowed two years at the end of the study to reduce the possibility that some birds in the data set were still alive (see above).

3. AGE-DEPENDENT BREEDING PERFORMANCE

3.1 ABSTRACT

I examined the effect of age on breeding performance in male and female Merlins (*Falco columbarius*) from a natural population using a long-term data set. In the analysis, I examined whether differences in chick hatch date and brood size associated with parents of different ages arose due to selection of superior individuals (differential mortality hypothesis) or to changes within individuals over time (constraint and restraint hypotheses). In addition, I examined the effect of longevity on production of recruits and lifetime reproductive success (LRS). For females, improvements in breeding performance with age were the result of the selection of superior breeders and there was less evidence to support the constraint or restraint hypotheses. Among males, changes in breeding performance with age were mostly the result of improvements within individuals early in their life (between age 1 and 2+). Production of recruits was not dependent on parental age at the time of breeding for either sex. Recruit production and LRS were both influenced by longevity, so that longer-lived birds produced more offspring over their lifetimes and thereby had a greater probability of producing recruits. The differences

between the sexes in terms of age-dependent breeding performance are likely a consequence of the differing roles the two parents play in reproduction. Male Merlins provide most of the food for the pair and their young during the breeding season and changes in hunting skill with age may account for individual improvements in breeding performance.

3.2 INTRODUCTION

An understanding of age-dependent reproduction is acknowledged as an integral component for several subdisciplines of evolutionary ecology, such as life history theory and population dynamics. Most iteroparous animal species exhibit age-specific patterns of breeding performance (Forslund and Pärt 1995) and often breeding performance is higher among older individuals (Clutton-Brock 1988, Newton 1989a, b, Sæther 1990). Studies of birds over the past 30 years have shown significant relationships between age and clutch size (Klomp 1970, Ross 1980, Forslund and Larsson 1992), time of breeding (review in Perdeck and Cave 1992), and the number of young fledged (Perrins and Moss 1974, Bryant 1979, Reese and Kadlec 1985). The general pattern is that breeding performance increases with age during early reproductive years to reach a high point at mid-life and then sometimes is followed by a decline in old age. Degenerative senescence in later life has been suggested in a number of bird studies (Coulson and Horobin 1976, Perrins 1979, Korpimäki 1988, Newton and Rothery 1997). Nevertheless, studies of Lifetime Reproductive Success (LRS) in birds have shown that longevity is the most important contributor to an

individual's lifetime reproductive output (reviewed in Newton 1989a).

In an excellent review, Forslund and Pärt (1995) describe three primary hypotheses to explain the general pattern of age-dependent reproduction: (1) the differential mortality hypothesis, (2) the constraint or breeding experience hypothesis and (3) the restraint hypothesis. The differential mortality hypothesis predicts that individuals of different phenotypic quality differ in age of first reproduction or survival probability. This leads to a progressive appearance or disappearance of phenotypes as a cohort ages. The constraint hypothesis predicts that the breeding performance of young birds improves as they get older because they acquire or improve certain skills that positively affect reproduction. Under the restraint hypothesis, younger individuals abstain from or put less effort into breeding because reproductive effort increases mortality (Williams 1966, Pugesek and Diem 1990). As birds age they invest more effort into current reproduction because future reproductive potential is smaller. The constraint and restraint hypotheses both act within individuals, and most (if not all) studies have not been able to distinguish between them (Wooller et al. 1990, Forslund and Pärt 1995). In actuality, all three hypotheses (constraint, restraint and differential mortality) can operate simultaneously within a population. Therefore, the central question regarding age dependent breeding performance in birds is how much of the age related trends observed in a population arise due to within-individual changes compared to between-individual differences.

The principle objective of this paper was to test the three major hypotheses concerning age and breeding performance in male and female Merlins (*Falco columbarius*). The Merlin is a small, monogamous, single-brooded raptorial bird that occurs in North America, Europe and Asia (Sodhi et al. 1992, 1993). Merlins, like other raptors, are unusual among birds in that males appear to invest substantially more energy in offspring than do females (Wijnandts 1984, Masman et al. 1988). During the incubation period, female Merlins are largely inactive, leaving the nest for only brief periods to feed. In contrast, males are very active, providing the majority of food for the female as well as for themselves. Males also provide most (Temple 1972), if not all, of the food during the nestling period (Sodhi et al. 1992). Perhaps as a consequence of this, most male Merlins exhibit delayed breeding by starting at 2 years of age while most females show no delay and begin breeding at age 1 (Lieske et al. 1997). Given these life-history traits, Merlins are attractive subjects to test hypotheses concerning age specific differences in breeding performance. Little is known on the effects of age on breeding performance in birds of prey compared to other bird groups. In particular, male raptors have received almost no attention (due mostly to the difficulties involved in their capture) despite their obvious importance in the reproductive effort. In this study, I used a combination of cross sectional and longitudinal data to test the three main hypotheses concerning age and breeding performance in male and female Merlins. Due to the non-experimental nature of the field study, however,

I was unable to distinguish completely between the constraint and restraint hypotheses and therefore combined these two.

As a second objective I examined the relationship between longevity and Lifetime Reproductive Success and also production of recruits for both male and female Merlins. I then attempted to relate observed trends in these measures to the cross-sectional data and the hypotheses concerning age dependent breeding performance in Merlins.

3.3 METHODS

3.3.1 Determination of Ages

Breeding males could be aged precisely if they had been banded as nestling birds or if they were first caught in their first year when they are separable from adult males (age 2+) based on plumage features (Temple 1972). The age of females could be determined only if they had been banded as nestlings. Breeding females unbanded at the time of first capture were assigned a minimum age of one. Adult males unbanded at the time of first capture were assigned a minimum age of two. The decision to assign ages in this way was based on a previous study that showed that 80% of all known aged females begin breeding at age 1 and 83% of all known aged males begin breeding by age 2 (Lieske et al. 1997). One potential problem with this approach is that the majority of female Merlins were of unknown age at the time of capture. This was due to at least two factors. The first was that females tend to have greater natal dispersal distances and thus far fewer females

compared to males returned to the study area to breed (James et al. 1989). Secondly, it was impossible to distinguish between yearling and adult female Merlins as was possible with males. In order to account for this potential problem I conducted most analyses separately for known-aged female Merlins and compared the results to those obtained from estimated-aged females. I also tested for differences in hatch date and brood size between known- and estimated age females. The inclusion of a few older birds in younger age classes should have acted to reduce the magnitude of any age related trends observed rather than enhance them (Newton and Rothery 1997, 1998). Thus, any significant trends observed had to be quite robust in order to support the proposed hypotheses.

3.3.2 Analyses and Hypothesis Testing

I analyzed the data for males and females separately because I was most concerned with how age-dependent breeding performance in each sex related to the proposed hypotheses. For both male and female Merlins, brood size, LRS, and number of recruits were not normally distributed ($P < 0.01$, Kolmogorov-Smirnov tests) a condition that did not change when these data were transformed ($\log_{10}[x+1]$). Therefore, for all analyses of these variables I used a combination of nonparametric tests (Zar 1984, Siegel and Castellan 1988) and randomization techniques (Crowley 1992, Adams and Anthony 1996). Hatch date was a normally distributed variable ($P > 0.05$, Kolmogorov-Smirnov tests) so analyses of this variable employed parametric tests (Zar

1984). However, when $0.05 < P < 0.25$ I employed randomization methods to determine the probability value as this maximized power and reduced the chance of committing a Type II error (Crowley 1992, Adams and Anthony 1996). I tested for differences in brood size and hatch date between estimated- and known-aged females by one-way analysis of variance (ANOVA) (Zar 1984). In addition I tested for a relationship between brood size and hatch date.

To assess the relationships between age and hatch date, age and brood size, longevity and LRS, and longevity and recruit production I used Kendall's tau correlation (Zar 1984, Siegel and Castellan 1988). For female Merlins, these analyses were conducted for known-age birds and estimated-age birds separately. One drawback to using Kendall's tau is that it did not allow for the detection of non-linear relationships. However, follow-up analyses were not constrained in this way (see below). For hatch date and brood size I also attempted to determine whether any observed general trends with age occurred within individuals (constraint and restraint hypotheses), or if they were the result of differential mortality, or both. To test for within-individual trends I examined data for breeding birds that were captured as yearlings and again as adults (age 2+). In addition I used paired *t*-tests (Zar 1984) to determine if there were any differences in breeding performance in birds captured at any time from ages 1-3 (inclusive) and again at any time from ages 4-6 (inclusive) I assigned age 3 as the mid-life cutoff because only one Merlin in the sample (a female) lived past age six. In my analyses of individuals captured before and after mid-

life, I used the breeding performance values that were separated by the greatest number of years. For example, if a bird was caught when aged 1, 2 and 5, I only used its breeding performance measures from ages 1 and 5 in the paired *t*-tests. I did this to maximize the likelihood of detecting trends within individuals. In order to conduct a further test of the constraint and restraint hypotheses, I compared hatch dates and brood sizes of yearling males that bred once to those of two year old males that bred once. I was interested in these two groups because I wanted to know whether waiting a year would improve LRS for male Merlins making only one breeding attempt. I used a *t*-test to compare hatch dates and a Mann-Whitney U-test to compare brood sizes (Zar 1984, Siegel and Castellan 1988).

To test the differential mortality hypothesis I separated the birds in each age class into two categories. Birds of any age could be divided into those that bred again in a later year ("lived") and those that did not ("died"). Birds were assumed to have died if they were never recaptured between 1985-1997. I used "died" and "lived" as two categories of the fixed effect factor in a randomized block analysis of variance (ANOVA) with age as the blocking factor (Zar 1984). This allowed me to examine within each age group whether any relationship existed between breeding success at a given age and survival to the next age class or in other words, whether poorly performing birds were more likely to die than more highly performing ones. I used mean values of hatch date and brood size in each cell of the block design. I did this because

the design was unbalanced (i.e., very unequal sample sizes within each category). Thus, I felt that the best approach to testing the differential mortality hypothesis was to use the mean values for brood size and hatch date for each cell in the analyses. I could not assess any interaction because each cell contained only a single value. Only birds up to age 5 were included in these analyses because the sample contained only one female and no male Merlins older than age 6. For females, estimated- and known-aged birds of different ages comprised separate blocks. For example, estimated-aged females of age 2 comprised one block and known-aged females of age 2 another.

The mean number of young produced by those birds living past a particular age category and those that died appeared to follow different trends for both male and known-age females (but not estimated-age females) for ages 1-3 (inclusive) versus ages 4-5 (inclusive) (i.e., before and after mid-life). To compare the trends in these two groups for males and known-age females I used the differences between the means of "lived" and "died" birds for each age category in a *t*-test (Zar 1984). The two categories in the *t*-tests were birds aged 1-3, and birds aged 4-5. Probability levels were determined by randomization methods (Crowley 1992, Adams and Anthony 1996). Splitting the data at mid-life did create a problem when testing the differential mortality hypothesis. If I used "died" and "lived" as two categories of the fixed effect factor in a randomized block analysis of variance (ANOVA) with age as the blocking factor (and keeping the sexes separate) it precluded finding statistically

significant differences (based on randomization methods) between the two categories as there were not enough possible permutations of the data to achieve $P_r < 0.05$. Non-parametric methods would have suffered a similar fate. Therefore, in this instance only it was necessary to combine data for males and known-age females in order to perform legitimate analyses. For birds aged 1-3 I used randomized block ANOVA (probability values calculated by randomization) and for birds aged 4-5 I used Friedman's ANOVA (Zar 1984). In both analyses males and females constituted separate blocks. For estimated-age females I did not partition the data into before and after mid-life groups.

To determine if recruitment of offspring was dependent upon the age of the parent I compared the observed versus expected recruitment values for each age category in a contingency table for male and female Merlins using Log-likelihood ratio analyses. I used Log-likelihood ratio analyses rather than Chi-squared analyses because $> 20\%$ of the expected frequencies were less than 5.0 (Zar 1984).

All tests were two-tailed and considered significant when $P < 0.05$. Parametric and non-parametric statistical tests were computed using Statistica for Windows (V 5.1) (StatSoft Inc. 1995). Randomization tests were conducted using the computer program RT (V 2.1) (Manly 1997). If the number of permutations for reshuffling and sampling the data were small (< 2000) I used exact permutation to calculate probability values. If the number of permutations was large, I performed 5000 replications and used the frequency distribution of

possible outcomes to calculate probability values (see Crowley 1992, Adams and Anthony 1996). Probability values calculated from randomization techniques are denoted as P_r . Means are reported \pm one SD. Unless otherwise stated, all analyses combined birds of known and estimated ages.

3.4 RESULTS

Of the 225 female Merlin captures, 53 cases were of known age (Fig. 3.1). For the 153 male captures 105 were of known age (Fig. 3.1). The mean lifespan for known-aged females was 3.15 ± 1.91 years and for known-aged males was 2.67 ± 1.51 years (Fig. 3.1). For birds of estimated age the mean lifespan for females was 1.81 ± 1.19 and for males 2.58 ± 1.18 . There was no difference in brood size ($F = 0.70$, $df = 1$, 223, $P_r = 0.46$) nor hatch date ($F = 1.28$, $df = 1$, 216, $P = 0.26$) when comparing estimated- and known-aged females.

Hatch date became earlier with age for both estimated-age females ($\tau = -0.189$, $n = 166$, $P < 0.001$) and known-age females ($\tau = -0.462$, $n = 52$, $P < 0.001$; Fig. 3.2). The relationship between hatch date and age also held for male Merlins ($\tau = -0.344$, $n = 150$, $P < 0.001$; Fig. 3.2). Within individuals, hatch date did not change for estimated-age females (mean difference = 1.26 ± 6.56 days, paired- $t = 1.26$, $n = 43$, $P_r = 0.22$) nor known-age females (mean difference = 2.43 ± 13.67 days, paired- $t = 0.47$, $n = 7$, $P_r = 0.65$), but, came to be substantially earlier for males (mean difference = 10.70 ± 5.46 days, paired- $t = 6.20$, $n = 10$, $P < 0.001$). For individuals captured before and after mid-life,

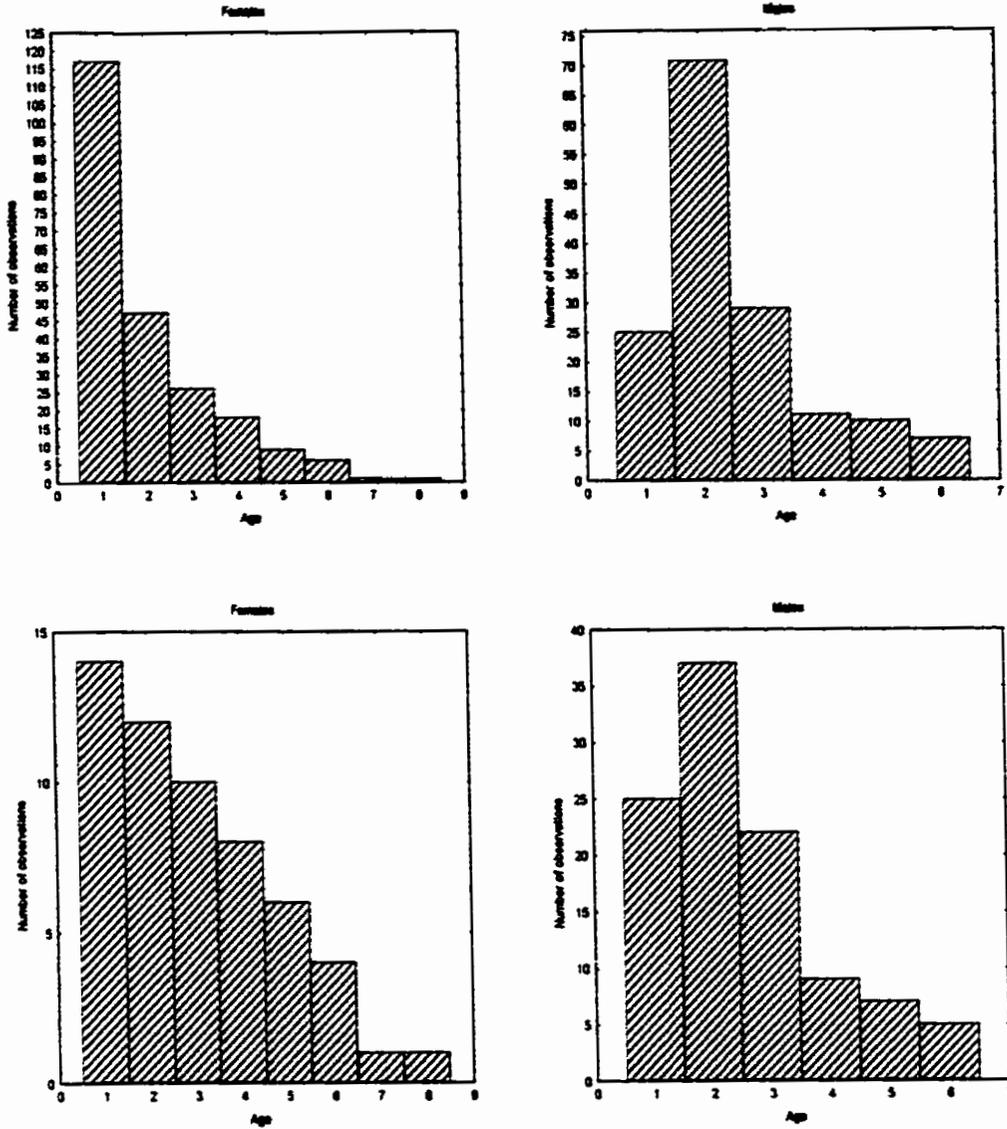


Figure 3.1. Age distributions of breeding female and male Merlins captured in Saskatoon, Saskatchewan (1985-1995). The top panels include birds of known and estimated age. Only known aged birds are shown in the bottom two panels.

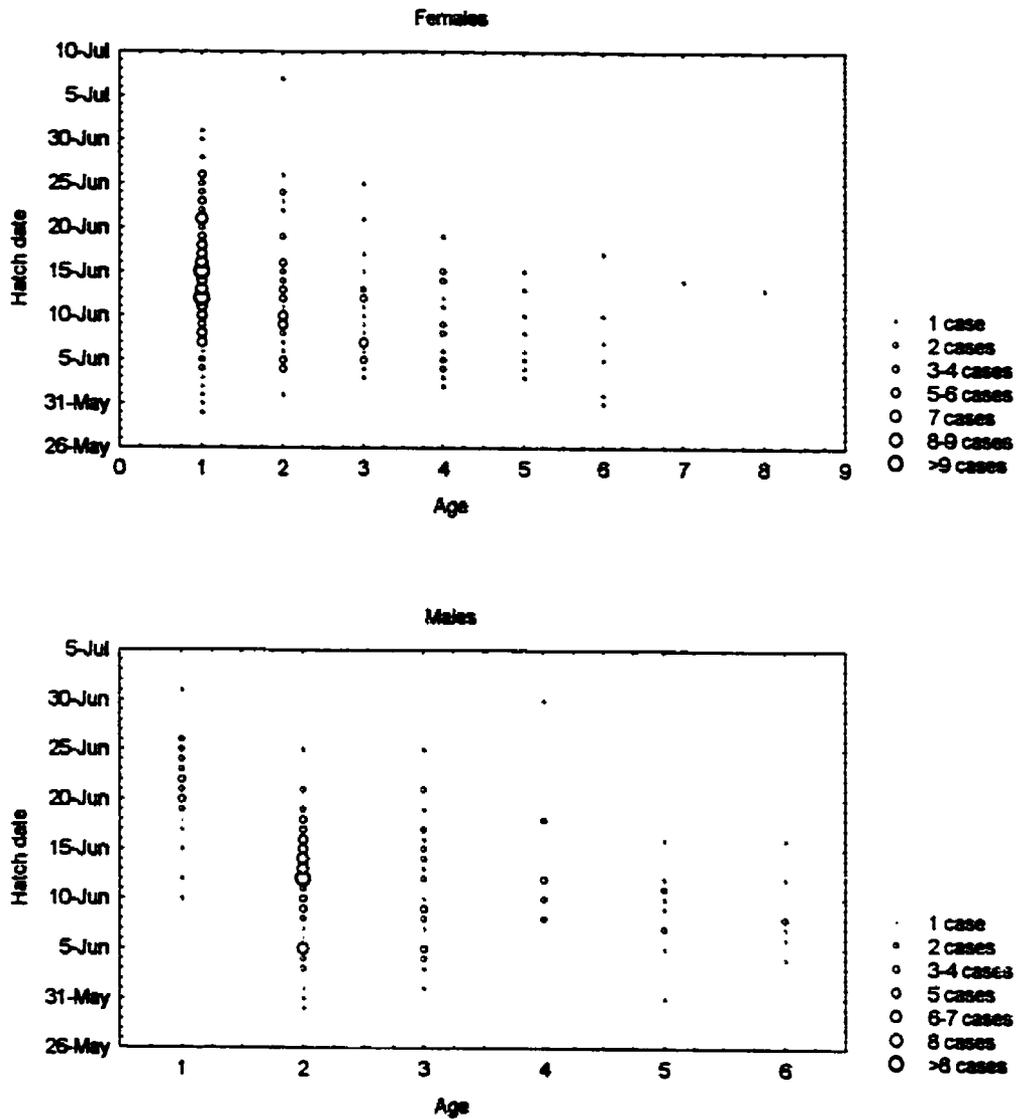


Figure 3.2. Scatter diagram of parent age and chick hatch date for female and male Merlins in Saskatoon. All captures for each individual are shown. There is a significant reduction in chick hatch date with age for both sexes.

there was no change in hatch date for females (mean difference = 2.87 ± 6.98 days, paired- $t = 1.59$, $n = 15$, $P_r = 0.082$), but, there was for males (mean difference = 2.41 ± 5.77 days, paired- $t = 1.72$, $n = 17$, $P_r = 0.0498$). Using analysis of variance blocked by age I found that birds surviving past each age category did have earlier hatch dates for females ($F = 7.32$, $df = 1, 9$, $P = 0.024$, Fig. 3.3). This trend was not apparent in males past age 1 and there was no difference in hatch date between those males that survived past each age class and those that did not ($F = 0.001$, $df = 1, 4$, $P = 0.98$; Fig. 3.3). Males that bred for the first time at age 2 (Mean = 12 June, $n = 45$) had chick hatch dates that were earlier than yearling male breeders (Mean = 22 June, $n = 14$, $t = 6.70$, $P < 0.001$). Males that initially bred at age 2 also produced more chicks (median = 5, $n = 46$) than yearling males only breeding once (median = 4, $n = 15$, $U = 208.5$, $P = 0.015$). Birds having earlier hatching chicks also had significantly larger broods for both females ($\tau = -0.194$, $n = 218$, $P < 0.001$) and males ($\tau = -0.243$, $n = 150$, $P < 0.001$).

The general trend for males was for brood size to increase with age ($\tau = 0.117$, $n = 153$, $P = 0.033$). Among known-age females, brood size did not increase with age ($r = 0.188$, $n = 56$, $P_r = 0.174$), but, did for estimated-age females ($\tau = 0.135$, $n = 169$, $P < 0.01$). For yearling breeders that were captured again as adults (age 2+), brood size did not change within estimated-age females (mean difference = -0.11 ± 1.00 chicks, paired- $t = 0.708$, $n = 43$, $P_r = 0.29$) nor known-age females (mean difference = 0.96 ± 1.31 chicks, paired- t

indicate sample sizes for each category (died:live).

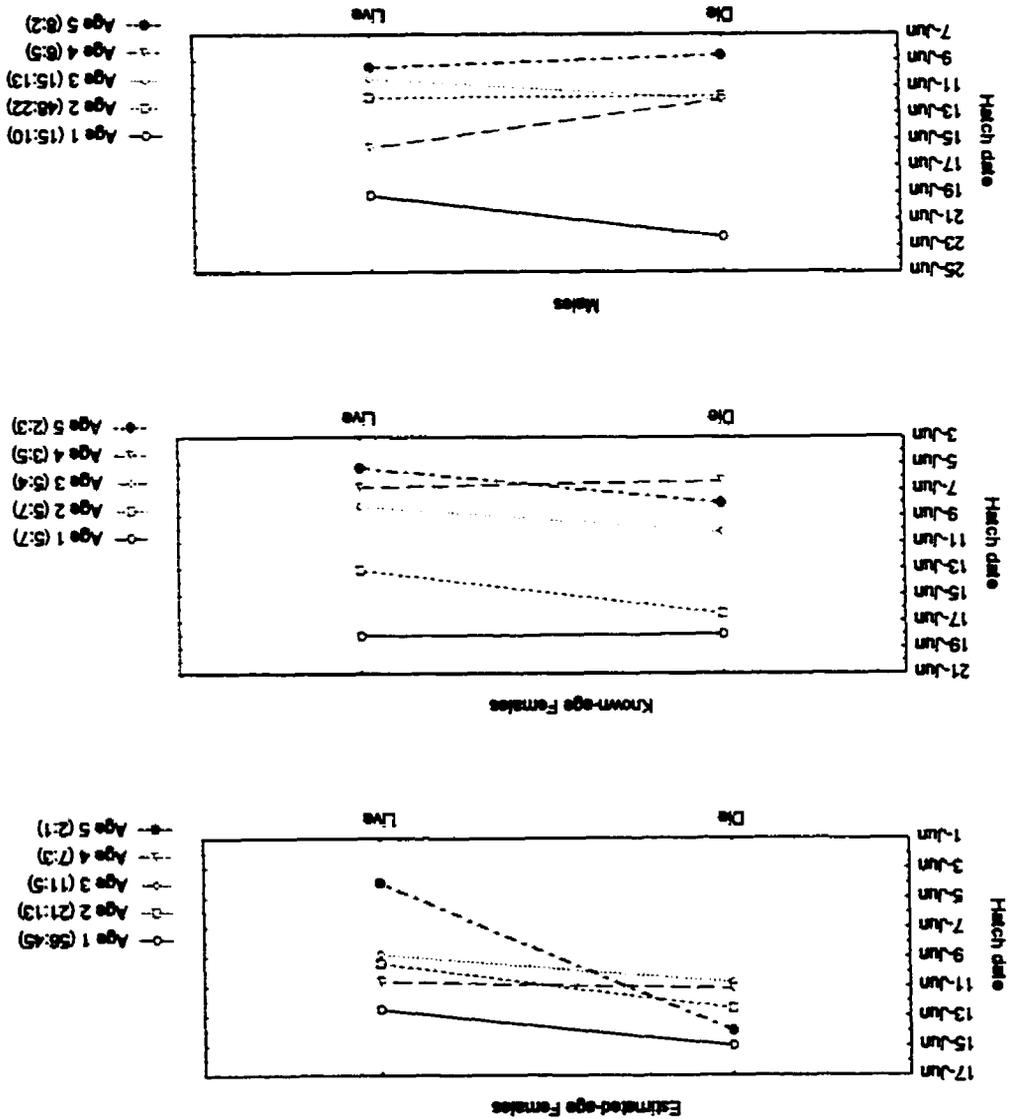
Connecting lines are used to illustrate equal aged birds. Numbers in the legend

chick hatch date for surviving versus dead females but not for males.

tests (blocked for age effects) revealed a significant overall difference in the

survived past or died at a particular age. Two-factor randomized block ANOVA

Figure 3.3. Mean chick hatch dates for Merlin parents in Saskatoon that



=1.95, $n = 7$, $P_r = 0.094$), but, did so within males (mean difference = 0.55 ± 0.72 chicks, paired- $t = 2.40$, $n = 10$, $P_r = 0.031$). No change in brood size was detected within individual females (mean difference = -0.07 ± 1.10 chicks, paired- $t = 0.234$, $n = 15$, $P_r = 0.51$) or males (mean difference = -0.29 ± 1.45 chicks, paired- $t = 0.84$, $n = 17$, $P_r = 0.25$) when comparing before and after mid-life.

The mean number of young produced by those birds living past a particular age category and those that died followed different trends for both male ($t = 4.28$, $df = 3$, $P_r < 0.05$) and known-age females ($t = 9.19$, $df = 3$, $P_r < 0.01$), but, not estimated-age females ($t = 3.89$, $df = 3$, $P_r = 0.10$) when comparing before and after mid-life (Fig. 3.4). For male and known-age female Merlins aged 1-3, the ANOVA test (blocked by age) revealed a nearly significant overall difference in the brood sizes of surviving versus dead birds ($F = 6.49$, $df = 1,5$, $P_r = 0.0625$). For male and known-age female Merlins aged 4-5, brood size was smaller for surviving birds compared to those that died (Friedman's ANOVA, $\chi^2 = 4.0$, $df = 1$, $n = 4$, $P = 0.046$, Fig. 3.4). For estimated-age females there was no difference between the "lived" and "died" categories ($F = 2.08$, $df = 1,4$, $P_r = 0.125$, Fig. 3.4).

As expected there was a positive correlation between age (i.e., longevity) and lifetime reproductive success for both male ($\tau = 0.662$, $n = 102$, $P < 0.001$) and female Merlins ($\tau = 0.728$, $n = 129$, $P < 0.001$; Fig. 3.5). Most Merlins (both sexes) bred only once and produced 5 or fewer chicks. Females

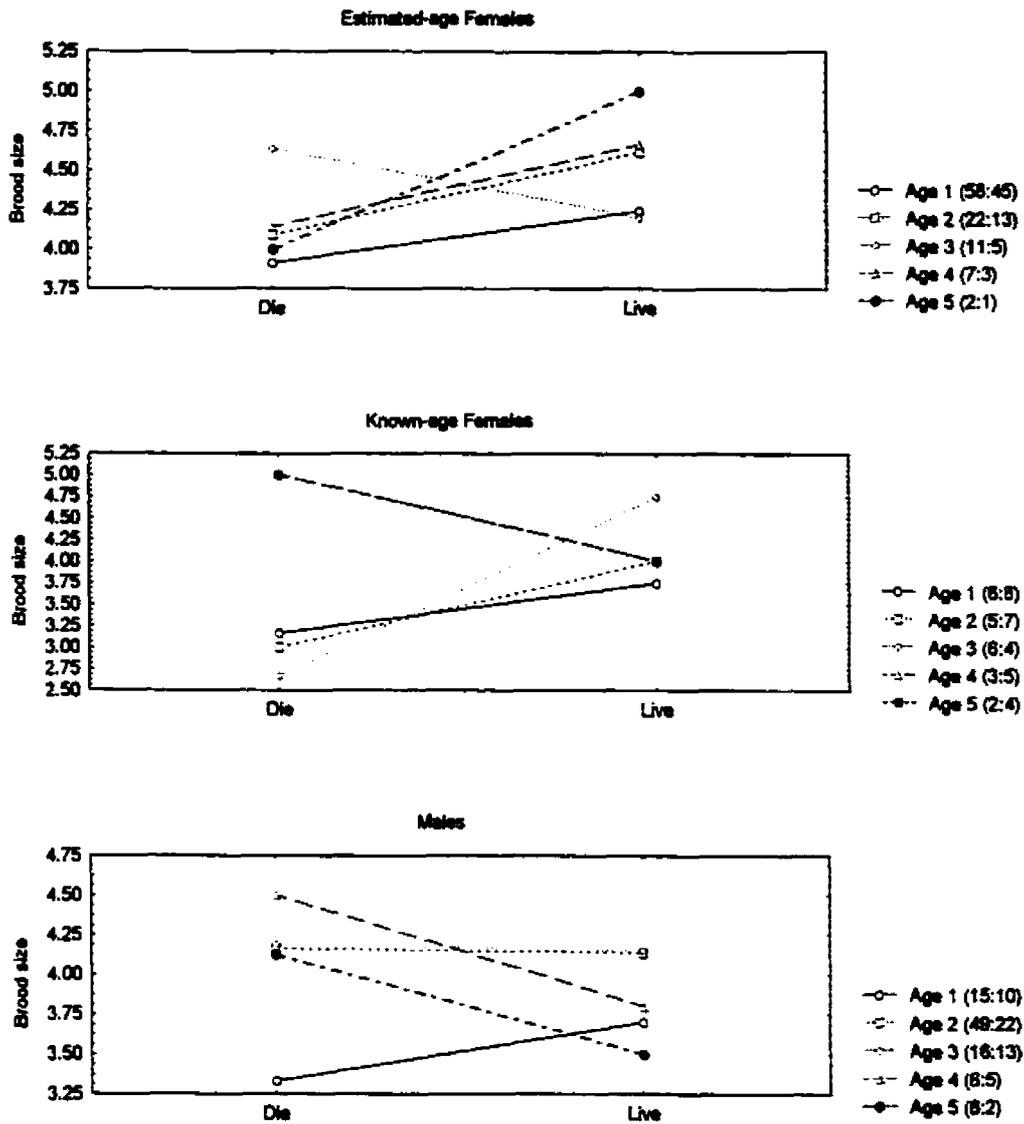


Figure 3.4. Mean brood sizes for Merlin parents in Saskatoon that survived past or died at a particular age. Note that for known-aged females, birds aged 4 and 5 produced the same mean number of chicks for both categories. Connecting lines are used to illustrate equal aged birds. Numbers in the legend indicate sample sizes for each category (died:lived).

produced a mean of 8.0 ± 6.0 chicks in their lifetimes whereas males produced a mean of 7.4 ± 5.9 chicks in their lifetimes. The maximum number of chicks produced by a male was 32 and for a female, 30.

The number of recruits produced by Merlins of each age class did not differ from the number expected by chance alone for each age class (Table 3.1). Thus, older birds produced more recruits over their lifetimes in both females ($\tau = 0.342$, $n = 129$, $P < 0.001$) and males ($\tau = 0.252$, $n = 102$, $P < 0.001$) simply because they lived longer and bred more times. It is noteworthy, however, that the oldest female Merlin in the sample (age 8) did not produce any recruits to the population.

3.5 DISCUSSION

Life history theory is based on the assumption that there are trade-offs between different life history traits (Stearns 1992). Lack (1947) was among the first to point out the existence of negative relationships among life history variables by showing that increased investment in one component may result in decreased investment in another. Some studies have suggested that patterns of age-dependent variation in breeding performance should be related both to chances for future survival and reproduction (Hamilton 1966, Emlen 1970, Charlesworth 1980). In several experimental studies, a cost of reproduction has been shown for several bird species (reviewed by Nur 1988; see also Gustafsson and Pärt 1990, Jacobsen et al. 1995, Wiehn and Korpimäki 1997). Individual performance in male and female Merlins provides clear evidence of

Table 3.1. Total number of young and recruits produced and the expected number of recruits for individual breeding attempts by female and male Merlins of different ages. For females $G = 3.93$, $df = 5$, $P = 0.56$. For males $G = 1.67$, $df = 5$, $P = 0.89$.

Age (yr)	Females			Males		
	Number of Young	Recruits Produced	Recruits Expected	Number of Young	Recruits Produced	Recruits Expected
1	467	35	31.8	87	5	6.6
2	193	12	13.1	295	24	22.4
3	107	9	7.3	121	11	9.2
4	78	2	5.3	46	2	3.5
5	39	3	2.7	40	3	3.0
6	27	1	1.8	30	2	2.3
Total	911	62		619	47	

age-dependent changes in reproduction for a natural population.

3.5.1 Between-individual Trends

Previous work has shown that Merlins in Saskatoon time their breeding so that the fledging phase falls during the period of peak production of juvenile House Sparrows (Sodhi and Oliphant 1993). Other workers have reported increased predation on juvenile prey individuals as the Merlin breeding season progresses (Newton et al. 1984). Secondly, the timing of molt is of fundamental importance for Merlins as they renew their feathers at the same time as raising offspring (Espie et al. 1996) and must accomplish both before fall migration. Thirdly, early hatching may be adaptive for Merlin chicks because they would have more time available for practicing hunting and for accumulating body reserves before winter as has been shown for other raptors (e.g., Tengmalm's Owl, *Aegolius funereus*; Korpimäki 1987). These lines of evidence, in association with the data from this study, suggest to me that timing of breeding is important for both Merlin parents and their offspring. Hatch date for Merlins did decrease during the study period (R. H. M. Espie, *unpublished data*). However, I am unable to say for certain whether Merlins were responding to some environmental trend (e.g., weather, change in House Sparrow breeding chronology, etc.) or if this decrease in hatch date over the study period was due to selection of superior breeders, or both. However, a repeatability analysis of hatch date for individual females ($n = 46$) has shown that hatch date is repeatable for the same individuals caught breeding in different years (Chapter

6).

When comparing before and after mid-life trends between non- and surviving birds a different strategy was suggested for both males and known-age females in terms of optimal brood size. Before mid-life, surviving birds tended to have larger broods than non-surviving birds. This was more apparent among the known-age females than among the males. After mid-life, those individuals (for both groups) having smaller broods tended to be more likely to survive to breed again. This may suggest that past mid-life, higher fecundity reduced future survival and hence LRS. However, it must be noted that these different strategies before and after mid-life were not apparent among the estimated-age females, and thus, my findings are not entirely conclusive. The cost of reproduction can only truly be investigated by experimentally manipulating the reproductive effort in individuals and determining how this influences their future reproduction and survival. For a number of other birds, the differential mortality hypothesis has received limited support (reviews in Martin 1995, Forslund and Pärt 1995). Most support has come from species such as: Song Sparrows *Melospiza melodia* (Nol and Smith 1987), Screech Owls *Otus asio* (Gehlbach 1989), Short-tailed Shearwaters *Puffinus tenuirostris* (Wooller et al. 1990) and Kittiwakes *Rissa tridactyla* (Coulson and Porter 1985, Aebischer and Coulson 1990). Some of the observed trends in hatch date and brood size in male and female Merlins were likely due to the disappearance of inferior individuals, but, some changes in breeding performance did occur within individuals, particularly

for males.

3.5.2 Within-individual Trends

Both the constraint and restraint effects act within individuals and potentially give rise to the same general trends explained by differential mortality. My analyses revealed no change in either chick hatch date or brood size within individual female Merlins, but, there were significant improvements in both measures within male Merlins as they aged. These changes within individual males were most noticeable early in life. These findings make sense when placed within the context of the ecology of birds of prey. Experimental and observational evidence strongly suggests that in raptors, food limits breeding performance (Newton 1986, Daan et al. 1988, Wiehn and Korpimäki 1997). Because male Merlins provide almost all food for themselves, their mates and their offspring during the breeding season (Sodhi et al. 1992), one would expect their ability to provide food to be the primary determinant of breeding success. Improved foraging skills have frequently been suggested as an explanation for increased reproductive success with age early in life (Lack 1968, Burger 1988, Newton 1989a, Pyle et al. 1991, Desrochers 1992, Forslund and Pärt 1995). According to life history theory, individuals should begin breeding when the benefits are greater than any benefits gained from a delay of reproduction (Promislow and Harvey 1990, Stearns 1992). A longer delay in age of first breeding for males compared to females has been reported for many raptors (see Newton 1979, Mearns and Newton 1984, Heyne and Wegner

1991). Most known-age female Merlins in Saskatoon begin breeding at age 1, whereas most males begin to breed at age two (Lieske et al. 1997). The simplest explanation for this observation is the different roles the two sexes play in reproduction which may constrain many yearling male Merlins from breeding. However, a one year delay for male Merlins that only bred once as adults significantly improved their LRS over their counterparts that only bred once as yearlings. From the field study, however, it was impossible for me to determine exactly how much of the observed change in male performance was due to a change in competence (i.e., constraint) or reproductive effort (i.e., restraint). Intelligent experimentation in this area could prove very useful in determining the influence of these two factors early in life for raptors and other birds. The idea that young breeders show reproductive restraint in order to increase subsequent performance has received little empirical support (Newton 1989a, Forslund and Pärt 1995, but see Pugsek 1981, Pugsek and Diem 1990, Weimerskirch 1992).

3.5.3 LRS and Recruitment

Lifetime Reproductive Success for Merlins of both sexes was highly correlated with age. This is not surprising, considering that for most animals studied thus far (reviews in Clutton-Brock 1988, Newton 1989a), longevity is the single most important factor accounting for variance in LRS measures. Since Newton's (1985) first report of LRS in female Sparrowhawks, it has come to be recognized as an extremely important measure of breeding performance.

Perhaps its greatest attribute as a measure of breeding performance is that it reveals the full extent to which reproduction varies among individuals with small annual differences potentially becoming larger and more detectable over an entire lifespan (Newton 1985, 1988, 1989a). Despite its value, however, LRS does not allow for the detection of trade-offs between reproduction and survival or perhaps even signs of senescence (i.e., innate deterioration in probability of survival or breeding performance with increasing age). For example, 4 and 5 year old Merlins (i.e., males and known-age females) surviving past these age classes tended to produce fewer offspring than those not surviving. This did not show up in the measures of LRS because these birds had done so well in previous breeding attempts that it masked any later reduction in breeding performance. Therefore, the longest lived birds having the highest LRS in the study were not always the best performers at each age. In fact, for Merlins past mid-life it appeared better to slightly reduce brood size in a given breeding attempt in order to increase the probability of surviving to breed again and thereby, maximize their LRS. A deterioration in performance in later life despite the accumulation of experience is likely attributable to degenerative senescence (*sensu* Abrams 1991, Newton and Rothery 1997, 1998). Medawar (1952) and Williams (1966) proposed that the evolution of senescence could be understood in terms of age-specific gene action whereby a mutation increases fitness early in life at the expense of reducing it later on. Another explanation is that there may be an accumulation of harmful mutations that reduce fitness in later life

(Medawar 1952, Partridge and Barton 1993). Although deterioration in breeding performance has obvious negative consequences, a slight reduction in breeding performance at later ages may not be entirely negative if there is some trade-off between survival and reproduction.

Recruitment of Merlins (in this case limited to locally produced offspring which subsequently returned to breed) was independent of the parent's age at the time of production. Thus, different-aged Merlins did not produce offspring that were more or less likely to be recruited. The total number of recruits produced in a bird's life depended on how long the bird lived. This was because these same birds tended to produce more chicks over their lifetimes and thus by sheer numbers and probability alone were able to produce more recruits. Newton (1989b) reported a similar finding for female Sparrowhawks. Therefore, anything that increased LRS would have in turn impacted recruitment. However, the fact that so few offspring returned (compared to the number produced) to the study area to breed probably limits my ability to draw conclusions from the recruitment data. A recent review of 22 long-term studies of birds suggests that individuals that disperse can differ from those that stay (or return), and thus using recruitment of breeding offspring to the local study plot in order to identify individual adaptations may be misleading (Lambrechts et al. 1999).

4. SELECTION PRESSURES ACTING ON BODY SIZE

4.1 Abstract

Using the long-term data set I tested whether body size influenced mortality and breeding performance in the Merlin. In the analyses I found that larger yearling females were more successful breeders with respect to brood size and chick hatch date, and were more likely to survive to adulthood. In yearling males, smaller individuals tended to have larger broods, whereas larger birds were more likely to survive to breed again. Among adult Merlins, body size had little influence on mortality or any of the measures of breeding performance. However, the trends between body size and brood size were almost significantly opposite between adult males and females. The results suggest that size selection in Merlins occurs early in life and that there exists different body size optima for males and females in terms of breeding performance and mortality. Moreover, the data for yearling males provides support for the sexual selection hypothesis in that smaller males tended to be superior breeders while larger ones tend to have higher survival. To my knowledge this is the first time this trade-off has been shown for a RSD bird species.

4.2 Introduction

Body size has been widely studied because it can influence many aspects of an individual's biology (Peters 1986). In birds and mammals, competition among males for the opportunity to mate is generally associated with male-biased size dimorphism (Selander 1965, Clutton-Brock 1988), and body size has been shown to affect annual reproductive success, survival and lifetime reproductive success in several bird species (Boag and Grant 1981, Fleischer and Johnston 1982, Price and Grant 1984, Gustafsson 1986, Newton 1986, 1989, Weatherhead and Clark 1994, Choudhury et al. 1996 and Rohwer et al. 1996).

Among mammals and birds, males are most frequently the larger sex (Andersson and Norberg 1981). One hypothesis advanced to explain this, the sexual selection hypothesis proposes that large body size in males is favoured because it confers reproductive advantages, but also, may carry with it some ecological cost such as reduced survival (Selander 1965). This hypothesis has received support from interspecific studies of sexual dimorphism and the intensity of competition among males for mates (Clutton-Brock et al. 1977, Webster 1992, Fairbairn and Preziosi 1994). Several studies have looked for evidence of increased survival costs due to large size in male-biased sexually dimorphic species, but, obtained mixed results. Examination of sexual size dimorphism and survival in birds (Promislow et al. 1992) and mammals (Promislow 1992) reveal that relative male mortality increases as sexual size dimorphism becomes more pronounced. In one study of Red-winged

Blackbirds (*Agelaius phoeniceus*), male survival was shown to decrease as size increased (Yasukawa 1987). However, other studies have found no evidence of intraspecific selection against large body size in male Red-winged Blackbirds (Searcy 1979, Weatherhead et al. 1987, Rohwer et al. 1996). In fact, larger male Red-winged Blackbirds may be better suited to survive the non-breeding period (Weatherhead et al. 1987, Weatherhead and Clark 1994). Most studies of body size in sexually dimorphic bird species have concentrated on male polygynous birds and in particular New World blackbirds (Icterinae) (Selander 1972, Searcy 1979, Yasukawa 1981, 1987, Orians 1985, Weatherhead and Clark 1994). Despite this extensive body of literature, the evidence for opposing selective forces limiting body size dimorphism in birds is equivocal.

In most birds of prey females exceed males in size (Amadon 1975, Newton 1979; i.e., reversed sexual dimorphism, RSD). More than 20 hypotheses have been proposed to account for the development of RSD in raptors (Newton 1979, Smith 1982, Temeles 1985, Mueller 1986, Pleasants and Pleasants 1988, Marti 1990). The literature concerning RSD has focussed largely on interspecific differences in the extent of dimorphism in order to explain the origins of the phenomenon. From this, it is evident that the degree of RSD in raptor species is related to diet. The more difficult the prey are to capture, the greater the degree of dimorphism (Newton 1979, Temeles 1985, Mueller 1986, but see Catry et al. 1999). What is lacking are data on intraspecific differences in survival and reproductive success for males and

females of RSD species. Thus, my aim in this study was to investigate a population of Merlins for evidence of intrasexual differences in mortality based on body size and the adaptive significance of body size, as it relates to breeding performance. Under the sexual selection hypothesis, I predicted that large male Merlins would have higher probability of survival, while small males would be superior breeders.

4.3 METHODS

4.3.1 Analysis of Body Size

I used Principal Components Analysis (PCA) to reduce six univariate measures into one overall index of size (Espie et al. 1996). The PCA was based on a correlation matrix of the raw measures and was done for males and females separately. The six measurements used in the PCA analysis were: (1) cube root of body mass (mass measured to nearest gram using a Pesola scale); (2) total length (from top of head to tip of tail); (3) tail length (base to tip); (4) wing chord of the unflattened wing (all measured to nearest millimeter using a wing ruler); (5) bill length (from distal edge of cere to tip of bill, measured to nearest 0.1 millimeter with a vernier caliper); and (6) tarsus length (measured to nearest 0.1 millimeter with a vernier caliper).

I tested for repeatability of the morphometric measurements and PC1 scores by one-way analysis of variance (ANOVA). This analysis quantified the amount of within-individual variance relative to the total (within and between) individual variance in the morphometric measures (Zar 1984, Lessells and Boag

1987). Repeatability is a valuable measure that can be used to assess the reliability of multiple measurements on the same individual (Lessells and Boag 1987). Repeatability was calculated separately for males and females, and only those individuals that were captured at least twice (in subsequent years) were included in the repeatability analyses.

Previous work has suggested that a relationship in Merlins exists between age and body size with yearling birds being significantly smaller than adults (see Warkentin et al. 1992, Wiklund 1996). Therefore, in all subsequent analyses I examined the effects of body size on selective mortality and breeding performance separately in yearlings and adults.

In order to test for selective mortality based on body size in adult (age 2+) male and female Merlins I used a randomized block ANOVA. I separated the birds in each age class into two categories. Birds of any age could be divided into those that bred again in a later year ("lived") and those that did not ("died"). Birds were assumed to have "died" if they were never recaptured between 1985-1997. I used "died" and "lived" as two categories of the fixed effect factor in a randomized block analysis of variance (ANOVA) with age as the blocking factor (Zar 1984). This allowed me to examine within each age group whether any relationship existed between body size at a given age and survival to the next age class or in other words, whether different size birds were more or less likely to die. I used mean values of wing chord in each cell of the block design. I did this because the design was unbalanced (i.e.,

unequal sample sizes within each category; Zar 1984). Thus, I felt that the best approach to testing the differential mortality hypothesis was to use the mean values for each cell in the ANOVA. I could not assess any interaction because each cell contained only a single value. Only birds up to age 5 were included in these analyses because the sample contained only one female and no male Merlins older than age 6. Paired *t*-tests were used to test for growth in wing chord within individuals as they aged (i.e., yearling vs. adults).

Measurement of breeding performance

4.3.2 Effects of Body Size on Breeding Performance

Of the four measures of breeding performance, brood size, lifetime reproductive success, and number of recruits were not normally distributed ($P < 0.05$, Kolmogorov-Smirnov tests) nor were those of transformed data ($\log_{10}[x+1]$). Therefore, I used nonparametric tests for analyses involving brood size and lifetime reproductive success (Zar 1984, Siegel and Castellan 1988). I also excluded zero values from the analyses involving brood size and lifetime reproductive success. I did this because complete breeding failures were usually due to stochastic events (i.e., shootings, nest tree destruction, etc.) and in this way did not reflect some biological inadequacy of the parents. To avoid pseudoreplication (Hurlbert 1984) correlation analyses only included data on individuals for the last time they were captured. To analyze the effect of body size on recruitment of offspring, I divided the data set into individuals that had produced at least one recruit and those that did not. I then used these as two

categories for an independent variable in a one-way ANOVA to test for differences in body size between those individuals (males and females separate) producing recruits and those that did not. Hatch date followed a normal distribution ($P > 0.05$, Kolmogorov-Smirnov tests), therefore I used linear regression to analyze the relationship between body size and hatch date (Zar 1984).

4.4 RESULTS

4.4.1 Body Size, Age and Selective Mortality

All morphometric variables followed a normal distribution pattern ($P > 0.05$, Kolmogorov-Smirnov tests). The morphometric measures and PC1 scores were all significantly repeatable for female Merlins and tarsus length was the only unrepeatable measure in males (Table 4.1). Wing chord had the highest repeatability of the univariate measures for both sexes (Table 4.1). Thus, the morphometric measurements as well as the PC1 scores were generally a reliable reflection of individual males and females (see also Wiklund 1996). In both males and females, total length and wing chord were the two variables most highly correlated with PC1 axis scores (Table 4.2). For subsequent analyses, I concluded that wing chord was the best single measure of body size in Merlins. I based this decision on several criteria: (1) it was one of the most repeatable and therefore precise measures, (2) it contributed heavily to the overall size of a bird as demonstrated by the PCA, (3) being an absolute measure (as opposed to a relative measure like PC1 score) it was

Table 4.1. Repeatability (r) based on ANOVA (Fr) of morphometric measures and PC1 scores for female and male merlins captured in Saskatoon (1985-95). Only those individuals captured two or more times were included in the calculation of repeatability. Yearling birds were included in the analyses.

Character	Females				Males			
	Mean (n)	SD	r	Fr (df)	Mean (n)	SD	r	Fr (df)
Mass	254.45 (260)	15.94	0.188	1.60* (63, 103)	166.41 (184)	11.47	0.508	3.48** (41, 59)
Total length	299.77 (265)	6.76	0.309	2.16** (68, 110)	269.63 (163)	6.48	0.367	2.37** (43, 60)
Tail length	134.32 (264)	3.97	0.373	2.54** (68, 110)	121.04 (181)	3.29	0.296	2.00** (42, 60)
Wing chord	219.37 (264)	4.49	0.721	7.65** (68, 109)	198.15 (184)	3.77	0.739	7.78** (43, 61)
Tarsus length	39.90 (265)	1.69	0.203	1.66** (68, 110)	36.63 (182)	1.54	-0.139	0.71 (43, 61)
Beak length	14.75 (265)	0.59	0.586	4.66** (68, 110)	12.41 (181)	0.60	0.656	5.50** (43, 60)
PC1 score			0.628	5.33** (63, 101)			0.745	7.98** (39, 55)

*= P<0.05, **=P<0.01.

Note: PCA was done for each sex separately, therefore both will have PC1 scores with a mean of zero and SD of one.

Table 4.2. Variable loadings on the first component of principal component analysis (PC of morphological measurements of merlins. PC1 captured 34.7% of the variance in female body size and 35.3 % of the variance in male body size. PCA was based on 225 female captures and 153 male captures.

Character	Females	Males
Mass (cube root)	0.425	0.694
Total length	0.783	0.736
Tail length	0.644	0.631
Wing chord	0.734	0.718
Tarsus length	0.394	0.277
Beak length	0.465	0.268

directly comparable across groups and studies, and (4) it was unaffected by sample size or extreme values. Only total length contributed more to the PCA scores, but, it was not nearly as repeatable a measure as wing chord. For males, PC1 score was highly repeatable, but I decided against its use based on points (3) and (4). Other recent analyses on body size in birds support this decision (Wyllie and Newton 1994, Wiklund 1996, but see Rising and Somers 1989, Freeman and Jackson 1990).

Among adults, surviving females ($F = 0.82$, $df = 1,3$, $P = 0.432$) and surviving males ($F = 1.61$, $df = 1,3$, $P = 0.29$) were not significantly different in size from those birds that died (Fig. 4.1). For yearlings, however, surviving males (mean wing chord = 196.6 mm, $n = 10$) were significantly bigger than those that died (mean wing chord = 194.1 mm, $n = 15$; $t = 2.10$, $P = 0.047$; Fig. 4.1). Females that survived their first year (mean wing chord = 219.4 mm, $n = 53$) were also significantly bigger than those that died (mean wing chord = 217.5 mm, $n = 63$; $t = 2.22$, $P = 0.029$; Fig.4.1).

For individuals that I first caught as yearlings and again as adults (age 2+), adult wing chord averaged 1.0 mm longer than when measured as yearlings for males and 0.46 mm longer in females. Neither difference was significant (one tailed paired t-tests; males $t = -1.05$, $n = 10$, $P = 0.16$; females $t = -0.96$, $n = 52$, $P = 0.17$). To have found a significant difference ($P = 0.05$) between first year and adulthood (given the sample sizes and variances), adult males' wing chord would have to be on average at least 1.84 mm longer and adult females 0.81 mm.

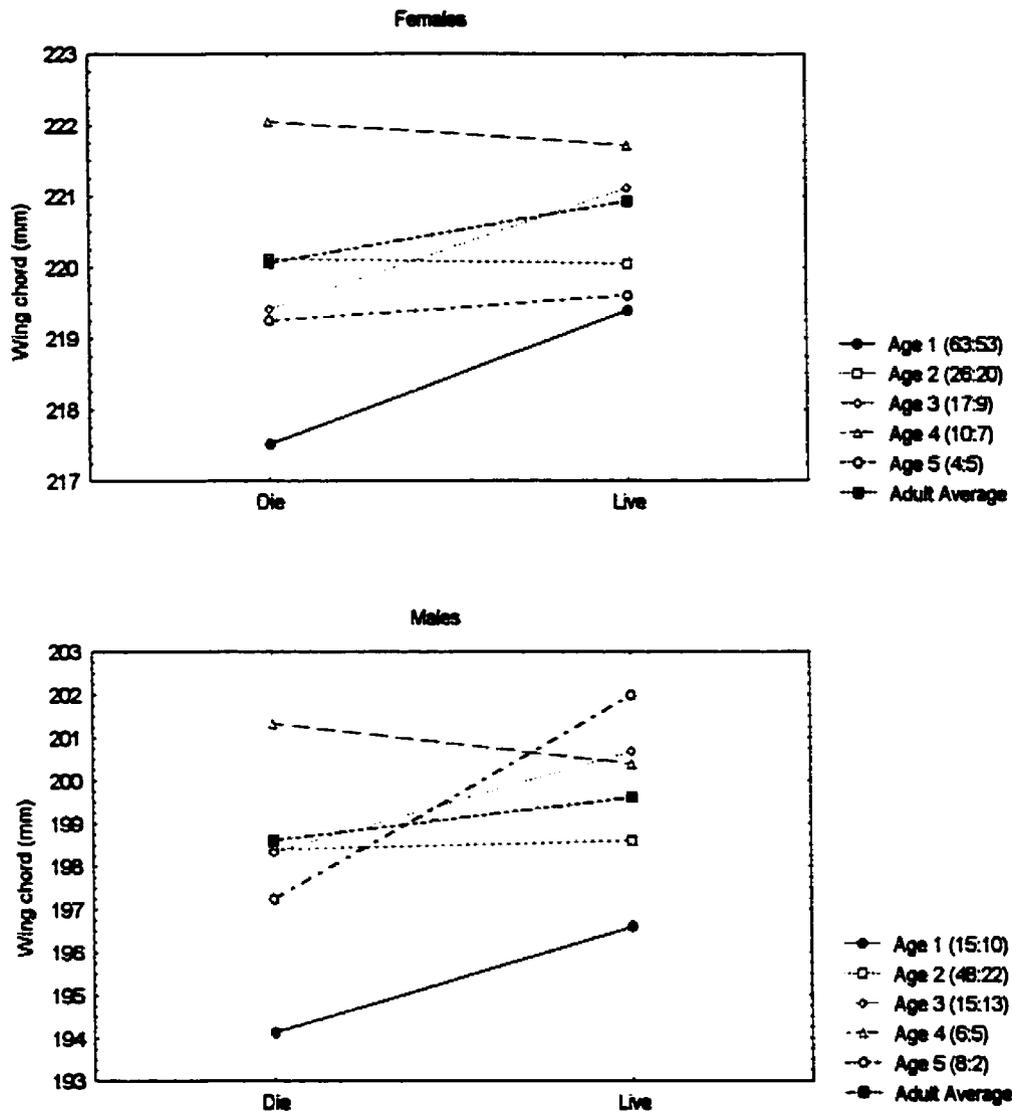


Figure 4.1. Mean wing chord for Merlins breeding in Saskatoon that survived past or died at a particular age. In yearlings, surviving birds were significantly bigger than those that died for females and males. Two-factor randomized block ANOVA tests (blocked for age effects) in adults (age 2+) revealed no significant overall difference in the wing chord of surviving versus dead females or males. Lines connect equal aged birds. Numbers in brackets indicate sample sizes for each age group (Die:Live).

4.4.2 Influence of Body Size on Breeding Performance

Wing chord was positively correlated with the brood size in yearling females ($\tau = 0.164$, $P = 0.010$) and significantly negatively correlated with brood size in yearling males ($\tau = -0.291$, $P = 0.052$; Fig. 4.2). There was no significant correlation between wing chord and brood size in adult female ($\tau = 0.022$, $P = 0.80$) or adult male Merlins ($\tau = -0.116$, $P = 0.126$; Fig. 4.3). Hatch date was negatively correlated with wing chord in yearling females ($r = -0.349$, $n = 112$, $P = 0.0016$) but was not correlated with wing chord in yearling males ($r = -0.024$, $n = 24$, $P = 0.91$; Fig. 4.4). Hatch date was not correlated with wing chord in adult female ($r = -0.195$, $n = 61$, $P = 0.13$) or adult male Merlins ($r = 0.130$, $n = 81$, $P = 0.25$; Fig. 4.5). Nonetheless, the relationships between wing chord and hatch date for adult males versus adult females was almost significantly different between the sexes ($P = 0.06$). Lifetime reproductive success was not correlated with wing chord in adult female ($\tau = 0.029$, $P = 0.738$, $n = 63$) or male Merlins ($\tau = -0.037$, $P = 0.62$, $n = 83$; Fig. 4.6).

During the study period a total of 1031 young were produced, all of which were banded. Of these chicks, only 61 individuals were recruited into the study area population (based only on captured birds with both sexes combined). Adult male and female Merlins that produced at least one recruit were not significantly different in terms of wing chord than those individuals that produced no recruits over their lifetime (Table 4.3).

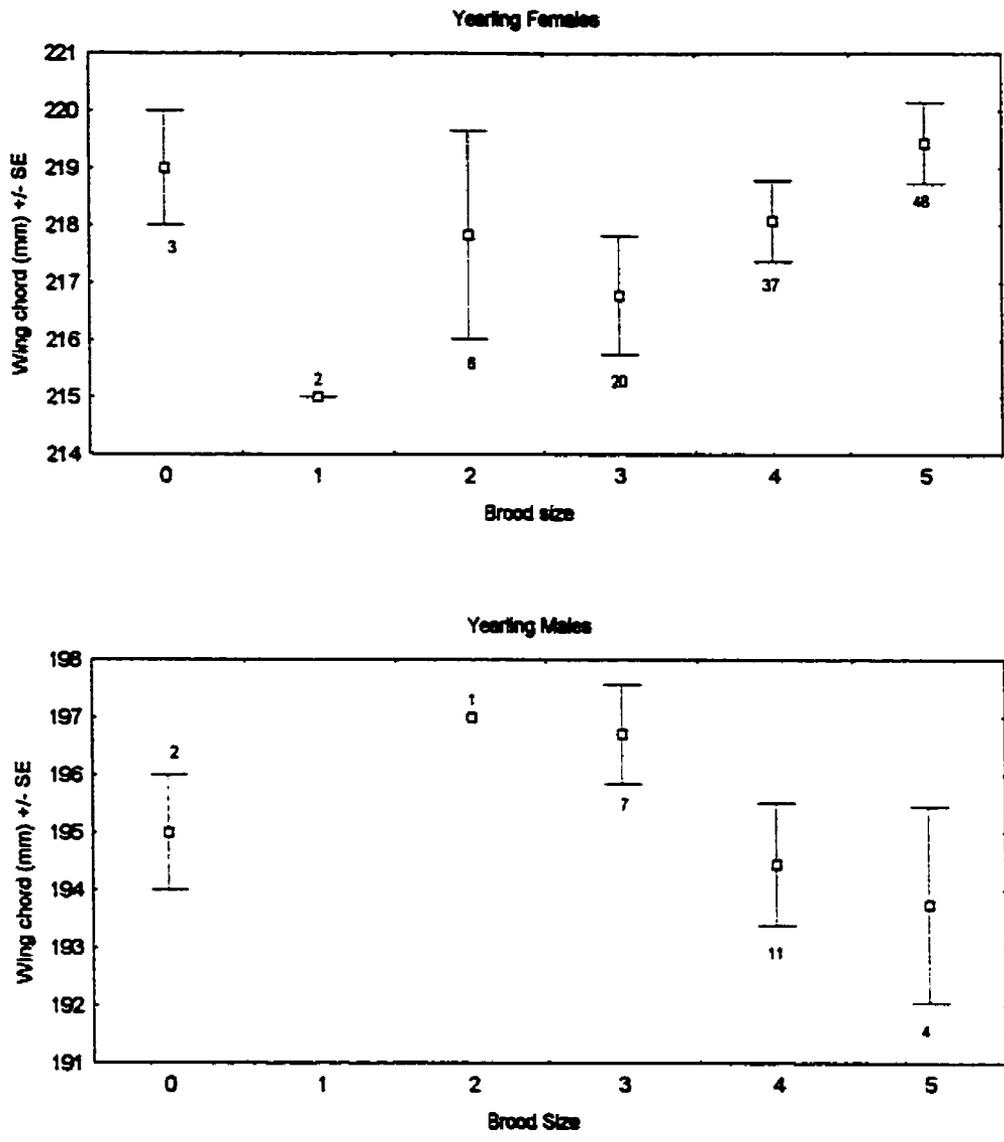


Figure 4.2. Mean wing chord and brood sizes of yearling Merlins breeding in Saskatoon. In females, brood size (excluding zeros) and wing chord were positively correlated and in males the two (excluding zeros) were negatively related. Numbers indicate sample sizes.

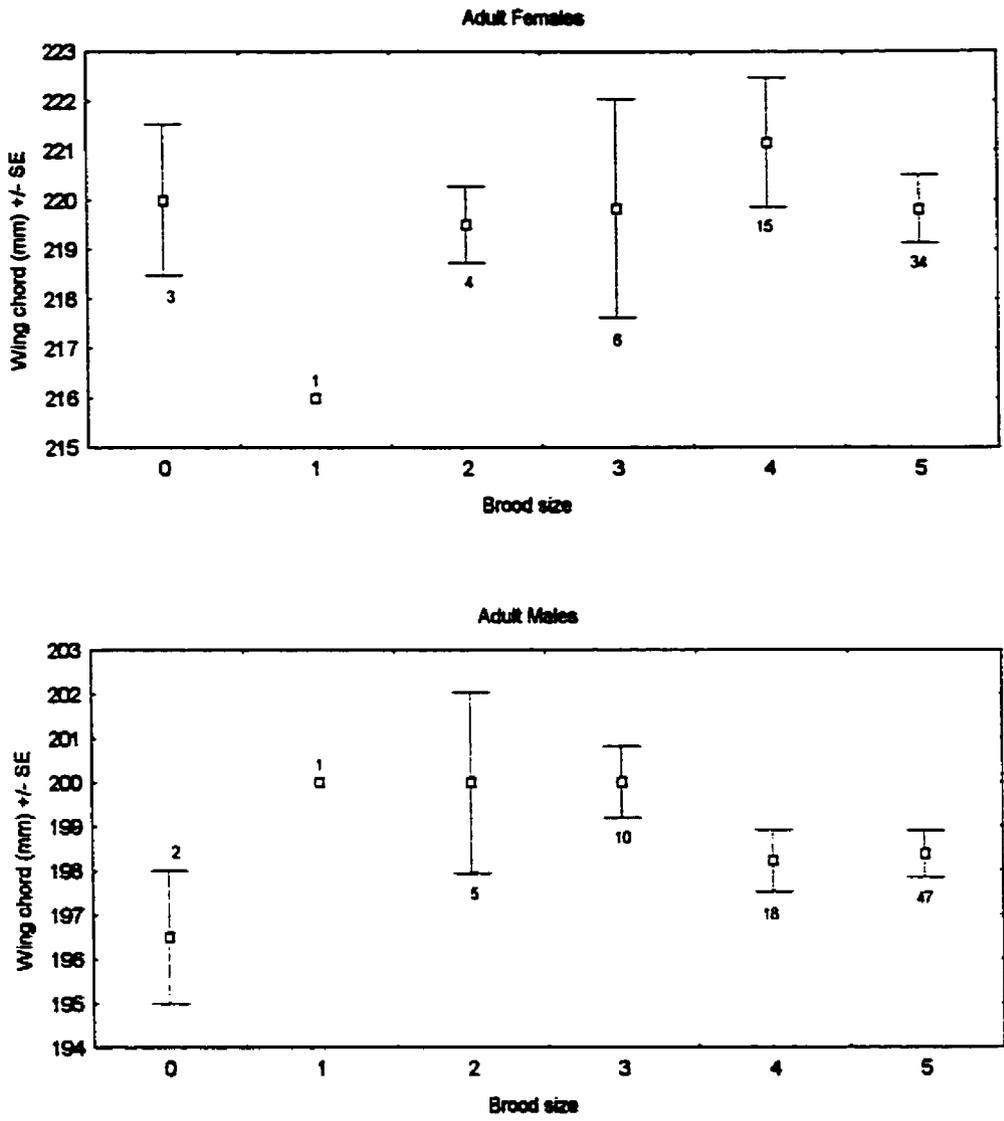


Figure 4.3. Mean wing chord and brood sizes of adult Merlins breeding in Saskatoon. In females, brood size (excluding zeros) and wing chord were not significantly correlated and in males the two were not significantly related. Only data from the last time a bird was captured are shown and included in the analysis. Numbers indicate sample sizes.

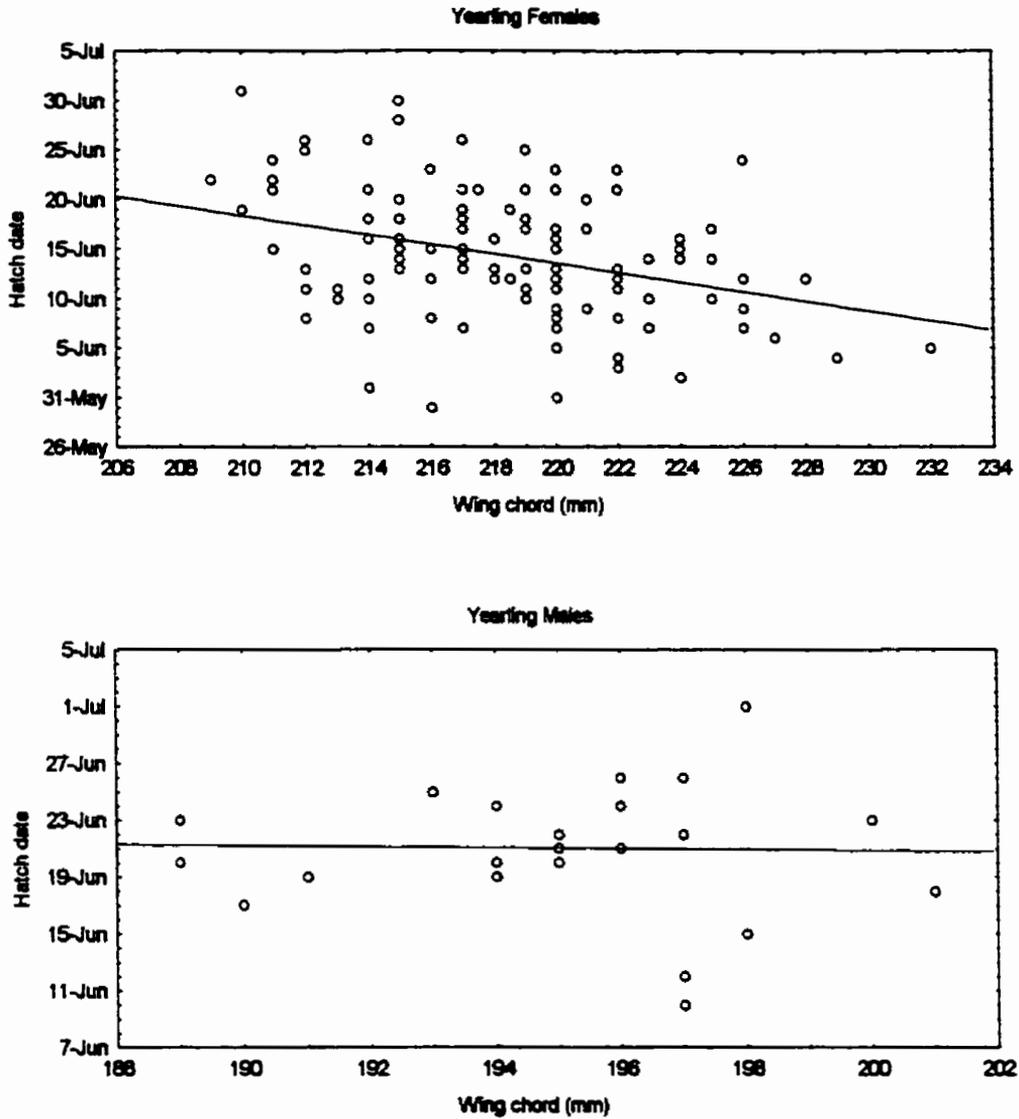


Figure 4.4. Scatter diagram of parent wing chord and chick hatch date for yearling female and yearling male Merlins breeding in Saskatoon. Chick hatch date and wing chord were significantly correlated in yearling females but not males. The line is a least squares line of best fit.

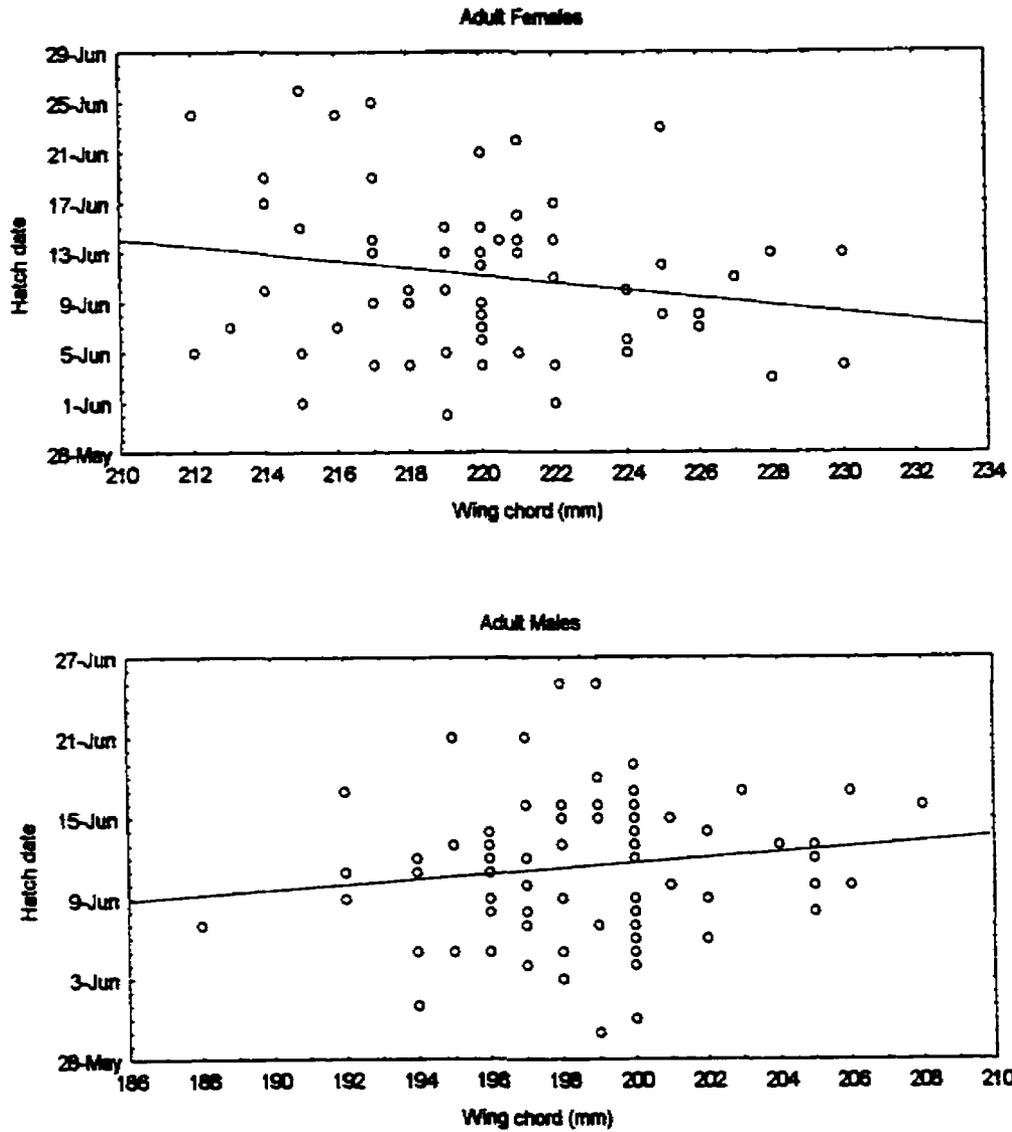


Figure 4.5. Scatter diagram of parent wing chord and chick hatch date for adult (age 2+) female and adult male Merlins breeding in Saskatoon. There is no significant relationship between hatch date and wing chord in either sex. The line represents a least squares line of best fit. Only data from the last time a bird was captured are shown and included in the analysis.

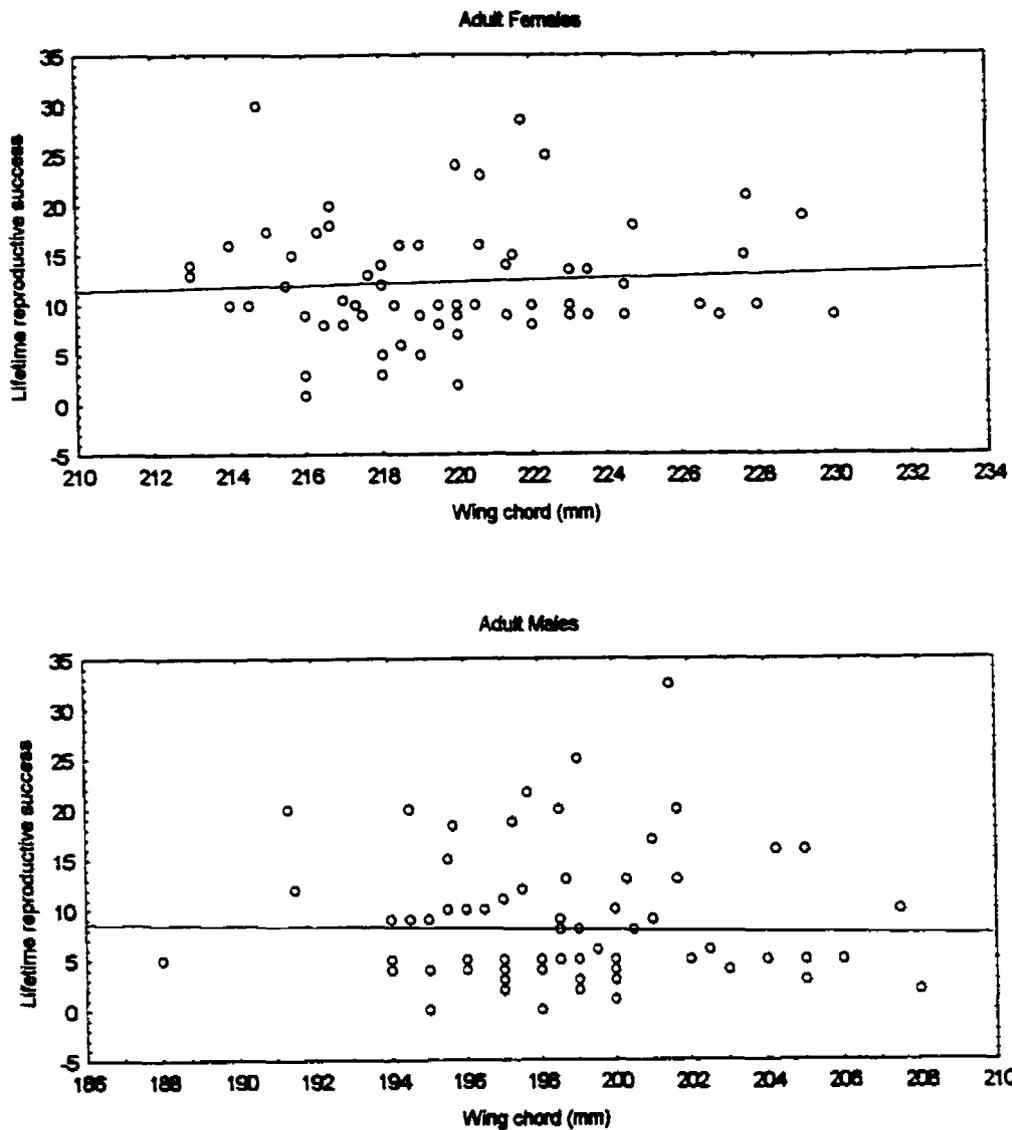


Figure 4.6. Scatter diagram of wing chord and lifetime reproductive success for adult (age 2+) female and adult male Merlins breeding in Saskatoon. There is no significant relationship between wing chord and LRS for either sex. Zero values were excluded from the analyses. The line represents a least squares line of best fit.

Table 4.3. Mean (+/- SE) wing chord for adult (age 2+) merlins that produced at least one recruit and those that produced no recruits over their lifetime. There were no significant differences found.

Sex	One + Recruit			No Recruits			F	P
	Mean	SE	n	Mean	SE	n		
Females	220.02	0.74	31	219.78	0.67	32	0.05	0.82
Males	198.43	0.59	30	198.74	0.48	55	0.16	0.69

4.5 DISCUSSION

4.5.1 Body Size, Age and Selective Mortality

Comparisons of wing lengths of yearling and adult birds revealed that the wings of older birds (particularly males) were significantly longer. This pattern is consistent with other work done on this and other sexually dimorphic species (Francis and Wood 1989, Warkentin et al. 1992, Weatherhead and Clark 1994, Wiklund 1996, but see Cade 1982, Marti 1990, Wyllie and Newton 1994). Some of this change in wing chord was likely caused by growth. However, the increase in wing chord of individual Merlins first caught as yearlings and again as adults was lower than the overall difference seen between yearling and adult birds. Moreover, among yearling male and female Merlins, larger individuals appeared to have higher survival or at least a higher likelihood of breeding again in the study area than smaller individuals. For adults, there was no evidence of selective mortality based on body size.

4.5.2 Influence of Body Size on Breeding Performance

Reproductive success most typically has been measured on a cross section of individuals from a population at one point in time. This method of collecting reproductive data suffers from several inherent flaws (see Clutton-Brock 1988, Newton 1989 for reviews), and the biggest drawback may be that cross sectional measures underestimate breeding performance by individuals. Newton (1985) was able to overcome these problems in underestimating reproductive success with his study of LRS in the Sparrowhawk (*Accipiter*

nisus), eventually concluding that lifespan was a major determinant of LRS as in other bird species (Newton 1989). Lifetime reproductive success in birds of prey has been studied in eight species: the Sparrowhawk (Newton 1985, 1988, 1989), the Osprey (*Pandion haliaetus*; Postupalsky 1989), the Tawny Owl (*Strix aluco*; Wallin 1988), the Eastern Screech Owl (*Otus asio*; Gehlbach 1989), the Ural Owl (*Strix uralensis*; Saurola 1989), Tengmalm's Owl (*Aegolius funereus*; Korpimäki 1992), the Merlin (Wiklund 1995) and the Barn Owl (*Tyto alba*; Marti 1997). Raptors are unusual among birds in that males appear to invest in offspring as much as, or more than, do females (Wijnandts 1984, Masman et al. 1988). Due to the difficulty involved in capturing male raptors, however, data on the breeding performance of males are scarce. For this study, each year on average $57.2 \pm 19\%$ (\pm SD) of males and $84.5 \pm 13.7\%$ (\pm SD) of females (Lieske et al. 1997) were captured. Thus, the estimates of LRS in male and female Merlins likely represent minimums.

Newton (1989) showed that in Sparrowhawks, larger females tend to have higher LRS than smaller ones. He explained that larger size may confer a survival advantage to these females and thus increase their LRS over smaller competitors. For male Sparrowhawks, there was a negative but non-significant relationship found between LRS and body size (Newton 1988). Korpimäki (1992) and Hakkarainen and Korpimäki (1991) found evidence suggesting that small male Tengmalm's Owls may have greater LRS than larger males in that small size allows them to produce young in both poor and good food years.

This notion is supported by experimental evidence showing that food stress influences brood size (Wiehn and Korpimäki 1997) and future reproductive output (Rohwer et al. 1996). The results suggest that production of offspring in Merlins is influenced by body size. In general, bigger female Merlins produced larger broods while smaller males tended to be more successful. The best evidence comes from the analyses of yearling breeders as I can be certain that these birds had equal prior breeding experience. Among male yearling breeders wing chord was significantly negatively correlated with the number of young produced. For yearling females the trend was significant, but, in the opposite direction. Although I did not examine whether food availability varied during the study period, the results from yearling Merlins support the idea that small males are superior breeders. For adults though, body size appeared to have no significant influence on brood size or lifetime reproductive success. Perhaps other factors such as age and experience (Chapter 3) are more important in determining the production of young in Merlins once birds reach adulthood.

Reproductive success has been shown to vary seasonally in a number of animal taxa including: fish (Schultz 1993), mammals (Clutton-Brock et al. 1982), and insects (Ohgushi 1991). Seasonal declines in reproductive success have been well documented in birds (Lack 1950, Perrins 1970, Newton and Marquiss 1984, Daan et al. 1988, Verhulst et al. 1995). In addition, time of breeding may influence the survival of offspring. Chicks that hatch early in the

season often survive better than late hatching individuals (Perrins 1965, Cooke et al. 1984, Martin and Hannon 1987). Previous work has shown that Merlins in Saskatoon time their breeding so that the fledging phase falls during the time of peak production of juvenile House Sparrows (*Passer domesticus*; Sodhi and Oliphant 1993). Thus, it appears that Merlins attempt to exploit this particularly vulnerable food supply. Other workers have reported increased predation on juvenile prey individuals as the Merlin breeding season progresses (Newton et al. 1984). Secondly, the timing of molt is of fundamental importance for Merlins as they must renew their feathers at the same time as raising offspring (Espie et al. 1996) and all of this must be accomplished before fall migration. Thirdly, early hatching is adaptive for chicks because they have more time available for practising hunting and for accumulating body reserves before winter as has been shown for other raptors (Korpimaki 1987). Therefore, I equated Merlins having an earlier hatch date with being superior breeders. For yearling female Merlins it appears that bigger birds tended to breed earlier than smaller ones. This finding agrees with Newton's (1988) data on female Sparrowhawks which showed that heavier females tended to breed earlier. In northern climates it has been speculated that bigger individuals may have an advantage over smaller ones in that they may be able to return earlier to breeding areas (Weatherhead and Clark 1994) or in the case of the Merlin, be able to remain on the breeding area the year round (Warkentin et al. 1990). Moreover, larger birds may be able to acquire better mates or territories by force even if they

arrive at the same time as smaller birds, and in this way be able to breed sooner. Thus, both dominance and bioenergetic constraints may favour large body size during the winter and early spring (Warkentin et al. 1990, Weatherhead and Clark 1994). In male Merlins, body size appears to have less influence on the time of breeding. For yearling and adult males, there was no significant relationship between wing chord and hatch date. It has been suggested that male raptors in general have some control over hatch date, because males of many RSD species (Merlins included) provide almost all food for the female during the early part of the breeding season (Newton 1979, Sodhi et al. 1992). My results did not support this idea.

The number of recruits produced by an individual over its lifetime is another useful measure of breeding performance. It has been stated that this may in fact be the best overall measure of reproductive success (Hepp et al. 1989, Newton 1989). For the Sparrowhawk, the number of recruits produced was correlated with LRS (Newton 1989). One might have expected that recruitment in Merlins to also be related to body size given that brood size and lifetime reproductive success were influenced to some extent by body size. The results showed, however, that parent size did not affect whether or not recruits were produced.

In conclusion, selective mortality associated with body size in yearling Merlins results in larger individuals of both sexes to be more likely to survive until the next breeding attempt. Among adults, selective mortality associated

with body size is weaker or non-existent. Body size also influences brood size and hatch date in Merlins, with small males and large females being the most successful breeders. Again, the effects are most evident in yearling birds with no previous breeding experience, but, more importantly though this study clearly shows that there exists different optima for each sex. Thus, for males there is a distinct trade-off, in early life at least, between survival and reproduction with respect to body size which supports the sexual selection hypothesis and life-history theory (Stearns 1992). To my knowledge this is the first study to clearly show this in a RSD species. It appears that female Merlins are not faced with this trade-off. Other factors not studied here acting both inside and outside the breeding season probably limit upper female body size.

5. MATE CHOICE FOR BODY SIZE AND CONDITION AND ITS INFLUENCE ON BREEDING PERFORMANCE

5.1 ABSTRACT

In this chapter I tested whether mate choice for body size (wing chord) and body condition (mass corrected for size) was repeatable in Merlins. In addition, I examined what affect these two factors had on breeding performance within mated pairs and whether they were heritable. For this paper I used three parameters to assess breeding performance: brood size, chick hatch date, and lifetime reproductive success (LRS). I calculated heritability from mid-parent on offspring regression. In the analyses I found that female choice of male body size was nearly repeatable, but, female choice for male body condition was not. There was no repeatability of choice by male Merlins for females body size or condition. Within mated pairs, larger females had significantly higher LRS and tended to have earlier chick hatch dates. There was no effect of male body size on any of the measures of breeding performance. Body condition of neither males nor females influenced breeding performance within mated pairs. Body size showed high heritability between parents and offspring, whereas, body condition did not. Characters closely related to fitness are generally thought to have low heritability. However, body size in Merlins may have higher

heritability because it is subject to less environmental influence than body condition.

5.2 INTRODUCTION

Nonrandom assortment of breeding pairs can arise through intersexual selection (mate choice) Darwin (1871). For organisms that reproduce sexually, some form of mate choice is likely beneficial. In most cases it is thought that only females exhibit mate choice because they tend to have greater reproductive investment (Trivers 1972, Williams 1975). Among monogamous species with biparental care, however, mate choice by both sexes may be expected (Trivers 1972, Sargent et al. 1986, Johnson 1988a, b, Gwynne and Simmons 1990, Jones and Hunter 1990, Johnstone et al. 1996, but see Dale and Slagsvold 1994). Mate choice in avian field studies has often been investigated by determining whether behavioural or morphological attributes are distributed nonrandomly among mated pairs (Searcy 1982, Johnson and Marzluff 1990). However, a nonrandom distribution does not necessarily mean that mate choice within individuals is consistent nor repeatable. Models of mate choice assume that there is a genetic component to individual preferences (Kirkpatrick and Ryan 1991, Møller 1994). If this is so, then mate choice should show some degree of consistency (Møller 1994). One can use repeatability analysis to estimate the consistency of mate choice, whereby, the amount of variance within individuals is compared to the total within and between individual variance of mate characteristics (Boake 1989, Møller 1994).

Traditionally, life history studies have looked at reproductive fitness in relation to the characteristics of individuals of only one sex (Clutton-Brock 1988, Newton 1989). This approach is less useful when parents share in the reproductive effort as is the case for many monogamous bird species including raptors (Newton 1979). In birds of prey for instance, where reversed sexual size dimorphism (RSD) is the norm, small males and large females are thought to be superior breeders (Newton 1979, 1988, Hakkarainen and Korpimäki 1991, Chapter 4). Thus, the combination of large females paired with small males should have increased breeding performance compared to other pairings. Other workers have posited that in birds the compatibility or complementary nature of mates may influence the breeding performance of both partners (Coulson 1972, Marzluff and Balda 1988, Choudhury et al. 1996, Ens et al. 1996). In order to show support for the compatibility hypothesis one must show that an individual does better with a mate of similar type than with a higher quality but dissimilar mate.

Warkentin et al. (1992) showed that Merlins mate assortatively and other work on Merlins has shown that body size and condition are related to breeding performance (Chapters 4 and 6). In this paper, I test for repeatability of female and male mate choice of body condition and wing chord (i.e., body size) in Merlins. I also test whether certain pairings (based on body size and body condition) resulted in improved breeding performance in Merlins. In addition, I regress mid-parent body condition and wing chord against those of their

offspring in order to calculate the heritability of the two traits.

5.3 METHODS

5.3.1 Quantification of body condition and body size

Ideally, one would directly measure fat content to measure body condition but this can be difficult to do in the field for a number of reasons. More typically ecologists have estimated body condition by comparing body mass or other measures of nutritional state among individuals after controlling for absolute body size (Jakob et al. 1996). For Merlins, six morphometric measures were recorded (see Espie et al. 1996 and Chapter 4) whenever breeding birds were captured. For this study to estimate overall body size in Merlins I used the length of the unflattened wing chord (measured to nearest 1.0 mm) as this measure was the best estimate of overall body size (Chapter 4; see Wyllie and Newton 1994, Wiklund 1996 for similar conclusions, but see Rising and Somers 1989, Freeman and Jackson 1990). Based on the recommendations of Jakob et al. (1996) I quantified body condition in Merlins by using the residual scores from a regression of the cube root of body mass (mass measured to nearest 1.0 g) on wing chord. The residual index is the most reliable estimate of body condition because it does not vary with body size as other estimates of condition do (e.g., ratio index, Jakob et al. 1996). I classified body condition indices as poor, medium or good (Marti 1990, Chastel et al. 1995). I did this by standardizing body condition indices ($Z = (X - \bar{X})/SD$) so that the distributions would have a mean of zero and a SD of 1.

Standardized condition indices were then categorized as poor ($Z < -0.43$), medium ($-0.43 < Z < 0.43$) and good ($Z > 0.43$) (Marti 1990, Chastel et al. 1995). I also classified body sizes of male and female Merlins as small, medium and large in the way outlined above. Body conditions and body sizes were calculated separately for males and females.

5.3.2 Analyses

I tested for repeatability of mate choice by male and female Merlins for body condition and wing chord (i.e., body size) measures by one-way analysis of variance (ANOVA). This analysis quantified the amount of within-individual variance relative to the total (within and between) individual variance in mate wing chord and body condition measures (Zar 1984, Lessells and Boag 1987, Møller 1994). Only those birds that were mated to different individuals (in subsequent years) were included in the repeatability analyses.

In order to test for the effects of body size and body condition of male and female parents I used two factor non-parametric ANOVA because the design was unbalanced (i.e., unequal replication, Zar 1984) and both brood size and LRS did not follow a normal distribution pattern ($P < 0.05$, Kolmogorov-Smirnov tests). The male parent acted as one factor and the female the other. For hatch date and brood size, mean values for a particular female (and her mates) were used so that individuals appeared no more than once in the analysis. I excluded zero values from the analyses involving brood size and lifetime reproductive success. I did this because complete breeding failures

were usually due to stochastic events (i.e., shootings, nest tree destruction, storms, etc.) and in this way did not reflect some biological inadequacy of the parents.

In order to calculate the heritability of body size and body condition in Merlins, I regressed the mid-parent wing chord and body condition measures with those obtained from male offspring that returned to breed in Saskatoon. I used only male offspring for this analysis as they return to breed in the study area much more often than females and thus sample sizes were higher. Heritability (h^2) was calculated as the slope (b) of the linear regression (Falconer 1981).

All tests were two-tailed and considered significant when $P < 0.05$. All statistical tests were computed using Statistica for Windows (V 5.1) (StatSoft Inc. 1995).

5.4 RESULTS

There was no repeatability of female choice for male body condition ($r = 0.083$, $F = 1.21$, $df = 20, 29$, $P = 0.31$) but for male wing chord female choice was nearly repeatable ($r = 0.247$, $F = 1.77$, $df = 23, 33$, $P = 0.064$). Even so, a regression of female wing chord on mates' wing chord did not show a significant trend ($r = 0.101$, $n = 24$, $P = 0.64$, Fig. 5.1). Among males there was no repeatability of choice for female body condition ($r = -0.217$, $F = 0.58$, $df = 24, 34$, $P = 0.92$) or female wing chord ($r = -0.234$, $F = 0.56$, $df = 25, 35$, $P = 0.93$).

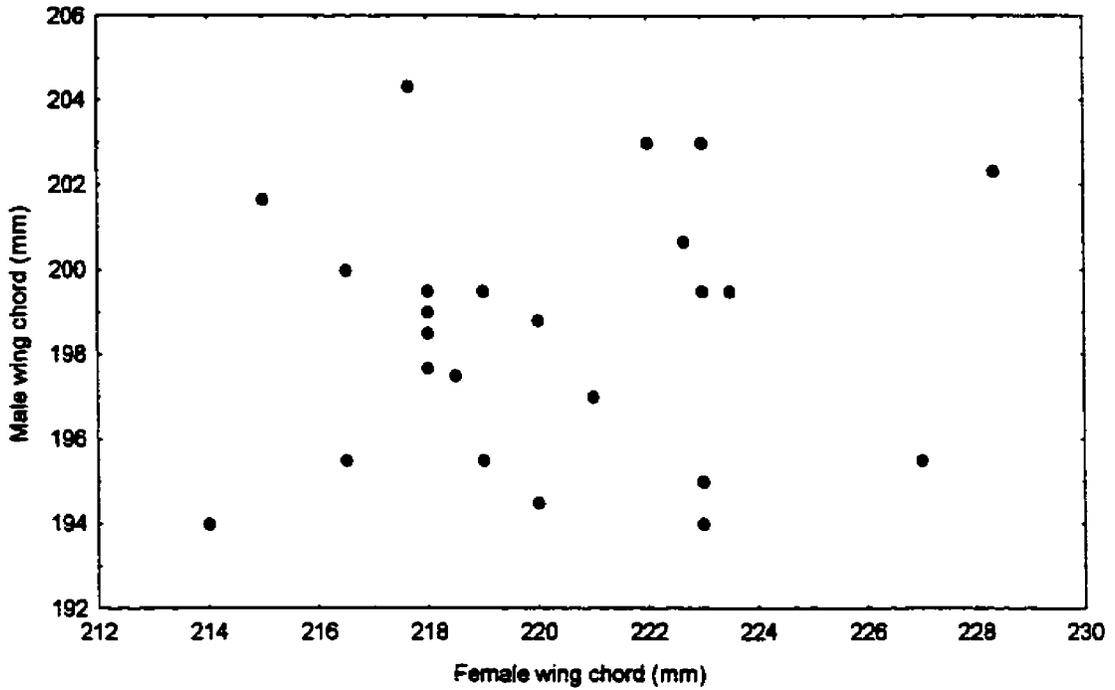


Figure 5.1. Scatter diagram of mean female wing chord and mean mates' wing chord for Merlins captured in Saskatoon. Only those females having two or more mates (different individuals) are included in the diagram. There is no significant relationship between female and mates' wing chord.

Two factor non-parametric ANOVA revealed that for mated pairs female body size influenced LRS and to a slightly lesser extent hatch date (Tables 5.1 and 5.2). The trend was for bigger females to have higher LRS and earlier hatching chicks (Table 5.2 and Fig. 5.2). There was no effect of male body size on breeding performance in mated pairs.

Based on the regression, there was no significant relationship between mid-parent and offspring body condition ($r = 0.099$, $n = 22$, $P = 0.66$, $h^2 = 0.032$, Fig. 5.3). However, there was a highly significant relationship between mid-parent and male offspring wing chord ($r = 0.633$, $n = 22$, $P < 0.01$, $h^2 = 0.624$, Fig. 5.4).

5.5 DISCUSSION

Choosing a particular mate can have direct benefits and influence things such as hatch date and the number of offspring produced. Indirect benefits may arise when benefits are manifested in increased fitness of the offspring (Promiankowski 1988, Promiankowski et al. 1991). Tests of assortative mating in Merlins showed that the productivity of pairs which included a yearling member was significantly lower than that of pairs with two adult birds (Warkentin et al. 1992). In their study Warkentin et al. (1992) were not able to conclusively show that assortative mating occurred between Merlins based on body size. Other studies have also shown no assortative mating based on body size in birds of prey (Marti 1990, Village 1990, Bortolotti and Iko 1992). In this study I show that there is a nearly statistically significant (and likely

Table 5.1. Results of nonparametric ANOVA tests for effects of body condition on breeding performance of male and female Merlins caught breeding in Saskatoon, Saskatchewan from 1985 to 1995.

hatch date			
Factor	df	H	P
Female	2	2.18	0.34
Male	2	1.08	0.58
Fem x Mal	4	2.05	0.73
brood size			
Female	2	1.48	0.48
Male	2	0.57	0.75
Fem x Mal	4	1.85	0.76
LRS*			
Female	2	3.51	0.17
Male	2	0.62	0.73
Fem x Mal	4	2.88	0.58

* LRS was calculated for an individual female and her mates.

Table 5.2. Results of nonparametric ANOVA tests for effects of body size on breeding performance of male and female Merlins caught breeding in Saskatoon, Saskatchewan from 1985 to 1995.

hatch date			
Factor	df	H	P
Female	2	5.41	0.067
Male	2	0.45	0.8
Fem x Mal	4	2.90	0.57
brood size			
Female	2	1.62	0.45
Male	2	0.09	0.95
Fem x Mal	4	2.91	0.57
LRS*			
Female	2	6.11	0.047
Male	2	0.17	0.92
Fem x Mal	4	2.57	0.63

* LRS was calculated for an individual female and her mates.

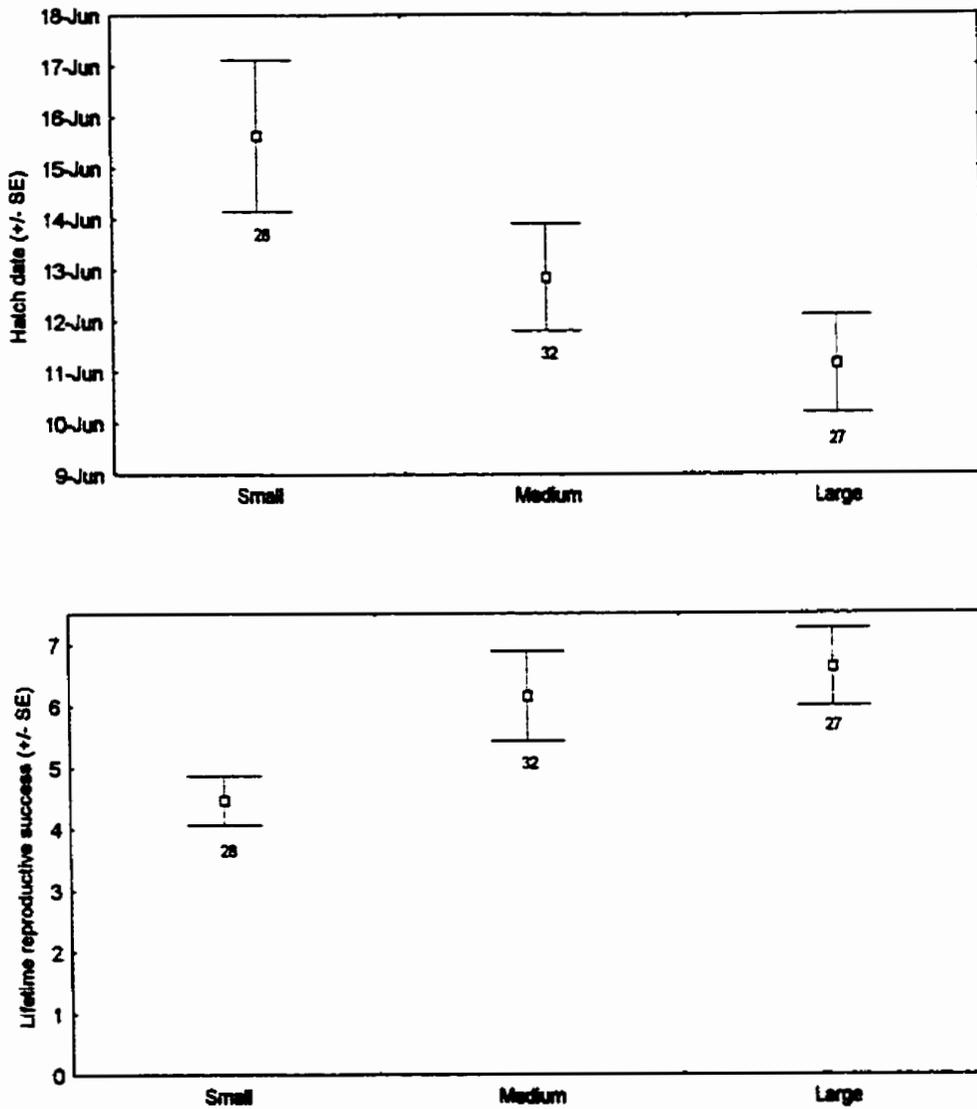


Figure 5.2. Lifetime reproductive success (LRS) and mean hatch date for different size female Merlins in Saskatoon. Large females had significantly higher LRS than small females (Dunn's test, $P < 0.05$). There were no other significant differences found.

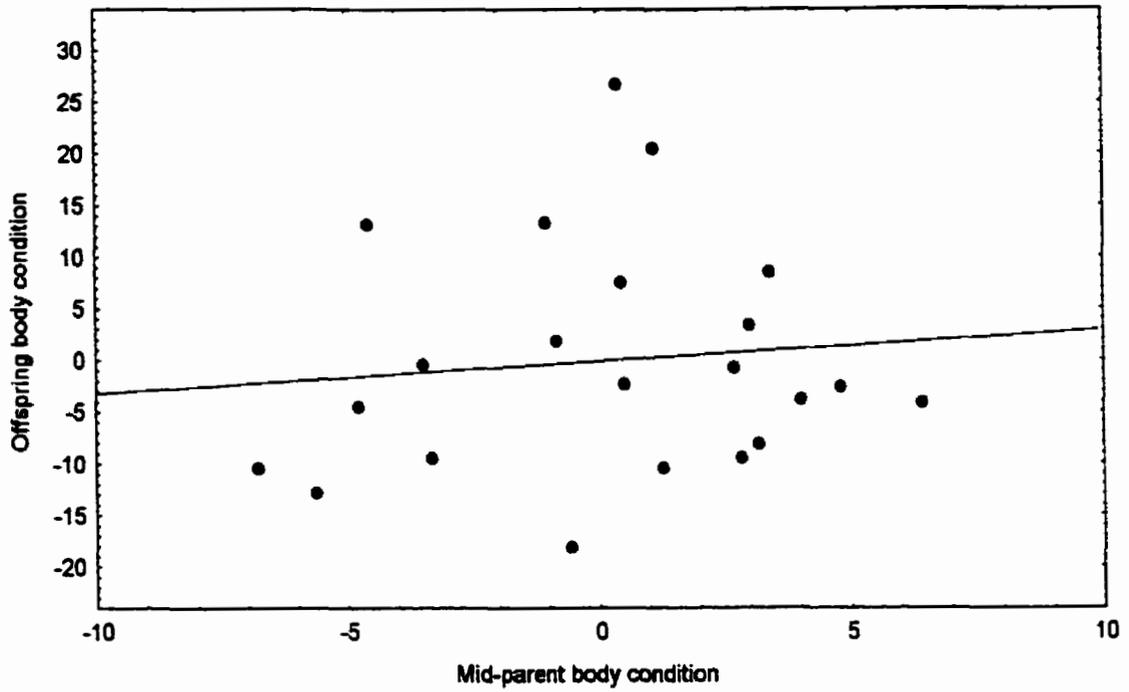


Figure 5.3. Scatter diagram of mid-parent body condition and male offspring body condition for Merlins in Saskatoon. There is no significant relationship between the two. The line represent a least-squares line of best fit.

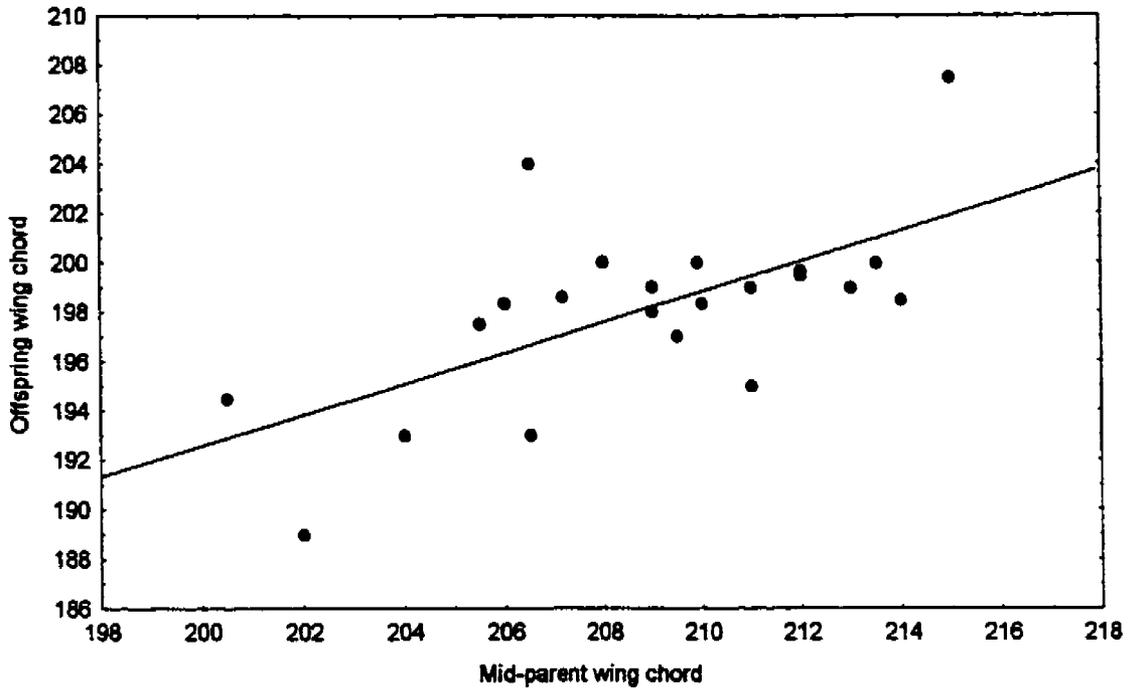


Figure 5.4. Scatter diagram of mid-parent wing chord and male offspring wing chord for Merlins in Saskatoon. Heritability ($h^2 = 0.624$) was calculated from the slope of the regression.

biologically significant) degree of repeatability in female choice of males based on wing chord (i.e., body size). Even so, for the same sample of pairings there was no trend for big (or small) females to be paired consistently with big or small males. This suggests to me that individual female Merlins consistently chose males of a particular size, but, that it was not necessarily in relation to their own size. Another possibility is that repeatability came about through restrictive means (e.g., males already paired and inaccessible) rather than by choice alone, and only males of a particular size were available to certain females. Female Barn Swallows (*Hirundo rustica*) appear to mate assortatively based on tail length (Møller 1992) and their choice of mates is repeatable and based on those males that are locally available Møller (1994). There was no repeatability of choice by male or female Merlins in terms of body condition of mates. Bortolotti and Iko (1992) found that American Kestrels mated assortatively based on body condition, but, they did not test whether mate choice for body condition was repeatable in kestrels.

Numerous hypotheses have been put forward to explain reversed sexual size dimorphism in raptors (Safina 1984, Mueller and Meyer 1985, Mueller 1986, Pleasants and Pleasants 1988). Previous work examining the Merlin sexes separately showed that smaller yearling males tend to have larger brood sizes and bigger yearling females had larger broods and earlier hatch dates. For both sexes bigger birds were more likely to survive to breed again. These trends did not hold for adult Merlins (Chapter 4). The results from this study

suggest that female body size alone influences LRS and to some extent hatch date with the trend being for larger females to have higher LRS and breed earlier. I caution readers that the results in this study could be partly influenced by the fact that I did not separate yearlings from adults as I did previously. Nevertheless, evidence from both studies suggests that the influence of male body size on breeding performance in Merlins is very limited. It has been suggested that male raptors in general should have some control over reproduction, because males of many RSD species (Merlins included) provide almost all food for the female during the early part of the breeding season (Newton 1979, 1988, Sodhi et al. 1992). It has been speculated that low resources at the beginning of the breeding season allow smaller males to be more efficient at providing food for their mostly inactive mates (Hakkarainen and Korpimäki 1991) or that small males are simply better hunters (Mueller 1986, Newton 1986, 1988). Even so, the results provide no evidence that particular pairings of Merlins (e.g., small males and large females) have higher breeding performance than other groupings and along the same lines, there was no evidence to support the compatibility hypothesis.

Body condition may be an important predictor of breeding performance in birds, given that the amount of reserves available will likely act on the rate of energy expenditure devoted to breeding (Drent and Daan 1980). Timing of reproduction and clutch size have been shown to be correlated with body condition in waterfowl (Ankney and MacInnes 1978, Raveling 1979, Cooke et

al. 1984, Alisauskas and Ankney 1985) and passerines (Price et al. 1988, reviews by Daan et al. 1988 and Meijer et al. 1988). From this study, however, there was no evidence suggesting that body condition within pairs was related to breeding performance and there was no support for the compatibility hypothesis either. This is in contrast to another study where I examined the sexes separately and found that body condition in female Merlins was negatively correlated to both hatch date and LRS (Chapter 6). For male Merlins, individuals in good condition tended to have smaller broods than those in poor condition (Chapter 6). It appears then, that these effects of body condition on breeding performance were 'cancelled out' when I considered the sexes in unison. Even if this is true, there was no repeatability of mate choice for body condition in either sex.

The question of how heritability and fitness are related is central to evolutionary biology and life history theory. In general, theoretical and empirical work has shown lower heritability for traits that exert strong influence on reproductive fitness either because little genetic variance remains in a population at equilibrium or because they are subject to additional environmental noise (Falconer 1981, Gustafsson 1986, Price and Schluter 1991). For Merlins, body size has high repeatability and heritability and for body condition the corresponding values are much lower (this study and Chapter 4). For Tree Swallows (*Tachycineta bicolor*) tarsus length was highly heritable whereas body mass was not (Wiggins 1989). In comparison, Phillips

and Furness (1999) showed high heritability for body condition in Arctic Skuas (*Stercorarius parasiticus*). Typically morphological traits (e.g., wing chord, beak length) show higher heritability because they are subject to less environmental influence than measures such as body condition (Price and Schluter 1991, Schluter and Gustafsson 1993). Therefore, while apparently counter to Fisher's theorem, the high degree of heritability for wing chord in Merlins is not completely at odds with the general trend for morphological traits in other birds.

Finally, the fact that large Merlin pairs tended to produce large offspring comes as no shock. However, the finding is interesting in that much work has suggested (and some shown) that smaller males and larger females tend to be superior breeders in RSD species. What may have been overlooked is the fact that large males can compensate for their inferiority by producing large female offspring. The same would hold true for small female Merlins producing small male offspring.

6. INFLUENCE OF TERRITORY QUALITY, BIRD QUALITY AND BODY CONDITION ON BREEDING PERFORMANCE

6.1 ABSTRACT

I examined the effects of territory quality, body condition and bird quality on breeding performance in male and female Merlins (*Falco columbarius*) from a long-term study in Saskatoon, Saskatchewan. In addition, I examined whether territory quality and body condition influenced survival, as well as, the production of recruits and lifetime reproductive success (LRS). For females, territory quality had little influence on any of the measures of breeding performance or survival. Even so, when females switched territories, they tended to move to ones of higher quality. Females in poorer body condition tended to have earlier chick hatch dates and higher LRS. Hatch date was repeatable for the same females occupying different territories but not for the same territories occupied by different females. Among males, birds surviving past each age category tended to occupy territories of higher quality and LRS was positively correlated with territory quality. The relationship between territory quality and LRS was heavily influenced by the poorest territories. When males switched territories, they too tended to go to ones of higher quality. Body condition had little influence on breeding performance or survival

in male Merlins. In addition, chick hatch date was not repeatable for the same males occupying different territories nor for the same territories occupied by different males. The differences between the sexes are likely a consequence of the differing roles the two parents play in reproduction. Male Merlins provide most of the food for the pair and their young during the breeding season and differences in habitat quality may have affected the effort needed by males to secure food. Females appear to have considerable control over the timing of breeding and their body condition is related to breeding performance.

6.2 INTRODUCTION

Differential breeding performance in birds is attributable to some degree to differences in either the quality of the birds themselves or the quality of the habitat chosen for breeding. Any effects of bird condition and quality could interact with the quality of habitat occupied and thus confound any interpretations of the effect of each factor alone. Most studies concentrate on one of the two aforementioned areas without considering the other (but see Högstedt 1980, van Noordwijk et al. 1980, Newton and Marquiss 1984, Goodburn 1991).

The breeding habitat of most species is not uniformly distributed in space and time, but rather, occurs as discrete habitat patches. As habitat changes, it becomes more or less suitable for species to breed in. This territory quality is thought to be a major factor in determining breeding performance in many territorial animal species (reviews in Newton 1992, Rodenhouse et al. 1997).

For example, the majority of land birds (81% of non-passerines and 84% of passerines) breed in pairs on territories (Lack 1968). Territories may differ widely in what they provide to their occupants (e.g., food resources, a refuge from predation, a nest building site, etc.; Rodenhouse et al. 1997). Various lines of evidence have been used to infer the existence of variation in territory quality. These have been reviewed by Ens et al. (1992). Although not as robust as those studies which are able to directly link territory quality to habitat features or critical resources, one of the most common procedures is to rank territories on the basis of the permanency of occupancy during the study period. Usually a positive relationship is found between the territory rank or quality and breeding performance (Ens et al. 1992, Newton 1991). However, a key difficulty with determining territory quality is to develop a measure that predicts breeding success, but, is measured independently of the performance or quality of the individuals breeding there (Newton 1991).

Life history theory predicts that parents should balance their current investment in offspring against their chances of survival and future reproduction (reviewed in Roff 1992, Stearns 1992) and thus, an individual's physiological state is potentially related to its evolutionary fitness. In birds, body condition may be an indicator of past foraging success, environmental stresses, and local food supplies. Body condition also may be an important predictor of breeding performance in birds given that the amount of reserves available will likely act on the rate or total amount of energy expenditure devoted to breeding (Drent

and Daan 1980). Timing of reproduction and clutch size have both been shown to be correlated with body condition in waterfowl (Ankney and MacInnes 1978, Raveling 1979, Cooke et al. 1984, Alisauskas and Ankney 1985) and passerines (Price et al. 1988, reviews by Daan et al. 1988 and Meijer et al. 1988). In some birds, however, breeding performance may depend more on direct input from foraging rather than on body reserves (Drent and Daan 1980, Winkler and Allen 1996) and in more abstract terms, the quality of individuals (foraging skills, nest defence, etc.; Coulson 1968, Coulson and Porter 1985, Coulson and Thomas 1985, Slagsvold and Lifjeld 1990, Riddington and Gosler 1995). In Sparrowhawks (*Accipiter nisus*), breeding performance is related to the body weight of females, with the most productive birds attaining and maintaining relatively high weights throughout the breeding season (Newton and Marquis 1984).

In this chapter, I examine the separate effects of territory quality and body condition and quality of parents on brood size and hatch date in Merlins. I also test whether habitat quality and body condition impact survival and more general measures of fitness such as Lifetime Reproductive Success (LRS) and recruitment.

6.3 METHODS

6.3.1 Quantification of Territory Quality

Like other falcons, the Merlin does not build its own nest. A previous study of nest site selection revealed that Merlins in Saskatoon show a

significant preference for breeding in old American Crow (*Corvus brachyrhynchos*) nests in the numerous spruce trees (*Picea* spp.) that have been planted in residential areas (Warkentin and James 1988).

Following Newton (1991), I assessed territory quality based upon temporal occupancy of nest places. I denoted nest place occupancy by determining if a nest in any particular year was closer to a nest used in a previous year or to its nearest neighbour in the same year. If a nest was closer to an old nest site then the pair was classified as occupying that nest place. If a nesting pair was closer to its nearest neighbour then I classified it as a new nest place. To account for changes in territory quality over time, I graded each nest place by giving it a separate score for each year, depending on its occupancy in a moving five-year period, centered on the year in question (Newton 1991, Espie et al. 1996). For example, nest places in 1987 were given a score (1-5), equal to the number of years occupied in the period 1985-1989. Nest places for the last two years of study were graded on occupancy in the last five years of the study. To examine the effect of territory quality on LRS I used the average score of all known nest places occupied by a bird during its lifetime. In this paper I equate nest place with territory.

6.3.2 Quantification of Body Condition

Ideally, one would directly measure fat content to assess body condition but this can be difficult to do in the field for a number of reasons. More typically, ecologists have estimated body condition by comparing body mass or

other measures of nutritional state among individuals after controlling for absolute body size (Jakob et al. 1996). For Merlins, I recorded body mass (measured to nearest 1.0 g) whenever breeding birds were captured. To estimate overall body size in Merlins I used the length of the unflattened wing chord (measured to nearest 1.0 mm) as this measure was the best estimate of overall body size (Chapter 4; see Wyllie and Newton 1994, Wiklund 1996a for similar conclusions, but also see Rising and Somers 1989, Freeman and Jackson 1990). Based on the recommendations of Jakob et al. (1996) I quantified body condition in Merlins by using the residual scores from a regression of the cube root of body mass on wing chord. The residual index is the most reliable estimate of body condition because it does not vary with body size as other estimates of condition do (e.g., ratio index, Jakob et al. 1996). I classified body condition indices as poor, medium or good (Marti 1990, Chastel et al. 1995). I did this by standardizing body condition indices ($Z = (X - \bar{X})/SD$) so that the distributions would have a mean of zero and a SD of 1. Standardized condition indices were then categorized as poor ($Z < -0.43$), medium ($-0.43 < Z < 0.43$) and good ($Z > 0.43$) (Marti 1990, Chastel et al. 1995). To assess the influence of body condition on LRS I used the average of the body condition scores obtained for an individual over its lifetime.

6.3.3 Analyses

In all instances I analyzed the data for males and females separately. I tested for repeatability of body condition measures by one-way analysis of

variance (ANOVA). This analysis quantified the amount of within-individual variance relative to the total (within and between) individual variance in the body condition measure (Zar 1984, Lessells and Boag 1987). Repeatability is a valuable statistic that can be used to assess the reliability of multiple measurements on the same individual (Lessells and Boag 1987). Only those individuals that were captured at least twice (in subsequent years) were included in the repeatability analyses.

Previous work has shown that Merlins select a particular subset of the American Crow nests that are available to them in the city (Warkentin and James 1988). For this study I was not concerned with nest site selection but rather whether the occupancy rate of nest places occurred at random. I used Chi-squared analysis to determine if nest places were occupied more or less frequently than expected by chance (Zar 1984). To test if there was any relationship between bird condition and territory quality, I used one-way ANOVA to test for differences in the body condition of male and female Merlins occupying different quality territories. I was also interested in the turnover of individuals at the same nest places and tested if body condition of different individuals occupying the same nest places was repeatable. To test for within individual changes in the occupation of different quality territories I examined territory quality for breeding birds that were captured as yearlings and again as adults (mean value for age 2+) using a paired *t*-test (Zar 1984). Because a large number of male Merlins delay breeding until age 2 (Lieske et al. 1997) I

also compared territory quality of birds captured when age 2 with the quality of territory occupied when they were older (mean value for age 3+). In order to conduct a test of whether delayed breeding allowed males to obtain better quality territories or whether they were in better body condition, I compared territory quality and body condition for yearling males that bred once to those of two year old males that bred once. I compared these two groups because a previous analysis showed that delayed breeding for males increased their LRS. I used a Mann-Whitney *U*-test to compare territory quality for the two groups and a *t*-test to compare body conditions (Zar 1984, Siegel and Castellan 1988).

Birds of any age could be divided into those that bred again in a later year ("lived") and those that did not ("died"). Birds were assumed to have "died" if they were not recaptured. I used "died" and "lived" as categories of the fixed effect factor in a randomized block ANOVA with age as the blocking factor (Zar 1984). This allowed me to examine within each age group whether any relationship existed between body condition and quality of territory occupied at a given age and survival to the next age class. In other words, were birds in poor condition (or on poor territories) more likely to die than birds in better condition (or on better territories). I used mean values of territory quality and body condition in each cell of the block design. I did this because the design was unbalanced (i.e., unequal sample sizes within each category). Body condition scores followed a normal distribution pattern for males and females ($P > 0.05$ Kolmogorov-Smirnov tests), but, territory quality did not follow a normal

distribution pattern ($P < 0.05$, Kolmogorov-Smirnov test). Thus, for analyses involving territory quality data in the blocked ANOVA, probability levels were determined by randomization methods (Crowley 1992, Adams and Anthony 1996). I could not assess any interaction because each cell contained only a single value. Only birds up to age 5 were included in these analyses because the sample contained only one Merlin (a female) older than age 6.

The mean body condition of those birds living past a particular age category and those that died appeared to follow different trends for females (but not males) for ages 1-3 (inclusive) versus ages 4-5 (inclusive) (i.e., before and after mid-life). To compare the trends in these two groups for females I used the differences between the means of "lived" and "died" birds for each age category in a t -test (Zar 1984). The two categories in the t -tests were birds aged 1-3 (inclusive), and birds aged 4-5 (inclusive).

Of the four measures of breeding performance, brood size, lifetime reproductive success, and the number of recruits were not normally distributed ($P < 0.01$, Kolmogorov-Smirnov tests) nor were those of transformed data ($\log_{10}[x+1]$). Therefore, I used nonparametric tests and randomization methods for analyses involving brood size and lifetime reproductive success (Zar 1984, Siegel and Castellan 1988, Crowley 1992, Adams and Anthony 1996). I also excluded zero values from the analyses involving brood size and lifetime reproductive success. I did this because complete breeding failures were usually due to stochastic events (i.e., shootings, storms, nest tree destruction,

etc.) and in this way did not necessarily reflect some biological inadequacy of the parents. To determine if territory quality influenced the production of recruits I used Log-likelihood ratio analyses. I used Log-likelihood ratio analyses rather than Chi-squared analyses because > 20% of the expected frequencies for males were less than 5.0 (Zar 1984). To analyze the effect of body condition on recruitment of offspring, I divided the data set into individuals that had produced at least one recruit and those that did not. I then used these as two categories for an independent variable in a one-way ANOVA to test for differences in body condition between those individuals producing recruits and those that did not. Hatch date followed a normal distribution ($P > 0.05$, Kolmogorov-Smirnov tests), therefore I used parametric tests to analyze the relationship between territory quality and body condition on hatch date (Zar 1984).

When testing for the effects of territory quality and body condition on hatch date and brood size, I restricted the analyses to include only those instances where particular individuals occupied different nest places, or put another way, particular nest places were occupied by different individuals. I also tested for the repeatability of hatch date for the same individuals occupying different nest places and for the same nest places occupied by different individuals. This analysis allowed me to quantify the separate effects of female, male and territory on this measure of breeding performance (Zar 1984, Goodburn 1991).

All tests were two-tailed and considered significant when $P < 0.05$. All statistical tests were computed using Statistica for Windows (V 5.1) (StatSoft Inc. 1995). Randomization tests were conducted using the computer program RT (V 2.1) (Manly 1997). If the number of permutations for reshuffling and sampling the data were small (< 2000) I used exact permutation to calculate probability values. If the number of permutations was large, I performed 5000 replications and used the frequency distribution of possible outcomes to calculate probability values (see Crowley 1992, Adams and Anthony 1996). Probability values calculated from randomization techniques are denoted as P_r . Means are reported \pm one SD.

6.4 RESULTS

I identified 59 separate nest places on which nesting occurred 308 times between 1985-1995. Not all nest places were occupied in a given year. The mean occupancy rate was 5.2 ± 3.4 years and the range was 1- 11 years. These 59 nest places were not occupied at random ($\chi^2 = 129.92$, $df = 58$, $P < 0.001$).

Body condition scores were repeatable for both females ($r = 0.249$, $F = 1.86$, $df = 54, 88$, $P < 0.01$) and males ($r = 0.383$, $F = 2.54$, $df = 32, 49$, $P < 0.01$). Thus, the body condition scores were relatively constant for individuals compared to the variation within the population. Body condition of different females on the same nest places was repeatable ($r = 0.130$, $F = 1.59$, $df = 47, 138$, $P = 0.021$). For different males on the same nest places, body condition

was not repeatable ($r = -0.028$, $F = 0.93$, $df = 37, 68$, $P = 0.59$). Adult female Merlins (age 2+) that had switched nest places occupied higher quality territories (mean = 3.17 ± 1.07) than they did when they were yearlings (mean = 2.73 ± 1.29 ; $t = 1.73$, $n = 42$, $P_r = 0.0448$). For males that switched nest places there was no significant change in territory quality between age 1 (mean = 3.13 ± 1.46) and age 2+ (mean = 2.88 ± 1.13 ; $t = 0.39$, $n = 8$, $P_r = 0.72$), but, a nearly significant change between age 2 (mean = 2.33 ± 0.87) and age 3+ (mean = 3.22 ± 1.12 ; $t = 1.92$, $n = 9$, $P_r = 0.0586$). It is also noteworthy that Merlins that initially bred on territories of rank 1 never switched to territories of rank 1 in a subsequent breeding attempt. Males that delayed breeding until age 2 (and only bred once) did not occupy better quality territories (median = 3.0, $n = 46$) than yearling males that only bred once (median = 3.0, $n = 13$; Mann-Whitney $U = 281.5$, $P = 0.74$).

Using analysis of variance blocked by age I found that female Merlins surviving past each age category did not occupy territories of different quality than those that died ($F = 0.87$, $df = 1,4$, $P_r = 0.25$; Fig. 6.1). Among males, however, birds surviving past each age category did occupy better quality territories than those same aged males that did not survive to breed again ($F = 5.93$, $df = 1,4$, $P_r = 0.03125$; Fig. 6.1).

Body condition of females varied significantly among the different quality territories ($F = 2.45$, $df = 4, 192$, $P = 0.047$; Fig. 6.2), however, the only difference occurred between birds occupying nest places of rank 4 and 5 ($P <$

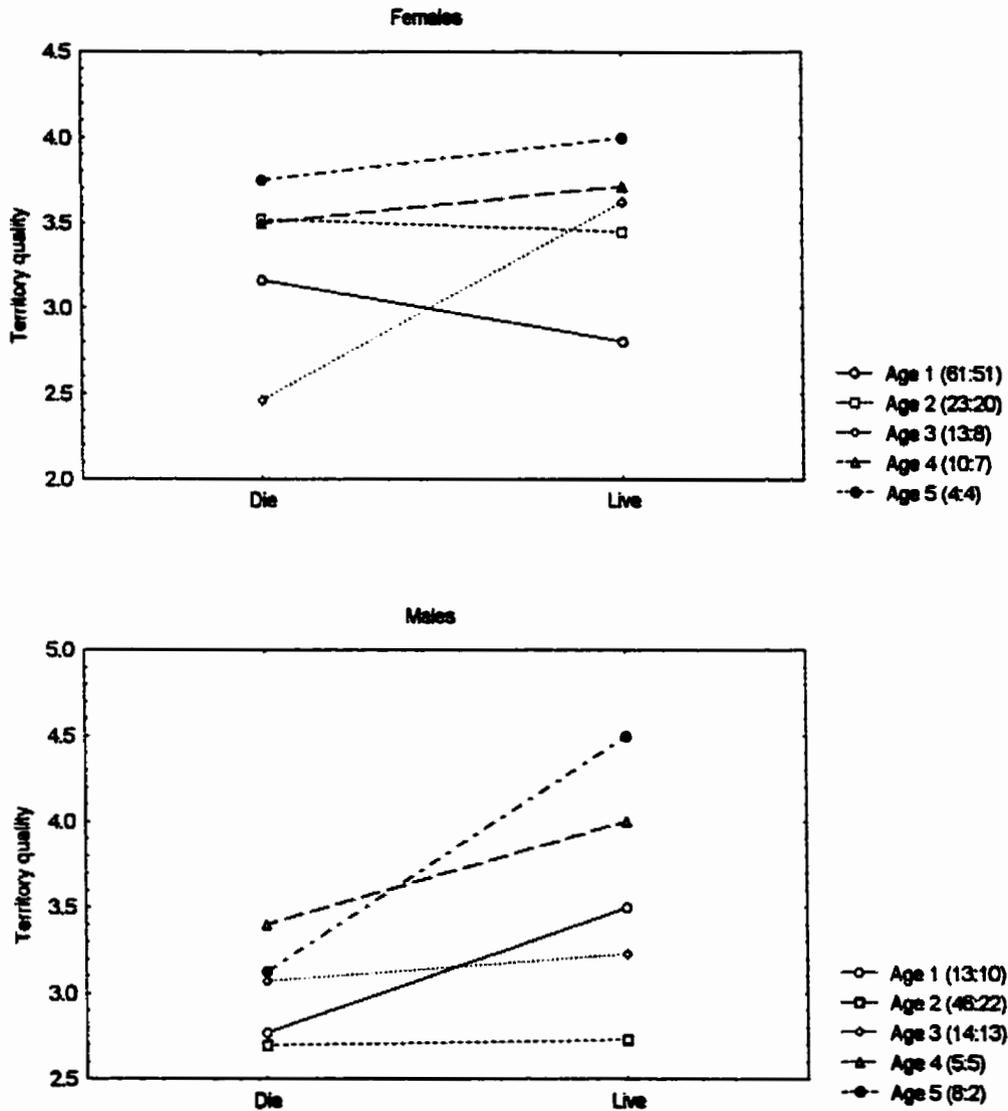


Figure 6.1. Mean quality of territory for Merlins in Saskatoon that survived past or died at a particular age. Two-factor randomized block ANOVA tests (blocked for age effects) revealed an overall difference in territory quality for surviving versus dead males but not for females. Connecting lines are used to illustrate equal aged birds. Numbers in the legend indicate sample sizes for each category (died:lived).

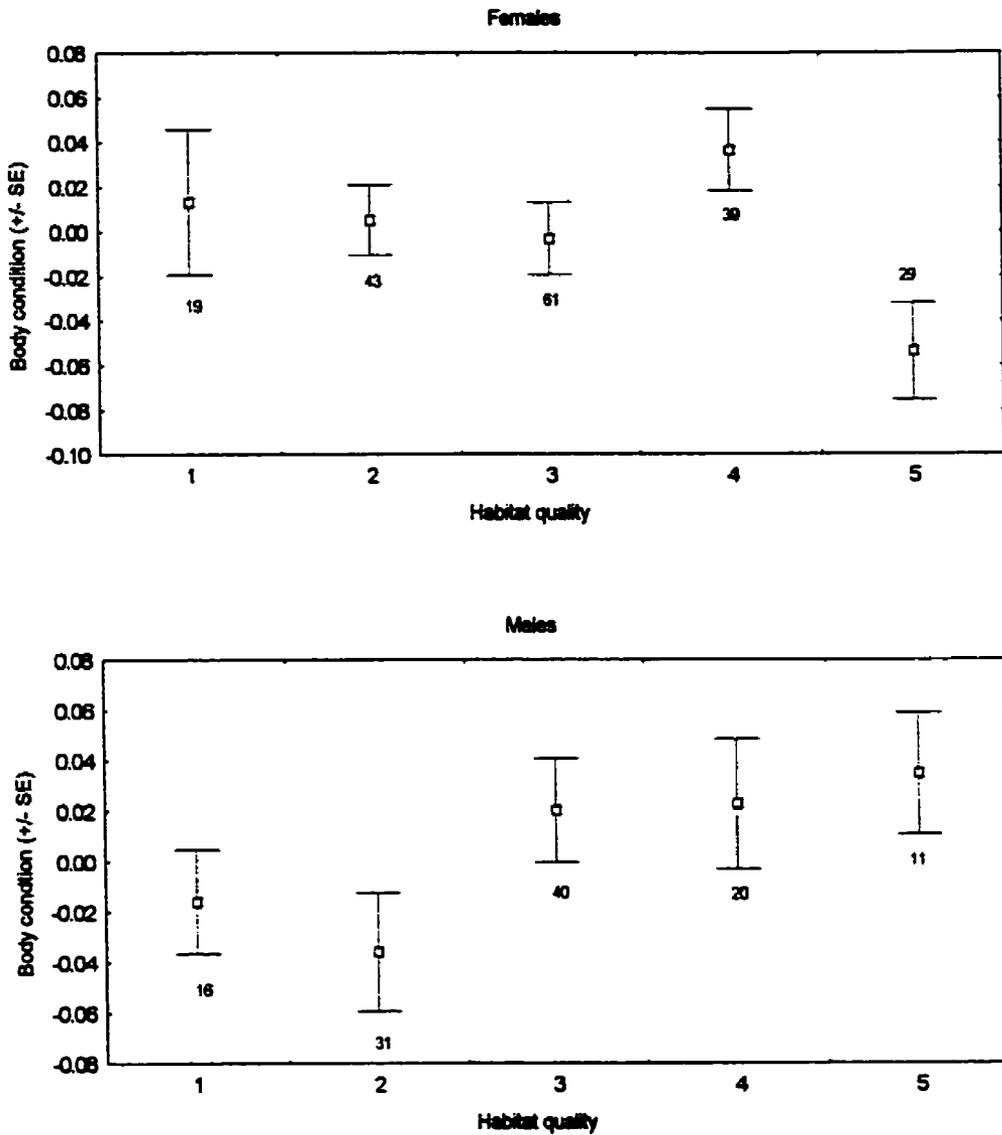


Figure 6.2. Mean body condition scores for male and female Merlins occupying different quality territories in Saskatoon. For females the only difference was that birds occupying territories of rank 5 had poorer body conditions than birds occupying rank 4 territories (Tukey's HSD test). For males, there were no differences found. Numbers indicate sample sizes.

0.05, Tukey's HSD test). For males, there was no difference in the body condition of birds occupying different quality territories ($F = 1.25$, $df = 4, 117$, $P = 0.29$; Fig. 6.2).

Among female Merlins, hatch date ($F = 0.82$, $df = 4, 184$, $P = 0.52$; Fig. 6.3) and brood size (Kruskal-Wallis $H = 3.49$, $n = 191$, $P = 0.48$, Fig. 6.4) were not different on the different quality territories. For males too, hatch date ($F = 0.39$, $df = 4, 115$, $P = 0.82$; Fig. 6.3) and brood size (Kruskal-Wallis $H = 3.35$, $n = 118$, $P = 0.50$, Fig. 6.4) were not affected by territory quality. Territory quality did not appear to influence LRS in female Merlins ($\tau = -0.028$, $n = 127$, $P = 0.64$; Fig. 6.5). On the other hand, in male Merlins territory quality was positively correlated to their LRS ($\tau = 0.205$, $n = 98$, $P < 0.01$; Fig. 6.5). However, when territories of rank 1 were eliminated from the analysis the relationship no longer held ($\tau = 0.118$, $n = 88$, $P = 0.102$). The nest places of different quality did not produce more or less recruits than expected by chance alone for females or males (Table 6.1). For the same nest places occupied by different females hatch date was not repeatable ($r = 0.020$, $F = 1.08$, $df = 47, 131$, $P = 0.361$). Hatch date was also not repeatable for the same nest places occupied by different males ($r = 0.119$, $F = 1.37$, $df = 37, 66$, $P = 0.132$).

The mean body condition of those female Merlins birds living past a particular age category and those that died followed different trends ($t = 5.26$, $df = 3$, $P = 0.0134$) when comparing ages 1-3 to ages 4-5 (i.e., before and after mid-life (Fig. 6.6). Thus, I partitioned the analysis to test for differences in body

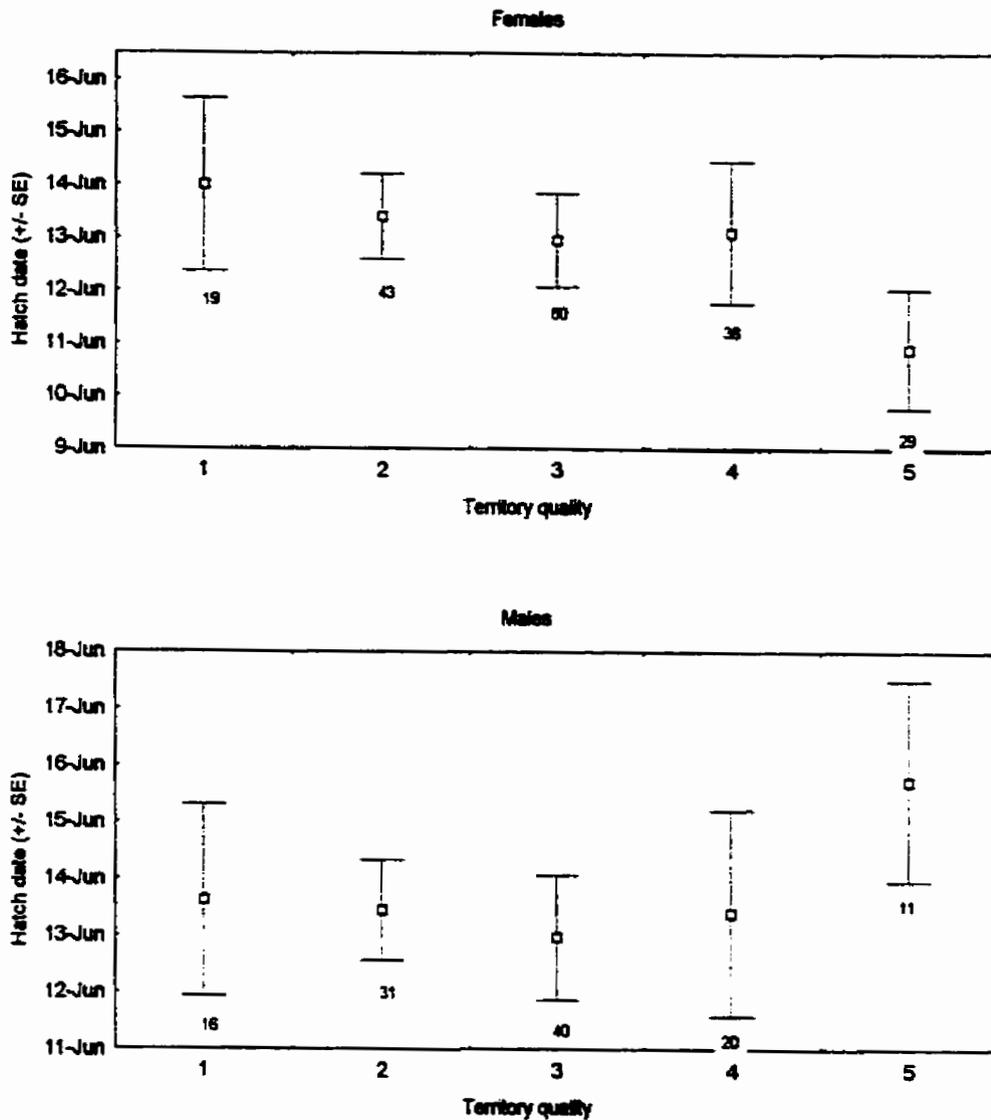


Figure 6.3. Mean chick hatch dates for breeding female and male Merlins in Saskatoon occupying different quality territories. There were no differences found for either sex. Numbers indicate sample sizes.

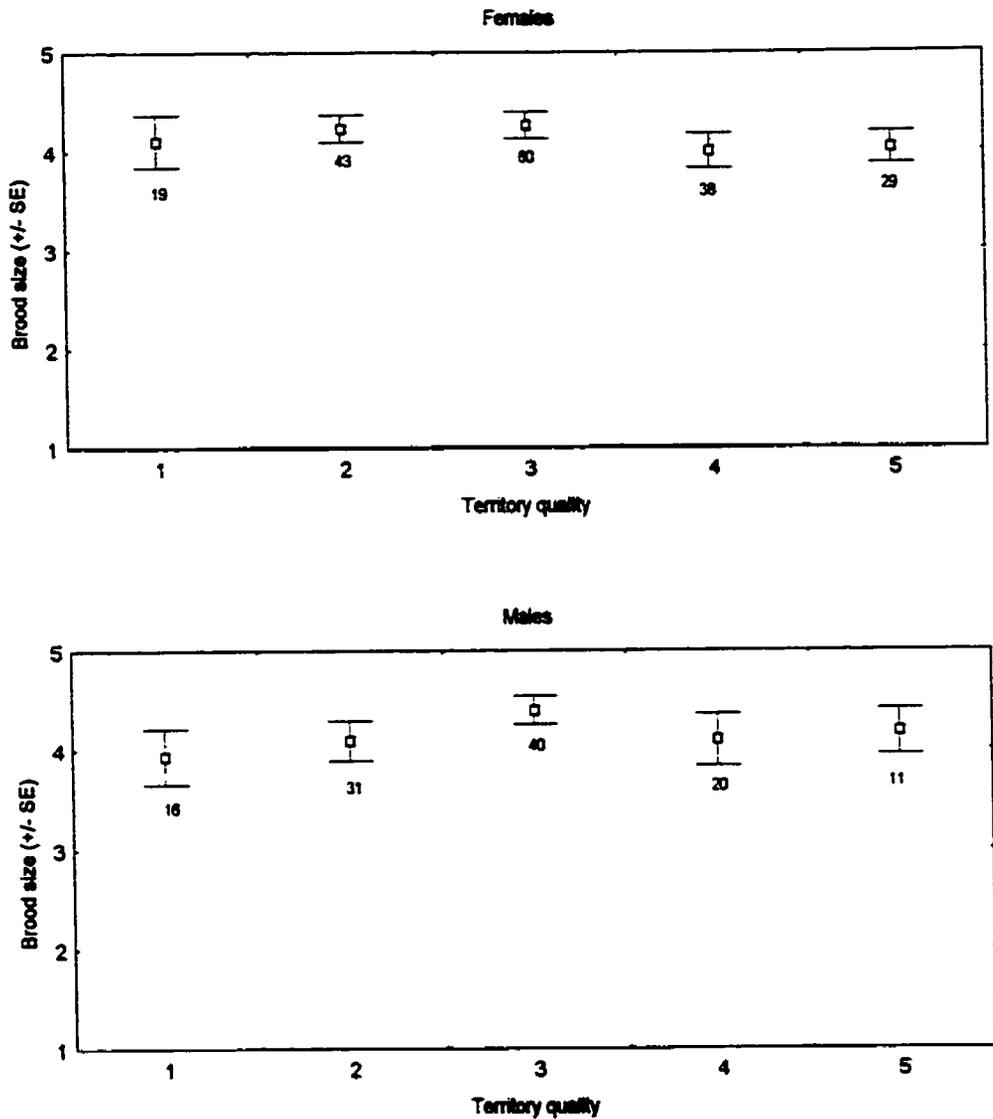


Figure 6.4. Mean brood sizes for breeding female and male Merlins in Saskatoon occupying different quality territories. There were no differences found for either sex. Numbers indicate sample sizes.

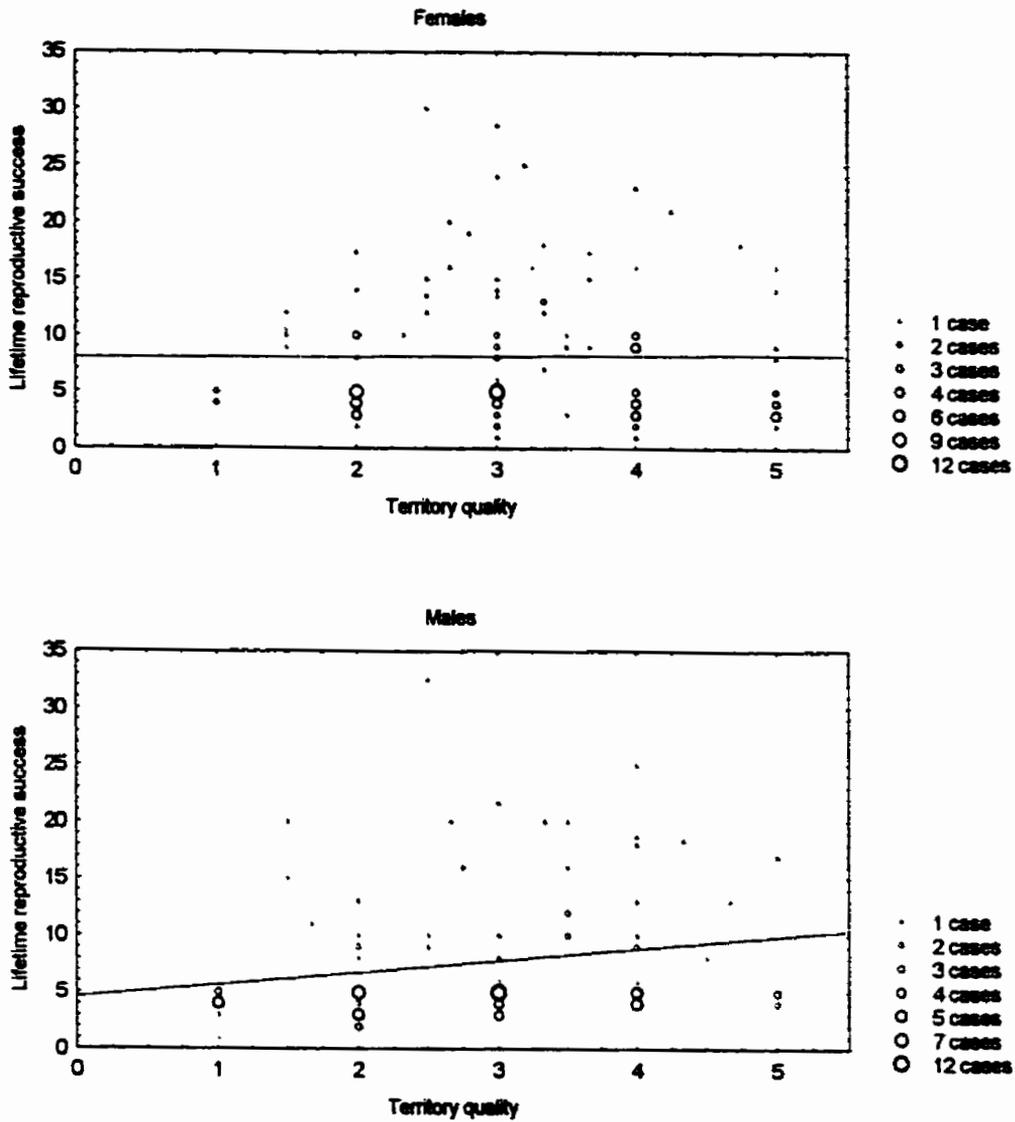


Figure 6.5. Scatter diagram of mean quality of territory occupied (over a bird's lifetime) and Lifetime Reproductive Success for female and male Merlins caught breeding in Saskatoon (1985-1995). For females there was no relationship between territory quality and LRS, but, for males the two were positively correlated. The line represents a line of best fit.

Table 6.1. Total number of young and recruits produced and the expected number of recruits for individual breeding attempts on different quality territories by female and male Merlins in Saskatoon.

For females, $G = 2.92$, $df = 4$, $P = 0.57$ and for males $G = 0.816$, $df = 4$, $P = 0.96$.

Habitat	Females			Males		
	Number of Young	Recruits Produced	Recruits Expected	Number of Young	Recruits Produced	Recruits Expected
1	78	7	5.6	63	5	4.5
2	182	12	13.1	127	7	9.0
3	260	14	18.7	178	13	12.5
4	156	15	11.2	82	7	5.8
5	117	9	8.4	46	3	3.3
Total	793	57		494	35	

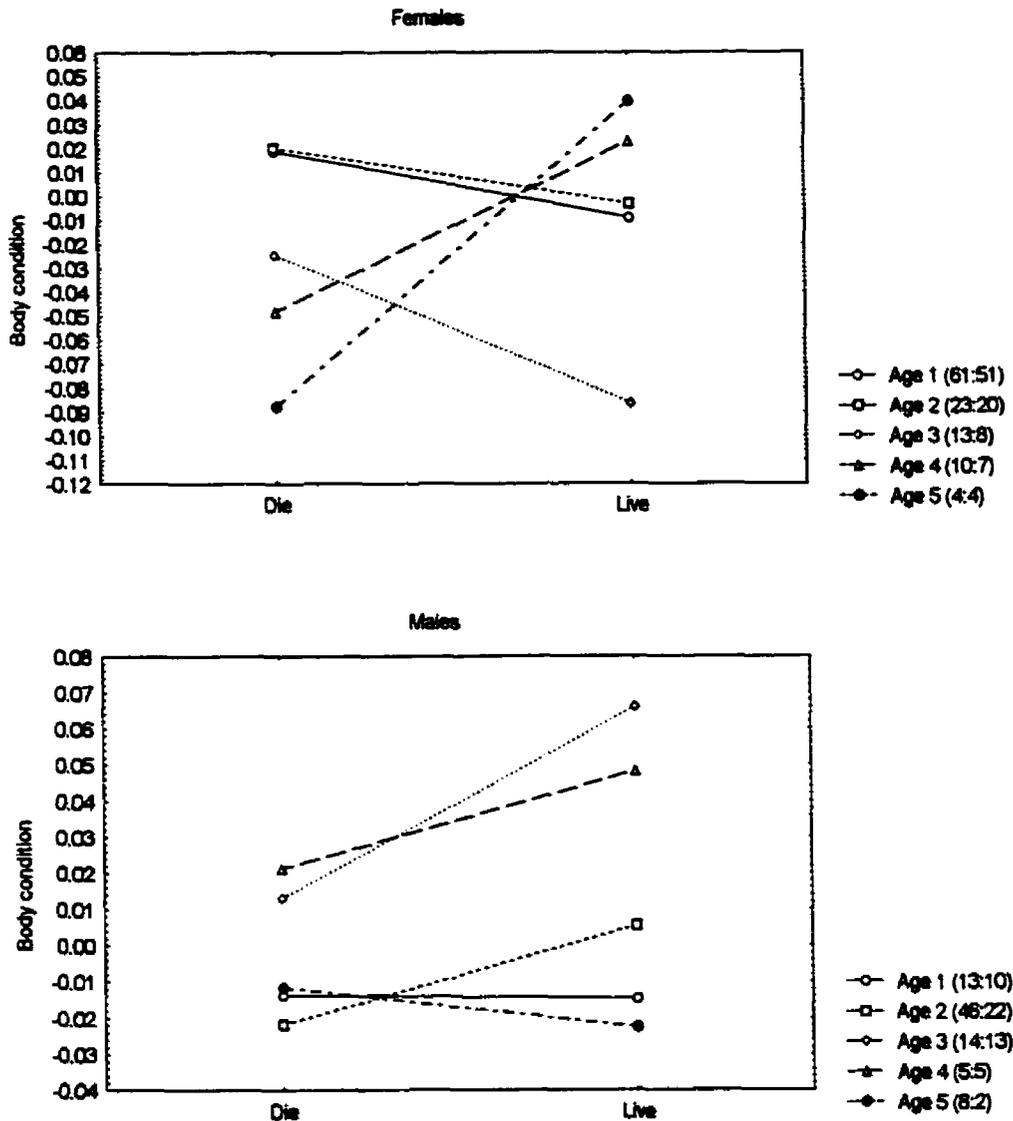


Figure 6.6. Mean body condition scores for Merlins in Saskatoon that survived past or died at a particular age. Two-factor randomized block ANOVA tests (blocked for age effects) revealed no overall difference in the body condition scores of surviving Merlins versus those that died. Connecting lines are used to illustrate equal aged birds. Numbers in the legend indicate sample sizes for each category (died:lived).

condition between dead and living birds in age classes 1-3 and 4-5 separately for females. For female Merlins aged 1-3, the ANOVA test (blocked by age) revealed no overall difference in the body condition of surviving versus dead females ($F = 9.89$, $df = 1,2$, $P = 0.088$; Fig. 6.6). For female Merlins aged 4-5, the same test showed no difference in the body condition of surviving versus dead birds ($F = 13.22$, $df = 1,1$, $P = 0.17$). For male Merlins surviving birds were not different in body condition compared to those that died ($F = 2.96$, $df = 1,4$, $P = 0.16$; Fig. 6.6). Males that delayed breeding until age 2 (and only bred once) did not have different body condition scores (mean = -0.0218 ± 0.116 , $n = 46$) than yearling males that only bred once (mean = -0.0138 ± 0.109 , $n = 13$; $t = 0.22$, $P = 0.82$).

Hatch date ($F = 1.60$, $df = 2, 188$, $P = 0.21$; Fig. 6.7) was not different among the female Merlins of different body condition. However, the lifetime average body condition of females was positively correlated with their lifetime average hatch date ($r = 0.220$, $n = 124$, $P = 0.014$). Among males hatch date was not different among the different body condition categories ($F = 0.43$, $df = 2, 117$, $P = 0.65$; Fig. 6.7) and there was no correlation between average lifetime body condition and average lifetime hatch date ($r = -0.029$, $n = 98$, $P = 0.77$). Brood size (Kruskal-Wallis $H = 8.96$, $n = 191$, $P = 0.011$) did differ among the female Merlins of different body condition, however, the only difference was that females in medium condition produced fewer offspring than birds in poor condition (Dunn's test $P < 0.05$; Fig. 6.8). Among males in different body

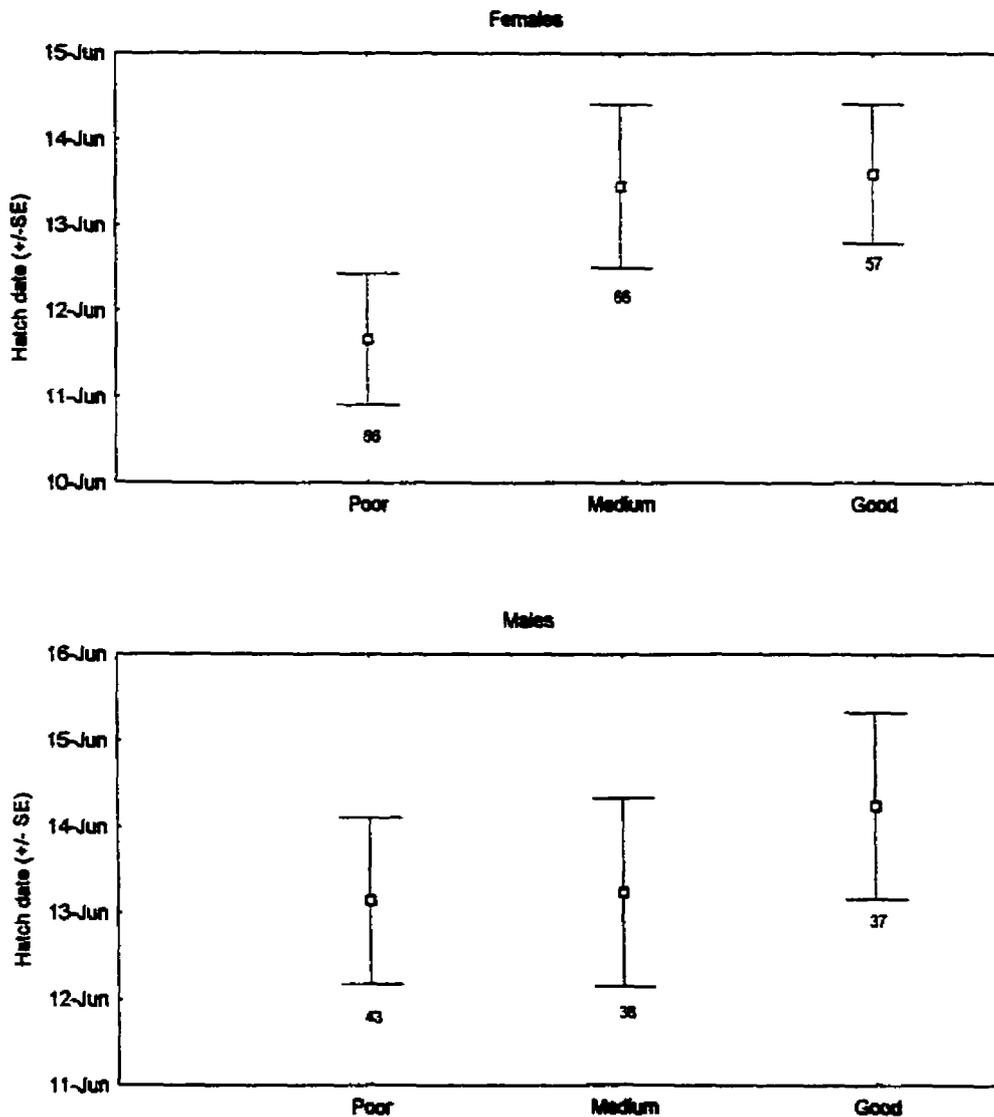


Figure 6.7. Mean chick hatch dates for Merlins of different body condition breeding in Saskatoon. There were no differences in chick hatch dates between the body condition categories for either sex. Numbers indicate sample sizes.

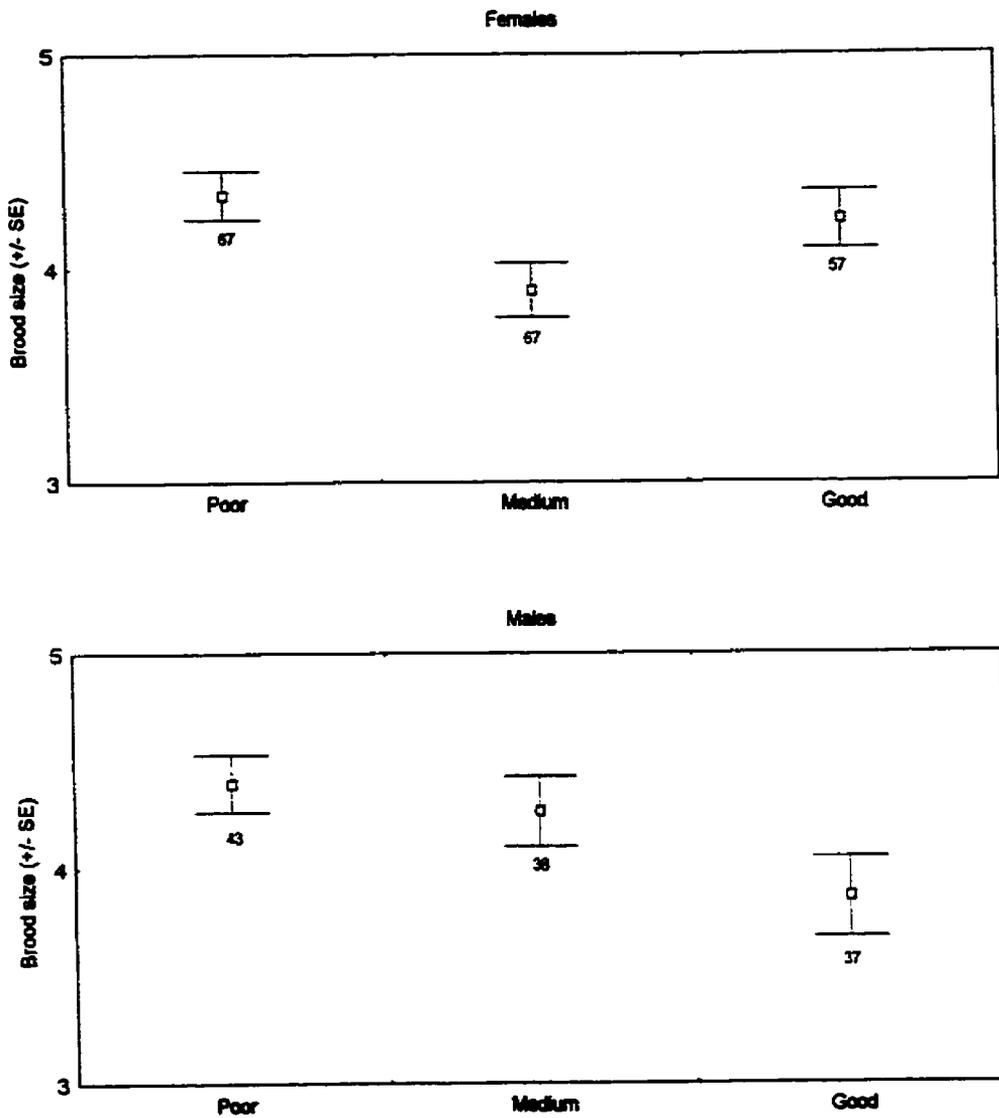


Figure 6.8. Mean brood sizes for Merlins of different body condition breeding in Saskatoon. For Females, only birds in Medium condition had smaller broods compared to birds in Poor condition. For males, birds in Good condition had nearly significantly smaller broods than birds in Poor and Medium condition. Numbers indicate sample sizes.

condition, there was a nearly significant difference in the brood sizes of the different groups ($F = 2.94$, $df = 2, 115$, $P = 0.0564$; Fig. 6.8). Those females in poor lifetime average body condition produced more chicks in their lifetimes than females in better body condition ($\tau = -0.136$, $n = 125$, $P = 0.025$; Fig. 6.9). Among males, there was no correlation between LRS and body condition ($\tau = -0.001$, $n = 96$, $P = 0.986$; Fig. 6.9). Recruitment of offspring did not vary among the Merlins of different body condition (Table 6.2). For the same female individuals occupying different nest places over their lifetimes, hatch date was repeatable ($r = 0.381$, $F = 2.50$, $df = 45, 66$, $P < 0.001$), but, among males occupying different nest places it was not ($r = 0.060$, $F = 1.37$, $df = 19, 23$, $P = 0.38$).

6.5 DISCUSSION

Tradeoffs between different fitness components are inevitable from a life history perspective and evidence from brood size manipulation studies in birds suggests that increased reproductive effort may affect parental body weight, future fecundity and survival (reviews in Roff 1992, Lessells 1991, Stearns 1992). However, some non-experimental field studies report a positive relationship between current reproduction and survival (Smith 1981, Safriel et al. 1984, Coulson and Porter 1985, Chapter 3). Van Noordwijk and de Jong (1986) posit that this positive relationship may result from variation in the resources available to different individuals. Alternatively, this relationship may be related to the quality (Coulson and Porter 1985, Coulson and Thomas 1985,

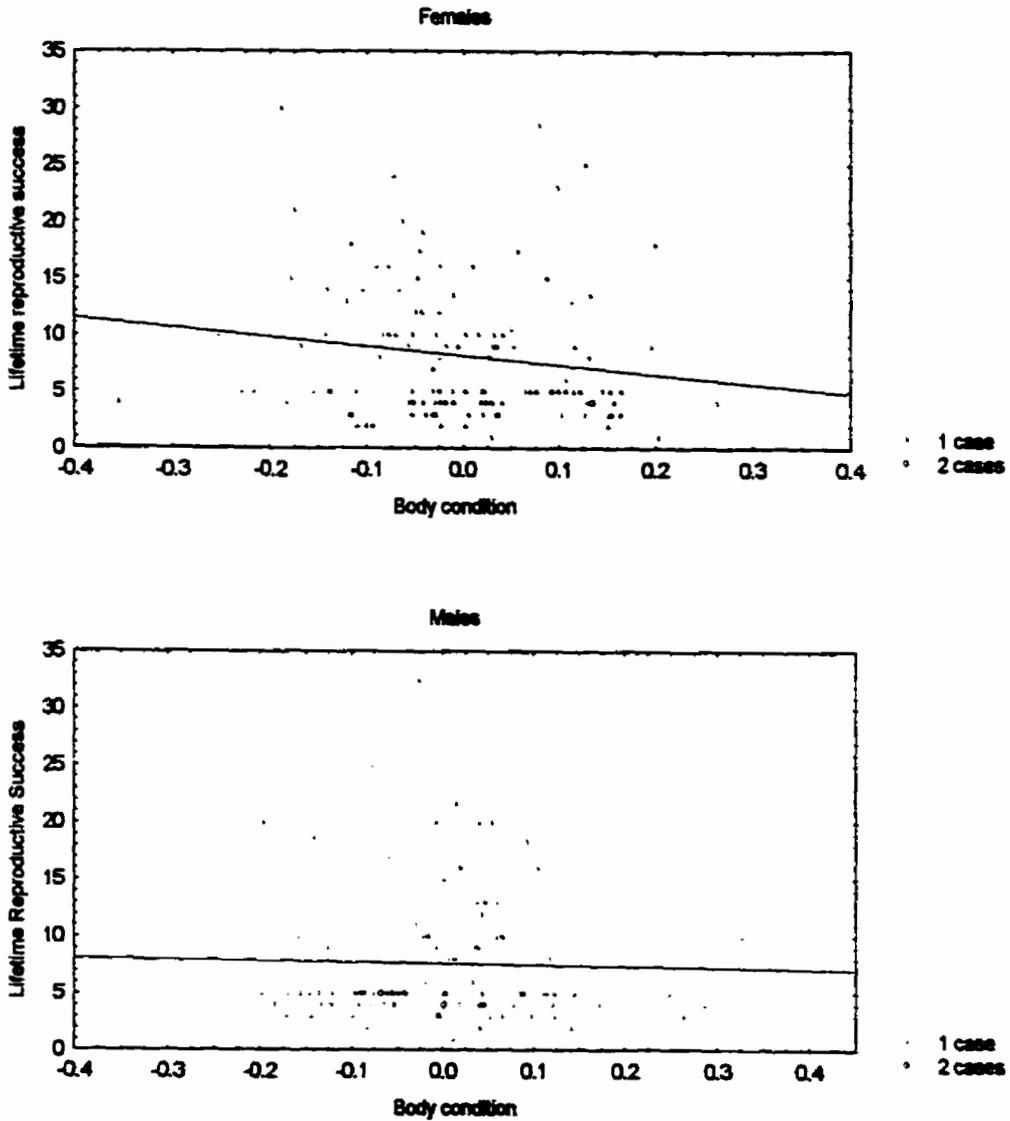


Figure 6.9. Scatter diagram of a bird's mean body condition (over a bird's lifetime) and Lifetime Reproductive Success for female and male Merlins caught breeding in Saskatoon (1985-1995). For females there was a negative correlation between body condition and LRS, but, for males the two were not related. The line represents a line of best fit.

Table 6.2. Mean (\pm one SD) body condition of merlins that produced at least one recruit and those that produced no recruits over their lifetime in Saskatoon. There were no significant differences found.

Sex	One + Recruit			No Recruits			F	P
	Mean	SD	n	Mean	SD	n		
Females	-0.01	0.10	43	-0.00	0.11	82	0.10	0.76
Males	-0.00	0.10	33	-0.00	0.11	63	0.02	0.88

Goodburn 1991) or the condition (Drent and Daan 1980) of the individuals concerned or the quality of territories occupied (Ens et al. 1992). This study of male and female Merlins provides evidence of the influence that body condition and bird quality, and to a lesser extent territory quality, have on reproduction in a natural population. This reinforces the notion that these factors may act in combination to influence breeding performance in birds and other taxa.

6.5.1 Influence of Territory Quality on Breeding Performance

There is a large body of evidence showing that habitat quality can influence breeding performance in birds (reviews in Ens et al. 1992, Rodenhouse et al. 1997). Merlin occupation of nest places was non-random and there are good data to show that Merlins select a subset of nest sites from larger number of possible nest sites that remained unused (Warkentin and James 1988). Except for a few specific circumstances (e.g., Viitala et al. 1995) little is known about how birds and other animals may assess territory quality. Some studies have shown that poor breeding performance in one year can lead to a change of breeding territory the next (Newton and Marquis 1982, Shields 1984, Sonerud 1985, Beletsky and Orians 1991, Korpimäki 1993, Newton 1993, Wiklund 1996b). Nevertheless, some avian species return in successive years to breed in the same territories or nest sites in spite of failure (Haig and Oring 1988). Birds that breed in the same area may benefit from previous experience in terms of obtaining food and mates, territory defense and evasion of predators (Greenwood and Harvey 1982, Moore and Ali 1984, Shields 1984, Dobson and

Jones 1986). Site fidelity is higher among male Merlins than females (Warkentin et al. 1991, Wiklund 1996b) and female birds in general tend to disperse farther than males (Newton 1979, 1986, Gavin and Bollinger 1988, Pärt and Gustafsson 1989, Village 1990, Korpimäki 1993). Mate fidelity is low among Merlins in the Saskatoon population (20% of pairings contained the same birds for two consecutive years; Warkentin et al. 1991) and appears largely related to the degree of site fidelity. Whereas site fidelity has been shown to make a difference in some species, there is no apparent benefit of site fidelity to Merlins in Saskatoon (Warkentin et al. 1991).

The results from this study indicate few links between territory quality and female productivity, timing of breeding, body condition or survival. Furthermore, hatch date was not repeatable for nest places occupied by different females. Even so, when female Merlins switched territories they tended to settle the next year in territories of higher quality and different females on the same nest places had significantly repeatable body conditions. Thus, females apparently use some cues to assess territory quality, however, these features do not appear to significantly enhance their breeding performance.

For male Merlins, territory quality did not appear to be related to hatch date, brood size or recruitment, but, when male Merlins switched territories they also tended to go to ones on higher quality. Male Merlins surviving past each age category did occupy nest places of higher quality and this relationship

between survival and territory quality may have contributed to the finding that LRS in males was influenced by territory quality. However, it must be noted that largest influence of territory quality on LRS in males apparently came from the low productivity of birds on territories of rank 1. Even so, longevity has been show to contribute most to a bird's LRS (Newton 1989, Chapter 3) and the increased survival of males on higher quality nest places likely allowed for higher LRS in those birds. This finding also reinforces the greatest attribute of LRS as a measure of breeding performance in that it reveals the full extent to which reproduction varies among individual male Merlins with small annual differences potentially becoming larger and more detectable over an entire lifespan (Newton 1985, 1988, 1989).

Body condition of different males occupying the same nest places was not repeatable and there was no difference in the body condition of birds on the different quality territories. In addition, hatch date for different males occupying the same nest places was not repeatable. Males that delayed breeding for a year did not obtain higher quality territories than males that bred as yearlings. Other work on birds has shown that delayed breeding allows individuals to obtain higher quality territories in some species (Stacey and Ligon 1987, Zack 1990, Koenig et al. 1992, review in Zack and Stutchbury 1992). Other work on Merlins (Chapter 3) has shown that a delay of breeding for 2 year old males increased their LRS significantly over those males that bred as yearlings. It seems then that some male Merlins delay breeding to improve skills (and

thereby enhance their LRS) rather than to obtain better territories and thereby enhance reproduction.

Some research has suggested a connection between territory quality and productivity such that there is competition a population for the best quality nest sites where potential productivity is greatest. For instance, Newton (1991) has shown for female Sparrowhawks that: 1) only a proportion of available nest places were occupied in any one year, 2) some places were favoured over others during a period of years, 3) better nest success on the most frequently occupied places, and 4) the presence of surplus birds. All four features have also been shown for the Peregrine (*Falco peregrinus*; Hickey 1942, Ratcliffe 1980). For the Saskatoon Merlin population, all features can be seen to some extent. More recently, Rodenhouse et al. (1997) have posited that population size may be regulated by site dependence. Site dependent population regulation has two major tenets: 1) environmentally caused heterogeneity among sites in suitability for reproduction and survival, 2) pre-emptive site occupancy with the tendency for individuals to move to sites of higher quality as they become available. Again, Merlins meet these precepts to some extent. Males on higher quality territories were more likely to survive to breed again the following season, and there was a tendency for both sexes to move to territories of higher quality when switching nest places. In addition males on higher quality territories did have higher LRS and a study of wintering Merlins in Saskatoon (Warkentin et al. 1990) showed that non-migratory birds nested the

following spring in higher quality nest places than migratory birds. Perhaps the absence of general trends in how territory heterogeneity influences breeding performance in the Saskatoon Merlin population may be related to the rather unique features of the species, the study area or a combination of these two factors. Merlins do not build their own nests and thus are limited to nesting in areas where corvids (American Crows and Black-billed Magpies *Pica pica*) have already built nests in the city (Sodhi et al. 1993). Corvids presumably select nest sites based on criteria which are different from those of Merlins, but, the result is that Merlins are restricted to areas of the city that corvids prefer for breeding (almost exclusively residential areas as opposed to industrial or commercial areas). House Sparrows act as the predominate prey of Merlins in Saskatoon (Sodhi and Oliphant 1993) and sparrows occur at a higher densities in the city compared to outside the city and in industrial areas (e.g., grain elevators, seed mills, rail yards) rather than in residential areas. Thus, the Merlin's primary food source is available in abundance, but, not in defensible quantities nor locations. In Saskatoon, hunting ranges of radio-tagged males had spatial overlap of up to 77% (Sodhi and Oliphant 1992). Based on this, Sodhi and Oliphant (1992) concluded that Merlins have non-exclusive hunting ranges due to at least three factors: 1) the high density of Merlins nesting in the city may make defense costly, 2) the prey base is abundant, widespread and stable in Saskatoon so there are few benefits to exclusive ranges and 3) the prey (small birds) are hard to defend because they are mobile and alert to the

presence of Merlins. Therefore, the abundance, accessibility and mobility of food in the city appears to negate some advantages of occupying a specific nest place to breed.

6.5.2 Influence of Bird Condition and Quality on Breeding Performance

The condition of parents early in the breeding season can influence breeding performance (Drent and Daan 1980, Birkhead and Nettleship 1982, Newton et al. 1983, Chastel et al. 1995). When faced with poor body condition early in the season, birds may respond by not breeding (Newton et al. 1983, Chastel et al. 1995) by reducing energy requirements through reducing clutch size (Drent and Daan 1980) or egg volume (Birkhead and Nettleship 1982, Martin 1987) or by delaying reproduction until body condition improves (Martin 1987). Newton et al. (1983) showed that female Sparrowhawks that did not lay eggs remained low in weight throughout the early part of the breeding season and were significantly lighter than breeders. Female Sparrowhawks also fluctuate greatly in weight during the year with the highest weights attained at the beginning of breeding in May and the lowest weights in August at the end of breeding (Newton et al. 1983). Male Sparrowhawk weights on the other hand, tended to fluctuate much less than females but followed the same trend. Although the body condition of breeding birds is important early in the season, less is known about how food abundance and body condition are related to breeding performance during the nestling period (Wiehn and Korpimäki 1997).

Among female Merlins, those birds surviving past each age category (up

until age 3) tended to be in poorer condition than those birds that did not survive to breed again. Another study (Chapter 3) has shown that these same individuals tended to have earlier hatching and larger broods. It may be that these superior breeders are investing in offspring at the expense of their own body condition. Other evidence to support this comes from the finding that those females in poorer lifetime body condition tended to have earlier chick hatch dates and higher LRS. However, the brood sizes of females in poor and good condition were the same while those of females in medium condition were significantly smaller. Another line of support for the cost of reproduction to adult parents comes from a study of molt in Merlins (Espie et al. 1996) where it was shown that females that continued molting through the breeding season had significantly smaller broods than those females that had arrested molt. Taken all together then, these findings suggest that higher fecundity may have reduced body condition through an increased cost of reproduction. However, it should be noted that cost of reproduction can only be truly investigated by manipulating the reproductive effort in individuals and determining how this influences their future reproduction and survival. Wiehn and Korpimäki (1997) found that supplementally fed female Eurasian Kestrels (*Falco tinnunculus*) were significantly heavier than those in the control groups and were able to produce more fledglings. Furthermore, supplementally fed Eurasian Kestrel females decreased their hunting effort over unfed females.

Food abundance directly influences body reserves stored by adult raptors

and other birds (Drent and Daan 1980, Newton et al. 1983, Dijkstra et al. 1982, Martin 1987, Korpimäki 1989, Chastel et al. 1995, Wiehn and Korpimäki 1997). In Saskatoon, Merlins time their breeding so that the fledging phase of their chicks falls during the time of peak production of juvenile House Sparrows (Sodhi et al. 1992, Sodhi and Oliphant 1993); likely, in order to exploit this particularly vulnerable food supply. Other workers have reported increased predation on juvenile prey as the Merlin breeding season progresses (Newton et al. 1984). Because male Merlins provide almost all food for themselves, their mate and their offspring during the breeding season (Sodhi et al. 1992), one would expect their ability to provide food to be the primary determinant of breeding success. Nevertheless, in general there was little to no association between body condition and breeding performance for male Merlins. In fact there was only one nearly significant trend; that males in good condition tended to produce smaller broods than their counterparts in poor and medium condition.

Merlins, like other raptors, are unusual among birds in that males appear to invest substantially more energy in offspring than do females (Wijnandts 1984, Masman et al. 1988). Moreover, for bird-eating raptors the breeding attempt hinges on the ability of the male to provide food (Newton 1986, 1988). If this is so then why was there no relationship between body condition and breeding performance in male Merlins? In their supplemental feeding experiment, Wiehn and Korpimäki (1997) found that male Eurasian Kestrels did

not adjust their parental effort within a season and they suggest that male parental effort is fixed at a level where survival is not jeopardized. In Merlins, hunting effort is highest during the nestling phase and is related to brood size so that males with larger broods show increased foraging effort (Sodhi 1993). Male raptors tend to vary less in weight than females and tend not to put on weight for breeding (Newton 1986). Perhaps the fact that Merlin males' body condition was unrelated to breeding is due to the food providing role they play in reproduction and that during the breeding season they may already be operating at the edge of their own safety margin in terms of body condition. If this is so then those males on higher quality territories may have gained a slightly better chance for survival through reduced hunting effort. Sodhi (1993) showed that males with high prey abundance in their hunting ranges spent less time flying than males with low prey abundance in their hunting ranges. Perhaps some high quality nest places allowed for slightly improved access with less energy expenditure to areas of higher prey abundance within the city.

The concept of individual quality was introduced by Coulson (1968) to emphasize the fact that not all individuals are equal. For Merlins I assessed bird quality through the repeatability of breeding performance (hatch date) for the same birds occupying different nest places (Van Noordwijk et al. 1980, Newton and Marquis 1984, Goodburn 1991, Hochachka 1993). For Merlins it appears that hatch date is largely determined by the quality of the female. In fact for males hatch date was not even repeatable. This finding runs counter to

that shown for Sparrowhawks where repeatability of laying date was greater for males than females (Newton and Marquis 1984). In addition, much of the reproductive potential of a female raptor is likely a function of the quality of her mate who will provide food for the breeding attempt (Newton 1979, 1986, 1988, Wijnandts 1984, Village 1990). Why then was repeatability not significant for male Merlins? It is thought that when individuals do not display repeatable performance, there may be nonrandom variation in quality within individuals. For instance in male Merlins breeding performance has been shown to improve with age probably as a consequence of improved foraging skills through increased experience (Chapter 3) and this may have reduced repeatability. A second possibility is that males adjusted their hunting effort to fit the situation at hand (Sodhi 1993). Moreover, birds should not repeat the conditions that caused the previous failure of reproduction (Hochachka 1993). This last notion probably has little bearing on this study though as all birds examined had produced at least one chick and complete failure at nests was quite uncommon (Sodhi et al. 1992).

7. CONCLUSIONS

My objective in this final chapter is to summarize the main findings of this thesis and to speculate on which of the factors studied were of greatest importance to breeding male and female Merlins.

Among females, improvements in breeding performance in relation to age were mostly due to the selection of superior breeders, and thus, supported the differential mortality hypothesis. For males, however, improvements occurred mostly within individuals early in life suggesting that they improved breeding performance by gaining experience in skills related to reproduction (i.e., nest defense, hunting, courtship). In both sexes, longevity influenced LRS and recruitment. Past mid-life, birds of both sexes with reduced brood size were more likely to survive to breed again whereas just the opposite was true for Merlins before mid-life.

For both sexes, body size appeared to influence breeding performance only among yearling birds. For yearling females, bigger birds tended to be better performers and were more likely to survive to breed again. Among yearling males, smaller birds had larger broods, but, larger males were more likely to survive to breed again. In adult Merlins, body size had little influence on breeding performance in either sex; however, the trends between body size

and brood size in the two sexes were different from each other suggesting increased fecundity by smaller males and larger females.

Mate choice of male body size by females was almost repeatable and suggests that individual females tended to choose the same size mates in subsequent breeding attempts. However, choice of male size was not related to the size of the female. There was no repeatability of female choice for body condition of male mates, nor male choice of female mates' body size or condition. There was no support for the compatibility hypothesis and among mated pairs, only large female body size improved breeding performance. There was no apparent effect of body condition on breeding performance among mated pairs. Body size showed high heritability between parents and male offspring. Body condition exhibited low heritability between parents and male offspring.

I found little evidence of the influence of territory quality on any of the measures of breeding performance for female Merlins. Even so, when females switched territories they tended to go to ones of higher quality. Females in poorer body condition tended to have earlier chick hatch dates and higher LRS than ones in better condition, which contradicted the results from Chapter 5. Hatch date was repeatable for the same females occupying different nest places, but, was not repeatable for the same nest places occupied by different females. Among males, birds surviving past each age category occupied higher quality territories than those that did not survive. In addition, LRS was

positively correlated with territory quality in males, but, this was mostly due to the heavy influence of the poorest quality territories. Like females, when males switched territories they tended to go to ones of higher quality. Male body condition was not related to breeding performance nor survival. Hatch date was not repeatable for the same males occupying different nest places.

The partitioning of roles between the Merlin sexes during the breeding season influences most aspects of their lives. Male Merlins improved breeding performance from increased experience and this is probably why so many in the Saskatoon population delay breeding until their second year. Females too benefit from experience, but, it does not appear to be as important as in males. This is a reflection of the heavy food provisioning role that males fulfil during breeding and the skills needed in capturing enough prey for successful reproduction. Perhaps the most interesting finding was that past mid-life in both sexes, birds with reduced brood sizes were more likely to survive to breed again. Just the opposite was shown for Merlins before mid-life. This suggests that there was a trade-off between fecundity and survival in the later stages of life.

Despite the large difference between the Merlin sexes in terms of body size, the evidence from my work suggests that body size did not have a pervasive influence on breeding performance. There was some consistency (i.e., repeatability) in the choice of mate size by females, but females did not appear to choose mates relative to their own size. Within mated pairs, female

body size did influence LRS and hatch date. However, this finding was probably due largely to the fact that I did not differentiate between age classes for the analysis and the majority of the females were in fact yearlings.

The only contradiction in results occurred between the finding in Chapter 5 that body condition in females (within mated pairs) did not influence breeding performance, whereas in Chapter 6 body condition was related to hatch date and LRS. I suspect that this was due to at least two things. The first is that it is possible that after controlling for the effects of male body condition (as in Chapter 5), the effects of female body condition on breeding performance were negligible. The second is that the two sections involved two types of analysis (ANOVA vs. linear regression), each with their own advantages and drawbacks. It is possible that the linear regression recorded a weak significant trend that was not detectable using ANOVA.

Territory quality appeared to have more influence on male Merlins than it did for females. Even so, it is obvious that for female Merlins a crucial resource during the breeding season is a male with an established territory, who is able to provide enough food for reproduction. Territory quality may have been more influential for males since they had to provide most food during the breeding season and any slight advantage gained in occupying particular territories was more noticeable in them. Despite the importance of a competent male and a place to nest to the breeding attempt, female Merlins appeared to have ultimate control over the timing of breeding as evidenced by the repeatability of hatch

date for them and the lack of it for males and nest places. This finding contradicts other work on raptors which suggest that males exercise control over the timing of breeding.

The findings from this study of Merlin breeding ecology came largely from the interpretation of observational evidence. In some cases this evidence was quite conclusive. Ideally, some of the less conclusive results would have been followed up with experimental evidence. This was not done with Merlins in Saskatoon for several reasons. The first and foremost was that any experiments would had to have been conducted in residential areas and it was often difficult even to obtain permission simply to climb the nest tree in order to band nestlings. The second was that any experiments carried out near the beginning or middle of the study could have negatively impacted subsequent measures of breeding performance. A third reason was that near the end of the study, sufficient funding was not available to conduct plausible experiments. Thus, some gaps in our understanding of Merlin ecology remain. For instance, more information is desirable concerning male non-breeders or "floaters". Does territory quality always have more influence on males than females? Is female choice for male body size repeatable under differing population densities? Would female mate choice be repeatable under more controlled laboratory conditions? In general, most aspects of raptor ecology are much better understood for females compared to males because males are more difficult to capture. In this study a relatively large number of breeding males were

captured, and I was fortunate to be able to include them in all of my analyses. This allowed me to find differences between the sexes that I did not expect to see when I began this work. I hope the same holds true for the reader.

8. LITERATURE CITED

CHAPTER 1

Clutton-Brock, T. H. 1988. Reproductive success. University of Chicago Press, Chicago.

Newton, I. 1989. Lifetime reproduction in birds. Academic Press, London.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, London.

CHAPTER 2

Barrowclough, G. F. and R. F. Rockwell. 1993. Variance of lifetime reproductive success: estimation based on demographic data. *American Naturalist* **141**:281-295.

Clark, W. S. 1981. A modified dho-gaza trap for use at raptor banding stations. *Journal of Wildlife Management* **45**:1043-1044.

James, P. C., A. R. Smith, L. W. Oliphant, and I. G. Warkentin. 1987. Northward expansion of the wintering range of the Richardson's Merlin. *Journal of Field Ornithology* **58**:112-117

James, P. C., I. G. Warkentin, and L. W. Oliphant. 1989. Turnover and dispersal in urban Merlins *Falco columbarius*. *Ibis* **131**:426-429.

Lieske, D. J. 1997. Population dynamics of urban Merlins. M.Sc. thesis. University of Saskatchewan, Saskatoon, Canada.

Lieske, D. J., L. W. Oliphant, P. C. James, I. G. Warkentin, and R. H. M. Espie. 1997. Age of first breeding in Merlins (*Falco columbarius*). *Auk*

114:288-290.

- Newton, I. 1989. Lifetime reproduction in birds. Academic, London, England**
- Oliphant, L. W. and E. Haug. 1985. Productivity, population density and rate of increase of an expanding Merlin population. Raptor Research 19:56-59.**
- Sodhi, N. S. 1991. Pair copulations, extra-pair copulations, and intraspecific nest intrusions in Merlin. Condor 93:434-437.**
- Sodhi, N. S., P. C. James, I. G. Warkentin, and L. W. Oliphant. 1992. Breeding ecology of urban Merlins (*Falco columbarius*). Canadian Journal of Zoology 70:1477-1483.**
- Sodhi, N. S. and L. W. Oliphant. 1993. Prey selection by urban-breeding Merlins. Auk 110:727-735.**
- Sodhi, N. S., L. W. Oliphant, P. C. James, and I. G. Warkentin. 1993. Merlin (*Falco columbarius*). The birds of North America (A. Poole and F. Gill, Eds.), No. 44. Academy of Natural Sciences, Philadelphia and American Ornithologists' Union, Washington, D. C., USA.**
- Temple, S. A. 1972. Sex and age characteristics of North American Merlins. Bird-Banding 43:191-196.**
- Warkentin, I. G., A. D. Curzon, R. E. Carter, J. H. Wetton, P. C. James, L. W. Oliphant, and D. T. Parkin. 1994. No evidence for extrapair fertilizations in the Merlin revealed by DNA fingerprinting. Molecular Ecology 3:229-234.**
- Warkentin, I. G., and P. C. James. 1988. Nest-site selection by urban Merlins.**

Condor **90**:734-738.

Weatherhead, P. J. and P. T. Boag. 1997. Genetic estimates of annual and lifetime reproductive success in male Red-winged Blackbirds. *Ecology* **78**:884-896.

CHAPTER 3

Abrams, P. A. 1991. The fitness costs of senescence: the evolutionary importance of events in early adult life. *Evolutionary Ecology* **5**:343-360.

Adams, D. C. and C. D. Anthony. 1996. Using randomization techniques to analyse behavioural data. *Animal Behaviour* **51**:733-738.

Aebischer, N. J. and J. C. Coulson. 1990. Survival of the Kittiwake in relation to sex, year, breeding experience and position in the colony. *Journal of Animal Ecology* **59**:1063-1071.

Bryant, D. M. 1979. Reproductive costs in the House Martin (*Delichon urbica*). *Journal of Animal Ecology* **48**:655-675.

Burger, J. 1988. Effects of age on foraging in birds. *Acta XIX Congressus Internationalis Ornithologici* **2**:1127-1140.

Charlesworth, B. 1980. Evolution in age-structured populations. Cambridge University Press, Cambridge, England.

Coulson, J. C. and J. Horobin. 1976. The influence of age on the breeding biology and survival of the Arctic Tern (*Sterna paradisaea*). *Journal of Zoology* **178**:247-260.

Coulson, J. C. and J. M. Porter. 1985. Reproductive success of the Kittiwake

- Rissa tridactyla*: the roles of clutch size, chick growth rates and parental quality. *Ibis* **127**:450-466.
- Clutton-Brock, T. H. 1988. *Reproductive success: studies of individual variation in contrasting breeding systems*. University of Chicago Press, Chicago, Illinois, USA.
- Crowley, P. H. 1992. Resampling methods for computation-intensive data analysis in ecology and evolution. *Annual Review of Ecology and Systematics* **23**:405-447.
- Daan, S., C. Dijkstra, F. Drent, and T. Meijer. 1988. Food supply and the annual timing of avian reproduction. *Acta XIX International Ornithological Congress* **1**:392-407.
- Desrochers, A. 1992. Age and foraging success in European blackbirds: variation between and within individuals. *Animal Behaviour* **43**:885-894.
- Emlen, J. H. 1970. Age specificity and ecological theory. *Ecology* **51**:588-602.
- Espie, R. H. M., P. C. James, I. G. Warkentin, and L. W. Oliphant. 1996. Ecological correlates of molt in Merlins (*Falco columbarius*). *Auk* **113**:363-369.
- Forslund, P. and K. Larsson. 1992. Age-related reproductive success in the Barnacle Goose. *Journal of Animal Ecology* **61**:195-204.
- Forslund, P. and T. Pärt. 1995. Age and reproduction in birds-hypotheses and tests. *Trends in Ecology and Evolution* **10**:374-378.
- Gehlbach, F. R. 1989. Screech-owl. In I. Newton (editor) *Lifetime*

- Reproduction in Birds, pp 315-326. Academic Press, London, England.
- Gustafsson, L. and T. Pärt. 1990. Acceleration of senescence in the Collared Flycatcher *Ficedula albicollis* by reproductive costs. *Nature* **347**:279-281.
- Hamilton, W. D. 1966. The moulding of senescence by natural selection. *Journal of Theoretical Biology* **12**:12-45.
- Heyne, K. H. and P. Wegner. 1991. Successful breeding of a first year male Peregrine (*Falco peregrinus*) in the wild. *Journal für Ornithologie* **132**:97-98.
- Jacobsen, K. O., K. E. Erikstad, and B. E. Saether. 1995. An experimental study of the costs of reproduction in the Kittiwake *Rissa tridactyla*. *Ecology* **76**:1636-1642.
- James, P. C., I. G. Warkentin, and L. W. Oliphant. 1989. Turnover and dispersal in urban Merlins *Falco columbarius*. *Ibis* **131**:426-429.
- Klomp, H. 1970. The determination of clutch size in birds: a review. *Ardea* **58**:1-54.
- Korpimäki, E. 1987. Timing of breeding of Tengmalm's Owl *Aegolius funereus* in relation to vole dynamics in western Finland. *Ibis* **129**:58-68.
- _____. 1988. Effects of age on breeding performance of Tengmalm's Owl *Aegolius funereus* in western Finland. *Ornis Scandinavica* **19**:21-26.
- Lack, D. 1947. The significance of clutch size. I. Intraspecific variation. *Ibis* **89**:302-352.
- _____. 1950. The breeding seasons of European birds. *Ibis* **92**:288-316.

- _____. 1968. *Ecological adaptations for breeding in birds*. Methuen, London, England.
- Lambrechts, M. M., J. Bondel, A. Caizergues, P. C. Dias, R. Pradel, and D. W. Thomas. 1999. Will estimates of lifetime recruitment of breeding offspring on small-scale study plots help us to quantify processes underlying adaptation? *Oikos* **86**:147-151.
- Lieske, D. J., L. W. Oliphant, P. C. James, I. G. Warkentin, and R. H. M. Espie. 1997. Age of first breeding in Merlins (*Falco columbarius*). *Auk* **114**:288-290.
- Manly, B. F. J. 1997. *RT Program Manual*. Cheyenne, Wy, USA.
- Martin, K. 1995. Patterns and mechanisms of age dependent reproduction and survival in birds. *American Zoologist* **35**:123-141.
- Masman, D., S. Daan, and C. Dijkstra. 1988. Time allocation in the Kestrel *Falco tinnunculus* and the principle of energy minimization. *Journal of Animal Ecology* **57**:411-432.
- Mearns, R. and I. Newton. 1984. Turnover and dispersal in a Peregrine *Falco peregrinus* population. *Ibis* **126**:347-355.
- Medawar, P. B. 1952. *An unsolved problem in biology*. H. K. Lewis, London, England.
- Newton, I. 1979. *Population ecology of raptors*. Poyser, Berhamsted, England.
- _____. 1985. Lifetime reproductive output of female Sparrowhawks. *Journal*

- of Animal Ecology **54**:241-253.
- _____. 1986. *The Sparrowhawk*. T. and A. D. Poyser, Calton, England.
- _____. 1988. Individual performance in Sparrowhawks: the ecology of two sexes. *Acta XIX Internationalis Ornithologici Congressus* **1**:125-154.
- _____. 1989a. *Lifetime reproduction in birds*. Academic, London, England.
- _____. 1989b. Sparrowhawk. In I. Newton (editor) *Lifetime Reproduction in Birds*. pp 279-296. Academic Press, London, England.
- Newton, I. and M. Marquiss. 1984. Seasonal trend in the breeding performance of Sparrowhawks. *Journal of Animal Ecology* **53**:809-829.
- Newton, I., E. R. Meek and B. Little. 1984. Breeding season foods of Merlins *Falco columbarius* in Northumbria. *Bird Study* **31**:49-56.
- Newton, I. and P. Rothery. 1997. Senescence and reproductive value in Sparrowhawks. *Ecology* **78**:1000-1008.
- _____. 1998. Age related trends in the breeding success of individual female Sparrowhawks *Accipiter nisus*. *Ardea* **86**:21-31.
- Noi, E. and J. N. M. Smith. 1987. Effects of age and breeding experience on seasonal reproductive success in the Song Sparrow. *Journal of Animal Ecology* **56**:301-313.
- Nur, N. 1988. The cost of reproduction in birds: an examination of the evidence. *Ardea* **76**:155-168.
- Partridge, L. and N. H. Barton. 1993. Optimality, mutation and the evolution of ageing. *Nature* **362**:305-311.

- Perdeck, A. C. and A. J. Cavé. 1992. Laying date in the Coot: effects of age and mate choice. *Journal of Animal Ecology* **61**:13-19.
- Perrins, C. M. 1970. The timing of birds' breeding seasons. *Ibis* **112**:242-255.
- Perrins, C. M. 1979. *British Tits*. Collins, London, England.
- Perrins, C. M. and D. Moss. 1974. Survival of young Great Tits in relation to age of female parent. *Ibis* **116**:220-224.
- Promislow, D. E. L. and P. H. Harvey. 1990. Living fast and dying young; a comparative analysis of life history variation among mammals. *Journal of Zoology* **220**:417-437.
- Pugesek, B. H. 1981. Increased reproductive effort with age in the California Gull (*Larus californicus*). *Science* **212**:822-823.
- Pugesek, B. H. and K. L. Diem. 1990. The relationship between reproduction and survival in known-aged California Gulls. *Ecology* **71**:811-817.
- Pyle, P., L. B. Spear, W. J. Sydeman, and D. G. Ainley. 1991. The effects of experience and age on the breeding performance of Western Gulls. *Auk* **108**:25-33.
- Reese, K. P. and J. A. Kadlec. 1985. Influence of high density and parental age on the habitat selection and reproduction of Black-billed Magpies. *Condor* **87**:96-105.
- Ross, H. A. 1980. The reproductive rates of yearling and older Ipswich Sparrows *Passerculus sandwichensis*. *Canadian Journal of Zoology* **58**:1557-1563.

- Saether, B. E. 1990. Age-specific variation in the reproductive performance of birds. *Current Ornithology* 7:251-283.
- Siegel, S. and N. J. Castellan. 1988. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York, New York, USA.
- Sodhi, N. S., P. C. James, I. G. Warkentin, and L. W. Oliphant. 1992. Breeding ecology of urban Merlins (*Falco columbarius*). *Canadian Journal of Zoology* 70:1477-1483.
- Sodhi, N. S. and L. W. Oliphant. 1993. Prey selection by urban-breeding Merlins. *Auk* 110:727-735.
- Sodhi, N. S., L. W. Oliphant, P. C. James, and I. G. Warkentin. 1993. Merlin (*Falco columbarius*). *The birds of North America* (A. Poole and F. Gill, Eds.), No. 44. Academy of Natural Sciences, Philadelphia and American Ornithologists' Union, Washington, D. C., USA.
- StatSoft, Inc. (1995). STATISTICA for Windows program manual. Tulsa, Ok, USA.
- Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press, Oxford, England.
- Temple, S. A. 1972. Sex and age characteristics of North American Merlins. *Bird-Banding* 43:191-196.
- van Balen, J. H. 1973. A comparative study of the breeding ecology of the Great Tit *Parus major* in different habitats. *Ardea* 61:1-93.
- Verhulst, S., J. H. van Balen, J. M. Tinbergen. 1995. Seasonal decline in

reproductive success of the Great Tit: variation in time or quality.

Ecology **76**:2392-2403.

Weimerskirch, H. 1992. Reproductive effort in long lived birds: age specific patterns of condition, reproduction and survival in the wandering albatross. *Oikos* **64**:464-473.

Wiehn, J. and E. Korpimäki. 1997. Food limitation on brood size: experimental evidence in the Eurasian Kestrel. *Ecology* **78**:2043-2050.

Wijnandts, H. 1984. Ecological energetics of the Long-eared Owl (*Asio otus*). *Ardea* **72**:1-92.

Williams, G. C. 1966. Natural selection, the costs of reproduction and a refinement of Lack's principle. *American Naturalist* **100**:687-690.

Wooler, R. D., J. S. Bradley, I. J. Skira, and D. L. Serventy. 1990. Reproductive success of Short-tailed Shearwaters *Puffinus tenuirostris* in relation to their age and breeding experience. *Journal of Animal Ecology* **59**:161-170.

Zar, J. H. 1984. Biostatistical analysis. Prentice Hall, Englewood Cliffs, New Jersey, USA.

CHAPTER 4

Amadon, D. 1975. Why are female birds of prey larger than males? - *Raptor Res.* **9**: 1-11.

Andersson, M. and Norberg, R. A. 1981. Evolution of reversed sexual dimorphism and role partitioning among predatory birds, with a size

- scaling of flight performance. - *Biol. J. Linn. Soc.* **15**: 105-130.
- Boag, P. T. and Grant, P. R. 1981. Intense natural selection in a population of Darwin's finches (*Geospizinae*) in the Galápagós. - *Science* **214**: 82-85.
- Cade, T. J. 1982. *The falcons of the world.* - Cornell Univ. press, Ithaca.
- Catry, P., Phillips, R. A. and Furness, R. W. 1999. Evolution of reversed sexual dimorphism in skuas and jaegers. - *Auk* **116**: 158-168.
- Choudhury, S., Black, J. M. and Owen, M. 1996. Body size, fitness and compatibility in Barnacle Geese *Branta leucopsis*. - *Ibis* **138**: 700-709.
- Clutton-Brock, T. H. 1988. Reproductive success. - In: Clutton-Brock, T. H. (ed.), *Reproductive success: studies of individual variation in contrasting breeding systems.* University of Chicago Press, pp. 472-475.
- Clutton-Brock, T. H., Harvey, P. and Rudder, B. 1977. Sexual dimorphism, socioeconomic sex ratio and body weight in primates. - *Nature* **269**: 797-800.
- Clutton-Brock, T. H., Guinness, F. E. and Albon, S. D. 1982. *Red deer. Behavior and ecology of two sexes.* - Edinburgh University Press.
- Cooke, F., Findlay, C. S. and Rockwell, R. F. 1984. Recruitment and the timing of reproduction in lesser snow geese. - *Auk* **101**: 451-458.
- Daan, S., Dijkstra, C., Drent, F. and Meijer, T. 1988. Food supply and the annual timing of avian reproduction.- *Proc. Int. Orn. Congr.* **19**: 392-407.
- Espie, R. H. M., James, P. C., Warkentin, I. G. and Oliphant, L. W. 1996. Ecological correlates of molt in Merlins (*Falco columbarius*). - *Auk* **113**:

363-369.

- Fairbairn, D. J. and Preziosi, R. F. 1994. Sexual selection and the allometry for sexual size dimorphism in the water strider, *Aquarius remigis*. - *Am. Nat.* **144**: 101-118.
- Fleischer, R. C. and Johnston, R. F. 1982. Natural selection on body size and proportions in House Sparrows. - *Nature* **298**:747-749.
- Francis, C. M. and Wood, D. S. 1989. Effects of age and wear on wing length of wood warblers. - *J. Field Ornithol.* **60**: 495-503.
- Freeman, S. and Jackson, W. M. 1990. Univariate metrics are not adequate to measure avian body size. - *Auk* **107**: 69-74.
- Gehlbach, F. R. 1989. Screech-Owl. - In Newton, I. (ed.), *Lifetime reproduction in birds*. Academic Press, pp. 315-326.
- Gustafsson, L. 1986. Lifetime reproductive success and heritability: Empirical support for Fisher's fundamental theorem. - *Am. Nat.* **128**: 761-764.
- Hakkarainen, H. and Korpimäki, E. 1991. Reversed sexual size dimorphism in Tengmalm's owl: is small male size adaptive? - *Oikos* **61**: 337-346.
- Hepp, G. R., Kenamer, R. A. and Harvey, W. F. 1989. Recruitment and natal philopatry of wood ducks. - *Ecology* **70**: 897-903.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. - *Ecological Monographs* **54**: 187-211.
- Jones, I.L. and Hunter, F.M. 1993. Mutual sexual selection in a monogamous seabird. - *Nature* **362**: 238-239.

- Korpimäki, E. 1986. Reversed size dimorphism in birds of prey especially in Tengmalm's owl *Aegolius funereus*: a test of the "starvation hypothesis". - *Ornis. Scand.* 17: 326-332.
- _____. 1987. Timing of breeding of Tengmalm's Owl *Aegolius funereus* in relation to vole dynamics in western Finland. - *Ibis* 129: 58-68.
- _____. 1992. Fluctuating food abundance determines the lifetime reproductive success of male Tengmalm's Owls. - *J. Anim. Ecol.* 61: 103-111.
- Lack, D. 1950. The breeding seasons of European birds. - *Ibis* 92: 288-316.
- Lieske, D. J., Oliphant, L. W., James, P. C., Warkentin, I. G. and Espie, R. H. M. 1997. Age of first breeding in Merlins (*Falco columbarius*). - *Auk* 114: 288-290.
- Lessells, C. M. and Boag, P. T. 1987. Unrepeatable repeatabilities: a common mistake. - *Auk* 104: 116-121.
- Marti, C. 1990. Sex and age dimorphism in the Barn Owl and a test of mate choice. - *Auk* 107: 246-254.
- Marti, C. 1997. Lifetime reproductive success in barn owls near the limit of the species' range. - *Auk* 114: 581-592.
- Martin, K. and Hannon, S. J. 1987. Natal philopatry and recruitment of Willow Ptarmigan in north central and north western Canada. - *Oecologia* 71: 518-524.
- Masman, D., Daan, S. and Dijkstra, C. 1988. Time allocation in the Kestrel *Falco tinnunculus* and the principle of energy minimization. - *J. Anim.*

- Ecol. **57**: 411-432.
- Møller, A. P. and Birkhead, T. R. 1991. Frequent copulations and mate guarding as alternative paternity guards in birds: a comparative study. - Behaviour **118**: 170-186.
- Mueller, H.C. 1986. The evolution of reversed sexual dimorphism in owls: an empirical analysis of possible selective factors. - Wilson Bull. **98**: 387-406.
- Newton, I. 1979. Population ecology of raptors. - Buteo books.
- _____. 1985. Lifetime reproductive output of female Sparrowhawks. - J. Anim. Ecol. **54**: 241-253.
- _____. 1986. The sparrowhawk. - T. and A. D. Poyser.
- _____. 1988. Individual performance in Sparrowhawks: the ecology of two sexes. -Proc. Int. Orn. Congr. **19**: 125-154.
- _____. 1989. Sparrowhawk. - In: Newton, I. (ed.), Lifetime reproductive success in Birds. Academic Press, pp. 279-296.
- Newton, I. and Marquiss, M. 1984. Seasonal trend in the breeding performance of sparrowhawks. - J. Anim. Ecol. **53**: 809-829.
- Newton, I., Meek, E. R. and Little, B. 1984. Breeding season foods of Merlins *Falco columbarius* in Northumbria. - Bird Study **31**: 49-56.
- Ohgushi, T. 1991. Lifetime fitness and evolution of reproductive pattern in herbivorous lady beetle. - Ecology **72**: 2110-2122.
- Orians, G. H. 1985. Blackbirds of the Americas. - Princeton University Press.

- Perrins, C. M. 1965. Population fluctuations and clutch size in the great tit *Parus major* L. - *J. Anim. Ecol.* **34**: 601-647.
- _____. 1970. The timing of birds' breeding seasons. - *Ibis* **112**: 242-255.
- Peters, R. H. 1986. The ecological implications of body size. - Cambridge Univ. Press.
- Pleasants, J.M., and Pleasants, B.Y. 1988. Reversed size dimorphism in raptors: evidence for how it evolved. - *Oikos* **52**: 129-135.
- Postupalsky, S. 1989. Osprey. - In: Newton, I. (ed.), Lifetime reproduction in birds. Academic Press, pp. 297-313.
- Price, T. D. and Grant, P. R. 1984. Life history traits and natural selection for small body size in a population of Darwin's finches. - *Evolution* **38**: 483-494.
- Promislow, D. E. L. 1992. Costs of sexual selection in natural populations of mammals. - *Proc. Roy. Soc. Lond. B* **247**: 203-210.
- Promislow, D. E. L., Montgomerie, R. and Martin, T. E. 1992. Mortality costs of sexual dimorphism in birds. - *Proc. Roy. Soc. Lond. B* **250**: 142-150.
- Rising, J. D. and Somers, K. M. 1989. The measurement of overall body size in birds. - *Auk* **106**: 666-674.
- Rohwer, S., Langston, N. and Gori, D. 1996. Body size and harem size in male red-winged blackbirds: manipulating selection with sex-specific feeders. - *Evolution* **50**: 2049-2065.
- Saurola, P. 1989. Ural Owl. - In: Newton, I. (ed.), Lifetime reproduction in

- birds. Academic Press, pp. 81-86.
- Schultz, E. T. 1993. The effect of birth date on fitness of female dwarf perch, *Micrometrus minimus* (Perciformes: Embiotocidae). - *Evolution* **47**: 520-539.
- Searcy, W. A. 1979. Sexual selection and body size in male red-winged blackbirds. - *Evolution* **33**: 649-661.
- Selander, R. K. 1965. On mating systems and sexual selection. - *Am. Nat.* **99**: 129-141.
- _____. 1972. Sexual selection and dimorphism in birds. - In: Campbell, B. (ed.), *Sexual selection and the descent of man*. Aldine, pp. 180-230.
- Siegel, S. and Castellan, N. J. 1988. *Nonparametric statistics for the behavioral sciences*. - McGraw-Hill.
- Smith, S. M. 1982. Raptor "reverse" dimorphism revisited: a new hypothesis. - *Oikos* **39**: 118-122.
- Sodhi, N. S., James, P. C., Warkentin, I. G. and Oliphant, L. W. 1992. Breeding ecology of urban Merlins (*Falco columbarius*). - *Can. J. Zool.* **70**: 1477-1483.
- Sodhi, N. S. and Oliphant, L. W. 1993. Prey selection by urban-breeding Merlins. - *Auk* **110**: 727-735.
- Sodhi, N. S., Oliphant, L. W., James, P. C. and Warkentin, I. G. 1993. Merlin (*Falco columbarius*). - In: Poole, A and Gill, F. (eds.), *The birds of North America*, No. 44. Academy of Natural Sciences, Philadelphia and

American Ornithologists' Union.

- Stearns, S. C. 1992. *The evolution of life histories*. - Oxford University Press.
- Temeles, E. J. 1985. Sexual size dimorphism of bird-eating hawks: the effect of prey vulnerability. - *Am. Nat.* **125**: 485-499.
- Verhulst, S., van Balen, J. H. and Tinbergen, J. M. 1995. Seasonal decline in reproductive success of the great tit: variation in time or quality? - *Ecology* **76**: 2392-2403.
- Wallin, K. 1988. Life-history evolution and ecology in the tawny owl (*Strix aluco*). Ph.D. dissertation. - Göteborg University, Göteborg.
- Warkentin, I. G., James, P. C. and Oliphant, L. W. 1990. Body morphometrics, age structure, and partial migration of urban Merlins. - *Auk* **107**: 25-34.
- Warkentin, I. G., James, P. C. and Oliphant, L. W. 1992. Assortative mating in urban-breeding Merlins. - *Condor* **94**: 418-426.
- Weatherhead, P. J. and Clark, R. G. 1994. Natural selection and sexual size dimorphism in red-winged blackbirds. - *Evolution* **48**: 1071-1079.
- Weatherhead, P. J., Greenwood, H. and Clark, R. G. 1987. Natural selection and sexual selection on body size in red-winged blackbirds. - *Evolution* **41**: 1401-1403.
- Webster, M. S. 1992. Sexual dimorphism, mating system and body size in new blackbirds (Icterinae). - *Evolution* **46**: 1621-1641.
- Wiehn, J. and Korpimäki, E. 1997. Food limitation on brood size: experimental evidence in the Eurasian Kestrel. - *Ecology* **78**: 2043-2050.

Wijnandts, H. 1984. Ecological energetics of the Long-eared Owl (*Asio otus*). - *Ardea* **72**:1-92.

Wiklund, C. G. 1995. Nest predation and life-span: components of variance in LRS among Merlin females. - *Ecology* **76**: 1994-1996.

_____. 1996. Body length and wing length provide univariate estimates of overall body size in the Merlin. - *Condor* **98**: 581-588.

Williams, G. C. 1975. *Sex and Evolution*. - Princeton Univ. press.

Wyllie, I. and Newton, I. 1994. Latitudinal variation in the body size of Sparrowhawks *Accipiter nisus* within Britain. - *Ibis* **136**: 434-440.

Yasukawa, K. 1981. Male quality and female choice of mate in the red-winged blackbird (*Agelaius phoeniceus*). - *Ecology* **62**: 922-929.

_____. 1987. Breeding and nonbreeding season mortality of territorial male red-winged blackbirds. - *Auk* **104**: 56-62.

Zar, J. H. 1984. *Biostatistical analysis*. - Prentice Hall.

CHAPTER 5

Alisauskas, R. T. and C. D. Ankney. 1985. Nutrient reserves and the energetics of reproduction in American Coots. *Auk* **102**:133-144.

Ankney, C. D. and C. D. MacInnes. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. *Auk* **95**:459-471.

Boake, C. R. B. 1989. Repeatability: its role in evolutionary studies of mating behavior. *Evolutionary Ecology* **3**:173-182.

Bortolotti, G. R. and W. M. Iko. 1992. Non-random pairing in American

- Kestrels: mate choice versus intra-sexual competition. *Animal Behaviour* **44**:811-821.
- Chastel, O., H. Weimerskirch, and P. Jouventin. 1995. Body condition and seabird reproductive performance: a study of three petrel species. *Ecology* **76**:2240-2246.
- Choudhury, S., J. M. Black and M. Owen. 1996. Body size, fitness and compatibility in Barnacle Geese *Branta leucopsis*. *Ibis* **138**:700-709.
- Clutton-Brock, T. H. 1988. Reproductive success. University of Chicago Press, Chicago.
- Cooke, F., C. S. Findlay, and R. F. Rockwell. 1984. Recruitment and the timing of reproduction in Lesser Snow Geese (*Chen caerulescens caerulescens*). *Auk* **101**:451-458.
- Coulson, J. C. 1972. The significance of the pair bond in the Kittiwake. *Proceedings International Ornithological Congress XV*:424-433.
- Daan, S., C. Dijkstra, F. Drent, and T. Meijer. 1988. Food supply and the annual timing of avian reproduction. *Acta XIX International Ornithological Congress* **1**:392-407.
- Dale, S. and T. Slagsvold. 1994. Male pied fly catchers do not choose mates. *Animal Behaviour* **47**:1197-1205.
- Darwin, C. 1871. The descent of man, and selection in relation to sex. John Murray, London.
- Drent, R. H. and S. Daan. 1980. The prudent parent: energetic adjustments in

- avian breeding. *Ardea* **68**:225-252.
- Ens, B. J., S. Choudhury, and J. M. Black. 1996. Mate fidelity and divorce in monogamous birds. In: *Partnerships in birds: The study of monogamy* (J. M. Black, Ed.). Oxford University Press, Oxford.
- Espie, R. H. M., P. C. James, I. G. Warkentin, and L. W. Oliphant. 1996. Ecological correlates of molt in Merlins (*Falco columbarius*). *Auk* **113**:363-369.
- Falconer, D. S. 1981. *Introduction to quantitative genetics*. Longham, New York.
- Freeman, S. and W. M. Jackson. 1990. Univariate metrics are not adequate to measure avian body size. *Auk* **107**:69-74.
- Gustafsson, L. 1986. Lifetime reproductive success and heritability: Empirical support for Fisher's fundamental theorem. *American Naturalist* **128**:761-764.
- Gwynne, D. T. and L. W. Simmons. 1990. Experimental reversal of courtship roles in an insect. *Nature* **346**:172-174.
- Hakkarainen, H. and E. Korpimäki. 1991. Reversed sexual size dimorphism in Tengmalm's owl: is small male size adaptive? *Oikos* **61**:337-346.
- Jakob, E. M., S. E. Marshall, and G. W. Uetz. 1996. Estimating fitness: a comparison of body condition indices. *Oikos* **77**:61-67.
- Johnson, K. 1988a. Sexual selection in pinyon jays I: female choice and male-male competition. *Animal Behaviour* **36**:1038-1047.

- _____. 1988b. Sexual selection in pinyon jays II: male choice and female-female competition. *Animal Behaviour* **36**:1048-1053.
- Johnson, K. and J. M. Marzluff. 1990. Some problems and approaches in avian mate choice. *Auk* **107**:296-304.
- Johnstone, R. A., J. D. Reynolds and J. C. Deutsch. 1996. Mutual mate choice and sex differences in choosiness. *Evolution* **50**:1382-1391.
- Jones, I. L. and F. M. 1993. Mutual sexual selection in a monogamous seabird. *Nature* **362**:238-239.
- Kirkpatrick, M. and M. J. Ryan. 1991. The evolution of mating preferences and the paradox of the lek. *Nature* **350**:33-38.
- Lessells, C. M. and P. T. Boag. 1987. Unrepeatable repeatabilities: a common mistake. *Auk* **104**:116-121.
- Marti, C. D. 1990. Sex and age dimorphism in the Barn Owl and a test of mate choice. *Auk* **107**:246-254.
- Marzluff, J. M. and R. P. Balda. 1988. The advantages of, and constraints forcing, mate fidelity in pinyon jays. *Auk* **105**:286-295.
- Masman, D., S. Daan, and C. Dijkstra. 1988. Time allocation in the Kestrel *Falco tinnunculus* and the principle of energy minimization. *Journal of Animal Ecology* **57**:411-432.
- Meijer, T. S., S. Daan, and M. Hall. 1988. Family planning in the Kestrel (*Falco tinnunculus*): the proximate control covariation of laying date and clutch size. *Behaviour* **114**:117-136.

- Møller, A. P. 1992. Sexual selection in the monogamous barn swallow (*Hirundo rustica*). II. Mechanisms of intersexual selection. *Journal of Evolutionary Biology* 5:603-624.
- _____. 1994. Repeatability of female mate choice in a monogamous swallow. *Animal Behaviour* 47:643-648.
- Mueller, H. C. 1986. The evolution of reversed sexual dimorphism in owls: an empirical analysis of possible selective factors. *Wilson Bulletin* 98:387-406.
- Mueller, H. C. and K. Meyer. 1985. The evolution of reversed sexual dimorphism in size: a comparative analysis of the Falconiformes of the western Palearctic. *Current Ornithology* 2:65-101.
- Newton, I. 1979. Population ecology of raptors. Poyser, Berhamsted, England.
- _____. 1988. Individual performance in Sparrowhawks: the ecology of two sexes. *Proceedings International Ornithological Congress XIX*:125-154.
- _____. 1989. Lifetime reproduction in birds. Academic, London, England.
- Phillips, R. A. and R. W. Furness. 1999. Measurement of heritability of hatching date and chick condition in parasitic jaegers. *Canadian Journal of Zoology* 76:2290-2294.
- Pleasants, J. M. and B. Y. Pleasants. 1988. Reversed size dimorphism in raptors: evidence for how it evolved. *Oikos* 52:129-135.
- Price, T., M. Kirkpatrick, and S. J. Arnold. 1988. Directional selection and the

- evolution of breeding date in birds. *Science* **240**:798-799.
- Price, T. and D. Schluter. 1991. On the low heritability of life history traits. *Evolution* **45**:853-861.
- Promiankowski, A. N. 1988. The evolution of female mate preferences for male genetic quality. *Oxford Surv. Evol. Biol.* **5**:136-184.
- Promiankowski, A., Y. Iwasa, and S. Nee. 1991. The evolution of costly mate preferences. I. Fisher and biased mutation. *Evolution* **45**:1422-1430.
- Raveling, D. G. 1979. The annual cycle of body composition of Canada Geese with special reference to control of reproduction. *Auk* **96**:234-252.
- Rising, J. D. and K. M. Somers. 1989. The measurement of overall body size in birds. *Auk* **106**:666-674.
- Safina, C. 1984. Selection for reduced male size in raptorial birds: the possible roles of female choice and mate guarding. *Oikos* **43**:159-164.
- Sargent, R. C., M. R. Gross, and E. P. van den Berghe. 1986. Male mate choice in fishes. *Animal Behaviour* **34**:545-550.
- Schluter, D. and L. Gustaffson. 1993. Maternal inheritance of condition and clutch size in the collared flycatcher. *Evolution* **47**:658-667.
- Searcy, W. A. 1982. The evolutionary effects of mate selection. *Annual Review of Ecology and Systematics* **13**:57-85.
- Sodhi, N. S., P. C. James, I. G. Warkentin, and L. W. Oliphant. 1992. Breeding ecology of urban Merlins (*Falco columbarius*). *Canadian*

Journal of Zoology 70:1477-1483.

StatSoft, Inc. (1995). STATISTICA for Windows program manual. Tulsa, Ok, USA.

Trivers, R. L. 1972. Parental investment and sexual selection. Sexual selection and the descent of man 1871-1971 (B. Campbell, Ed.). Aldine, Chicago.

Village, A. 1990. The Kestrel. T. and A. D. Poyser, London, England.

_____. 1992. Assortative mating in urban-breeding Merlins. Condor 94:418-426.

Wiggins, D. A. 1989. Heritability of body size in cross-fostered tree swallow broods. Evolution 43:1808-1811.

Wijnandts, H. 1984. Ecological energetics of the Long-eared Owl (*Asio otus*). Ardea 72:1-92.

Wiklund, C. G. 1996. Body length and wing length provide univariate estimates of overall body size in the Merlin. Condor 98:581-588.

Williams, G. C. 1975. Sex and evolution. Princeton University Press, Princeton, NJ.

Wyllie, I. and I. Newton. 1994. Latitudinal variation in the body size of Sparrowhawks *Accipiter nisus* within Britain. Ibis 136:434-440.

Zar, J. H. 1984. Biostatistical analysis. Prentice Hall, Englewood Cliffs, New Jersey, USA.

CHAPTER 6

- Adams, D. C. and C. D. Anthony. 1996. Using randomization techniques to analyse behavioural data. *Animal Behaviour* **51**:733-738.
- Alisauskas, R. T. and C. D. Ankney. 1985. Nutrient reserves and the energetics of reproduction in American Coots. *Auk* **102**:133-144.
- Ankney, C. D. and C. D. MacInnes. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. *Auk* **95**:459-471.
- Beletsky, L. D. and G. H. Orians. 1991. Effects of breeding experience and familiarity on site fidelity in female red-winged blackbirds. *Ecology* **72**:787-796.
- Birkhead, T. R. and D. N. Nettleship. 1982. Adaptive significance of egg size and laying date in Thick-billed Murres *Uria lomvia*. *Ecology* **63**:300-306.
- Chastel, O., H. Weimerskirch, and P. Jouventin. 1995. Body condition and seabird reproductive performance: a study of three petrel species. *Ecology* **76**:2240-2246.
- Cooke, F., C. S. Findlay, and R. F. Rockwell. 1984. Recruitment and the timing of reproduction in Lesser Snow Geese (*Chen caerulescens caerulescens*). *Auk* **101**:451-458.
- Coulson, J. C. 1968. Differences in the quality of birds nesting in the centre and on the edge of a colony. *Nature* **217**:478-479.
- Coulson, J. C. and J. M. Porter. 1985. Reproductive success of the kittiwake *Rissa tridactyla*: the roles of clutch size, chick growth rates and parental quality. *Ibis* **127**:450-466.

- Coulson, J. C. and C. S. Thomas. 1985. Differences in the breeding performance of individual kittiwake gulls *Rissa tridactyla*. Behavioural Ecology: Ecological Consequences of Adaptive Behaviour (R. M. Sibly and R. H. Smith, Eds.). Blackwell Scientific Publications, Oxford, UK.
- Crowley, P. H. 1992. Resampling methods for computation-intensive data analysis in ecology and evolution. Annual Review of Ecology and Systematics 23:405-447.
- Daan, S., C. Dijkstra, F. Drent, and T. Meijer. 1988. Food supply and the annual timing of avian reproduction. Acta XIX International Ornithological Congress 1:392-407.
- Dijkstra, C., L. Vuursteen, S. Daan, and D. Masman. 1982. Clutch size and laying date in the kestrel *Falco tinnunculus*: effect of supplementary food. Ibis 124:210-213.
- Dobson, F. S. and W. T. Jones. 1986. Multiple causes of dispersal. American Naturalist 126:855-858.
- Drent, R. H. and S. Daan. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68:225-252.
- Ens, B. J., M. Kersten, A. Brenninkmeijer and J. B. Hulscher. 1992. Territory quality, parental effort and reproductive success of oystercatchers (*Haematopus ostralegus*). Journal of Animal Ecology 61:703-715.
- Espie, R. H. M., P. C. James, I. G. Warkentin, and L. W. Oliphant. 1996. Ecological correlates of molt in Merlins (*Falco columbarius*). Auk

113:363-369.

Freeman, S. and W. M. Jackson. 1990. Univariate metrics are not adequate to measure avian body size. *Auk* **107:69-74.**

Gavin, T. H. and E. K. Bollinger. 1988. Reproductive correlates of breeding site fidelity in Bobolinks (*Dolichonyx oryzivorus*). *Ecology* **69:96-103.**

Goodburn, S. F. 1991. Territory quality or bird quality? Factors determining breeding success in the Magpie *Pica pica*. *Ibis* **133:85-90.**

Greenwood, P. J. and P. H. Harvey. 1982. The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics* **13:1-21.**

Hickey, J. J. 1942. Eastern populations of the Duck Hawk. *Auk* **59:176-204.**

Hochachka, W. M. 1993. Repeatable reproduction in Song Sparrows. *Auk* **110:603-613.**

Högstedt, G. 1980. Evolution of clutch size in birds: adaptive variation in relation to territory quality. *Science* **210:1148-1150.**

Jakob, E. M., S. E. Marshall, and G. W. Uetz. 1996. Estimating fitness: a comparison of body condition indices. *Oikos* **77:61-67.**

Koenig, W. D., F. A. Pitelka, W. J. Carmen, R. L. Mumme, and M. T. Stanback. 1992. The evolution of delayed dispersal in cooperative breeders. *Quarterly Review of Biology* **67:111-150.**

Korpimäki, E. 1989. Breeding performance of Tengmalm's Owl *Aegolius funereus*: effects of supplementary feeding in a peak vole year. *Ibis* **131:51-56.**

- _____. 1993. Does nest hole quality, poor breeding success or food depletion drive the breeding dispersal of Tengmalm's Owl. *Journal of Animal Ecology* **62**:606-613.
- Lack, D. 1968. *Ecological adaptations for breeding in birds*. Methuen, London, England.
- Lessells, C. M. 1991. The evolution of life histories. *Behavioural Ecology* (J. R. Krebs and N. B. Davies, Eds.). Blackwell Scientific Publications, Oxford, UK.
- Lessells, C. M. and P. T. Boag. 1987. Unrepeatable repeatabilities: a common mistake. *Auk* **104**:116-121.
- Lieske, D. J., L. W. Oliphant, P. C. James, I. G. Warkentin, and R. H. M. Espie. 1997. Age of first breeding in Merlins (*Falco columbarius*). *Auk* **114**:288-290.
- Manly, B. F. J. 1997. *RT Program Manual*. Cheyenne, Wy, USA.
- Marti, C. D. 1990. Sex and age dimorphism in the Barn Owl and a test of mate choice. *Auk* **107**:246-254.
- Martin, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. *Annual Review of Ecology and Systematics* **18**:453-487.
- Masman, D., S. Daan, and C. Dijkstra. 1988. Time allocation in the Kestrel *Falco tinnunculus* and the principle of energy minimization. *Journal of Animal Ecology* **57**:411-432.
- Meijer, T. S., S. Daan, and M. Hall. 1988. Family planning in the Kestrel

- (*Falco tinnunculus*): the proximate control covariation of laying date and clutch size. *Behaviour* 114:117-136.**
- Moore, J. and R. Ali. 1984. Are dispersal and inbreeding avoidance related? *Animal Behaviour* 32:94-112.**
- Newton, I. 1979. Population ecology of raptors. Poyser, Berhamsted, England.**
- _____. 1985. Lifetime reproductive output of female Sparrowhawks. *Journal of Animal Ecology* 54:241-253.**
- _____. 1986. The Sparrowhawk. T. and A. D. Poyser, Calton, England.**
- _____. 1988. Individual performance in Sparrowhawks: the ecology of two sexes. *Acta XIX Internationalis Ornithologici Congressus* 1:125-154.**
- _____. 1989. Lifetime reproduction in birds. Academic, London, England.**
- _____. 1991. Habitat variation and population regulation in Sparrowhawks. *Ibis* 133:76-88.**
- _____. 1992. Experiments on the limitation of bird numbers by territorial behaviour. *Biological Review* 67:129-173.**
- _____. 1993. Age and site fidelity in female sparrowhawks. *Animal Behaviour* 46:161-168.**
- Newton, I. and M. Marquiss. 1982. Food, predation and breeding season in sparrowhawks. *Journal of Zoology (London)* 197:221-240.**
- _____. 1984. Seasonal trend in the breeding performance of Sparrowhawks. *Journal of Animal Ecology* 53:809-829.**

- Newton, I, M. Marquiss and A. Village. 1983. Weights, breeding and survival in European sparrowhawks. *Auk* **100**:344-354.
- Newton, I., E. R. Meek and B. Little. 1984. Breeding season foods of Merlins *Falco columbarius* in Northumbria. *Bird Study* **31**:49-56.
- Noordwijk, A. J. van, J. H. Balen, and W. Scharloo. 1980. Heritability of ecologically important traits in the Great Tit. *Ardea* **68**:193-203.
- Noordwijk, A. J. van and Jong, G., de. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. *American Naturalist* **128**:137-142.
- Pärt, T. and L. Gustafsson. 1989. Breeding dispersal in the Collared Flycatcher (*Ficedulla albicollis*): possible causes and reproductive consequences. *Journal of Animal Ecology* **58**:305-320.
- Price, T., M. Kirkpatrick, and S. J. Arnold. 1988. Directional selection and the evolution of breeding date in birds. *Science* **240**:798-799.
- Ratcliffe, D. A. 1980. *The Peregrine Falcon*. T. and A. D. Poyser, Calton, England.
- Raveling, D. 1979. The annual cycle of body composition of Canada Geese with special reference to control of reproduction. *Auk* **96**:234-252.
- Riddington, R. and A. G. Gosler. 1995. Differences in reproductive success and parental qualities between habitats in the Great Tit *Parus major*. *Ibis* **137**:371-378.
- Rising, J. D. and K. M. Somers. 1989. The measurement of overall body size

- in birds. *Auk* **106**:666-674.
- Rodenhouse, N. L., T. W. Sheery and R. T. Holmes. 1997. Site-dependent regulation of population size: a new synthesis. *Ecology* **78**:2025-2042.
- Roff, D. A. 1992. The evolution of life histories; theory and analysis. Chapman and Hall, New York, USA.
- Safriel, U. N., M. P. Harris, M. L. and C. K. Britton. 1984. Survival of breeding oystercatchers *Haematopus ostralegus*. *Journal of Animal Ecology* **53**:867-877.
- Shields, W. M. 1984. Factors affecting nest and site fidelity in Adirondack Barn Swallows (*Hirundo rustica*). *Auk* **101**:780-789.
- Siegel, S. and N. J. Castellan. 1988. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York, New York, USA.
- Smith, J. N. M. 1981. Does high fecundity reduce survival in song sparrows? *Evolution* **35**:1142-1148.
- Slagsvold, T. and J. T. Lifjeld. 1990. Influence of male and female quality on clutch size in Tits (*Parus* spp.). *Ecology* **71**:1258-1266.
- Sodhi, N. S. 1991. Pair copulations, extra-pair copulations, and intraspecific nest intrusions in Merlin. *Condor* **93**:434-437.
- _____. 1993. Proximate determinants of foraging effort in breeding male Merlins. *Wilson Bulletin* **105**:68-76.
- Sodhi, N. S., P. C. James, I. G. Warkentin, and L. W. Oliphant. 1992. Breeding ecology of urban Merlins (*Falco columbarius*). *Canadian*

- Journal of Zoology 70:1477-1483.**
- Sodhi, N. S. and L. W. Oliphant. 1992. Hunting ranges and habitat use and selection of urban-breeding Merlins. Condor 94:743-749.**
- _____. 1993. Prey selection by urban-breeding Merlins. Auk 110:727-735.**
- Sodhi, N. S., L. W. Oliphant, P. C. James, and I. G. Warkentin. 1993. Merlin (*Falco columbarius*). The birds of North America (A. Poole and F. Gill, Eds.), No. 44. Academy of Natural Sciences, Philadelphia and American Ornithologists' Union, Washington, D. C., USA.**
- Sonerud, G. A. 1985. Nest hole shift in Tengmair's Owl (*Aegolius funereus*) as defense against nest predation involving long term memory in the predator. Journal of Animal Ecology 54:179-192.**
- Stacey, P. B. and J. D. Ligon. 1987. Territory quality and dispersal options in the acorn woodpecker, and a challenge to the habitat saturation model of cooperative breeding. American Naturalist 130:654-676.**
- StatSoft, Inc. (1995). STATISTICA for Windows program manual. Tulsa, Ok, USA.**
- Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, UK.**
- Village, A. 1990. The Kestrel. T. and A. D. Poyser, London, England.**
- Viitala, J., E. Korpimäki, P. Palokangas, and M. Kolvula. 1995. Attraction of kestrels to vole scent marks visible in ultraviolet light. Nature 373:425-427.**

- Warkentin, I. G., and P. C. James. 1988. Nest-site selection by urban Merlins. *Condor* **90**:734-738.
- _____. 1991. Influence of site fidelity on mate switching in urban-breeding Merlins (*Falco columbarius*). *Auk* **108**:294-302.
- _____. 1992. Assortative mating in urban-breeding Merlins. *Condor* **94**:418-426.
- Wiehn, J. and E. Korpiäki. 1997. Food limitation on brood size: experimental evidence in the Eurasian Kestrel. *Ecology* **78**:2043-2050.
- Wijnandts, H. 1984. Ecological energetics of the Long-eared Owl (*Asio otus*). *Ardea* **72**:1-92.
- Wiklund, C. G. 1996a. Body length and wing length provide univariate estimates of overall body size in the Merlin. *Condor* **98**:581-588.
- _____. 1996b. Determinants of dispersal in breeding Merlins (*Falco columbarius*). *Ecology* **77**:1920-1927.
- Winkler, D. W. and P. E. Allen. 1996. The seasonal decline in tree swallow clutch size: physiological constraint or strategic adjustment? *Ecology* **77**:922-932.
- Wyllie, I. and I. Newton. 1994. Latitudinal variation in the body size of Sparrowhawks *Accipiter nisus* within Britain. *Ibis* **136**:434-440.
- Zack, S. 1990. Coupling delayed breeding with short distance dispersal in cooperatively breeding birds. *Ethology* **86**:265-286.
- Zack, S. and B. J. Stutchbury. 1992. Delayed breeding in avian social

**systems: the role of territory quality and "floater" tactics. Behaviour
123:194-219.**

**Zar, J. H. 1984. Biostatistical analysis. Prentice Hall, Englewood Cliffs, New
Jersey, USA.**