AN ABSTRACT OF THE THESIS OF

Peter J. Loschl for the degree of Master of Science in Wildlife Science presented on March 13, 2008.
Title: Age-specific and Lifetime Reproductive Success of Known Age Northern Spotted Owls on Four Study Areas in Oregon and Washington.

Abstract approved:

_____

Eric D. Forsman

Northern Spotted Owls (*Strix occidentalis caurina*) are a long-lived forest owl and range-wide declines in their numbers have resulted in the species being listed as threatened under the endangered species act. While many studies have been focused on population trends and reproductive performance of Spotted Owls from different age-classes, none have examined age related performance or lifetime reproductive success of individual owls. Using data from known age Spotted Owls on four long-term demography studies in Oregon and Washington, I conducted separate analyses to examine the functional relationship of age and reproductive success, measured as the number of young fledged (NYF), and to examine lifetime reproductive success.

In my age-specific analysis, I used a mixed models approach to account for repeated measures on individual owls. I found that the standard 3-level age-class approach (1-year-old, 2-year-old, adult) often used in Spotted Owl research was a poor fit relative to curvilinear and threshold models that allowed for age-dependent variation beyond age 3. A quadratic age effect was more often supported for males,

whereas a threshold effect indicating a linear increase in NYF from ages 1 to 4 was most supported in the analyses of female data. Females tended to achieve a maximum in reproductive performance at earlier ages than males, and there appeared to be a negative relationship between the age when a maximum in mean NYF was reached and overall fecundity, as reported in earlier studies. Temporal variability in numbers of young fledged at each age was best modeled with a categorical year variable as opposed to a cyclic biennial ("even-odd") year effect.

Lifetime reproductive success of Spotted Owls, measured as the total numbers of fledglings and recruits produced by individuals, varied widely. For owls with relatively complete data, the number of lifetime fledglings ranged from 0 to 20 and the number of lifetime offspring that were observed as recruits within study areas ranged from 0 to 7. There was a significant positive relationship between the number of lifetime young fledged and the number that later recruited locally. Seventy five percent of females and 67% of males bred at least once. Whereas 17% of females and 16% of males produced 50% of the offspring fledged by each sex, only 9% of females and 7% of males produced 50% of the banded young that were later observed as recruits. Thirty nine percent of females and 30% of males produced no fledglings and 64% of females and 69% of males produced no local recruits. Thus while most owls fledged at least 1 offspring, most did not produce any fledglings that recruited locally during the study. Cumulative proportions of individual owls that first bred at different ages indicated that females tended to initiate their breeding at earlier ages than males. Whereas 36% of females bred first at ages 1 or 2, only 19% of males bred first before

age 3. Of the owls that bred, 98% of females and 91% of males bred at least once by age 6.

Compared to owls on the three Oregon study areas, owls on the Cle Elum Study Area in the eastern Cascades of Washington bred early (>50% by age 2), had higher mean numbers of fledglings (>1) at most ages, and had short mean lifespans (6 years). On the Oregon study areas, owls first bred at later ages (>50% at age ≥3), had lower mean numbers of fledglings (0.4–0.7) at most ages, and had longer mean lifespans (7–9 years). These patterns appear consistent with a compensatory relationship between reproduction and survival that was suggested in at least one previous study. Life history theory is also consistent with the idea that where lower and more variable non-juvenile survival occurs (as has been documented on Cle Elum), selection pressure for earlier breeding and greater offspring production at each attempt are to be expected. Nevertheless, it is unclear if local conditions such as prey abundance, harsh winter conditions, or predation pressure act proximately to influence reproduction and survival of Spotted Owls in these studies, or if the variability in patterns of age-specific reproductive success and components of lifetime reproduction on these study areas reflect adaptive life history responses among populations of Spotted Owls. It is likely that both plasticity and life history adaptations underlie the differences and patterns that were revealed, but tests of these hypotheses were beyond the scope of my study.

Age-specific and Lifetime Reproductive Success of Known Age
Northern Spotted Owls on Four Study Areas in Oregon and Washington

by
Peter J. Loschl

A THESIS

submitted to

Oregon State University

In partial fulfillment of
the requirements for the
degree of

Master of Science

Presented March 13, 2008
Commencement June 2008

Master of Science thesis of Peter J. Loschl presented on March 13, 2008.

APPROVED:

_____

Major Professor, representing Wildlife Science

_____

Head of the Department of Fisheries and Wildlife

_____

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

_____

Peter J. Loschl, Author

ACKNOWLEDGMENTS

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

LIST OF FIGURES

LIST OF FIGURES (continued)

LIST OF TABLES

LIST OF APPENDICES

AGE-SPECIFIC AND LIFETIME REPRODUCTIVE SUCCESS OF KNOWN AGE
NORTHERN SPOTTED OWLS ON FOUR STUDY AREAS IN OREGON AND
WASHINGTON

CHAPTER 1

GENERAL INTRODUCTION

Peter J. Loschl

Despite the listing of Northern Spotted Owls (*Strix occidentalis caurina*) as a threatened species under the U.S. Endangered Species Act in 1990 (USDI 1990) and the subsequent implementation of the Northwest Forest Plan (USDA and USDI 1994), populations continue to decline on federal and non-federal lands in many areas (Anthony et al. 2006). Management plans for federal lands have their basis in descriptive research that has provided information on general life history characteristics, habitat relationships, and area requirements of Spotted Owls (e.g., Forsman et al. 1984, Thomas et al. 1990, Carey et al. 1992, Franklin et al. 2000). In addition, extensive capture-recapture studies have been used to examine survival rates, reproductive rates, and population trends of the owl (Franklin et al. 1996, Lint et al. 1999, Anthony et al. 2006). While these efforts have provided critical data for the assessment of Spotted Owl population dynamics and spurred advances in mark-recapture methodology (White and Burnham 1999), Noon and Franklin (2002) emphasized a need to move beyond the focus on estimation of population trends to a focus on mechanistic explanations for the observed variation in life history characteristics. Researchers have logically argued, that for a species at risk of extinction, where intervention to arrest population declines is desired, it is important to understand the relative contributions of factors that relate to declines (Noon and Franklin 2002, Courtney et al. 2004).

Variation in breeding success among individuals is of interest to ecologists because of the implications for natural selection. Discerning patterns of reproductive success and their causes are important for understanding species' life histories and

population dynamics (Stearns 1992). Whereas "cross-sectional" studies assess fitness during a particular series of years or recapture occasions and thus represent only a single episode or relative snapshot of selection for long-lived iteroparous species (Endler 1986), longitudinal data provide several advantages for examining species life history traits. Summary data of breeding success over the entire lifespan of identifiable individuals takes into account tradeoffs between survival and reproduction, which are the two major components of lifetime reproductive success (LRS). As such, LRS is often considered a proxy measure of individual fitness. In addition, data collected from known age individuals monitored over long periods is ideal for closer examination of age-specific performance.

An increase in breeding performance with age has been widely documented in birds (Newton 1989a, Saether 1990, Martin 1995), and a number of hypotheses have been advanced to explain this relationship (Curio 1983, Forslund and Pärt 1995). In long-lived iteroparous species, a pattern commonly described is one in which breeding performance increases most markedly in the early years of life before reaching a maximum in middle age (Newton 1989a, Forslund and Pärt 1995). A number of studies have also shown declines in reproductive performance later in life, a trend often attributed to senescence (Newton and Rothery 1997, 2002, Nielsen and Drachmann 2003, González-Solís et al. 2004).

Variation in reproductive performance of birds has often been examined through the relationships between individual traits (e.g, laying date, clutch size, numbers of fledglings) and environmental or ecological conditions. Such relationships

are explored in the context of the adaptive significance of life history traits (Lack 1947, 1948), but variation due to non-environmental causes such as age (Ryder 1981) is also important. In some studies of Spotted Owls, the absence of clear relationships between key environmental parameters such as the amount of forest habitat and reproductive success or survival has led to speculation that individual variation may account for much of the unexplained variance in demographic rates (Olson et al. 2004, Dugger et al. 2005). Carefully assessing the influence of age on vital rates of both male and female Spotted Owls may help to explain why there is such high variation in vital rates regardless of the condition of the habitat that is occupied.

Virtually all previous studies of Northern Spotted Owls have coded owl age categorically with all owls ≥3 years old coded as "adults". However, as Martin (1995) pointed out, comparisons based on limited age-class data yield conservative estimates of age-dependent effects because means for prime age birds are minimized if data for the older age-class includes a pattern of improvement with age that is followed by senescence. Thus, the pattern of increased reproductive success with age-class that has been documented in Spotted Owls (Burnham et al. 1996, Franklin et al. 1999, Anthony et al. 2006) reveals nothing about age-dependent performance among adults. No published studies have related reproduction of Spotted Owls to specific age in years. Nor have previous studies analyzed reproductive performance of male Spotted Owls.

Long-term mark-recapture studies produce the type of data that are needed to examine LRS. Despite logistical difficulties of collecting these data for individuals

from wild populations, studies of LRS have been completed for a number of long-lived bird species (Postupalsky 1989, Saurola 1989, Wooller et al. 1989, Krüger and Lindstrom 2001, Krüger 2005, Linkhart and Reynolds 2006). Studies of LRS typically involve analysis of "longitudinal" data collected over the entire breeding lifespans of identifiable individuals, but to date, no studies on LRS in the Northern Spotted Owl have been published. Instead, several studies have conferred estimates of "fitness potential" on Spotted Owls (Franklin et al. 2000, Zimmerman et al. 2003, Olson et al. 2004) based on estimates of survival and reproduction of owls occupying individual territories. These "territory-specific" estimates were used to gauge the importance of forest composition and configuration (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005), and in correlations with territory occupancy rates, to assess whether the species meets the assumptions of an ideal despotic distribution (Zimmerman et al. 2003). Elsewhere, fitness has been discussed relative to inbreeding, hybridization, and introgression, such as gene flow between Northern and California Spotted Owl populations (Courtney 2004), but a lack of data has generally constrained researchers to speculation regarding potential negative effects of these factors. Fitness benefits have been attributed to habitat and/or prey selection (LaHaye et al. 1997, Ward et al. 1998, Smith et al. 1999) with the abundance or accessibility of larger prey being suggested as contributing to reproductive success, and therefore improved fitness (but see Forsman et al. 2001). LaHaye et al. (1997) used fledging success and nest productivity as fitness measures. In all of these studies, measures of fitness were conferred on individuals or pairs, but were based on limited data from

study periods that were short relative to the potential lifespan (≥20 years) of Spotted Owls.

In my study, I estimated LRS as numbers of fledglings (LRS_F) and numbers of recruits (LRS_R) produced by male and female Spotted Owls on four study areas in Oregon and Washington from 1986–2005. I modeled relationships between LRS (based on fledglings) and both lifespan and annual nest success. I describe individual variation in LRS for males and females and modeled the relationship between numbers of fledglings and recruits produced by individuals. I also describe life history traits other than LRS that are revealed from lifetime data. These included lifespan, age at first breeding, number of breeding attempts, breeding lifespan, annual nest success, breeding dispersal, and numbers of mates. I discuss results for males and females from different study areas in the context of life history theory.

In my study of age-dependent reproduction, I examined the functional relationship of numeric age and reproduction to identify the range over which age-specific effects operate. My modeling approach was focused on the form of this relationship rather than an examination of a suite of predictor variables that included age and other covariates. I modeled biologically plausible functional patterns of age and reproductive success in order to identify the ages over which increases in performance occurred and the age when maximum annual reproduction was achieved. I also wanted to explore the possible occurrence of a senescent decline in reproduction of older owls. To meet these objectives, I constructed models of age that included linear, quadratic, cubic, asymptotic, and threshold effects. Finally, I wanted to

compare effects modeled using the 3-level age-class approach with functional patterns that could include variation across adult ages.

The four study areas used in my analyses included two areas in the Oregon Coast Ranges (Tyee and Oregon Coast Ranges), one area on the west slope of Cascades Range in Oregon (H. J. Andrews), and one area on the east slope of the Cascades Range in Washington (Cle Elum). These study areas spanned the broad range of climatic conditions in which Spotted Owls occur in Oregon and Washington, from the relatively cool and dry conditions on the east slope of the Cascades to the more mesic forests of western Oregon.

I present my analysis of age-specific reproductive success in Chapter 2 and my analysis of lifetime reproductive success in Chapter 3. I then provide a synthesis of conclusions from these two studies in Chapter 4. This research is the first to assess Northern Spotted Owl reproductive performance using a continuous age-specific explanatory variable, the first to include separate analyses for males and females, and the first to examine summary data on reproductive success of individual Spotted Owls over entire recorded lifespans. Results generated from this research provide new perspectives on life history characteristics of Spotted Owls in different regions and also provide insights into the gender roles for the species.

CHAPTER 2

AGE-SPECIFIC REPRODUCTIVE SUCCESS OF NORTHERN SPOTTED OWLS
IN OREGON AND WASHINGTON

Peter J. Loschl

INTRODUCTION

An increase in breeding performance with age has been widely documented in birds (Clutton-Brock 1988, Newton 1989a, Saether 1990) and a number of hypotheses have been advanced to explain this relationship (Curio 1983, Forslund and Pärt 1995). In long-lived iteroparous species, a pattern commonly described is one in which breeding performance increases most markedly in the early years of life before reaching a maximum in middle age (Newton 1989a, Forslund and Pärt 1995). A number of studies have also shown declines in reproductive performance later in life, a trend often attributed to senescence (Newton and Rothery 1997, 2002, Nielsen and Drachmann 2003, González-Solís et al. 2004). Discerning patterns of reproductive success and their causes are important for understanding species' life histories and population dynamics (Stearns 1992).

Variation in reproductive performance of birds has often been examined through the relationships between individual traits (e.g, laying date, clutch size, numbers of fledglings) and environmental or ecological conditions. Such relationships are explored in the context of the adaptive significance of life history traits (Lack 1947, 1948), but variation due to non-environmental causes such as age (Ryder 1981) is also important. In some studies of Spotted Owls (*Strix occidendalis*), the failure to link key environmental parameters, such as the amount or structure of forest habitat, to a significant proportion of the variance in reproductive success or survival (Olson et al. 2004, Dugger et al. 2005) has led to speculation that individual variation may account for much of the unexplained variance in demographic rates. Therefore,

assessing the influence of age on vital rates of Spotted Owls should help to better understand why there is such high variation in vital rates regardless of the condition of the habitat occupied.

Investigating associations of individual reproductive success and age must be done against a backdrop of temporal variation. Previous studies have indicated significant cyclic biennial patterns in Spotted Owl reproduction with greater numbers of young fledged in even-numbered years than in odd-numbered years (Franklin et al. 1999, Olson et al. 2004, Dugger et al. 2005, Anthony et al. 2006). However, in a meta-analysis of fecundity of Spotted Owls in 15 different study areas Franklin et al. (1999) found equal support for both the cyclic biennial and variable time (year) effects; and Anthony et al. (2006) noted a weakening of the cyclic biennial effect as more years of data were collected. It has been suggested that the cyclic biennial year pattern in fecundity of Spotted Owls may reflect an energetic cost of reproduction in the previous year (Anthony et al. 2006) or annual variation in the effects of weather on reproduction or prey abundance (Wagner et al 1996, Franklin et al. 1999, Courtney et al. 2004). Regardless, accounting for this temporal variation is important for investigating the effects of age on reproductive success.

While a pattern of increased reproductive success with age has been well documented in Spotted Owls, published reports on this relationship have all been based on studies in which "adult" owls were lumped into a single age-class ($\geq$3 years old) and compared with 1- or 2-year-old owls (Burnham et al. 1996, Franklin et al. 1999, Anthony et al. 2006). There are no published studies relating reproduction to

specific age in years. Nor have previous studies analyzed male reproductive performance as a function of age. Although Olson et al. (2004) and Dugger et al. (2005) included both male and female age-classes as separate variables in analyses of territory-specific reproductive success in Spotted Owls, their studies were restricted to a subset of territories with at least three years of reproductive data and no missing values. As such, territories included must have been occupied by pairs for ≥3 years, a criterion that may have biased the data towards higher quality sites and a subset of the older owls in the overall population. To my knowledge, my study is the first to assess Northern Spotted Owl reproductive performance using a continuous age-specific explanatory variable and the first to include separate analyses for males and females. In this study, I examined age-related trends in reproduction of Spotted Owls based on the number of young fledged by known-age individuals on four study areas in Oregon and Washington during 1988–2005.

Although, it has been established that younger age-classes of Spotted Owls have lower reproductive performance, variation in the performance of adult owls (≥3 years old) has not been studied. Hence, analysis of data from known age individuals may reveal variability among adults of different ages and lead to better understanding of individual effects on Spotted Owl demography. Using data from 16 studies spread across the range of the owl, Franklin et al. (1999) observed greater variation in fecundity of 2-year-olds than for 1-year-olds or adults. This may suggest that most gains in reproductive performance occur in this early age range (ages 1–3), but it reveals nothing about age-dependent variation in adult performance. Martin (1995)

pointed out that comparisons based on limited age-class data yield conservative estimates of age-dependent effects because means for prime age birds are minimized if data for the older age-class includes a pattern of improvement with age that is followed by senescence. Thus, studying the functional relationship of age and reproduction is one method of identifying a wider range of ages over which age-specific effects operate. Furthermore, methods that allow for the examination of this relationship in the oldest age-classes may reveal senescence—a decrease in reproductive success of older owls.

In this study, my goal was to identify patterns of age-specific reproductive performance, measured as the number of young fledged, for males and females on four study areas in Oregon and Washington. My modeling approach was focused on the form of this relationship rather than an examination of a suite of predictor variables that included age and other covariates. My objectives were to model biologically plausible functional patterns of age and reproductive success in order to identify the ages over which increases in performance occurred and the age when maximum annual reproduction was achieved. I also wanted to explore the possible occurrence of a senescent decline in reproduction of older owls. To meet these objectives, I constructed models of age that included linear, quadratic, cubic, asymptotic, and threshold effects. Finally, I wanted to compare effects modeled using the 3-level age-class approach with functional patterns that could include variation across adult ages.

I used a mixed models approach that enabled direct modeling of covariance among repeated observations of owls that were checked for reproduction in more than

one year. Thus where other studies have sometimes rarified data using a single observation per bird to overcome the lack of independence between repeated measures, I was able to account for any such lack of independence in the models. Moreover, the mixed model approach allows for the specification of random individual effects providing a more powerful approach for examining patterns at the individual level. Thus the possibility that age-related increases in productivity are a sampling artifact due to early mortality of inferior reproducers, as opposed to real age-related differences, can be better examined in the mixed model (Curio 1983, Newton 1989a, Forslund and Pärt 1995). Therefore, not only does the inclusion of a random individual effect allow for inferences to the broader population of owls studied, but functional patterns of age-specific reproduction reveal fitness consequences of age at the individual level.

METHODS

Study Area

I used data from three study areas in Oregon and one study area in Washington (Fig. 2.1, Table 2.1). The Tyee Study Area (TYE) and Oregon Coast Ranges Study Area (OCR) were located in the southern and central Coast Ranges of Oregon, respectively. The H. J. Andrews Study Area (HJA) was located on the west slope of Cascades Range in Oregon, and the Cle Elum Study Area (CLE) was located on the east slope of the Cascades Range in Washington. Size of the four study areas ranged from 1741–3919 km^2 (Table 2.1). These areas included four of the eight study areas that comprise

the federal monitoring plan for the Northern Spotted Owl (Lint et al. 1999, Anthony et al. 2006). One of the four study areas (HJA) was primarily on federal lands administered by the USDA Forest Service (USFS). The other three were in areas that included a mixture of federal lands administered by the USFS or USDI Bureau of Land Management (BLM), and non-federal lands owned by private landowners. These study areas have been described previously by Forsman et al. (1996a) and Anthony et al. (2006).

FIGURE 2.1. Locations of four study areas where data used in analyses of age-specific and lifetime reproductive success of Northern Spotted Owls were collected.

TABLE 2.1. Study areas and sample sizes used in the analysis of age-specific reproductive success of Northern Spotted Owls in Oregon and Washington.

Study Area	Study acronym	Years used in analysis	Area (km^2)	No. owl years (No. individuals)[a]	
				Females	Males
Oregon					
Tyee	TYE	1990–2005	1741	790 (169)	814 (172)
Oregon Coast	OCR	1990–2005	3919	574 (127)	594 (126)
H. J. Andrews	HJA	1988–2005	1526	432 (91)	380 (96)
Washington					
Cle Elum	CLE	1991–2005	1784	249 (52)	208 (54)

[a]Included known age owls that were monitored for reproductive success (number of young fledged). Number of owl years is the number of recorded reproductive outcomes, including repeated observations on some individuals. The number of individual owls is in parentheses. Years with < 5 known age owls were excluded from analysis.

All four study areas were characterized by mountainous terrain that was predominantly covered by coniferous forests. These forests included a diverse mixture of age-classes that ranged from early seral vegetation on recent clear-cuts to forests that were over 450 years old on areas that had never been cut. Species composition of vegetation on all four areas was dominated by Douglas-fir (*Pseudotsuga menziesii*) in associations with other conifer and hardwood species. The three study areas in Oregon were dominated by Douglas-fir in association with western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), red alder (*Alnus rubra*), and big leaf maple (*Acer macrophylum*). Forest species composition on CLE included mixed associations of Douglas-fir, grand fir, and ponderosa pine (*Pinus ponderosa*), with stands of ponderosa pine predominating on south exposures and mixed stands of Douglas-fir and grand fir predominating elsewhere.

The four study areas spanned a broad range of climatic conditions in which Spotted Owls occur in Oregon and Washington, from the relatively cool and dry conditions on the east slope of the Cascades (CLE) to the more mesic forests of western Oregon (OCR, TYE, HJA), where maritime influences are more pronounced. The HJA and CLE study areas were at moderate elevations (~400–2084 m) in the Cascades where the ground was often covered by snow in winter. The OCR and TYE areas were at lower elevations (38–1418 m) in the Coast Ranges where snow was infrequent and most precipitation occurred as rain.

Field Methods

A standard protocol was followed on each of the four study areas for conducting field surveys and collecting data on reproductive success (Franklin et al. 1996, Lint et al. 1999). Surveys to locate Spotted Owls were conducted annually between 1 March and 31 August, and were designed to confirm the identity of all banded owls in each study area and to document the number of young produced by each owl. Owls were initially marked with a color-coded plastic leg band on one leg and a uniquely numbered USFWS aluminum leg band on the opposite leg (Forsman et al. 1996b) and their identities were thereafter confirmed through visual observations of color bands. In rare cases when the identity of an owl was in question, owls were recaptured to read their numbered leg band and change the color band if necessary. Loss of color bands was nearly zero, and loss of numbered leg bands was zero (Franklin et al. 1996).

Owls first captured as fledglings or subadults were classified as 0, 1 or 2 years old based on plumage attributes (Forsman 1981, Moen et al. 1991). Owls first banded

when they were >2 years old were identified as "unknown age adults" and recorded as

≥3 years old. Since observers did not know the exact age of owls first captured as

adults, and since few Spotted Owls were banded prior to the initiation of the

demography studies, samples of known age owls for my study grew annually with the

recruitment of young banded in previous years (Fig. 2.2).
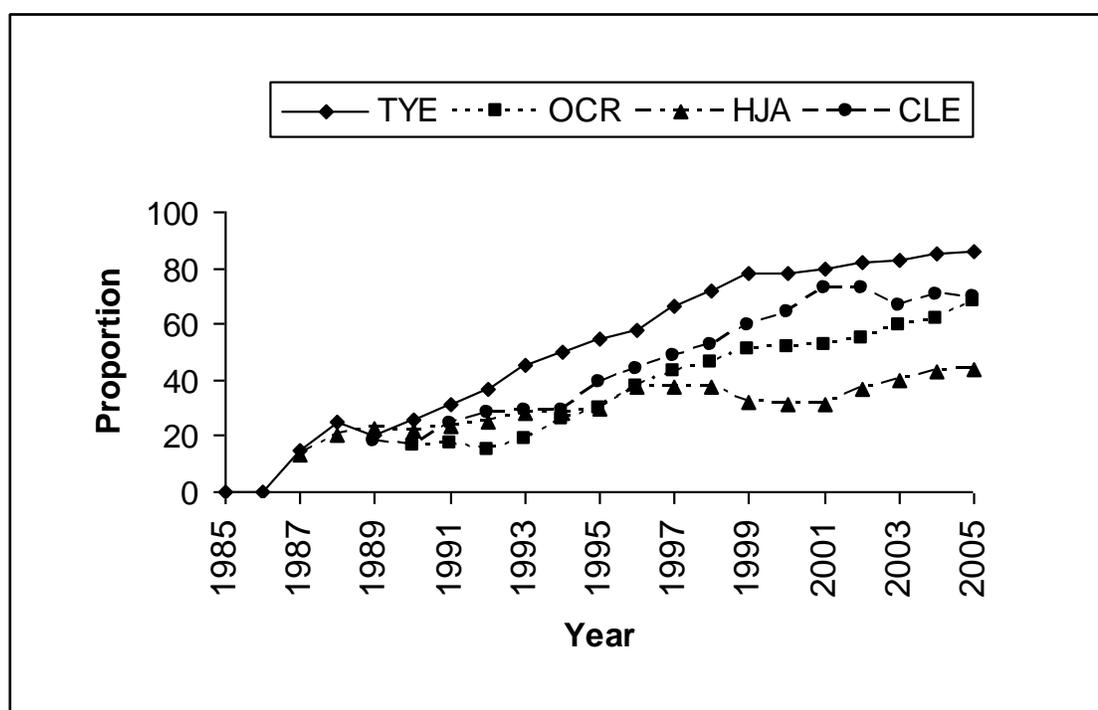
FIGURE 2.2. Proportions of color banded non-juvenile Northern Spotted Owls observed annually that were classified as known age individuals on four study areas in Washington and Oregon. Years with less than five observations were not graphed. Known age owls were first banded as juveniles or as 1- or 2-year olds, whereas minimum age (unknown age) owls were first banded as adults (≥3 years old).

Observers used a combination of calling surveys and live lure surveys to

relocate owls each year (Forsman 1983, Franklin et al. 1996). Once owls were

visually located the primary method used to determine their nesting status and number

of young produced was to offer the owls live mice, which they would then capture and carry to their nests or fledged young (Reid et al. 1999, Franklin et al. 1996). By doing this on at least two occasions, it was usually possible to determine the location of the nest tree and to document the number of fledglings produced, which was used as the estimate of annual productivity (Lint et al. 1999). Each territory was surveyed at least three times each year before it was coded as unoccupied.

Nesting status was determined primarily in April and May, and the number of young fledged (NYF) was determined in June–August. Young were not considered "fledged" until they were observed out of the nest tree. If it was determined that an owl did not nest or nested and failed to produce offspring, NYF was coded as zero. In all analyses of age-specific reproductive success I used NYF (range 0–3) as the measure of reproductive success.

I coded the data so that estimates of annual NYF for males and females were based on the same criteria. To do this I made several simplifying assumptions. First, within a territory, the number of young fledged annually was attributed to each pair member or territory holder including cases when the pair status was not certain. Thus, the male and female on each territory were coded as producing the same number of fledglings, regardless of whether they displayed pair behavior or not. Second, single males were coded as producing zero fledglings when they were monitored to the same protocol standards required for single females or pairs. And third, any "extra owls" on territories were coded as producing zero fledglings. An extra owl was defined as a second individual of the same sex found on a territory that was not the primary

territory holder. Extra pair paternity in the Northern Spotted Owl has never been documented and is assumed to be rare; therefore I felt it was most reasonable to attribute any young to the primary territory holders, and to assign the production of zero young to the few extra owls that were observed.

Statistical Analyses

My observational units were "owl years", defined as a banded owl of known identity in a year in which it was monitored to the protocol standards required for reproductive success (Franklin et al. 1996, Lint et al. 1999). My analyses were restricted to known age owls and there was no requirement that pair status be confirmed. Hence, single owls checked for reproductive success were included in the analysis. Other than feeding mice to confirm color bands and determine reproductive status, owls were not intentionally manipulated for the purpose of avian research or experiments. The only exception included a small number of owls that were radio-marked. The latter owls were included in the sample if they were wearing tail mount radios, but were excluded ($n = 34$ individuals; 64 owl years) if either they or their mates were wearing backpack radios because of concerns that backpack radios could have influenced reproduction (Foster et al. 1992). A few known-age Spotted Owls ($n = 8$ individuals; 15 owl years) that exhibited pair behavior with Barred Owls (*Strix varia*) or Barred Owl/Spotted Owl hybrids were also excluded in the years of those observations. The net result was a data set of 4041 owl years from 887 individual owls (Table 2.1). The sample included 2045 female owl years and 1996 male owl years, of which 97% and 92%, respectively, occurred when an owl of the opposite sex was also confirmed on the

territory.

Since most data on reproductive success were collected from paired owls, there was a lack of independence between male and female data. In addition, preliminary plots and regression analyses of pooled male and pooled female data from the four study areas indicated strong main effects and interaction effects of year and study area ($F_{females} = 3.20_{44,1963}$, $P<0.001$; $F_{males} = 2.68_{44,1920}$, $P<0.001$). Consequently, male and female data for each study area were analyzed separately, resulting in eight separate analyses of age-specific reproductive effects, each of which was carried out in a two-stage approach similar to that of Franklin et al. (2004).

The longitudinal nature of my study led to a lack of independence among repeated measures on individual owls. Therefore, I conducted the first phase of each analysis to identify an appropriate error structure to account for correlation of measures of NYF for individual owls monitored in multiple years. This "error structure analysis" was then followed by an "effects analysis" in which I investigated functional relationships between age and reproduction. I used the PROC MIXED procedure in SAS® 9.1 (SAS Institute 2004) to run all models. Due to small samples during early years on three study areas, I truncated the data so that each analysis included only the data from the set of consecutive years with five or more observations. Because mark-recapture studies were initiated in different years and varied in size, the starting year for age-specific analyses also varied (Table 2.1). I conducted all effects analyses with a set of 15 a priori models that included what I felt were biologically plausible functional relationships between age and reproduction

(Table 2.2). I used Akaike's Information Criterion (Akaike 1973) corrected for small

sample size (AIC$_c$) to rank and compare models (Burnham and Anderson 2002) in

both stages of each analysis. The model with the lowest AIC$_c$ was considered the one

best supported by the data, but models within 2 AIC units of the best model were

considered to be "competitive". I also computed Akaike weights (w_i), for each model

in order to assess model selection uncertainty and the degree to which competitive

models were supported by the data (Buckland et al. 1997, Burnham and Anderson

2002).

TABLE 2.2. A priori models used in analyses of age-specific reproductive success of
Northern Spotted Owls on four study areas in Oregon and Washington.

Model structure	Description
yr	Year effect only
eo	Even-odd year (cyclic biennial) effect only
age	Numeric age effect only
age + age2	Quadratic age effect only
age + age2 + age3	Cubic age effect only
ageclass	Effect of categorical age-class (S1, S2, or Adult) only
iage	Effect of inverse age only
age4	Threshold model with numeric age effect from ages 1–4 only
age + yr	Additive effects of age and year
age + age2 + yr	Additive effects of quadratic age and year
age + age2 + eo	Additive effects of quadratic age and even-odd yr (cyclic biennial)
age + age2 + age3 +yr	Additive effects of cubic age and year
ageclass + yr	Additive effects of categorical age-class (S1, S2, or Adult) and year
iage + yr	Additive effects of inverse age and year
age4 + yr	Additive effects of numeric age from ages 1–4 and year

In the effects analysis, I further dealt with model selection uncertainty by model averaging the predicted responses. I computed weighted averages and unconditional variance estimates from the subset of top ranked models (2–4 models for each analysis) in which the model weights summed to ≥95% of the Akaike weight. Whereas estimates of NYF at each age from any top or competitively ranked model are conditional on a single model, and measures of precision are likely to be overestimated, model averaging allowed for unconditional variance estimates and multimodel inference (Burnham and Anderson 2002). Lastly, I combined model selection results across areas for the four male and four female analyses. This was possible because negative log-likelihoods for independent datasets (samples of males or females) are independent; thus AIC values are additive. I summed AIC_c values ($n = 4$) for each model for both males and females and recomputed AIC_c weights. Combined results for males and females represent a weighted sum for each gender because AIC_c values are smaller for individual analyses with fewer data.

Error structure analysis. PROC MIXED enabled the specification of both fixed and random effects as well as structuring of the error covariance matrix. In the error structure analysis I fit a global model {$NYF = \beta_0 + \beta_1(age) + \beta_2(age^2) + \beta_3(yr)$} to each data set using different covariance structures. Age was the integer value of owl age in years (treated as a continuous variable), age^2 was a quadratic effect of age, and yr was a categorical variable for year. Age, age^2, and yr were fixed effects and were selected based on preliminary model results from the pooled (across study areas) data. I included band number as a random effect in all models to account for variance

associated with individual owl effects. For each data set (sex/study area combination) the global model was executed with 10 candidate variance structures: variance components (VC), compound symmetric (CS), first-order autoregressive (AR(1)), 1-band toeplitz (TOEP(1)), 2-banded toeplitz (TOEP(2)), 3-banded toeplitz (TOEP(3)), heterogeneous toeplitz 1 (TOEPH(1)), heterogeneous toeplitz 2 (TOEPH(2)), log linear variance (LOCAL=EXP(AGE)), and log linear variance (LOCAL=EXP(AGE YR)) (SAS Institute 2004). In this analysis I used restricted maximum likelihood estimation which uses only the numbers of covariance parameters (but no fixed effects) in calculations of fit statistics (Wolfinger 1993).

Modeling Age-specific Effects. Once I identified an appropriate error structure (based on AIC_c model selection) for each of the eight data sets, I evaluated the 15 a priori candidate models to investigate temporal and age-specific reproductive patterns (Table 2.2).

I examined time dependent effects by including either a categorical year (yr) or an even-odd year (eo) variable. Substituting these effects in several models allowed me to identify the best form of these temporal factors for inclusion in models of age-specific reproductive success. Year (yr) was included as an additive effect in all age-specific models but interactions of yr and age were not modeled due to a lack of old known age owls in early years.

To test different functional relationships of age and reproduction I modeled patterns of age-specific reproduction as linear (age), quadratic (age age^2), cubic (age age^2 age^3), and asymptotic (iage) age effects. I considered a quadratic effect of age

because some studies of medium and long-lived birds have shown an increase in performance through middle age, followed by a decline in older ages. I also believed a cubic effect was possible if the relation of reproductive success and age differed among young, middle-age, and old owls. I predicted there might be a steep increase, constant, and declining pattern (possibly due to senescence) of success in these three life periods, respectively. I modeled an inverse age relationship to test the prediction that reproductive success increased sharply with age during early years, but where increases due to age related benefits (e.g., previous experience) diminished over older ages (Sydeman et al. 1991). I also included a categorical age-class (ageclass) model that provided the nearest approximation to models previously used by Anthony et al. (2006) and others to model age-specific reproductive performance of Spotted Owls. In this model, known age owls were classified as 'S1' for 1-year-old owls, 'S2' for 2-year-old owls, or 'AD' for owls that were ≥3 years old. Inclusion of the age-class model allowed me to evaluate the most commonly used age classification for Spotted Owls alongside more complex or finer scale formulations of age. Finally, I included a true threshold model (age4) in which reproductive success increased at a constant rate up to age 4, and then leveled off. To model this effect I created a new age variable (age4) that was coded with age for owls of age 1–3, and with 4 for owls ≥ age 4. I selected a threshold at age 4 because previous studies suggest that differences in Spotted Owl fecundity among age-classes vary by study area. For example, Franklin et al. (1999) found that estimates for 2-year-olds exhibited greater variation across study areas than either 1-year-olds or adult females. Given this variable grouping of

2-year-old owls with either 1-year-olds or adults, I determined that a threshold at age 4 (above age 3 but early in adult life) was more likely to fit the data than a threshold at a later age. Although age4 was the most explicit model I used to examine a point at which mean annual NYF is maximized and then remains constant, I also considered the age-class and inverse age models to be "threshold-type" models as they predict constant or lesser improvements after initial gains, but not declines in late life.

RESULTS

In my analyses, temporal effects were stronger when modeled as variable year-effects as opposed to cyclic biennial (even-odd) effects. The most common relationship between age and annual productivity was a quadratic relationship for males and a threshold (or asymptotic) relationship for females. In addition, the top ranked and competitive models indicated that mean annual NYF peaked at earlier ages for females than for males. Furthermore, there appeared to be a negative relationship between overall productivity and the age at which mean annual NYF peaked. Finally, age specific models generally fit the data better than age-class models, suggesting that age-class models were an oversimplification of the age-effect on reproduction.

On all study areas observations of old females outnumbered those of old males and the oldest known age owls on three of four study areas were females (Fig. 2.3). Only on CLE did data for males and females include observations through the oldest documented age (16 years). But on CLE there was less opportunity to observe owls over age 16 because only 10 individuals that were resighted were from cohorts that

preceded the first year (1989) of the study. Considering all resights of owls from cohorts before 1989, only one CLE owl (10%) was confirmed to have survived past age 10, whereas the proportion of known age owls living past age 10 on the HJA, TYE, and OCR areas was 41, 43, and 65%, respectively ($n = 23, 49, 51$). These estimates suggest longer lifespans for owls on the Oregon study areas. In each of the three Oregon studies, the oldest females included in age-specific analyses were three years older than the oldest known age males.
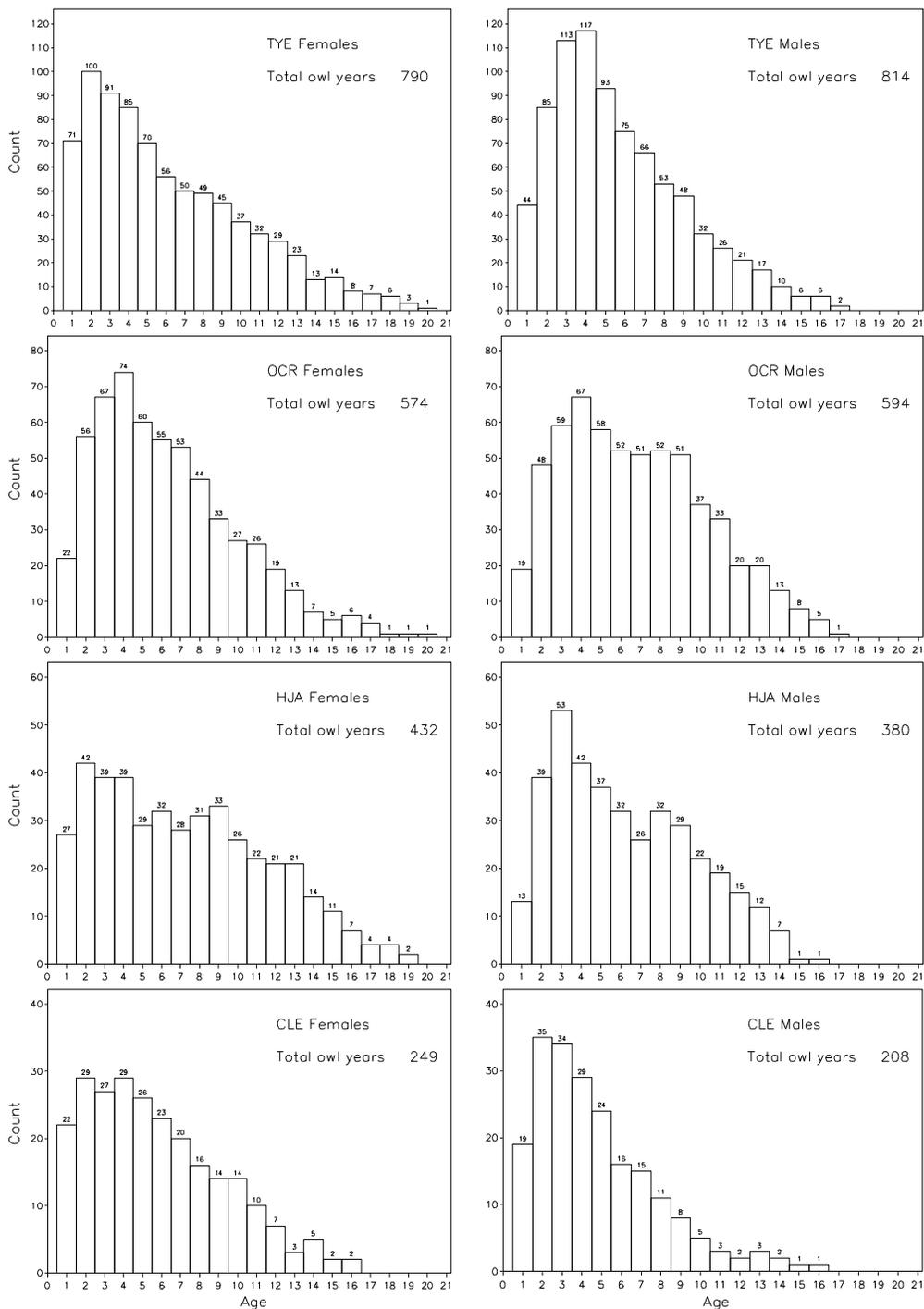
FIGURE 2.3. Comparative plots showing the frequency of individual observations ("owl years") in each age for samples used in the analysis of age-specific reproductive performance of Northern Spotted Owls on four study areas in Oregon and Washington 1988–2005.

Error Models

In five of eight cases, the top ranked model from the error structure analysis was either the first-order autoregressive (AR(1)) or the log-linear LOCAL=EXP(AGE YR) model (Appendix A). Therefore, I used these two error structures for all analyses, including three cases in which other error structures were a slightly better fit. I did this for consistency but also to maintain a year component in the covariance structure, as was the case for all other analyses.

Effects Models

The categorical year effect (yr) was included in all top and competitive models for each of the eight analyses (Table 2.3). However, yr by itself was never a top model or competitive with a top model in any analyses. Models with the cyclic biennial year effect (eo) were always outperformed by models containing yr, and eo ranked last out of the 15 a priori models in four of the eight analyses (Table 2.3). Age effects were included in all top and competitive models, but the form of the relation between age and mean annual NYF varied among areas and sexes (Table 2.3, Fig. 2.4). One result common to all analyses was that simple linear models of age and reproduction were not supported. The top ranked a priori models (all including yr) were the threshold age4 model (three datasets), the quadratic age model (three datasets), the asymptotic age model (one dataset), and the age-class model (one dataset). In five analyses there were no competitive models and the top ranked model had considerable weight ($w_i \geq$ 0.56; Table 2.3). Threshold-type models that included constant or only minimal increases in mean annual NYF after an initial increase during early life were most

commonly supported for females, whereas models that included a mid-life maximum

and late life decline in mean annual NYF tended to fit the data for males better (Table

2.3). These patterns remained evident in the model averaged plots (Fig. 2.4). The

combined model selection results from the four analyses for each sex indicated that the

threshold age4 model provided the best fit for females ($w_i = 0.98$) and that the

quadratic age model was the best fit for males ($w_i = 0.74$) (Table 2.4).

TABLE 2.3. Model selection results for the effects of age and year on the mean annual number of young fledged by Northern Spotted Owls on four study areas in Oregon and Washington, 1988–2005.[a]

Study area/ model	-2log(L)	k	ΔAIC_c[b]	w_j	Study area/ model	-2log(L)	k	ΔAIC_c[b]	w_j
TYE females					**TYE males**				
age4 yr	1831.4	20	0.00	0.80	age4 yr	1800.8	35	0.00	0.42
age age2 age3 yr	1831.7	22	4.45	0.09	age age2 yr	1799.2	36	0.60	0.31
iage yr	1835.9	20	4.50	0.08	age age2 age3 yr	1797.6	37	1.13	0.24
age age2 yr	1837.0	21	7.68	0.02	iage yr	1806.9	35	6.02	0.02
ageclass yr	1837.5	21	8.23	0.01	ageclass yr	1806.9	36	8.22	0.01
age yr	1862.5	20	31.10	0.00	age age2 eo	1854.3	22	25.50	0.00
yr	1877.3	19	43.77	0.00	age yr	1831.1	35	30.30	0.00
age4	1908.5	5	46.05	0.00	age4	1864.3	20	31.28	0.00
iage	1913.3	5	50.88	0.00	age age2	1864.6	21	33.72	0.00
age age2 age3	1910.3	7	51.94	0.00	age age2 age3	1863.2	22	34.38	0.00
age age2	1914.6	6	54.22	0.00	iage	1869.6	20	36.59	0.00
age age2 eo	1913.2	7	54.87	0.00	yr	1842.7	34	39.71	0.00
ageclass	1917.5	6	57.05	0.00	ageclass	1873.1	21	42.23	0.00
age	1939.6	5	77.17	0.00	age	1896.3	20	63.26	0.00
eo	1956.6	5	94.18	0.00	eo	1907.2	20	74.17	0.00
OCR females					**OCR males**				
age age2 yr	1005.2	35	0.00	0.36	age age2 yr	1205.2	21	0.00	0.52
iage yr	1008.3	34	0.82	0.24	age age2 age3 yr	1203.2	22	0.16	0.48
age4 yr	1008.3	34	0.82	0.24	iage yr	1224.0	20	16.64	0.00
age age2 age3 yr	1005.2	36	2.28	0.12	age4 yr	1229.3	20	21.94	0.00
age yr	1011.8	34	4.37	0.04	ageclass yr	1230.6	21	25.40	0.00
ageclass yr	1013.6	35	8.44	0.01	age yr	1237.8	20	30.51	0.00
yr	1025.5	33	15.77	0.00	yr	1250.6	19	41.12	0.00
age age2 eo	1084.3	21	48.15	0.00	age age2 eo	1301.3	7	66.73	0.00
eo	1098.9	19	58.46	0.00	age age2	1319.3	6	82.67	0.00

TABLE 2.3. Continued.

Study area/model	-2log(L)	k	ΔAIC$_c$[b]	w_j	Study area/model	-2log(L)	k	ΔAIC$_c$[b]	w_j
age4	1165.6	19	125.12	0.00	age age2 age3	1317.9	7	83.31	0.00
iage	1166.1	19	125.63	0.00	age	1334.6	5	95.95	0.00
age	1166.4	19	125.88	0.00	age4	1340.5	5	101.83	0.00
age age2	1164.3	20	126.00	0.00	age	1349.0	5	110.29	0.00
age age2 age3	1164.3	21	128.15	0.00	ageclass	1349.7	6	113.03	0.00
ageclass	1173.1	20	134.81	0.00	eo	1355.5	5	116.79	0.00
HJA females					HJA males				
age4 yr	938.2	22	0.00	0.65	age age2 yr	832.4	23	0.00	0.56
ageclass yr	938.8	23	2.78	0.16	age age2 age3 yr	832.2	24	2.04	0.20
iage yr	941.1	22	2.86	0.16	age4 yr	837.8	22	3.10	0.12
age age2 age3 yr	939.7	24	5.97	0.03	iage yr	837.8	22	3.10	0.12
age age2 yr	946.0	23	9.96	0.00	ageclass yr	842.7	23	10.29	0.00
age yr	953.6	22	15.32	0.00	age age2 eo	884.5	6	15.22	0.00
yr	961.6	21	21.13	0.00	age yr	852.5	22	17.80	0.00
age age2 eo	1008.6	7	38.20	0.00	age age2	893.9	5	22.54	0.00
age4	1023.2	5	48.65	0.00	iage	897.4	4	24.01	0.00
iage	1023.5	5	48.94	0.00	age age2 age3	893.7	6	24.44	0.00
eo	1025.6	5	51.04	0.00	age4	899.7	4	26.31	0.00
ageclass	1024.3	6	51.83	0.00	yr	865.7	21	28.75	0.00
age age2 age3	1024.4	7	53.97	0.00	ageclass	904.2	5	32.80	0.00
age age2	1026.6	6	54.10	0.00	age	908.9	4	35.49	0.00
age	1029.6	5	55.06	0.00	eo	915.1	4	41.68	0.00
CLE females					CLE males				
ageclass yr	593.7	20	0.00	0.62	iage yr	510.7	19	0.00	0.59
age4 yr	598.3	19	2.24	0.20	age4 yr	513.1	19	2.37	0.18
iage yr	599.3	19	3.20	0.13	ageclass yr	510.8	20	2.55	0.16
age age2 age3 yr	597.2	21	5.93	0.03	age age2 age3 yr	511.2	21	5.48	0.04

TABLE 2.3. Continued.

Study area/model	-2log(L)	k	$\Delta AIC_c{}^b$	w_j	Study area/model	-2log(L)	k	$\Delta AIC_c{}^b$	w_j
yr	607.1	18	8.68	0.01	age age2 yr	514.4	20	6.13	0.03
age age2 yr	602.9	20	9.17	0.01	age yr	524.3	19	13.64	0.00
age yr	606.3	19	10.19	0.00	yr	531.6	18	18.45	0.00
eo	649.1	5	21.99	0.00	age age2 eo	559.9	7	21.73	0.00
age age2 eo	646.7	7	23.73	0.00	age4	570.0	5	27.60	0.00
ageclass	653.5	6	28.45	0.00	ageclass	568.9	6	28.62	0.00
age4	660.5	5	33.32	0.00	iage	571.4	5	28.93	0.00
age age2 age3	657.1	7	34.19	0.00	age age2 age3	567.6	7	29.47	0.00
iage	661.6	5	34.48	0.00	age age2	571.2	6	30.90	0.00
age	666.0	5	38.85	0.00	eo	573.4	5	30.95	0.00
age age2	664.8	6	39.79	0.00	age	581.4	5	39.00	0.00

[a] Listed for each model are the fixed additive age and/or time effects (model), twice the negative value of the maximized log-likelihood function (-2log(L)), difference between the AIC_c estimate of the selected model and the top model AIC_c (ΔAIC_c), and the Akaike weight (w_j). All models were executed as mixed-effects models with a random individual owl effect and with a first-order auto regressive (AR1) covariance structure except for TYE males and OCR females where a log-linear (LOCAL=EXP(AGE YR)) covariance structure was used.

[b] AIC_c values for the top models in analyses of females were: TYE = 1872.5, OCR = 1079.9, HJA = 984.7, CLE = 637.4 and in analyses of males were: TYE = 1874.1, OCR = 1248.8, HJA = 881.5, CLE = 552.7.

TABLE 2.4. Model selection results from the combined analysis of the effects of age and year on the mean annual number of young fledged by Northern Spotted Owls on four study areas in Oregon and Washington, 1988–2005.[a] Models are listed in order of increasing $\sum AIC_c$ values. Akaike weights (w_j) indicate the relative fit of 15 a priori models from the combined results for each gender.

Model	AIC$_c$ values				$\sum AIC_c$	ΔAIC_c[b]	w_j
	TYE	OCR	HJA	CLE			
Females							
age4 yr	1872.5	1080.7	984.7	639.6	4577.5	0	0.98
iage yr	1877.0	1080.7	987.6	640.6	4585.9	8.4	0.01
age age2 age3 yr	1877.0	1082.1	990.7	643.3	4593.1	15.6	0.00
ageclass yr	1880.8	1088.3	987.5	637.4	4594.0	16.5	0.00
age age2 yr	1880.2	1079.9	994.7	646.6	4601.4	23.9	0.00
age yr	1903.6	1084.2	1000.0	647.6	4635.4	57.9	0.00
yr	1916.3	1095.6	1005.8	646.1	4663.8	86.3	0.00
age age2 eo	1927.4	1128.0	1022.9	661.1	4739.4	161.9	0.00
eo	1966.7	1138.3	1035.7	659.4	4800.1	222.6	0.00
age4	1918.6	1205.0	1033.3	670.7	4827.6	250.1	0.00
iage	1923.4	1205.5	1033.6	671.9	4834.4	256.9	0.00
age age2 age3	1924.5	1208.0	1038.7	671.6	4842.8	265.3	0.00
ageclass	1929.6	1214.7	1036.5	665.8	4846.6	269.1	0.00
age age2	1926.7	1205.9	1038.8	677.2	4848.6	271.1	0.00
age	1949.7	1205.7	1039.8	676.2	4871.4	293.9	0.00
Males							
age age2 yr	1874.7	1248.8	881.5	558.9	4563.9	0	0.74
age age2 age3 yr	1875.2	1249.0	883.6	558.2	4566.0	2.1	0.26
iage yr	1880.1	1265.4	884.6	552.7	4582.8	18.9	0.00
age4 yr	1874.1	1270.7	884.6	555.1	4584.5	20.6	0.00
ageclass yr	1882.3	1274.2	891.8	555.3	4603.6	39.7	0.00
age yr	1904.4	1279.3	899.3	566.4	4649.4	85.5	0.00
yr	1913.8	1289.9	910.3	571.2	4685.2	121.3	0.00
age age2 eo	1899.6	1315.5	896.7	574.5	4686.3	122.4	0.00
age age2	1907.8	1331.5	904.1	583.6	4727.0	163.1	0.00
age age2 age3	1908.5	1332.1	906.0	582.2	4728.8	164.9	0.00
iage	1910.7	1344.7	905.5	581.7	4742.6	178.7	0.00
age4	1905.4	1350.6	907.8	580.3	4744.1	180.2	0.00
ageclass	1916.3	1361.8	914.3	581.4	4773.8	209.9	0.00
age	1937.3	1359.1	917.0	591.7	4805.1	241.2	0.00
eo	1948.2	1365.6	923.2	583.7	4820.7	256.8	0.00

[a] Listed for each model are the fixed additive age and/or time effects (model), Akaike's Information Criteria (AIC$_c$) values, summed AIC$_c$ values for each model for each sex ($\sum AIC_c$), difference between the $\sum$AICc estimates of each model and the top model (with the lowest $\sum AIC_c$ value), and the Akaike weights (w_j). All models were executed as mixed-effects models with a random individual owl effect and with a first-order auto regressive (AR1) or log-linear (LOCAL=EXP(AGE YR)) covariance structure.
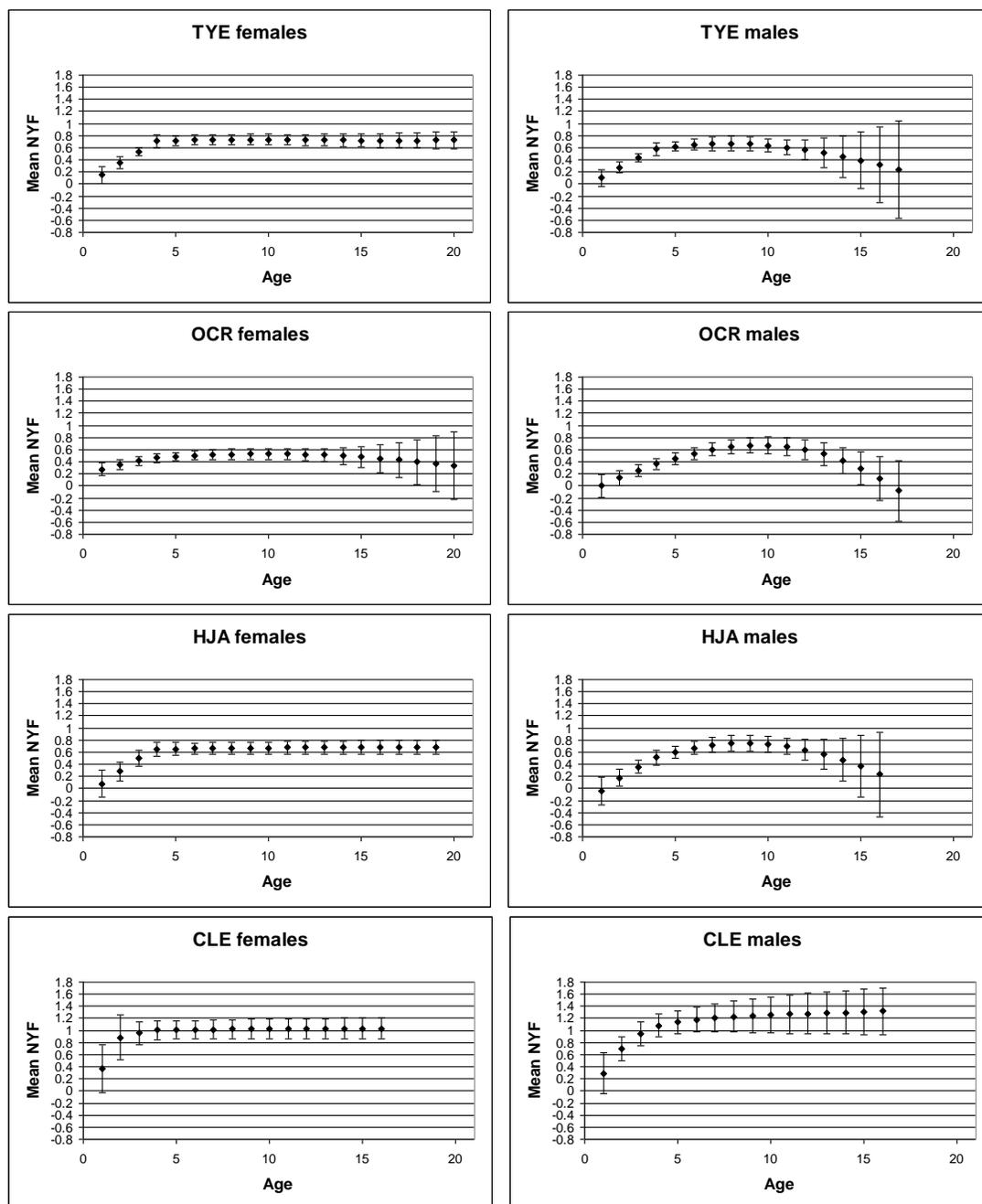
FIGURE 2.4. Model averaged predicted estimates and unconditional 95% confidence intervals that describe the relation of age and mean annual number of young fledged by known age female and male Northern Spotted Owls on four study areas in Oregon and Washington. All models included year as a categorical fixed effect and each plot represents an average of the mean number of fledglings predicted at each age over all years computed from the highest ranked models that summed to 95% AIC weight for each analysis.

Individual Study Areas

TYE was one of two study areas in which the top a priori model (threshold age4) was the same for both sexes. The top ranked model provided a substantially better fit to the TYE female data ($w_i = 0.80$; Table 2.3) than all other models, indicating that mean annual NYF increased at a constant rate from ages 1–4 and remained constant thereafter (Fig 2.4). Model averaged estimates included the top model and two additional models (asymptotic age and cubic age) but had little effect on the overall pattern of age-specific reproductive success predicted by the top model alone (Fig 2.4). There was strong evidence of a continued increase between ages 3 and 4 because each model averaged estimate fell outside the unconditional confidence interval of the other. For TYE males, the threshold age4 model had less weight ($w_i = 0.42$) and two additional models were supported (Table 2.3). The quadratic age ($\Delta AIC_c = 0.60$, $w_i = 0.31$) and cubic age ($\Delta AIC_c = 1.13$, $w_i = 0.24$) models were competitive and point estimates of mean annual NYF increased with age to a maximum at age 8 and 7 years, respectively, and decreased thereafter. Model averaged estimates for TYE males included the top and competitive models only and indicated that mean annual NYF increased at a decreasing rate through about age 8 and declined thereafter (Fig 2.4). However, unconditional confidence intervals were particularly large at older ages and each age-specific estimate above age 3 fell within every interval around estimates at older ages. Therefore, there was not strong evidence of an age effect among ages ≥ 4, but an increase between ages 3 and 4 was supported because each estimate fell outside the unconditional confidence interval of the other. In contrast to the cubic age effect

for OCR males, the cubic effect for TYE males included a sharper initial increase in mean annual NYF with a peak at an earlier age followed by a more gradual decline after the peak (Appendix B). These patterns were also evident in the model averaged plots (Fig. 2.4).

On OCR, the top a priori model for both sexes was the quadratic age model, but competing models were different for each sex (Table 2.3). For both sexes, the point estimates from the quadratic age model increased to a maximum at age 9 before beginning to decline (Appendix B). The weight of evidence for the quadratic age model was stronger for males ($w_i = 0.52$) than for females ($w_i = 0.36$). Competing models were the asymptotic age model and threshold age4 model for females and the cubic age model for males. Model averaged estimates for OCR females included the top model and three additional models (asymptotic age, threshold age4, and cubic age) and indicated an increase in mean annual NYF with age through about ages 9–11, followed by a possible decrease in reproductive success over older ages (Fig 2.4). However, large unconditional confidence intervals added uncertainty to the pattern above about age 12 (Fig 2.4). Furthermore, each model averaged age-specific estimate above age 3 fell within every interval for estimates at older ages resulting in uncertainty about the pattern of reproductive success over ages ≥ 4. However, despite lack of evidence for changes among ages ≥ 4, reproductive success for OCR females increased beyond age 3 because the trend continued upward and model averaged age-specific estimates from ages 5–12 were greater than the age 3 estimate based on a lack of overlap of estimates and unconditional confidence intervals. For OCR males, the

model averaged estimates from the quadratic and cubic age models indicated an increase in mean annual NYF with age through about age 10 followed by a decrease in reproductive success over older ages (Fig 2.4). There was strong evidence of an increase beyond age 6 because the trend continued upward and model averaged estimates for ages 6 and 9 fell outside the unconditional confidence intervals for one another (Fig 2.4). There was also strong evidence of a decrease in mean annual NYF in older ages, as unconditional confidence intervals for age-specific estimates for ages 8–11 and ages 13–17 did not include any estimates from the alternate age ranges.

On HJA, the top ranked model for females was the threshold age4 model, indicating that mean annual NYF increased at a constant rate from ages 1–4 and remained constant thereafter. There were no competing models. Model averaged estimates for females included the top model and two additional models (age-class and asymptotic age) but had little effect on the overall pattern of age-specific reproduction predicted by the top model alone (Fig 2.4). There was strong evidence of a continued increase between ages 3 and 4 because each model averaged estimate fell outside the unconditional confidence interval of the other. The model that best fit the data for HJA males included a quadratic age effect in which mean annual NYF increased up to age 9 and then declined (Appendix B). There were no competing models. Model averaged estimates for HJA males included the top ranked and three other models (cubic age, threshold age4, and asymptotic age) and followed a pattern similar to TYE males. Model averaged estimates increased at a decreasing rate through about age 9 and suggested the start of a decline in reproductive success at older ages (Fig 2.4).

However, beyond about age 11, unconditional confidence intervals were large and each age-specific estimate above age 5 fell within every interval around estimates at older ages. Despite the lack of strong evidence for differences among ages ≥ 6, mean annual NYF for HJA males increased beyond age 5 because model averaged estimates for ages 8–9 were greater than the age 5 estimate based on a lack of overlap of unconditional confidence intervals (Fig 2.4).

On CLE, the top ranked models for females and males were the age-class model and the asymptotic age model, respectively. There were no competitive models. For females, differences between the least squares means estimates from the top model indicated that, on average, 1-year-olds produced 0.69 (95% CI = 0.23 to 1.14) fewer fledglings than 2-year-olds and 0.71 (95% CI = 0.33 to 1.10) fewer fledglings than owls ≥ 3 years old. The mean annual NYF for 2-year-olds and older owls did not differ. Model averaged estimates for CLE females included the top model and two additional models (age4 and asymptotic age) but had little effect on the overall pattern of age-specific reproduction predicted by the age-class model alone. Model averaged estimates indicated that age 1 females had lower reproductive success than older females, but that mean NYF for females ages 2–16 did not differ (Fig 2.4). For CLE males the top ranked model indicated a sharp increase in mean NYF with each year through the early adult ages followed by slightly increasing productivity in middle and later ages. Model averaged estimates for CLE males included the top ranked and three other models (age4, age-class, and cubic age) and indicated a pattern similar to the asymptotic age model but with a more gradual increase in mean annual

NYF after about age 6 (Fig 2.4). After an increase in mean annual NYF from ages 1–3, wide unconditional confidence intervals indicated uncertainty about a continued gradual increase over middle and older ages (Fig 2.4). There was strong evidence of an increase between ages 2 and 3 because each estimate fell outside the unconditional confidence interval of the other. Evidence for an increase beyond age 3 was that the trend continued upward and estimates from ages 6–11 were greater than the estimate at age 3 based on a lack of overlap of estimates and unconditional confidence intervals. In contrast to results for males on other areas, the quadratic model was a poor fit for CLE males ($w_i = 0$). Although there were no competing models, the age4 threshold model ranked second and was nearly competitive for both sexes on CLE (Table 2.3).

DISCUSSION

Despite the model selection uncertainty incorporated in model averaged age-specific estimates, there was strong evidence of an increase in mean annual reproductive success during adult ages of males and females on all three study areas in Oregon. I concluded, therefore, that differences revealed by a 3-age-class model failed to reflect the true magnitude and duration (span of ages) of gains between early life and peak performance in at least some cases. The mean annual number of young produced generally increased from age 1–4, and thereafter, either plateaued or followed a quadratic pattern. Where quadratic models fit better, mean annual NYF varied across adult ages and there was a decline after middle age. For males in particular, there was

some evidence for reproductive senescence in later years. The most common threshold-type model, especially for females, provided evidence of variation in mean annual NYF through only the second adult year. On all areas the mean annual number of young produced by females reached a peak at earlier ages than males. My models also revealed that a simple cyclic biennial year effect was inferior to a non-cyclic categorical year effect for capturing inter-annual variation in reproductive success. This was not surprising given the weakening of that trend as more years of data have been added (Anthony et al. 2006). Moreover, there is little biological rationale for such a pattern given the absence of any known climatic or prey related fluctuations that correspond with cyclic biennial year patterns on my study areas. While my analytical approach was not designed to directly estimate or quantify differences in reproductive performance or functional relationships of age and reproduction between genders or study areas, differences were revealed through the differential fit of the same models of age-specific performance for different subsets of data from known age owls.

Temporal Effects

My analysis provided little support for a consistent biennial pattern of high and low reproduction in even and odd years. This pattern, which was prominent on some demography study areas in the 1990s (Forsman et al. 1996a, Franklin et al. 2004, Olson et al. 2004), has become less pronounced in recent years (Anthony et al. 2006). While similar fluctuations or cycles in reproductive performance have been linked to cyclic fluctuations in prey populations of several European owl species (Korpimäki

and Hakkarainen 1991, Brommer et al. 2002a), no such links have been established for Spotted Owls. This may be due to the lack of concomitant studies of prey population dynamics to address such questions. Researchers have long speculated that, for Spotted Owls, fluctuations in reproductive success and the number of pairs that breed may relate to fluctuations in prey abundance (Forsman et al. 1984, Barrows 1985, Gutiérrez 1985), but only 2 studies (Ward et al. 1998, Rosenberg et al. 2003) have explicitly examined relationships between Spotted Owl reproductive success and prey abundance. My results suggest that non-cyclic year effects are the norm, at least on the four areas I examined. This finding does not negate the likely influence of prey dynamics on reproductive success of Northern Spotted Owls, but does suggest that those effects are more random than they are predictable. Fortunately, most researchers have not made too much of cyclic reproductive patterns relative to Spotted Owls. For example, Dugger et al. (2005) avoided focus on the cyclic biennial pattern and discussed high performance of experienced males during even-numbered years in terms of interactive effects of experience and years with different overall reproductive performance. Given that their study spanned only six years, it seems appropriate that they modeled time effects with the cyclic biennial parameter, but then described their findings in more general biological terms. The absence of biological arguments for a continued biennial oscillation in productivity and the addition of more years of data to owl demography data sets, should allow for more detailed models and the inclusion of time variant variables that may reveal mechanisms underlying temporal variation.

Male and Female Patterns

Functional patterns. Martin (1995:343) described five general forms of the shapes of age-dependent effects in birds and noted that "…steepness of the improvement curve, the duration of peak performance and the occurrence of senescence varies with advancing age, across life history stage and species." A general pattern that emerged in my study was that quadratic age models fit the data in most analyses for males whereas the threshold model provided the best fit for females. These age-dependent patterns were also evident in the model averaged estimates, although unconditional confidence intervals reflected greater uncertainty around mean annual NYF at older ages in some data sets. For females on the TYE, HJA, and CLE areas, there was fairly strong evidence for a constant level of reproductive success following an early life increase. For males, evidence for a decline in estimates of mean annual NYF from middle to later ages was strong only on OCR, but model averaged point estimates followed the same pattern on TYE and HJA. The combined model selection results were in strong agreement with a superior fit of the threshold age4 model for females and a quadratic age model for males.

A quadratic relation between age and reproduction has been found in other studies of moderate to long-lived birds such as *Accipiter nisus* (Newton and Rothery 1997) and *Accipiter gentilis* (Nielsen and Drachmann 2003), and may be an indication of senescence. In a study of Common Buzzards (*Buteo buteo*), Krüger and Lindstrom (2001) found a quadratic relation between the number of breeding attempts and

reproductive output measured as the number of fledglings per breeding pair. While the quadratic model fit the data for males and females, predicted numbers of fledglings in late attempts declined sharply only for males. This finding was similar to my model results for OCR.

It is inappropriate to assume senescence in a fitness correlate simply due to significance of a negative quadratic effect (Newton and Rothery 1997, Catry et al. 2006). Where only linear and quadratic models are considered, a superior quadratic fit may be due to the curvilinear pattern or a non-constant increase in reproductive estimates as opposed to a decline in later ages. More direct examinations of reproductive senescence have involved: (1) age-specific estimation of residual reproductive value (Newton and Rothery 1997) or foraging performance (Catry et al. 2006), (2) within individual comparisons of performance in ages of peak performance and late life (Newton and Rothery 1997, Laaksonen et al. 2002, Catry et al. 2006), (3) accounting for the influence of extreme values associated with terminal (last) breeding events (Rattiste 2004, Catry et al. 2006), and (4) accounting for performance in various stages of the reproductive cycle (Rockwell 1993). In this study I modeled additional functional patterns of age-dependent effects that, if superior, should have fit the data better than the quadratic model. Nevertheless, documenting and measuring senescence in wild birds is wrought with practical, methodological, and analytical difficulties (Nisbet 2001). Additional models (and longer data sets) would be needed to reveal reproductive senescence and, more importantly, the proximate mechanisms for any late life declines. For example, the inclusion of breeding experience may

influence the fit or interpretation of different models for age. Pyle et al. (2001) found that both a linear age effect and a quadratic experience effect on annual reproductive success in Cassin's Auklets (*Ptychoramphus aleuticus*) were stronger for males than females. In a study of northern elephant seals (*Mirounga angustirostris*), Sydeman et al. (1991) reported that a quadratic relation of age and weaning success was replaced by a linear relation when an adjustment was made for experience (number of previous years a pup was produced). In the same analysis, the quadratic relation of experience with weaning success was enhanced by an adjustment for age; declining performance was thus attributed to reproductive "burnout". At least one study on Spotted Owls examined the relation between experience and reproductive success. Dugger et al. (2005) found that Spotted Owl fecundity was strongly influenced by male experience (coded as presence or absence on the territory in the previous year), and that this influence varied depending on whether it was a year in which average productivity in the population was high or low. Models with age-class and experience were fit separately due to concerns that the variables were confounded, but since nearly half of the observations of owls not present in the previous year were from adults, the effect of experience was important independent of age. Power to detect age effects may have been reduced (relative to experience effects) due to small samples. Nonetheless, the importance of male experience was clear. Disentangling the independent effects of age, experience, and other variables (e.g., environmental and phenotypic) will lead to a better understanding of age-dependent effects such as senescence in Spotted Owls, but was beyond the scope of my study.

Age at maximum performance. In addition to differences in functional relationships supported for each sex, females tended to achieve maximum reproductive performance (or greatest increases in mean annual NYF) at younger ages than males. For example, the top model for TYE indicated that productivity peaked at age 4 for both sexes, but greater model selection uncertainty was indicated by competitive models for males that indicated a peak at about age 7–8. Similarly, the top ranked model for OCR indicated that annual productivity peaked at age 9 for both sexes, but competitive models predicted maximum reproductive success at age 4 for females and age 10 for males. Top ranked models for HJA, indicated that females reached a maximum at age 4, whereas for males, estimates increased up to age 9. On CLE, coefficients from the top ranked model for females indicated that differences in mean annual NYF occurred only between 1-year-old owls and all other ages. Hence, CLE females reached near maximum performance at age 2. Interpretation of the top ranked model for CLE males was less clear, but a prediction plot indicated substantial increases in mean annual NYF through about age 3–5   As a post hoc test to see if the age-class model was somewhat representative of a lower (below age 4) threshold model for CLE females, I executed an "age2" model with owls coded as age2 = 1 for 1-year-olds and age2 = 2 for owls that were ≥2 years old. Consistent with the interpretation above, AIC_c for the age2 model was lower than that of all the 15 a priori models. Although model averaging indicated additional uncertainty about the age when maximums were achieved, within areas, a trend towards a more rapid increase to peak or near peak performance for females remained evident.

My results suggest that Spotted Owls are like many other birds of prey in that females tend to breed at an earlier age than males (Newton 1979, Korpimäki 1988, Lieske 1997). It is unlikely that this is due to physiological differences between males and females, because, in Spotted Owls, both sexes are physiologically mature at 1 year of age. A more likely explanation is that, in species like the Spotted Owl, where males provision the female and young, females are able to breed at an earlier average age than males because they can pair with older more experienced males on established territories. In contrast, regardless of whether they pair with young or old females, young males have the daunting task of acquiring and defending a territory and learning the best places to hunt in order to provide enough food for the female and young. Ward et al. (1998) estimated energetic costs of Spotted Owls during the breeding period and found that the cost associated with egg production was small relative to that required by a male to feed itself, a female, and one young. Based on the calculations of Ward et al. (1998), Smith et al. (1999:27) noted that a male Spotted Owl must increase the amount of food he procures by 276% in order to provision the female and a juvenile through the fledging stage.

Korpimäki (1988) described effects of age on breeding performance of Tengmalm's Owls (*Aegolius funereus*) that were similar to my findings for Spotted Owls. In that study, females showed the greatest increase in the mean annual number of fledglings produced between ages 1 and 2, whereas males also had substantial improvement between age 2 and older owls. When different constellations of male and female age-classes were compared, male age was more important for breeding

performance than female age. A positive relationship between the age-class of males and numbers of prey items stored in nests was consistent with the view that improved hunting skills and experience was a mechanism for age-dependent breeding performance. Thus, inadequate provisioning skills may reduce both the ability to secure a mate as well as the reproductive performance of young males. Our data for Spotted Owls appear consistent with the former in that most observations were from paired owls and within each area samples of 1- and 2-year-old females were usually larger than males of the same age (Fig. 2.3). Our data are also consistent with the latter in that, within areas, model averaged point estimates of mean NYF for 1- and 2-year-old males were lower than estimates for females of the same age. Similarly, Espie et al. 2000, attributed gender differences in breeding performance of Merlins (*Falco columbarius*) in Saskatchewan, Canada, to changes in hunting skill with age.

Patterns Among Areas

Another pattern that emerged from my analysis was that the age at which owls reached maximum mean annual NYF appeared to be negatively correlated with average annual fecundity (as reported for my study areas by Anthony et al. 2006). Results from the analyses of female data illustrate this relationship most clearly. Females on CLE had the highest mean annual fecundity among all areas examined by Anthony et al. (2006), and in my analysis they reached a maximum in mean annual NYF by age 2. Females on the other areas that I examined did not reach maximum mean annual NYF until they were ≥ 4 years old. The pattern of rapid increase to peak performance on CLE as compared to a slow increase to highest output at older ages on OCR, which had

comparatively low mean annual fecundity (Anthony et al. 2006), suggests intraspecific variation in life history patterns among Spotted Owls in different regions. Anthony et al. (2006) suggested that high annual fecundity of owls in eastern Washington might be a compensatory response to lower non-juvenile survival, a view that ascribes adaptive significance to inter-populational differences in vital rates of Spotted Owls. Life history theory predicts earlier maturation and high reproductive output where mortality rates are high. In several respects, my data appear consistent with the view that, among meta-populations, Spotted Owls may fall at slightly different positions along a slow-fast (*sensu* Saether 1987) life history continuum.

My results may have implications for how data are coded or what data are included in future analyses. In previous studies of Spotted Owls, the terms "age-class" and "age-specific" have usually been used to describe differences or comparisons of vital rates or other life history traits among juveniles, subadults (often segregated into two classes: 1- and 2-year-olds), and adults. Given that Spotted Owls of both sexes are capable of reproduction at age 1, I avoided use of the term "subadult" in reference to my own data and results herein and used numeric descriptors as much as possible. Grouping non-juveniles into one of three age-classes, and in particular lumping all adults in one age-class, allowed researchers to include all banded owls checked for reproductive success in analyses of reproductive performance. However, in only one of eight analyses described herein did age-specific variation in productivity fit best when modeled using the 3-level age-class coding used in virtually all previous analyses of Spotted Owl reproduction (Forsman et al. 1996a, Anthony et al. 2006).

The implications of not accounting for the unexplained variation in "adult" performance when 3-age-class models are used are unclear, as there are always trade-offs between computational complexity and the precision or accuracy of vital rates.

Although my samples were generally large and adequate to model covariance among repeated measures and a variety of age-dependent relationships, there were differences in sample sizes among areas that could have influenced the results. Smaller data sets (e.g., CLE) tended to support simple relationships between age and reproduction, whereas larger samples supported more complicated age-specific patterns. For example, the simple 3-level age-class model was supported (or nearly supported, in three of the four smallest data sets from CLE and HJA, but was not supported in the four largest datasets from OCR and TYE. All samples suffered from small numbers of individuals in the oldest ages and the effect for small data sets may have been that too few data for old owls were available to support quadratic and other curvilinear patterns of age-specific productivity.

To my knowledge, my study is the first to examine functional patterns of age-specific reproductive success for known age Spotted Owls and to document age-specific variation in reproductive output of adult owls. My study is also the first to explore age-related performance in a parallel modeling framework for both males and females. My findings do not demonstrate functional relations per se but provide more general results relative to age-specific patterns of reproduction in the Spotted Owl. Without experimental approaches and a suite of additional variables, it is impossible to do more than speculate as to what drives the observed patterns. Nevertheless, my

results indicate that modeling age as a continuous variable using data from only the known age individuals can lead to additional insights relative to age dependent performance, life history, and gender roles in the Spotted Owl. However, additional studies in which an attempt is made to disentangle the effects of experience, age, and environmental factors may provide insights into the adaptive significance of reproductive senescence and other age-dependent patterns of reproduction

Finally, the biological significance of age-dependent variation in reproduction of adult Spotted Owls is unclear. For a species that usually produces one or two offspring during a single nest attempt, mean differences of less than one fledgling between the lowest and highest levels of success may be difficult to conceive of as biologically meaningful. However, given the long potential lifespan of any individual (at least five individuals in my study were known to have survived for ≥ 20 years) small improvements in reproductive success with age may translate into a considerable fitness advantage.

CHAPTER 3

LIFETIME REPRODUCTIVE SUCCESS OF NORTHERN SPOTTED OWLS
IN OREGON AND WASHINGTON

Peter J. Loschl

INTRODUCTION

Despite its listing as a threatened species under the U.S. Endangered Species Act in 1990 (USDI 1990) and the subsequent implementation of the Northwest Forest Plan (USDA and USDI 1994), populations of Northern Spotted Owls (*Strix occidentalis caurina*) continue to decline on federal and non-federal lands in many areas (Anthony et al. 2006). Management plans for federal lands have their basis in descriptive research that has provided information on general life history characteristics, habitat relationships, and area requirements of Spotted Owls (e.g., Forsman et al. 1984, Thomas et al. 1990, Carey et al. 1992, Franklin et al. 2000). In addition, extensive capture-recapture studies have been employed to examine age-specific survival rates and reproductive rates of the owl (Franklin et al. 1996, Lint et al. 1999). While these efforts have provided critical data for the assessment of Spotted Owl population dynamics and spurred advances in mark-recapture methodology (White and Burnham 1999), Noon and Franklin (2002) emphasized a need to move beyond the focus on estimation of population trends to a focus on mechanistic explanations for the observed variation in life history characteristics. Researchers have logically argued that for a species at risk of extinction, where intervention to arrest population declines is desired, it is important to understand the relative contributions of factors that relate to declines (Noon and Franklin 2002, Courtney et al. 2004).

Fitness is an integral concept in ecological theory and has been addressed or utilized in a variety of ways with respect to Spotted Owls. Several studies have conferred estimates of "fitness potential" on Spotted Owls based on estimates of

survival and reproduction of owls occupying individual territories (Franklin et al. 2000, Zimmerman et al. 2003, Olson et al. 2004). These "territory-specific" estimates of fitness potential were used to gauge the importance of forest composition and configuration (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005), and in correlations with territory occupancy rates, to assess whether the species meets the assumptions of an ideal despotic distribution (Zimmerman et al. 2003). Other discussions of Spotted Owl fitness have addressed inbreeding, hybridization, and introgression, such as gene flow between Northern and California Spotted Owl populations (Courtney 2004) but were typically constrained by a lack of data and, therefore, restricted to speculation regarding potential negative effects of these factors. In a few studies, fitness benefits have been attributed to habitat and/or prey selection (LaHaye et al. 1997, Ward et al. 1998, Smith et al. 1999), with the abundance or accessibility of larger prey being suggested as contributing to reproductive success and, therefore, improved fitness (but see Forsman et al. 2001). In some cases, "fitness" was simply recorded as reproductive success or mean productivity of successful nests (LaHaye et al. 1997). Iverson (2004) noted the importance of reproductive success as a component of fitness and defined success as the production of at least one young at Spotted Owl activity centers during a three year study. However, his sample size, methods, and conclusions were challenged by Livezey (2005). In all of these studies, measures of fitness were conferred on individuals or pairs, but were based on limited data from study periods that were short relative to the potential lifespan ($\geq$ 20 years) of Spotted Owls. To date, no study has been conducted

to estimate the cumulative reproductive success of individuals as a proxy for fitness from a representative sample of Spotted Owls throughout their entire reproductive lifespans.

Estimates of individual lifetime reproductive success (LRS) are considered useful measures of biological fitness because they combine data on survival and reproductive output into a single measure of performance (Clutton-Brock 1988, Newton 1989a). Studies of LRS typically involve analysis of "longitudinal" data collected over the entire breeding lifespan of identifiable individuals. In contrast, "cross-sectional" studies assess fitness during a particular series of years or recapture occasions representing only a single episode or snapshot of selection (Endler 1986). Despite logistical difficulties of collecting these data for individuals from wild populations, studies of LRS have been completed for a number of long-lived birds including Osprey (*Pandion haliaetus*; Postupalsky 1989), Ural Owl (*Strix Uralensis*; Saurola 1989), Short-tailed Shearwater (*Puffinus tenuirostris*; Wooller et al. 1989), Goshawk (*Accipiter gentilis*; Krüger 2005), and Flammulated Owl (*Otus flammeolus*; Linkhart and Reynolds 2006). However, this is the first study of LRS in the Northern Spotted Owl.

The practical difficulties of collecting adequate data for studies of LRS in long-lived species are well known (Newton 1989a). In most cases, marked or otherwise identifiable individuals must be monitored over their entire breeding lives, and accurate counts of offspring raised to independence are needed. Where recruited offspring are used as a measure of individual LRS, other complications arise. All

young produced need to be marked or otherwise identifiable so that they can eventually be scored as recruits upon entry to the breeding or territorial population. But even when all offspring are marked, undetected dispersal due to recruitment outside a study area and potential bias in the quality of young that recruit locally versus those that leave a study area may confound efforts to utilize numbers of recruited offspring as a surrogate for individual fitness (Lambrechts et al. 1999, but see Brommer et al. 2004). For some species, obtaining comparable data for each sex may be difficult or even impossible because sex biases in natal or adult dispersal, trapability, or feather recovery contribute to differential recaptures of males and females and result in less complete, often insufficient, data for one sex (Newton 1985, 1989b, Korpimäki 1992, Marti 1997, Laaksonen et al. 2004, Krüger 2005, Linkhart and Reynolds 2006). Also, the occurrence of extra-pair fertilizations or intraspecific brood parasitism in some species can complicate measurement of LRS for males or females, respectively (Merilä and Sheldon 2000, Oli et al. 2002).

In most studies of LRS in raptors, only breeding individuals are included because it is their association with a specific territory and nest site that allows for annual observations. Individuals that nest are included, whereas individuals that never attempt to nest are not, simply because they cannot be consistently located. Thus, the range of individual variation in LRS often begins at zero, with the lowest values recorded for individuals that failed in their observed nesting attempts. The unavoidable exclusion of an "invisible fraction" of the population (Grafen 1988), either because they died young or never bred, limits samples and the amount of

variation in LRS. As a result, patterns and inferences from most studies of LRS have been to breeding individuals as opposed to the populations.

Although it is generally accepted that the number of descendants left in future generations is superior to single generation counts of offspring as a measure of individual fitness (Clutton-Brock 1988, Newton 1989a), the majority of studies of LRS have used counts of fledglings as a measure of fitness because of the difficulties of documenting recruits in future generations. Nonetheless, both proxy estimates of individual fitness have been shown to be good estimates of long-term genetic contributions (Brommer et al. 2004) despite criticisms that the measures are rate-insensitive and fail to account for the timing of reproduction (McGraw and Caswell 1996, Brommer et al. 2002b). Many avian studies of LRS have shown a strong relationship between the number of offspring raised to independence and the number recruited to the breeding or territorial population (Newton 1989b, Saurola 1989, Wooller et al. 1989, Korpimäki 1992, Brommer et al. 1998, Wiens and Reynolds 2005).

In this study my objectives were to: (1) estimate LRS for male and female Spotted Owls on four study areas in Oregon and Washington, (2) model some of the relationships between LRS and components of reproduction (lifespan and annual nest success), (3) describe individual variation in LRS for males and females, (4) examine the relationship between numbers of fledglings and recruits produced by individuals, and (5) describe life history traits other than LRS that are revealed from lifetime data

(lifespan, age at first breeding, number of breeding attempts, breeding lifespan, annual nest success, breeding dispersal [site fidelity], and numbers of mates [mate fidelity]).

Spotted Owls are somewhat unusual in that they defend their territories regardless of whether they are nesting or not (Lint et al. 1999, Anthony et al. 2006). As a result, researchers are generally able to use annual calling surveys to locate and confirm the nesting status and number of young produced by many, if not most, of the resident owls in the population, regardless of whether they are breeding or not (Reid et al. 1999). While an invisible fraction of individuals never resighted exists within populations of interest in almost every LRS study, including this one, my inclusion of all territorial individuals, including those that never bred, has consequences for variation in LRS, mean estimates of LRS and its components, and scope of inference.

METHODS

Study Area

I utilized data from three study areas in Oregon and one study area in Washington (see Chapter 2 Fig. 2.1, Table 3.1). The Tyee Study Area (TYE) and Oregon Coast Ranges Study Area (OCR) were located in the southern and central Coast Ranges of Oregon, respectively. The H. J. Andrews Study Area (HJA) was located on the west slope of the Cascade Range in Oregon, and the Cle Elum Study Area (CLE) was located on the east slope of the Cascade Range in Washington. Size of the four study areas ranged from 1741–3919 km^2 (Table 3.1). These areas included four of the eight study areas that comprise the federal monitoring program for the Northern Spotted Owl (Lint et al.

1999, Anthony et al. 2006). The HJA was primarily on federal lands administered by

the USDA Forest Service (USFS). The other three areas included a mixture of federal

lands administered by the USFS or USDI Bureau of Land Management (BLM), and

non-federal lands owned by private landowners. These study areas have been

described previously by Forsman et al. (1996a) and Anthony et al. (2006).

TABLE 3.1. Description of the four study areas and data used in the analysis of lifetime reproductive success of 336 Northern Spotted Owls in Oregon and Washington. Numbers of individuals in each sample that were resighted in 2005 (the last year of the study) are given in parentheses.

Study Area	Study area acronym	Years[a]	Area (km^2)	Number of owls[b] Female	Male
Oregon					
Tyee	TYE	1985–2005	1741	54 (11)	73 (13)
Oregon Coast Ranges	OCR	1990–2005	3919	29 (7)	47 (11)
H. J. Andrews	HJA	1987–2005	1526	41 (9)	47 (5)
Washington					
Cle Elum	CLE	1989–2005	1784	24 (2)	21 (1)

[a] Periods of mark-recapture studies on each area. Some owls banded on these areas prior to the initiation of the formal demography studies were also used in the analysis of LRS.
[b] Includes known age owls produced as fledglings from 1986 to 1992 (seven cohorts) that were not missed in more than two adult years and that were never marked with a backpack radio transmitter.

All four study areas were characterized by mountainous terrain that was

predominantly covered by coniferous forests. These forests included a diverse

mixture of age classes that ranged from early seral vegetation on recent clear-cuts to

forests that were over 450 years old on areas that had never been cut. Species

composition of vegetation on all four areas was dominated Douglas-fir (*Pseudotsuga*

menziesii) in associations with other conifer and hardwood trees, including western

hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), red alder (*Alnus*

rubra), and big leaf maple (*Acer macrophylum*). On the southernmost study area (TYE), Pacific madrone (*Arbutus menziesii*), California laurel (*Umbellularia californica*), and grand fir (*Abies grandis*) were also common canopy trees. Forest species composition on CLE included mixed associations of Douglas-fir, grand fir, and ponderosa pine (*Pinus ponderosa*), with stands of ponderosa pine predominating on south exposures and mixed stands of Douglas-fir and grand fir predominating elsewhere.

The four study areas spanned a comparatively broad range of climatic conditions, from the relatively cool and dry forests on the east slope of the Cascades (CLE) to mesic maritime forests of western Oregon (OCR, TYE, HJA). The HJA and CLE study areas were at moderate elevations (~400–2084 m) in the Cascades where the ground was often covered by snow in winter. The OCR and TYE areas were at lower elevations (~38–1418 m) in the Coast Ranges, where snow was infrequent and most precipitation occurred as rain.

Field Methods

A standard protocol was followed on all study areas for conducting field surveys and collecting data on reproductive success of owls that were marked with leg bands (Franklin et al. 1996, Lint et al. 1999). Individual field surveys were conducted to fulfill one or more of the demography study objectives including: 1) determine territory occupancy status, 2) confirm the identity of all banded owls, 3) determine nesting status, and 4) determine reproductive success, measured as the number of young that left the nest tree.

All adults and young were initially marked with a color-coded plastic leg band and a numbered USFWS aluminum leg band, and their identities were thereafter confirmed through visual observation of color bands (Forsman et al. 1996b). Most owls were only trapped once or twice in their lives with second captures typically corresponding with the recapture of individuals banded as fledglings and relocated after they settled on territories. Estimates of annual recapture probabilities of banded non-juveniles on all areas were high with means ranging from 0.82 for all banded owls on HJA to 0.92 for banded males on TYE (means computed from annual estimates reported in Anthony et al. 2006; Appendix D). Loss of color bands was nearly zero and loss of numbered leg bands was zero (Franklin et al. 1996). Approximately 90% of the records summarized for my analysis of LRS were from owls that were coded as paired (9356 out of 10 419 records) and only a small percentage of the mates of paired owls were unidentified (5% and 2% of the mates of banded males and females, respectively), either because they were not banded or a color band could not be observed.

Owls first banded as fledglings or subadults were identified as "known age" and recorded as 0, 1, or 2 years old based on plumage attributes (Forsman 1981, Moen et al. 1991). Owls first banded when they were ≥3 years old were identified as "unknown age adults" and recorded as ≥3 years old. I use the term "non-juvenile" to refer to owls of age ≥1 year. Since observers did not know the exact age of owls first captured at ages ≥3 and since few owls were banded prior to the initiation of our demography studies, samples of known age owls available for this study grew

annually with recruitment to the territorial population of young banded in previous years (see Chapter 2, Fig. 2.2).

Field personnel used a combination of calling surveys and live lure surveys to relocate owls each year (Forsman 1983, Franklin et al. 1996, Reid et al. 1999). The primary method used to determine nesting status and number of young produced was to offer the owls live mice, which they would then capture and carry to their nests or fledged young (Franklin et al. 1996, Reid et al. 1999). By doing this on 1–3 occasions each year, it was usually possible to document the nesting status of the owls, and if they were nesting, to determine the location of the nest tree and document the number of young that left the nest tree, which I used as the estimate of annual productivity (Lint et al. 1999).

Nesting status was determined primarily in April and May, and the number of young that left the nest was determined in June–August. Young were not considered "fledged" until they were observed out of the nest tree. If it was determined an owl did not nest or nested and failed to produce offspring, the number of young fledged was coded as zero.

Data Preparation

I combined data from the demography studies into a single file with one record for each banded owl for each year that it was resighted. I use the term "resight" to indicate the annual confirmation of an individual as being alive, either through initial banding or through observation of its color band. If an owl was "missed" (not resighted but known to be alive due to a resight in a later year) I did not add a record

for the missing year. Data were summarized for 2193 individual owls and 10 419 resights and included 984 known age owls (45% of all individuals) resighted in 4583 owl years (44% of all resights). Of 2880 young counted as fledglings in the demography studies, 2686 (93%) were banded. Most cases in which fledglings were not banded were cases in which juveniles disappeared and were presumed dead before they could be banded.

Variables recorded for all owls included sex, lifespan, cohort, and a radio transmitter code to indicate any years in which an owl was carrying a radio-transmitter. Cohort for each owl was the birth year and was explicit for individuals originally banded as fledglings and inferred for owls first banded as 1- or 2-year-olds. Lifespan was recorded as the age, in years, during the last year that an owl was resighted. For known age owls resighted in 2005, age equaled the true lifespan for individuals that did not survive to 2006. This was an unknown outcome, but was likely for at least some individuals. However, given the high annual survival rates of adult Spotted Owls in these studies (range = 0.86–0.89; Table 2.13. Anthony et al. 2006), lifespan and other summary measures of reproductive success for individuals alive in 2005 were probably biased low.

I evaluated LRS of each individual based on the cumulative numbers of fledglings (LRS_F) and recruits (LRS_R) produced by an individual over its lifespan. I defined a recruit as any banded fledgling later found alive as a non-juvenile within the local study area, regardless of the recruit's occupancy status. Thus, fledglings confirmed alive in later years as unpaired territory holders or even as apparent floaters

were counted towards the LRS_R of their parents. I only counted banded young that recruited locally, because the opportunity to detect off-study recruits was inconsistent over time due to variable effort, but also because my study areas varied in their relative isolation from other mark-recapture studies and banding projects.

A common approach for reducing bias in studies of LRS has been the application of a "2-year-rule", whereby individuals observed alive in the last two years of a study were excluded from analysis on the assumption that they may not have concluded their breeding lives. This rule has been used in studies of *Accipiter nisus* (Newton 1985), *Aegolius furnereus* (Korpimäki1992), *Tyto alba* (Marti 1997), *Strix uralensis* (Brommer et al. 1998), *Strix aluco* (Brommer et al. 2005), *Accipiter gentilis* (Krüger 2005). In my study, application of this 2-year-rule would have exacerbated a negative bias by excluding many of the oldest and most fecund individuals still alive in 2004–2005. This problem arose because the mark-recapture study periods in my sample were short (16–21 years; Table 3.1) relative to the potential lifespan of Spotted Owls (>20 years). As such, a small number of owls had completed relatively long lives by 2003 and application of the 2-year-rule led to a disproportionate exclusion of older owls from the sample. Nevertheless, using criteria described below, study periods were sufficient to encompass relatively complete data for many males and females, including a moderate number of owls that lived long lives (Fig. 3.1).
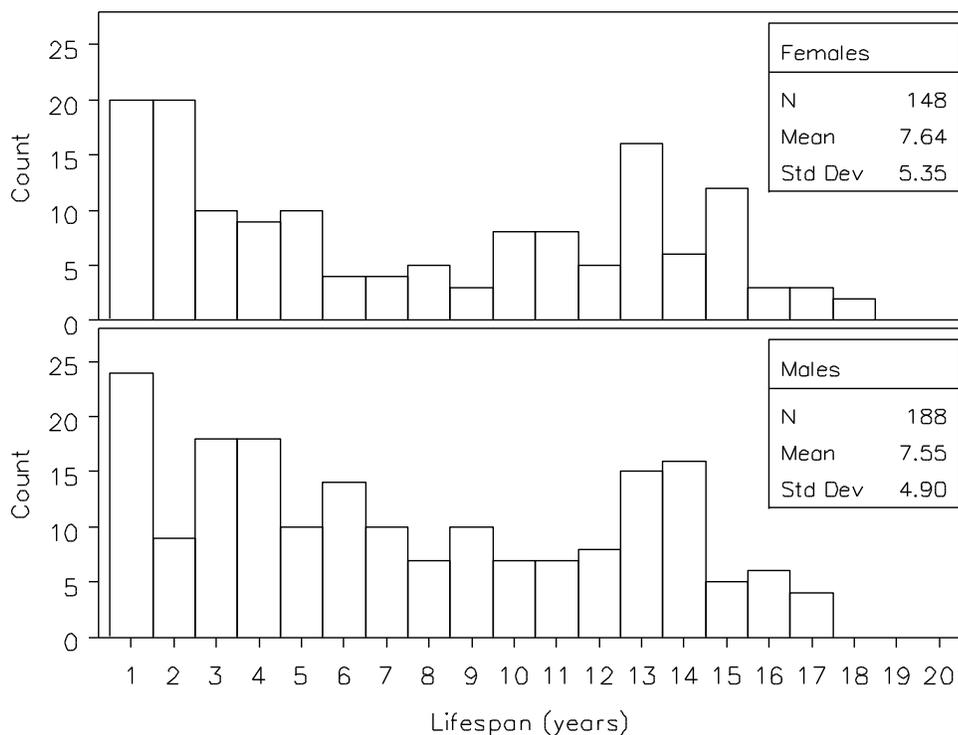
FIGURE 3.1. Frequency distributions (counts) of lifespans of female and male Northern Spotted Owls included in the analysis of lifetime reproductive success on four study areas in Oregon and Washington. Data are from the 1986–1992 cohorts. The last year of observation was 2005.

To reduce the negative biases caused by including owls that were still alive at the end of my study, I restricted the analysis of LRS to individuals in seven early cohorts that had either completed their lives and breeding or nearly so. I selected 1986 as the first cohort to avoid sparse data in any individual cohort and 1992 as the last cohort to reduce the proportion of data from owls that survived to the last year of the study (Figs. 3.2 and 3.3). Therefore, data for analysis included some owls that were ≥13 years old at the end of the study (Table 3.1), but excluded younger owls that had

more recently entered the sample and whose lifespan and long-term productivity were

likely to be more strongly underestimated based on cumulative data through 2005.
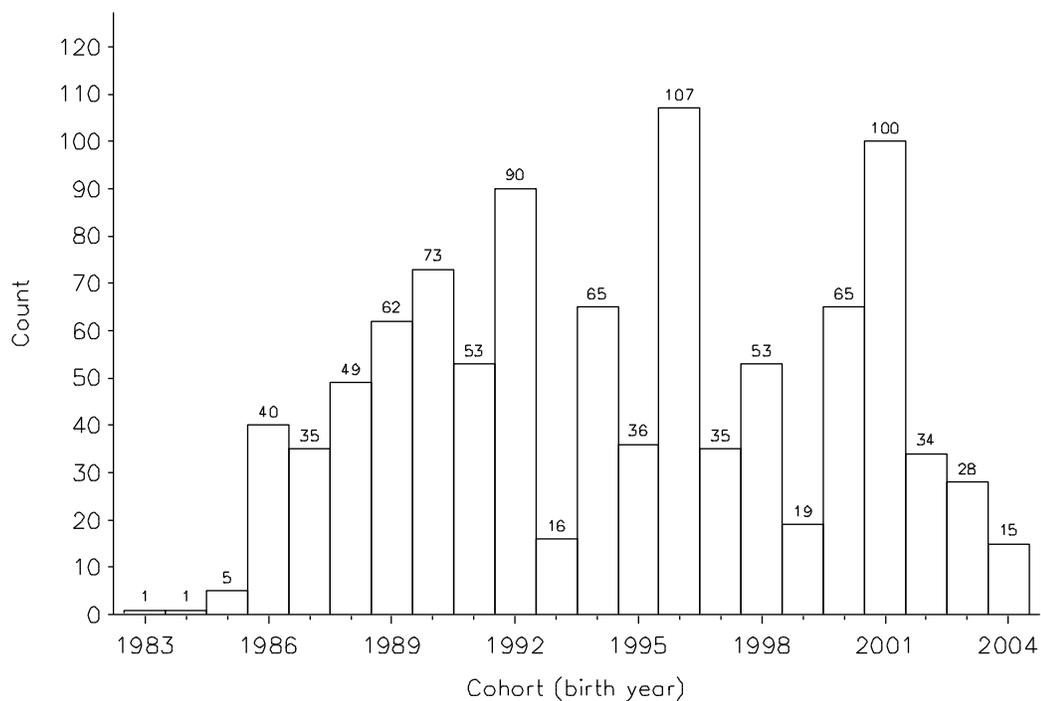
FIGURE 3.2. Frequency distribution of cohort (birth year) for 982 known age Northern Spotted Owls that were resighted as non-juveniles (age ≥ 1) on four demography studies in Oregon and Washington through the year 2005.
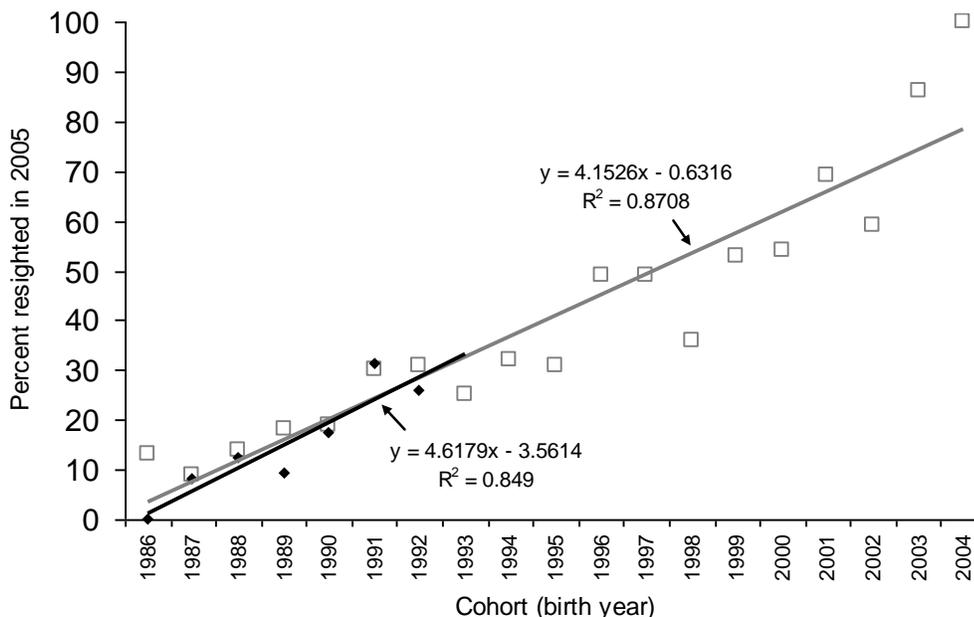
FIGURE 3.3. Percent of known age Northern Spotted Owls from each cohort that were observed as non-juveniles and resighted in 2005. Calculated for cohorts with >5 individuals. Proportions were estimated from all known age owls (squares, $n = 975$) and from the subset of owls used in the analysis of LRS (diamonds, $n = 336$). Trend lines and R^2 values are presented for each data set.

I further restricted my analysis of LRS to known age individuals that were

never marked with backpack radios and that had ≤ 2 missing resights after age 2. I

had some concern that backpack radios may have influenced reproduction (Foster et

al. 1992). Two years of missing adult resights was a compromise between one year,

which would have excluded 42 additional owls (13%), and $\geq$ three years, which I

believed was likely to reflect longer absences associated with unconfirmed breeding

dispersal that may have included nesting on an unknown or unmonitored territory. I

included owls not resighted as 1- or 2-year-olds on the assumption that these owls

were "missed" because they were still dispersing and thus unlikely to breed (Forsman

et al. 2002). These two restrictions led to a 16% reduction in the sample of owls from the 1986–1992 cohorts ($n = 402$, Fig. 3.2), resulting in a subsample of 336 owls with few or no missing resights from the time they first entered the sample until they disappeared and were never seen again. Twenty-one owls were excluded because they were carrying backpack radios during part of their life.

Within a territory, I attributed the nesting status and number of young fledged annually to each pair member or territory holder in cases when the pair status was not certain. Thus, the male and female on each territory were coded as nesting or not nesting and as producing the same number of fledglings, regardless of whether they were observed to display pair behavior or not. Single males were coded as producing zero fledglings when they were monitored to the same protocol standards required for single females or pairs, and "extra owls" were coded as producing zero fledglings. An extra owl was defined as a second individual of the same sex found on a territory that was not the primary territory holder. Because extra-pair paternity in the Northern Spotted Owl has never been observed, it is assumed to be rare. Therefore I felt it was most reasonable to attribute any young to the primary territory holders and to assign the production of zero young to the few extra owls that were observed. Since pair status was uncertain in only 2.6% of cases when a male and female were detected and was most often associated with at least one owl without a resight record, it was very unlikely that nest attempts or fledglings were attributed to the wrong individual.

I made the simplifying assumption that owls did not breed or produce young in years when reproduction was uncertain. This may have resulted in an underestimate

of the reproductive performance of some individuals, but I believe this bias was small because most of these cases were situations in which owls appeared to be non-nesting and could not be consistently located in the same location during the breeding season.

Nesting status and fledgling output were known for most owls that were resighted. Of 10 419 resights in the demography studies, protocol standards for determining nesting status were achieved in 7570 resights (73%), including 3509 resights when it was determined that owls were not nesting. Protocol standards for determining the number of fledglings produced were met in 8822 resights (85%), including 5349 resights when zero young were fledged by individuals.

In addition to LRS_F and LRS_R, other summary data for each individual included the number of breeding attempts, number of successful attempts, number of mates, number of breeding dispersal events, number of different territories occupied, and the number of adult years when the owl was not resighted. For individuals that made at least one nest attempt, I also calculated nest success, annual success, breeding experience, and breeding lifespan.

The number of breeding attempts was the number of years when an owl made a nesting attempt as indicated by repeated deliveries of food to a nest, presence of a brood patch on a female (in hand), or the observation of eggs, nestlings, or fledglings. The number of successful nesting attempts was the number of years when an owl produced ≥1 fledgling. Nest success was the proportion of breeding attempts that resulted in ≥1 fledgling. Annual success was the average number of fledglings per nesting attempt. Breeding experience was the span of years across which an owl was

observed to have nested based on the first and last years the owl was observed nesting. Breeding lifespan was the span of years from an owl's first observed nesting attempt to its last resight. Thus, breeding experience equals breeding lifespan for owls that nested in their last resight year. The number of mates was the number of different banded owls with which each individual shared a territory over the study period, without a requirement that they actually make a breeding attempt. The number of breeding dispersal events was the number of times that a non-juvenile owl changed territories and did not necessarily indicate the number of different territories an owl used because some individuals dispersed (or returned) to previously used territories (Forsman et al. 2002). Therefore, I also reported the number of different territories used by each owl as the cumulative number of different territories where resights occurred. Finally, I recorded the number of adult years that each owl was "missed" as the cumulative number of missing resight records (based on gaps) between age 2 and the last resight.

For each resighting, I recorded pair experience as the cumulative number of years that the owl was found to be paired with its current mate. Any gaps in resights of a mate were not counted towards an individual's count of pair experience (i.e., I did not assume the pair was intact due to an apparent missed resight of its mate). Therefore, pair experience was underestimated for owls whose mate had not changed but simply failed to be resighted. I also recorded the number of consecutive years that each individual owl made a nesting attempt and the number of consecutive years each owl successfully produced fledglings. For these estimates I did not continue the

counts if the owl was missed, thus I only counted nest attempts and nest success that occurred over consecutive resights without gaps.

I defined generation time as the mean age of successfully breeding females or "average age of the mothers of newborn offspring" (Futuyma 1998:563), calculated as the mean of the mean ages of known age females that produced fledglings in each of the last three years of my study. I used data from 2003–2005 to compute generation time since those where years when the recorded ages of known age owls were most representative of the real age distribution of all breeding owls.

When negative bias in estimates of LRS or its components was not of concern (e.g., age at first breeding), I used a larger subset of owls to examine trends in the data. I pooled across areas for graphical presentations when issues regarding lack of independence or study area differences were not of concern. To assess other components of reproduction (e.g., age at first breeding and nest success) I restricted the analysis to owls that bred at least once. I also presented data on maximum LRS and its components from the entire sample of banded owls for which data were summarized, including unknown age owls.

Statistical Analyses

Because my data on reproductive success of paired males and females were not independent, I analyzed the data from males and females separately. I used generalized linear models (PROC GENMOD; SAS Institute 2004) to examine relationships between the two measures of LRS. Due to the count nature of the data I used Poisson log-linear models with number of recruits as the response and number of

fledglings as the explanatory variable. For analysis of factors that influenced LRS, I used a Poisson log-linear model to examine the explanatory power of lifespan and annual success on the number of fledglings produced. In each case, I began with a relatively full model and tested for overdispersion (that is, when the variance for count data is greater than its mean, which is contrary to Poisson-distributed counts) with a deviance goodness-of-fit test. This test examines the magnitude of the deviance statistic relative to its degrees of freedom (Ramsey and Schafer 2002). When the p-value from a deviance goodness-of-fit test was small (<0.05) I used a quasi-likelihood approach in which I estimated a correction factor for the standard error and the chi-square statistic of each coefficient. This correction factor is the square root of DEVIANCE/DOF, and is implemented with the DSCALE option in SAS PROC GENMOD (SAS Institute 2004, Allison 1999). I tested for among-study-area differences in the effects of components by pooling data and including area and interaction terms for area and components of interest in the Poisson regressions. I conducted all analyses with SAS 9.1 software. Results are reported as means ± SE.

RESULTS

Maximum Values Observed

Maximum values of reproductive success and associated components of breeding were sometimes observed for owls that were not included in my analysis of LRS (Appendix E). The maximum number of lifetime fledglings produced by any individual was 22 and the maximum number of local recruits was seven. The greatest number of

breeding attempts was 15 and the maximum number of successful breeding attempts was 11. Although most individuals did not nest or produce fledglings in consecutive years, a few were assiduous in their nesting attempts and production of fledglings. Only 37% of owls were observed nesting in ≥2 consecutive resights and only 24% produced fledglings in ≥2 consecutive resights. Since these counts do not account for gaps when owls were missed, these percentages are likely to be slight overestimates. The maximum number of consecutive years that an owl made nesting attempts was 12 and the maximum number of consecutive years that owls nested successfully was seven.

The longest lifespans recorded were ≥20 years for five owls, four of which were still alive in the last year of this study. These represent a new published longevity record for Northern Spotted Owls in the wild. However, a female that was banded in Northern California as an adult in 1983 and last observed alive in 2003, survived to at least 23 years old (A. Franklin pers. comm.).

The maximum number of mates for any individual was six. The maximum number of breeding dispersal events was six and the maximum number of different territories an owl was resighted at was five. The maximum breeding experience for an owl was 17 years for an owl first and last observed nesting at ages 3 and 19, respectively. The maximum breeding lifespan for any individual was 18 years for an owl first observed breeding at age ≥3 and last resighted at age ≥20. The oldest age at last breeding was ≥20 for three owls, two of which produced fledglings in their last observed nest attempt. Four individuals (two pairs) had the greatest pair experience;

each pair was confirmed together during 15 resights. Both pairs were found on two different territories, each individual having made a single breeding dispersal.

Pooled Data

Of 148 females and 188 males that met the criteria for inclusion in the analysis of LRS, 109 females (74%) and 130 males (69%) attempted to nest at least once, and 104 females (70%) and 115 males (61%) successfully produced fledglings at least once. Of the owls that made ≥1 attempt, 5% of females and 14% of males never produced a single fledgling. However, the majority of fledglings were produced by only a few individuals. Seventeen percent of females and 16% of males produced 50% of the offspring that were fledged by each sex (Figs. 3.4 and 3.5). Considerable numbers of owls with short lifespans produced no fledglings, whereas all females with lifespans ≥ 8 years and all males with lifespans ≥ 10 years produced ≥1 lifetime fledgling (see section on components of reproduction below). Only 36% of females and 31% of males successfully produced recruits (Fig. 3.4). As in the case of fledglings, the vast majority of recruits were produced by a small minority of especially productive individuals. Of the recruits found for each sex, 50% were produced by 9% of females and 7% of males (Figs. 3.4, 3.5).
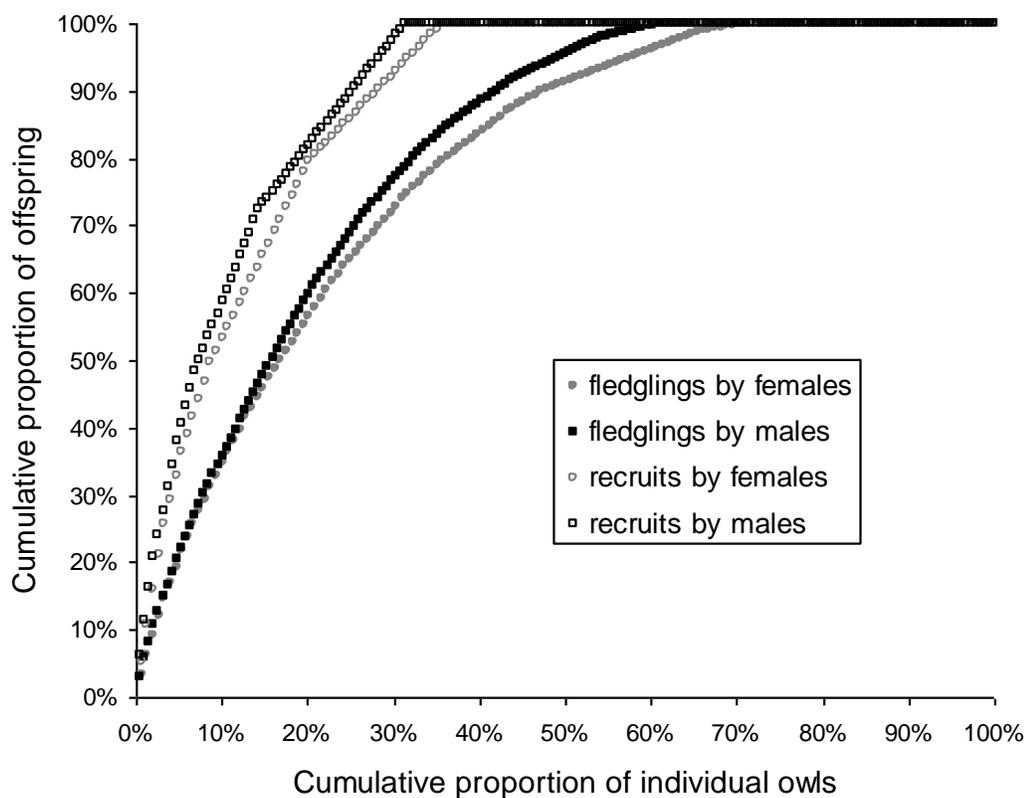
FIGURE 3.4. Percentages of offspring fledged and recruited by varying percentages of male and female Northern Spotted Owls from the 1986–1992 cohorts based on data collected through 2005. Data are pooled from four study areas in Oregon and Washington and include 601 fledglings and 113 recruits produced by 148 females, and 611 fledglings and 116 recruits produced by 188 males. Plots include all owls used in the analysis of LRS ordered from highest to lowest productivity along the horizontal axis.
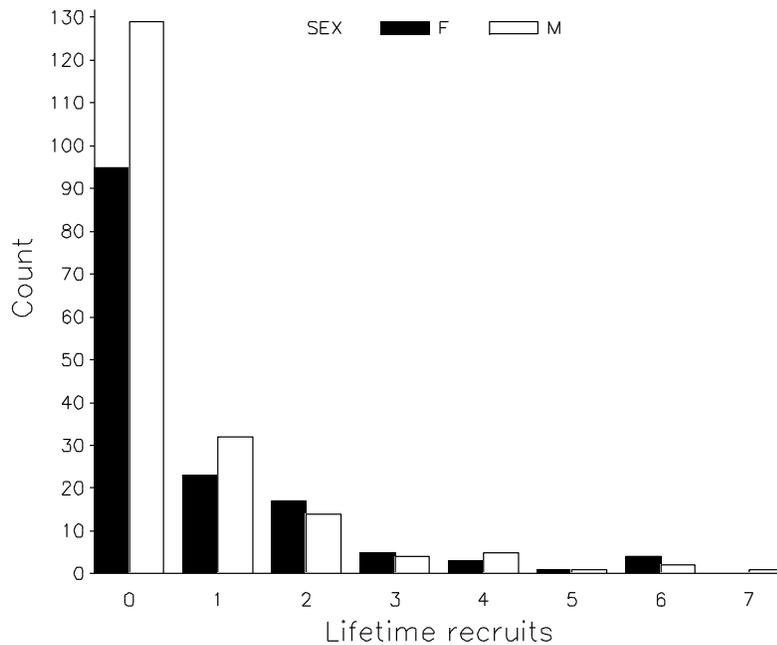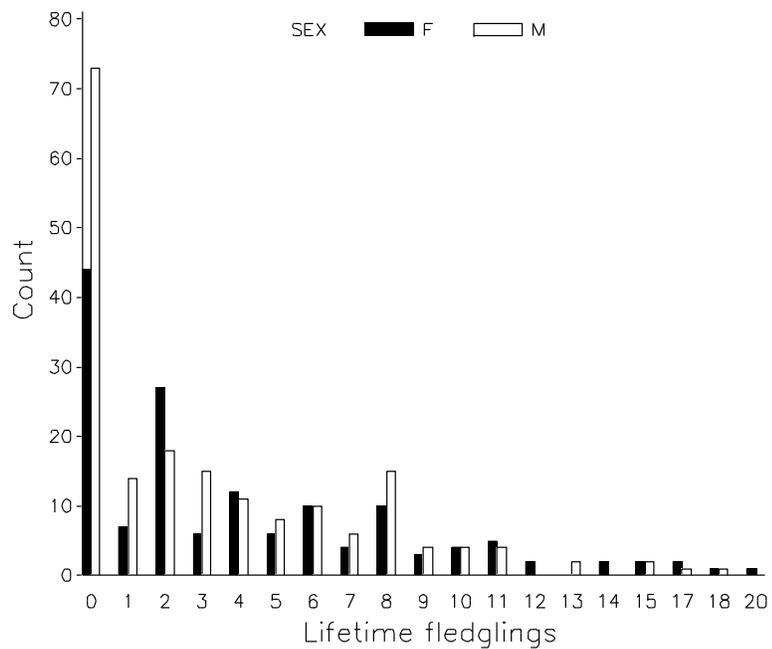
FIGURE 3.5. Distribution of lifetime reproductive success measured in fledglings and recruits produced by 148 female and 188 male Northern Spotted Owls from the 1986–1992 cohorts on four study areas in Oregon and Washington from data on observations through 2005.

Poisson regressions for the pooled male and pooled female data from all areas indicated that the numbers of offspring that recruited to local territories (LRS_R) were significantly related to the numbers of lifetime fledglings produced (LRS_F) (females: $\hat{\beta} = 0.21 \pm 0.02$, wald $\chi^2 = 136.21$, df = 1, P < 0.001; males: $\hat{\beta} = 0.23 \pm 0.02$, wald $\chi^2 = 188.39$, df = 1, P < 0.001; Fig. 3.6). The p-values from deviance goodness of fit tests were large for both sexes (males = 0.999, females = 0.890), indicating that the data were not overdispersed.
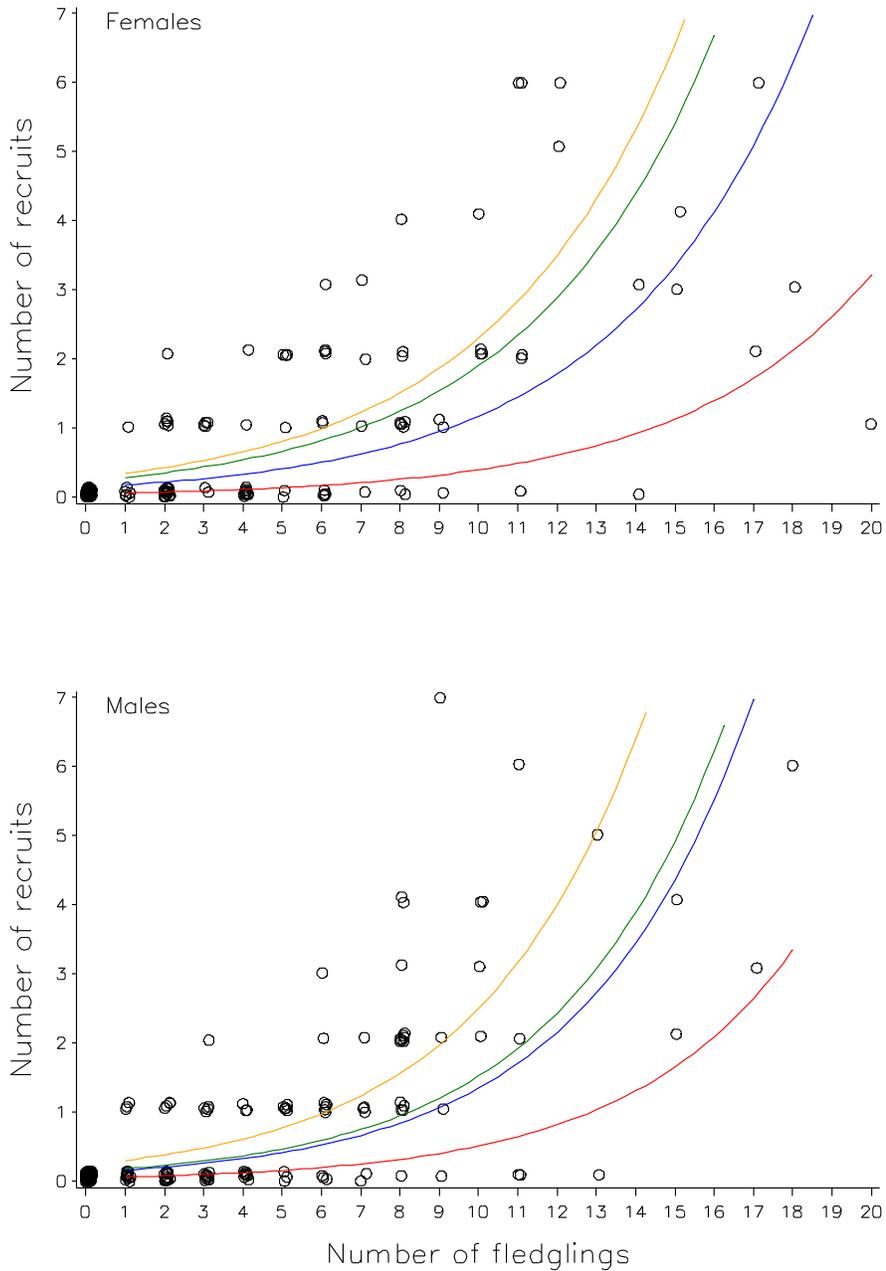
FIGURE 3.6. Numbers of fledglings that recruited locally in relation to lifetime fledglings produced by individual Northern Spotted Owls from the 1986–1992 cohorts on four study areas in Oregon and Washington through 2005. Circles represent individual owls ($n = 148$ females, 188 males) and are jittered to show multiple owls that had the same numbers of fledglings and recruits. Trend lines show study area effect determined with Poisson regression with a log-link function. Red = Cle Elum, Blue = H. J. Andrews, Green = Oregon Coast Ranges, Orange = Tyee.

Components of LRS

Poisson regressions for the pooled male and pooled female data from all areas indicated that LRS_F of individual owls was significantly related to lifespan (females: $\hat{\beta} = 0.19 \pm 0.01$, wald $\chi^2 = 288.30$, df = 1, P < 0.001; males: $\hat{\beta} = 0.20 \pm 0.01$, wald $\chi^2 = 208.65$, df = 1, P < 0.001; Fig. 3.7) after accounting for an area effect ($F_{females} = 9.98_{3,143}$, P<0.001; $F_{males} = 9.583_{3,183}$, P<0.001). P values from deviance goodness of fit tests were small for both sexes (<0.001 for males and 0.001 for females), indicating that the data were overdispersed.

Poisson regressions for the pooled male and pooled female data from all areas indicated that LRS_F was also related to annual success for owls that bred at least once (females: $\hat{\beta} = 0.48 \pm 0.13$, wald $\chi^2 = 13.10$, df = 1, P < 0.003; males: $\hat{\beta} = 0.66 \pm 0.11$, wald $\chi^2 = 38.75$, df = 1, P < 0.001; Fig. 3.8), but without an area effect ($F_{females} = 0.37_{3,104}$, P=0.78; $F_{males} = 0.81_{3,125}$, P=0.49). The p-values from deviance goodness of fit tests were small for both sexes (0 for males and females), indicating that the data were overdispersed.
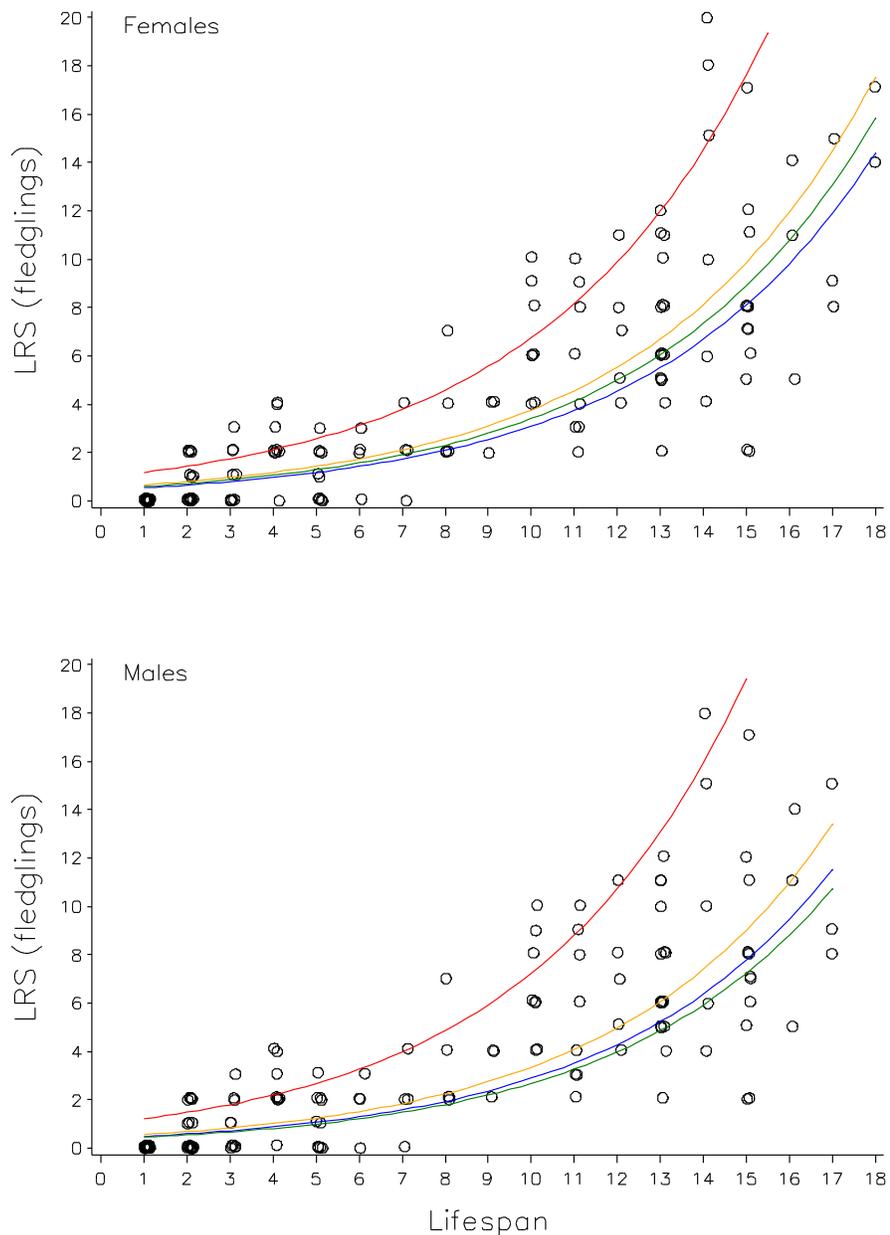
FIGURE 3.7. Lifetime production of fledglings in relation to lifespan of 148 female and 188 male Northern Spotted Owls from the 1986–1992 cohorts on four study areas in Oregon and Washington through 2005. Circles represent individual owls and are jittered to show multiple owls that had the same number of fledglings and lifespan. Trend lines show study area effect determined with Poisson regression with a log-link function. Red = Cle Elum, Blue = H. J. Andrews, Green = Oregon Coast Ranges, Orange = Tyee.
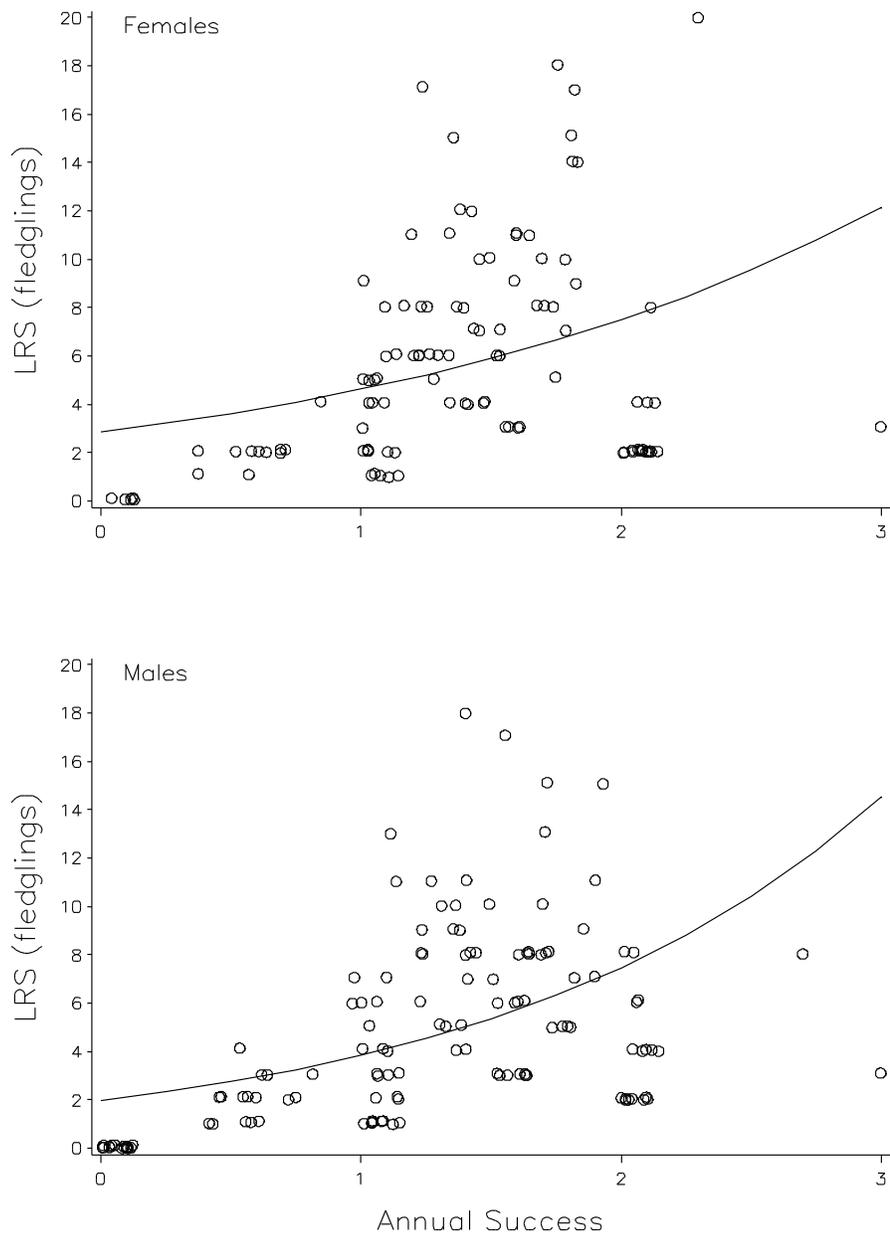
FIGURE 3.8. Lifetime production of fledglings in relation to annual nest success of 109 female and 130 male Northern Spotted Owls that made at least one breeding attempt on four study areas in Oregon and Washington during the period 1986–2005. Circles represent individual owls and are jittered to show multiple owls that had the same number of fledglings and estimates of annual success. Trend lines were determined with Poisson regression with a log-link function. Parent birds are from 1986–1992 cohorts and annual success was the mean number of offspring per breeding attempt.

Modifying the original criteria to include data from 1986–1996 cohorts increased the sample from 336 to 526 individuals (231 females and 295 males) for a closer examination of age at first breeding on each study area. The results from these data were similar to those from the 7-cohort sample. Seventy five percent of females and 67% of males bred at least once. For owls that bred, 36% of females and 19% of males first bred at ages 1 or 2, and 98% of females and 91% of males bred at least once by age 6 (Appendix D). The age at which owls first attempted to nest roughly fit a negative binomial distribution, with few birds of either sex breeding as 1-year-olds, the majority of birds first breeding when they were 2–5 years old, and a few individuals not breeding until they were ≥ 6 years old (Fig. 3.9, Appendix D). Males tended to breed for the first time at a slightly older age than females (Fig. 3.9, Appendix D).
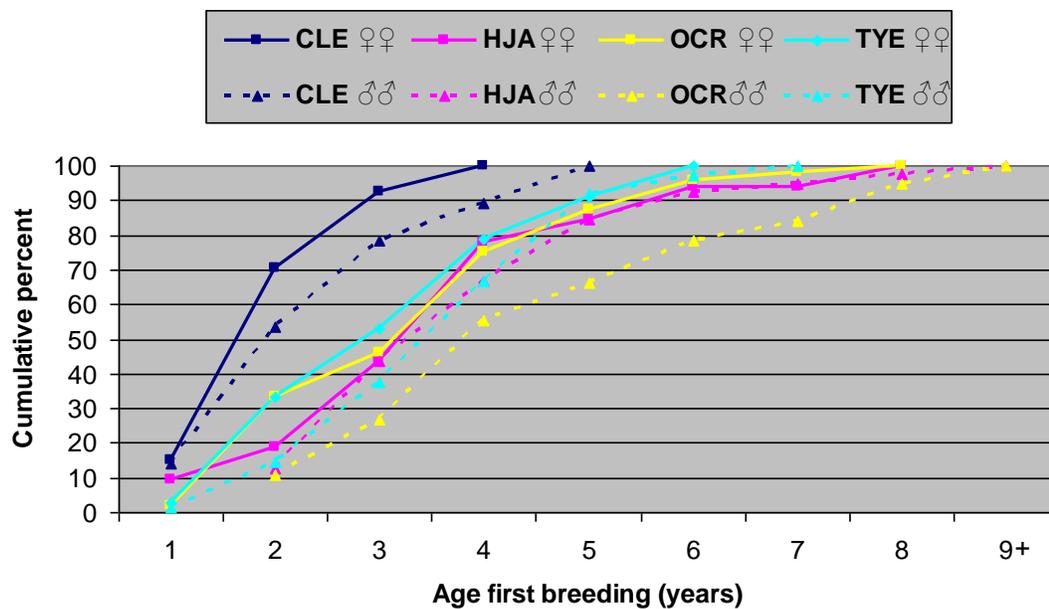
FIGURE 3.9. Cumulative proportions of female and male Northern Spotted Owls that began breeding at different ages on four study areas in Oregon and Washington. Data are for 371 owls from the 1986–1996 cohorts that bred at least once, never had a backpack radio, and were not missed in more than two adult years.

Although a few owls moved among multiple territories, 63% of females and 64% of males were located at only one territory during their recorded lifespan. Thus breeding dispersal was not observed for most owls.

During the last three years of the study, the mean age of females that produced ≥ 1 fledgling was 8.5, 9.0, and 8.8, respectively. Mean generation time, calculated as the mean of these three estimates was 8.8 years.

Individual Study Areas

Including owls that never bred, the mean number of fledglings produced by individual owls (LRS_F) was lowest for males at HJA and highest for females at CLE (Table 3.2). The mean number of recruits (LRS_R) was also lowest for HJA males and TYE females had the highest estimate of mean recruits. Within study areas, point estimates of LRS were always higher for females than males (Table 3.2). The median LRS_R for both sexes on all areas was zero and indicated that most owls produced no recruits. The proportion of fledglings that were later recruited, expressed as the ratio of means (LRS_R/LRS_F), ranged from a low of 0.08 for both sexes on CLE to a high of 0.30 for TYE males. This indicated that on average, about one in 10 fledglings of CLE owls and one in three fledglings from TYE males was recruited into the local population (was resighted in a later year).

TABLE 3.2. Descriptive lifetime statistics for 148 female and 188 male Northern Spotted Owls from the 1986–1992 juvenile cohorts on four study areas in Oregon and Washington based on observations through the year 2005. For each summary variable the maximum and minimum estimates are listed in bold and italics, respectively[a].

Study Area/Variable	Females[a] Mean ± SE	Median	Range	Males[a] Mean ± SE	Median	Range
Cle Elum						
Lifespan	6.17 ± 1.04	4	1–16	*5.67 ± 0.99*	4	1–16
Lifetime fledglings	**5.33 ± 1.24**	2.5	0–20	4.86 ± 1.18	3	0–17
Lifetime recruits	0.42 ± 0.17	0	0–3	0.38 ± 0.19	0	0–3
Breeding attempts	3.25 ± 0.68	2	0–11	3.00 ± 0.70	2	0–11
Successful attempts	**2.96 ± 0.64**	1.5	0–10	2.43 ± 0.60	2	0–9
Mates	1.75 ± 0.22	1	1–5	1.48 ± 0.29	1	0–4
Dispersal events	0.38 ± 0.16	0	0–3	0.43 ± 0.15	0	0–2
Territories used	1.33 ± 0.14	1	1–4	1.43 ± 0.15	1	1–3
Missed adult resights	*0.21 ± 0.10*	0	0–2	0.24 ± 0.12	0	0–2
H. J. Andrews						
Lifespan	7.20 ± 0.90	4	1–18	6.94 ± 0.71	6	1–17
Lifetime fledglings	3.22 ± 0.61	2	0–14	*2.51 ± 0.45*	1	0–11
Lifetime recruits	0.44 ± 0.12	0	0–3	*0.32 ± 0.09*	0	0–2
Breeding attempts	2.46 ± 0.41	1	0–9	*2.13 ± 0.35*	1	0–9
Successful attempts	1.90 ± 0.34	1	0–8	*1.55 ± 0.28*	1	0–7
Mates	1.66 ± 0.18	1	0–5	*1.40 ± 0.17*	1	0–6
Dispersal events	*0.32 ± 0.10*	0	0–2	0.62 ± 0.18	0	0–5
Territories used	*1.29 ± 0.09*	1	1–3	1.43 ± 0.12	1	1–4
Missed adult resights	0.54 ± 0.12	0	0–2	0.45 ± 0.11	0	0–2
Oregon Coast Ranges						
Lifespan	**9.28 ± 0.79**	9	2–17	8.87 ± 0.76	9	1–17
Lifetime fledglings	4.07 ± 0.68	3	0–15	3.38 ± 0.53	2	0–15
Lifetime recruits	0.79 ± 0.20	0	0–4	0.51 ± 0.13	0	0–4
Breeding attempts	**3.55 ± 0.48**	3	0–9	2.79 ± 0.38	2	0–8
Successful attempts	2.59 ± 0.40	2	0–8	2.11 ± 0.32	1	0–8
Mates	1.62 ± 0.15	1	1–4	1.53 ± 0.18	1	0–5
Dispersal events	0.62 ± 0.17	0	0–4	0.55 ± 0.12	0	0–3
Territories used	1.55 ± 0.14	1	1–3	1.53 ± 0.11	1	1–3
Missed adult resights	**0.76 ± 0.15**	1	0–2	0.66 ± 0.11	0	0–2

TABLE 3.2. Continued

Study Area/Variable	Females[a]			Males[a]		
	Mean ± SE	Median	Range	Mean ± SE	Median	Range
Tyee						
Lifespan	7.74 ± 0.76	6	1–18	7.63 ± 0.54	7	1–17
Lifetime fledglings	4.13 ± 0.60	2	0–17	3.19 ± 0.46	2	0–18
Lifetime recruits	**1.15 ± 0.25**	0	0–6	0.95 ± 0.19	0	0–7
Breeding attempts	3.37 ± 0.48	2	0–15	2.82 ± 0.36	2	0–13
Successful attempts	2.56 ± 0.39	1	0–11	2.01 ± 0.28	1	0–10
Mates	**1.87 ± 0.15**	1.5	0–5	1.71 ± 0.13	2	0–4
Dispersal events	**0.80 ± 0.16**	0	0–6	0.59 ± 0.10	0	0–4
Territories used	**1.61 ± 0.10**	1	1–4	1.52 ± 0.08	1	1–4
Missed adult resights	0.33 ± 0.08	0	0–2	0.32 ± 0.07	0	0–2

[a] Sample sizes for males and females by study area were: CLE (24,21); HJA (41,47); OCR (29,47); TYE (54,73).

The estimated mean lifespan was shortest for males at CLE and longest for females at OCR (Table 3.2, Fig. 3.10). Within areas, point estimates of mean lifespan were always greater for females than males (Table 3.2, Fig. 3.10). Exclusionary criteria resulted in lower estimates of lifespan in most cases, particularly for females (Fig. 3.10).
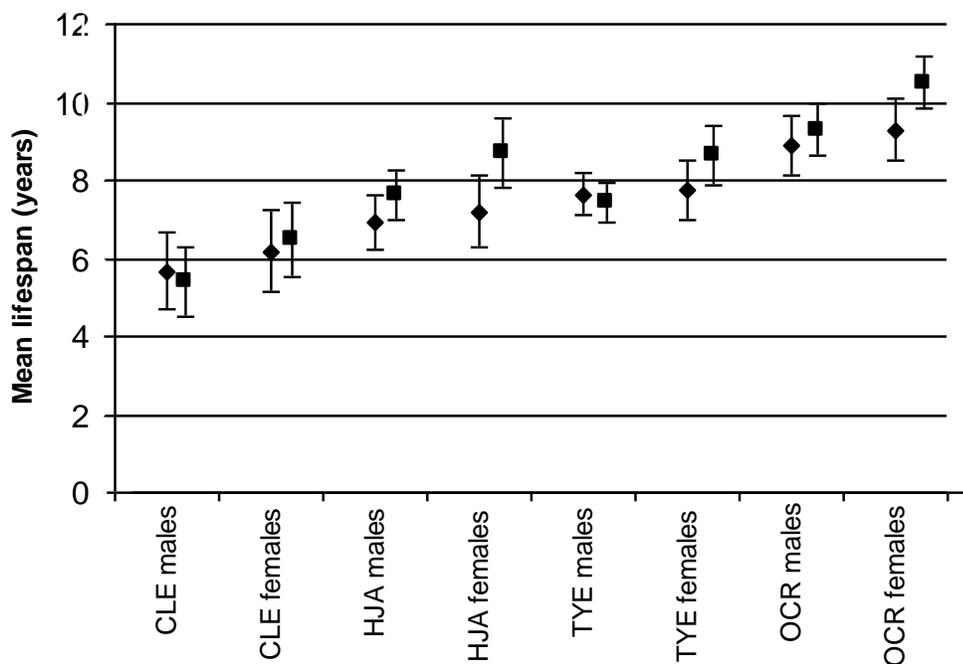
FIGURE 3.10. Estimated mean lifespan of male and female Northern Spotted Owls from the 1986–1992 cohorts on four study areas in Oregon and Washington. Bars indicate one standard error. Plot shows estimates from data used in the analysis of LRS (diamonds, $n = 336$) and estimates based on less restrictive samples that included owls marked with backpack radios and owls missed for three or more adult years (squares, $n = 401$).

The mean number of breeding attempts was greatest for OCR females and lowest for HJA males (Table 3.2). The mean number of successful attempts was highest for CLE females and lowest for HJA males. Again, within areas, point estimates of these means were higher for females than males and medians were considerably smaller than means, indicating the skewed nature of the data (Table 3.2). The success rate expressed as the ratio of means (successful breeding attempts to total breeding attempts) was greatest for CLE females (0.91) and lowest for TYE males (0.71), indicating that, on average, CLE females produced ≥1 fledgling in nine out of every 10 nesting attempts, whereas TYE males produced ≥1 fledgling in seven out of every 10 attempts.

The proportion of owls that made at least one breeding attempt during their lifespan ranged from 0.63 for HJA females to 0.86 for OCR females. For owls that made at least one attempt, the mean nest success was lowest for TYE males (0.66 ± 0.05) and highest for CLE females (0.88 ± 0.06). The mean number of fledglings produced per nest attempt ranged from 1.04 ± 0.08 for TYE males to 1.60 ± 0.21 for CLE males.

For the individual owls from the 1986–1996 cohorts that bred, the median age at first breeding was 2 for both sexes on CLE, 3 for TYE females, and 4 for TYE males and for both sexes on HJA and OCR (Appendix D). On most areas, males began to breed later than females on average and the final age when 100% of males had first bred was older than females (Fig. 3.9). Age at first breeding was particularly low on CLE where 70% of females and 54% of males first bred by age 2. In contrast

to the early breeding by CLE owls, it was not until age 5 or 6 that 70% of the males first bred on the Oregon study areas (Fig. 3.9).

Mate and Territory Fidelity

The median number of breeding dispersal events and territories used by owls on all areas were 0 and 1 respectively, indicating that most males and females were found at only one territory (Table 3.2). Mean numbers of breeding dispersal events ranged from a low of 0.32 ± 0.10 for females at HJA to 0.80 ± 0.16 for females at TYE. The mean number of different territories that owls were resighted at ranged from 1.29 ± 0.09 for HJA females to 1.61 ± 0.10 for TYE females (Table 3.2).

On CLE, HJA, and OCR, the median number of mates for both sexes was 1. Since a small proportion of owls were only observed as single unpaired individuals, this reflected the fact that it was most common for owls to only have one lifetime mate. On TYE the median number of mates for females and males was 1.5 and 2.0, respectively. The mean number of mates was lowest for HJA males and highest for TYE females. Within all areas, point estimates of the mean numbers of mates were always greater for females than males (Table 3.2). The percentage of owls recorded as having no mates was 16% for males and 5% for females. Owls with no mates appeared to have shorter lifespans than owls that had mates. Of 37 owls that had no recorded mates, 25 (67%) were only resighted at age 1, four (11%) were last resighted at age 2, and only eight (22%) were resighted when they were ≥ 3 years old. Thus failure to acquire a mate appeared to be mainly due to death at an early age, although

some owls may have dispersed and formed a pair at a territory that was unknown to us.

DISCUSSION

Differences among study areas in my study may reflect variations in life history strategies that reflect responses to local conditions. Although general patterns in birds have included negative correlations between body mass and reproductive output (Saether 1987) and positive correlations between body mass and lifespan (Newton 1998), several studies of North American strigiforms did not neatly fit these patterns. For example, Marti (1997) described a passerine-like life history strategy for Barn Owls (*Tyto alba*) in Utah where owls achieved equivalent or greater productivity compared with other owl species, but in a much shorter time. He noted that early maturation, large clutches, multiple clutches, and low survival were characteristics of species that evolved in harsh environments. In contrast, Linkhart and Reynolds (2004, 2006) found that Flammulated Owls (*Otus flammeolus*), one of the smallest owls in North America, had low annual reproductive output and a lifespan exceeded only by much larger owls. Notwithstanding difficulties in measuring longevity in long-lived species and the resultant problems of plotting relationships between owl mass and lifespan, a perfect pattern should not be expected because varying environmental constraints also shape life history characteristics of different species. In a similar way, it should not be unexpected that intra-specific variation in life history traits may stem

from differences in local environments under which populations of Spotted Owls exist.

The patterns that I observed suggest that Spotted Owls are similar to many other birds in that a small proportion of individuals on all study areas produced the majority of fledglings and recruits. Krüger and Lindstrom (2001) found that 17% of female and male Common Buzzards (*Buteo buteo*) produced 50% of all fledglings. Linkhart and Reynolds (2006) found that 18% of female and 24% of male Flammulated Owls produced half of all fledglings and (Postupalsky 1989) reported similar percentages for Osprey (16% of females and 24% of males). For female Ural Owls, 50% of fledglings were produced by 23% of individuals in one study (Saurula 1989) and by 18% in another (Brommer et al. 1998). Wiens and Reynolds (2005) found that 20% of the individual Goshawks that bred (pooled data for sexes) produced half of all fledglings and about 10% produced half of all local recruits. My inclusion of owls that never bred reduced the proportion of individuals producing 50% of the fledglings and recruits relative to studies that included only breeding individuals. Thus, at least some of the so-called "invisible fraction" of owls that die before breeding (Grafen 1988) were included in my analysis of LRS. Therefore it is not surprising that my estimates of 17% of females and 16% of males producing 50% of fledglings were at the low end of the range observed for different species. My results for recruits were comparable to those of Wiens and Reynolds (2005), in that the proportion of owls producing 50% of recruits was about half that of individuals producing 50% of fledglings.

LRS_F was highest for males and females on the CLE Study Area in Washington, a finding consistent with a previous analysis in which annual female fecundity on CLE was higher than in all other study areas within the range of the Northern Spotted Owl (Anthony et al. 2006). The greatest number of fledglings produced by any individual was 22 by a female on CLE that was not included in the analysis of LRS because she was an unknown age owl and wore a backpack radio early in the study period. This owl was ≥ 18 years owl (at least three times the mean lifespan for CLE females) when last resighted in 2004. The mean numbers of banded young that recruited locally (LRS_R) were higher on the TYE and OCR areas than on CLE and HJA. Despite the differences in where the highest LRS_F and LRS_R were recorded, there was a strong positive association between LRS_F and LRS_R that included an area effect but no interaction. This result indicated that, within study areas, LRS_F was a good predictor of LRS_R. In comparing the relationship between the two, some researchers only included individuals that produced ≥ 1 fledgling (Newton 1989b, Saurola 1989, Korpimäki 1992), presumably because non-breeders or birds that nested and failed were difficult to detect. My results for samples that included breeders as well as non-breeders were consistent with findings in those studies and additional regressions of the two proxy measures of fitness restricted to individual Spotted Owls with LRS_F>0 produced results that were also qualitatively the same.

Mean LRS for female Ural Owls, measured as fledglings, from two studies in Finland was 8.2 ± 0.5 (Saurola 1989) and 6.7 (Brommer et al. 1998). These estimates

were above our highest estimate for female Spotted Owls (CLE $\bar{x} = 5.3 \pm 1.2$), but were more comparable to estimates for both sexes on CLE when only the owls that bred were examined (female, $\bar{x} = 6.4 \pm 1.4$, $n = 20$; male, 6.8 ± 1.3 $n = 15$). My results for Spotted Owls were also somewhat comparable to the estimates for Flammulated Owls in Colorado (female, $\bar{x} = 4.3 \pm 0.8$, $n = 46$; male, 6.9 ± 1.2 $n = 22$), where sexual differences were attributed, in part, to a sex bias in breeding dispersal (Linkhart and Reynolds 2006).

Brommer et al. (2004) estimated generation time of Ural Owls at 6.4 years. In their study, lifetime fledgling data collected during a study period that spanned 2–3 generations was a good predictor of long-term contributions to future generations. My estimate of an 8.8 year generation time based on pooled data, for female Spotted Owls that bred on four study areas, was longer than that of Ural owls. Our study periods were about twice this generation time.

Although the mean lifespan of owls on CLE (6 years) was shorter than on the Oregon study areas (7–9 years), mean estimates of LRS_F for CLE owls were 29–93% greater than for owls of the same sex on the other areas. For the subset of owls that bred at least once, mean lifespans were about 7 years on CLE and ranged from 9–11 years for owls on the Oregon studies. On all areas, LRS_F was influenced positively by annual nest success, but the mean age at first breeding for both sexes was slightly lower on CLE than on the other areas. This likely contributed to the higher lifetime fledgling output of owls on CLE, in spite of their shorter mean lifespan. These patterns appear consistent with a compensatory relationship between

reproduction and survival as suggested by Anthony et al. (2006), but it is unclear if demographic parameters vary in a way that leads to common lifetime fledgling production or recruits across areas.

Lifespan has been identified as a major determinant of LRS in most studies. When lifespan is unknown, researchers have often used breeding lifespan or experience as a surrogate (Krüger and Lindstrom 2001, Linkhart and Reynolds 2006), usually assuming that the first observed nest attempt was the first breeding event for individuals. Saurola (1989) estimated lifespan of 82 known age female Ural Owls at 7.9 ± 0.4 years and breeding lifespan of all females at 4.9 ± 0.3 years. Brommer et al. (1998) estimated breeding lifespan of females Ural Owls at 3.3 years. Breeding lifespan of male Flammulated Owls, the sex with low breeding dispersal, was 4.3 ± 0.8 years and the ages at first breeding for two known age individuals were 5 and 6, suggesting a mean lifespan of about 8–9 years. Breeding lifespan for female and male Common Buzzards was 2.8 ± 0.2 and 2.2 ± 0.2 years, respectively. My results for Spotted Owls are most similar to those of Saurola's (1989) for female Ural Owls. Mean lifespan for females on CLE was about 6.2 ± 1.0 years based on all females and 7.2 ± 1.1 for those that bred. On the three Oregon study areas, mean lifespans for females ranged from 7–9 for all owls and was 10 for the females on each area that bred. Longer lifespans of Spotted Owls on some of my study areas contributed to longer breeding lifespans (range 5.9 ± 1.1 to 7.6 ± 0.9 for females), but an earlier age at first reproduction likely contributed as well. Saurola's estimate of mean age at first reproduction for Ural Owls (4.1 ± 0.18) was slightly higher than my estimates for

female Spotted Owls (range 2.2 ± 0.8 on CLE to 3.9 ± 1.8 OCR). For the owls from the 1986–1996 cohorts that bred, 76% of CLE females and 54% of CLE males did so before age 3. On the Oregon areas fewer than 35% of each gender first bred by age 2. Assuming that age at first breeding is correlated with age at settlement on a territory, opportunity to assign known ages to CLE females was likely greater than for owls in other samples because more recruited to the territorial population as 1- or 2-year-olds.

Mean nest success of owls that bred at least once was highest for CLE females (0.88 ± 0.06) and lowest for TYE males (0.66 ± 0.05). It was interesting that TYE males had the lowest number of fledglings per nest attempt, but the highest ratio of lifetime fledglings to recruits. One male on TYE produced seven recruits from a total of only nine lifetime fledglings, twice the mean LRS_F and seven times the mean LRS_R for all TYE males.

Since most owls with zero mates were young, including seven 1- and 2- year-olds last resighted as extra owls, they likely had a higher than average propensity to disperse. Therefore, most owls without mates probably did not live long enough to establish themselves on territories, but some may have done so after dispersing to an unknown location.

In a study like mine with samples from widely different areas, some variation is expected because environmental forces shape life histories and these forces tend to vary with geographic location. Differences between the CLE owls and those on the Oregon study areas may reflect life history responses to regional variation in climate, vegetation, or prey abundance under which Northern Spotted Owls have evolved. For

example, early onset of reproduction, high annual and lifetime fledgling output, and shorter lifespans of CLE owls may be a product of a more variable and harsher environment in the eastern Cascades in Washington than in the other study areas. Additional factors such as the presence of multiple species of large avian predators (Northern Goshawks, Great-horned owls *Bubo virginianus*) and dynamics of the regional prey base may also contribute to fluctuations in survival that have led to increased and early reproduction by CLE owls. Conversely, longer lifespans and lower reproductive output of owls on the Oregon areas may reflect better the notion of "bet hedging" (Boyce 1988, Franklin et al. 2000) whereby individuals forgo reproduction in favor of somatic maintenance (or, in essence—survival).

Compared to the other study areas included in my sample, CLE had comparatively cold winters and high prey abundance. One might postulate that these environmental factors accounted for the shorter average lifespan and higher productivity of owls on CLE. However, Stearns (1992) noted that while patterns in life history characteristics such as size, age at maturity, and lifespan are most evident at higher taxonomic levels (e.g., among species), they weaken but do not disappear within populations of species. Therefore, while among study area differences may reflect plasticity in life history traits of owls exposed to varying environments, they also seem consistent with general predictions of life history theory regarding fitness traits. Thus variation among study areas described here may be the equivalent of positions along a slow-fast continuum (*sensu* Saether 1987), but within species and thus on a finer and more subtle scale.

Anthony et al. (2006) suggested that higher annual fecundity of Spotted Owls in eastern Washington, which included CLE, might be a compensatory response to lower survival. They also noted a decline in apparent survival on CLE and four other areas, although on CLE the decline was nearly but not significant (95% CI for β for a linear time trend overlapped 0). I submit that it may not be low survival, but variable survival that shapes reproductive parameters observed for CLE owls. Only for CLE was the best model structure one in which a variable time effect alone was more important than all other models (Anthony et al. 2006; Table 13). In fact, the only area where this time structure was included in the top model was CLE. Otherwise, apparent survival was either constant or varied by age-class, time trend (linear or quadratic), presence of barred owls, or some combination of these effects. Therefore, among the temporal variables considered, non-patterned yearly variation best described survival of only the CLE owls. This finding seems consistent with the view that a temporally variable environment exists on CLE and a consequence is variable annual survival relative to other areas where Spotted Owl demography studies have been conducted.

Although some researchers have made adjustments to LRS to account for undetected adult dispersal or non-local recruitment (Brommer et al. 2004, Linkhart and Reynolds 2006), I did not do so for several reasons. Variation among studies in the quality, amount, and extent of suitable habitat within and outside of study boundaries would complicate my ability to correct LRS for dispersal in a standardized way. Furthermore, because breeding dispersal was infrequent (median = 0 for males

and females on all four areas), I assumed that an adjustment to measures of LRS to account for offspring that may have been produced following undetected emigration was not necessary.

A number of biases may have influenced my estimates of LRS and other components. The inclusion of some owls that were alive at the end of the study period, mortality or a failure to capture and band fledglings prior to dispersal, and missed resights all may have led to an underestimation LRS. These were addressed in part through my criterion for the inclusion of owls in my analysis of LRS. Also, it was unclear if a gender bias in detection rates of young owls led to the greater proportion of males without a mate in my sample or if there were simply more single young males. Excluding owls with backpacks and owls that were missed in ≥3 years after age 2 appeared to bias lifespan estimates downward. In most cases I believe that biases were similar on all areas and for males and females. Therefore, I do not believe these issues had strong effects on my results, especially where comparisons of the results among study areas were discussed.

The challenges of collecting adequate data on LRS of long long-lived species have been stated clearly before (Newton 1989a) and are evident in this study. Continued and consistent efforts to monitor individual performance on Spotted Owl demography studies will result in greater returns with respect to complete data on lifetime reproductive output. Without experiments, however, is it not possible to determine conclusively whether differences among areas represent phenotypic plasticity or life history adaptations. Nevertheless, these data offer a new perspective

on individual variation in Spotted Owl fitness and other components of lifetime

reproductive success.

CHAPTER 4

SYNOPSIS AND CONCLUSIONS

Peter J. Loschl

Despite intensive study over a period of more than 30 years, mechanisms that influence reproductive success, and thus individual fitness, in Spotted Owls are poorly understood. In fact, several factors that can be used to examine individual reproductive performance have received little attention or have been used in only a crude way. Longitudinal data restricted to known age individuals monitored over long periods have never been used to model age-specific breeding performance or lifetime reproduction of Spotted Owls. I used data collected from 1986–2005 on four study areas in Oregon and Washington to describe and compare both the functional patterns of age-specific reproductive performance and lifetime reproductive success of male and female Northern Spotted Owls. Patterns that I observed suggest that Spotted Owls are similar to many other birds in that reproductive success improved with age (Saether 1990, Martin 1995, Forslund and Pärt 1995) and a small proportion of individuals on all study areas produced the majority of fledglings and recruits (Clutton-Brock 1988, Newton 1989a). Results from my analyses provide new data and insights on life history variation and gender roles of Spotted Owls.

AGE-SPECIFIC REPRODUCTION

My age-specific analysis indicated that threshold, quadratic, cubic, or asymptotic age models were a better fit to most data than was the traditional 3-level age-class models used in most previous studies of Spotted Owls (e.g., Forsman et al. 1996a, Anthony et al. 2006). Differences between males and females and among study areas were revealed through the differential fit of models of age-specific performance for

different subsets of data from known age owls. The mean annual number of young

fledged (NYF) generally increased from age 1–4, and either plateaued or followed a

quadratic pattern thereafter. For males in particular, there was some evidence for

reproductive senescence in later years. On all areas, the mean annual number of

young produced by females reached a peak at earlier ages than males. Where

quadratic models fit better, mean NYF varied across adult ages and there was a decline

after middle age. The most common threshold-type model, especially for females,

provided evidence of variation in mean annual NYF through only age 4. Despite the

uncertainty incorporated in model averaged estimates, there was strong evidence of an

increase in reproductive success past age 3 for each sex on the three study areas in

Oregon. Therefore, differences revealed by a 3-level age-class model failed to reflect

the true magnitude and duration (span of ages) of gains between early life and peak

performance, particularly on the Oregon study areas.

A biennial pattern of high and low reproduction in even and odd years that was

prominent on some demography study areas in the 1990s (Forsman et al. 1996a,

Franklin et al. 2004, Olson et al. 2004) has become less pronounced in recent years

(Anthony et al. 2006), and was not included in any of the top models in my analysis.

Similar fluctuations or cycles in reproductive performance have been linked to cyclic

fluctuations in prey populations of several European owl species (Korpimäki and

Hakkarainen 1991, Brommer et al. 2002a). No such links can be established for

Spotted Owls because there have been no concomitant, long-term studies of any of the

major prey in their diet. My results suggest that non-cyclic year effects are the norm

on the four areas I examined, but this in no way negates the likely influence of prey dynamics on reproductive success of Northern Spotted Owls.

Quadratic age models fit the reproductive data in most analyses for males, whereas threshold models generally provided the best fit for females. These patterns were also evident in the model averaged estimates. Evidence was fairly strong for a constant level of reproductive success through the oldest ages after an early life increase for TYE, HJA, and CLE females. For males, evidence for a decline in estimates of mean annual NYF from middle to later ages was strong only on OCR, but point estimates followed the same pattern on TYE and HJA. Combined model selection results were in strong agreement with a superior fit of the threshold age4 model for females and a quadratic age fit for males.

While a quadratic relation of age and reproduction has been found in other studies of moderate to long-lived birds such as *Accipiter nisus* (Newton and Rothery 1997) and *Accipiter gentilis* (Nielsen and Drachmann 2003) and may be an indication of senescence, significance of a negative quadratic effect alone is not sufficient to prove senescence in a fitness correlate (Newton and Rothery 1997, Catry et al. 2006). Where only linear and quadratic models are considered, a superior quadratic fit may be due to a curvilinear pattern or a non-constant increase in reproductive estimates as opposed to a decline in later ages. I modeled additional functional patterns of age-dependent effects that, if superior, should have fit the data better than quadratic or linear models. Nevertheless, documenting and measuring senescence in wild birds is wrought with practical, methodological, and analytical difficulties (Nisbet 2001) and

additional models (and longer data sets) would be needed to reveal reproductive senescence or the proximate mechanisms for any late life declines in performance (Catry et al. 2006). For example, breeding experience may influence the fit or interpretation of different models for age (Sydeman et al. 1991, Pyle et al. 2001) and one study of Spotted Owls indicated that female fecundity was influenced by male experience (coded simply as presence or absence of the male on the territory in the previous year), and that this influence varied depending on whether it was a year in which average productivity in the population was high or low (Dugger et al. 2005). Therefore, disentangling the independent effects of age, mate age, experience, and other variables (e.g., environmental and phenotypic) may eventually lead to a better understanding of the mechanisms underlying age-dependent reproduction in Spotted Owls. However, this was beyond the scope of my study.

Females achieved a maximum reproductive performance at younger ages than males. Although my top ranked models suggested that productivity peaked at age 4 for both sexes on TYE and at age 9 for both sexes on OCR, competitive models indicated a later peak (age 7–8) for TYE males and an earlier peak (age 4) for OCR females. On HJA, top ranked models indicated that the mean annual NYF by females reached a maximum at age 4, whereas male estimates increase up to age 9. On CLE, the top ranked models indicated that the mean annual NYF for females reached a maximum at age 2 whereas males had substantial increases in mean annual NYF through about age 3–5. Model averaging indicated additional uncertainty about the

ages when maximums were achieved, but the trend towards a more rapid increase to peak or near peak performance for females remained evident.

These results were similar to findings for other birds of prey in which females tended to breed at an earlier age than males (Newton 1979, Korpimäki 1988, Lieske 1997). For Spotted Owls it is not likely that this is due to physiological differences, because both sexes are physiologically mature at 1 year of age. A more likely explanation is that, because males provision the female and young during nesting, females can breed at an earlier average age than males by pairing with older more experienced males on established territories. In contrast, regardless of the age and experience of their mate, males must acquire and defend a territory and learn the best places to hunt in order to provide enough food for the female and young. Smith et al. (1999:27) estimated that a male Spotted Owl must increase the amount of food he procures by 276% in order to provision himself, the female and a juvenile through the fledging stage.

Korpimäki (1988) described relationships between age and breeding performance of Tengmalm's Owls (*Aegolius funereus*) that were similar to my findings for Spotted Owls. In that study, females showed the greatest increase in mean annual NYF between ages 1 and 2, whereas males also had substantial improvement between age 2 and older owls. Different constellations of male and female age-classes suggested that male age was more important for breeding performance than female age. Also, a positive relationship between the age-class of males and numbers of prey items stored in nests was consistent with the view that

improved hunting skills and experience was a mechanism for age-dependent breeding performance. Thus, inadequate provisioning skills may reduce both the ability to secure a mate as well as reproductive performance of young male Tengmalm's Owls. Unfortunately, no such data on prey stores were available for Spotted Owls, and estimates of prey numbers found in pellets are of limited use in quantifying relationships of individual owls, their prey, and reproductive success (see Forsman et al. 2002).

Another pattern that I noted was that the age when owls reached the mean maximum annual reproductive performance appeared to be negatively correlated with the average annual fecundity reported for the four study areas that I examined. Females on CLE had the highest mean annual fecundity out of 16 study areas examined by Anthony et al. (2006) and CLE females reached a maximum in mean annual NYF at age 2 in my study. On the Oregon study areas females did not reach a maximum in mean annual NYF until age 4 or older. The rapid increase to peak performance on CLE as compared to a slow increase to highest mean output at older ages on OCR (which had one of the lowest estimates of fecundity reported by Anthony et al. 2006), may indicate intra-specific variation in life history patterns of Spotted Owls in different regions.

LIFETIME REPRODUCTION

My analysis of LRS indicated that a small proportion of owls produced a majority of the total offspring and the total number of fledglings per individual was strongly

correlated with lifespan. This pattern is typical of most of the other long-lived birds that have been studied (Clutton-Brock 1988, Newton 1989a, Brommer et al. 1998, Linkhart and Reynolds 2006). The mean number of lifetime fledglings was highest for males and females on the CLE Study Area in Washington, a finding consistent with a previous analysis in which annual female fecundity on CLE was higher than in all other study areas within the range of the Northern Spotted Owl (Anthony et al. 2006). However, the mean number of an individual's young that recruited locally was higher on the TYE and OCR areas than on CLE and HJA. Despite these differences, there was a strong positive association between numbers of fledglings and numbers of recruits that included an area effect but no interaction. This result indicated that, for individuals within study areas, the number of fledglings was a good predictor of the number of recruits produced.

Although the estimated mean lifespan of owls on CLE (6 years) was shorter than on the Oregon study areas (7–9 years), mean estimates of lifetime fledglings for CLE owls were 29–93% greater than for owls of the same sex on the other areas. Mean lifespans of owls that bred were 7 years on CLE and ranged from 9–11 years for owls on the Oregon studies. On all areas, the number of lifetime fledglings was influenced positively by annual nest success, but the mean age at first breeding was slightly lower on CLE than on the other areas. This likely contributed to the higher reproductive output of owls on CLE, in spite of their shorter mean lifespan. For owls from the1986–1996 cohorts that bred at least once, 70% of females and 54% of males on CLE did so before age 3, whereas fewer than 35% of males and females on the

Oregon study areas bred before age 3. These patterns may indicate a compensatory relationship between reproduction and survival (Anthony et al. 2006), but it is unclear if demographic parameters vary in a way that leads to common lifetime fledgling production or recruits across areas.

My inclusion of some individuals that were alive at the end of the study likely caused a downward bias in both lifespan and lifetime reproductive success, particularly for OCR which had the largest proportions of female and male owls (24% and 23 %, respectively) resighted in 2005. In contrast, CLE had the lowest proportions of females (5%) and males (8%) resighted in 2005. Additionally, fewer OCR owls were from the earliest cohorts included relative to HJA and TYE. Therefore, even with less opportunity to achieve long lifespans during my limited study period, OCR males and females had the longest point estimates of mean lifespan for each sex. Since estimated mean lifespans were longest on OCR and shortest on CLE, more data and complete histories for OCR will likely increase the disparity in lifespan among these areas, but this may result in numbers of lifetime fledglings that are more similar for the two study areas.

LIFE HISTORY

Although general patterns in birds have included negative correlations between body mass and reproductive output (Saether 1987) and positive correlations between body mass and lifespan (Newton 1998), several studies of North American strigiforms did not neatly fit these patterns. For example, Marti (1997) described a passerine-like life

history strategy for Barn Owls (*Tyto alba*) in Utah where owls achieved equivalent or greater productivity compared with other owl species, but in a much shorter time. He noted that early maturation, large clutches, multiple clutches, and low survival were characteristics of species that evolved in harsh environments. In contrast, Flammulated Owls (*Otus flammeolus*), one of the smallest owls in North American, had low annual reproductive output and a lifespan exceeded only by much larger owls (Linkhart and Reynolds 2004, 2006). Notwithstanding difficulties in measuring longevity in long-lived species and the resultant problems of plotting the relationship between owl mass and lifespan, a perfect pattern should not be expected because varying environmental constraints also shape life history characteristics of different species. In a similar way, it should not be unexpected that intra-specific variation in life history traits may stem from differences in local environments under which populations of Spotted Owls have evolved.

In a study like mine, with samples from widely different areas, some variation is expected because environmental forces shape life histories and these forces tend to vary with geographic location. Differences between the CLE owls and those on the Oregon studies may reflect life history responses to regional variation in climate, vegetation, or prey abundance under which northern Spotted Owls have evolved. For example, early onset of reproduction, high annual and lifetime fledgling output, and shorter lifespans of CLE owls may be a product of a more variable and harsher environment on the east slope of the Cascades in Washington than on the other study areas. Additional factors such as the presence of multiple species of large avian

predators (Northern Goshawks, Great-horned Owls *Bubo virginianus*) and dynamics

of the regional prey base may also contribute to fluctuations in survival that have led

to increased and early reproduction by CLE owls. Conversely, longer lifespans and

lower reproductive output of owls on the Oregon areas may reflect better the notion of

"bet hedging" (Boyce 1988, Franklin et al. 2000), whereby individuals forgo

reproduction in favor of somatic maintenance.

Among the study areas included in my sample, CLE had comparatively cold

winters and high prey abundance. One might postulate that these proximate

environmental factors accounted for the shorter average lifespan and higher

productivity of owls on CLE. However, Stearns (1992) noted that while patterns in

life history characteristics such as size, age at maturity, and lifespan are most evident

at higher taxonomic levels, they weaken but do not disappear within populations of the

same species. Shorter lives and higher fecundity on CLE may reflect more than just

current environment, but also may reflect variation in life history traits among regions

or populations. Thus, these differences among study areas may be adaptive and may

the equivalent of positions along a slow-fast continuum (*sensu* Saether 1987), but

within species and thus on a finer and more subtle scale.

Anthony et al. (2006) suggested that high fecundity of owls in eastern

Washington might be a compensatory response to lower survival, a view that ascribes

adaptive significance to differences in vital rates of Spotted Owls from different study

areas. Life history theory predicts earlier maturation and high reproductive output

where mortality rates are high. I submit that not just low, but variable survival may

shape reproductive parameters observed for CLE owls. Only for CLE was the best model structure one in which a variable year effect alone was more important than all other models (Anthony et al. 2006; Table 13). In fact, the only area where a variable year effect was included in the top model was CLE. Top models for other areas indicated that apparent survival was either constant or varied by age-class, time trend (linear or quadratic), presence of barred owls, or some combination of these effects. Therefore, among the temporal variables considered, non-patterned yearly variation best described survival of CLE owls. This finding seems consistent with the view that a temporally variable environment exists on CLE and a consequence is more variable and lower average annual survival relative to other areas where Spotted Owl demography studies have been conducted.

OVERVIEW

My results may have implications for how data are coded or what data are included in future analyses of demographic rates of Spotted Owls. In previous studies of Spotted Owls, the terms "age-class" and "age-specific" have usually been used to describe differences or comparisons of vital rates or other life history traits among juveniles, subadults (often segregated into two classes: 1- and 2-year-olds), and adults. Grouping non-juveniles into age-classes, and in particular lumping all adults in one age-class, allowed researchers to include all banded owls checked for reproductive success in analyses of reproductive performance and survival. However, my results indicate that only for CLE females was age-specific variation in reproductive success

best described with the age-class coding used in virtually all previous analyses of Spotted Owl reproduction (Forsman et al. 1996a, Anthony et al. 2006). The implications of not accounting for the unexplained variation in "adult" performance when 3-level age-class models are used are unclear, as there are always trade-offs between computational complexity and the precision or accuracy of vital rates.

Although my samples were generally large and adequate to model covariance among repeated measures and a variety of age-dependent relationships, differences in sample sizes may have influenced my results. All samples suffered from small numbers of individuals in the oldest ages and the effect for small data sets may have been that too few data for old owls were available to support quadratic and other curvilinear patterns of age-specific productivity.

To my knowledge, my study is the first to examine functional patterns of age-specific reproductive success for known age Spotted Owls and to document age-specific variation in reproductive output of adult owls. My study is also the first to explore age-related performance in a parallel modeling framework for both males and females. My findings do not demonstrate functional relations per se but provide more general results relative to age-specific patterns of reproduction in the Spotted Owl. Without experimental approaches and a suite of additional variables, it is impossible to do more than speculate as to what drives the observed patterns. Nevertheless my results indicate that modeling age as a continuous variable, using data from known age individuals, can lead to additional insights relative to age dependent performance, life history, and gender roles in the Spotted Owl. However, additional studies in which an

attempt is made to disentangle the effects of experience, age, and environmental factors may provide insights into the adaptive significance of reproductive senescence and other age-dependent patterns of reproduction.

For a species that usually produces one or two offspring during a nest attempt, mean differences of less than one fledgling between the lowest and highest levels of success may be difficult to conceive of as biologically meaningful. However, given the long potential lifespan of any individual (5 individuals on my study areas were known to have survived for ≥ 20 years) small improvements in reproductive success with age may translate into a considerable fitness advantage.

Although large samples of individuals have been monitored over long study periods, data on Spotted Owls are only now approaching adequacy for interpretation with respect to lifetime reproduction. My criteria for identifying owls with relatively complete data allowed for only 15% of all of the banded non-juveniles observed to be used in my analysis of LRS. However, I was able to use 39% of all non-juvenile resights in my examination of age-specific reproduction since complete lifetime data were not needed for that analysis. All data were collected in conjunction with demographic studies initiated from 1985 to 1990 (Anthony et al. 2006) and continued to present. Without the rigorous, consistent, and continuous survey approach employed in these studies, my analysis would not have been possible. As known age individuals continue to recruit to territorial populations and as studies span the complete lives of more individuals, researchers can look forward to more complete data that should allow more definitive analyses of age-specific and LRS in the future.

BIBLIOGRAPHY

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267–281 in B. N. Petrov and F. Csaki, editors. Second International Symposium on Information Theory. Akademiai Kiado, Budapest, Hungary.

Allison, P. D. 1999. Logistic regression using the SAS System: theory and application. Cary, NC: SAS Institute, Inc.

Anthony, R. G., E. D. Forsman, A. B. Franklin, D. R. Anderson, K. P. Burnham, G. C. White, C. J. Schwarz, J. Nichols, J. E. Hines, G. S. Olson, S. H. Ackers, S. Andrews, B. L. Biswell, P. C. Carlson, L. V. Diller, K. M. Dugger, K. E. Fehring, T. L. Fleming, R. P. Gerhardt, S. A. Gremel, R. J. Gutiérrez, P. J. Happe, D. R. Herter, J. M. Higley, R. B. Horn, L. L. Irwin, P. J. Loschl, J. A. Reid, and S. G. Sovern. 2006. Status and trends in demography of Northern Spotted Owls, 1985–2003. Wildlife Monographs 163.

Barrows, C. W. 1985. Breeding success relative to fluctuations in diet for Spotted Owls in California. In: Ecology and management of the Spotted Owl (Ed. by R. J. Gutiérrez and A. B. Carey), pp. 50–54. General Technical Report PNW GTR 185. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Boyce, M. S. 1988. Bet hedging in avian life histories. Pages 2131–2139 in Acta XIX Congressus Internationalis Ornithologici (H. Ouellet, Ed.). National Museum of Natural Science, Ottawa, Ontario.

Brommer, J. E., H. Pietiäinen, and H. Kolunen. 1998. The effect of age at first breeding on Ural Owl lifetime reproductive success and fitness under cyclic food conditions: Journal of Animal Ecology 67: 359–369.

Brommer, J. E., H. Pietiäinen, and H. Kolunen. 2002a. Reproduction and survival in a variable environment: Ural Owls (*Strix uralensis*) and the three-year vole cycle. Auk 119:544–550.

Brommer, J. E., J. Merilä, and H. Kokko. 2002b. Reproductive timing and individual fitness. Ecology Letters 5:802–810.

Brommer, J. E., L. Gustaffson, H. Pietiäinen, and J. Merilä. 2004. Single generation estimates of individual fitness as proxies for long term genetic contribution. American Naturalist 163:505–517.

Brommer, J. E., K. Ahola, and T. Karstinen. 2005. The colour of fitness: plumage coloration and lifetime reproductive success in the tawny owl. Proceedings of the Royal Society of London. B 272:935–940.

Burnham, K. P., D. R. Anderson, and G. C. White. 1996. Meta-analysis of vital rates of the Northern Spotted Owl. Studies in Avian Biology 17:92–101.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York.

Buckland, S. T., K. P. Burnham, and N. H. Augustin. 1997. Model selection: an integral part of inference. Biometrics 53:603–618.

Carey, A. B., S. P. Horton, and B. L. Biswell. 1992. Northern Spotted Owls: influence of prey base and landscape character. Ecological Monographs 62(2):223–250.

Catry, P., R. A. Phillips, B. Phalan, and J. P. Croxall. 2006. Senescence effects in an extremely long-lived bird: the Grey-headed Albatross *Thalassarche chrysostoma*. Proceedings of the Royal Society. B 273:1625–1630.

Clutton-Brock, T. H., ed. 1988. Reproductive success. Studies of individual variation in contrasting breeding systems. University of Chicago Press, Chicago, Illinois.

Courtney, S. P., J. A. Blakesley, R. E. Bigley, M. L. Cody, J. P. Dumbacher, R. C. Fleischer, A. B. Franklin, J. F. Franklin, R. J. Gutiérrez, J. M. Marzluff, and L. Stukowski. 2004. Final Report. Scientific evaluation of the status of the Northern Spotted Owl. Sustainable Ecosystems Institute, Portland, Oregon. Document taken from the web http://www.sei.org/owl/finalreport/OwlFinalReport.pdf on February 27, 2005.

Curio E. 1983. Why do young birds reproduce less well. Ibis 125:400–404.

Dugger, K. M., Wagner, F., Anthony, R. G., and Olson, G. S., 2005. The relationship between habitat characteristics and demographic performance of Northern Spotted Owls in southern Oregon: The Condor, v. 107, p. 863–878.

Endler, J. A. 1986. Natural selection in the wild. Princeton University Press, Princeton, New Jersey.

Espie, R. H. M., L. W. Oliphant, P. C. James, I. G. Warkentin and D.J. Lieske. 2000. Age-dependent breeding performance in Merlins (*Falco columbarius*). Ecology 81:3404–3415.

Forslund, P., and T. Pärt. 1995. Age and reproduction in birds—hypotheses and tests. Trends in Ecology and Evolution 10:374–378.

Forsman, E. D. 1981. Molt of the Spotted Owl. Auk 98:735–742.

Forsman, E. D. 1983. Methods and materials for locating and studying Spotted Owls. USDA Forest Service General Technical Report PNW-162.

Forsman, E. D., E. C. Meslow, and H. M. Wight. 1984. Distribution and biology of the Spotted Owl in Oregon. Wildlife Monographs 87:1–64.

Forsman, E. D., S. Destefano, M. G. Raphael, and R. J. Gutierrez [EDS.]. 1996a. Demography of the Northern Spotted Owl. Proceedings of a Workshop, Ft. Collins, Colorado, December 1993. Studies in Avian Biology. 17. Cooper Ornithological Society. Camarillo, CA.

Forsman, E. D., A. B. Franklin, F. M. Oliver, and J. P. Ward. 1996b. A color band for Spotted Owls. Journal of Field Ornithology 67:507–510.

Forsman, E. D., I. A. Otto, S. G. Sovern, M. Taylor, D. W. Hayes H. Allen, S. L. Roberts, and D. E. Seaman. 2001. Spatial and temporal variation in diets of Spotted Owls in Washington. Journal of Raptor Research 35(2):141–150.

Forsman, E. D., R. G. Anthony, J. A. Reid, P. J. Loschl S. G. Sovern, M. Taylor, B. L. Biswell, A. Ellingson, E. C. Meslow, G. S. Miller, K. A. Swindle, J. A. Thrailkill, F. F. Wagner, and D. E. Seaman. 2002. Natal and breeding dispersal of Northern Spotted Owls. Wildlife Monographs 149:35.

Foster, C. C., E. D. Forsman, E. C. Meslow, G. S. Miller, J. A. Reid, F. F. Wagner, A. B. Carey, and J. B. Lint. 1992. Survival and reproduction of radio marked adult Spotted Owls. Journal of Wildlife Management 56:91–95.

Franklin, A. B., D. R. Anderson, E. D. Forsman, K. P. Burnham, and F. F. Wagner. 1996. Methods for collecting and analyzing demographic data on the Northern Spotted Owl. Studies in Avian Biology 17:12–20.

Franklin, A. B., K. P. Burnham, G. C. White, R. G. Anthony, E.D. Forsman, C. Schwarz, J. D. Nichols, and J. Hines. 1999. Range-wide status and trends in Northern Spotted Owl populations. Colorado Cooperative Fish and Wildlife Research Unit, USGS, Biological Resources Division, Colorado State University, Ft. Collins, CO, and Oregon Cooperative Fish and Wildlife Research Unit, USGS, Biological Resources Division, Department of Fish and Wildlife, Oregon State University, Corvallis, OR.

Franklin, A. B., D. R. Anderson, R. J. Gutiérrez, and K. P. Burnham. 2000. Climate, habitat quality, and fitness in Northern Spotted Owl populations in northwestern California. Ecological Monographs 70:539–590.

Franklin, A. B., R. J. Gutiérrez, J. D. Nichols, M. E. SeamanS, G. C. White, G. S. Zimmerman, J. E. Hines, T. E. Munton, W. S. LaHaye, J. A. Blakesley, G. N. Steger, B. R. Noon, D.W. H. Shaw, J. J. Keane, T. L. McDonald, and S. Britting. 2004. Population dynamics of the California Spotted Owl (*Strix occidentalis occidentalis*): a meta-analysis. Ornithological Monographs 54:1–54.

Futuyma, D. J. 1998. Evolutionary biology, third edition. Sinauer Associates, Inc., Sunderland, Massachusetts.

González-Solís, J., P. H. Becker, L. Jover, X. Ruiz. 2004. Individual changes underlie age-specific pattern of laying date and egg-size in female Common Terns (*Sterna hirundo*). Journal of Ornithology 145:129–136.

Grafen A. 1988. On the uses of data on lifetime reproductive success. In: Reproductive success. Studies of individual variation in contrasting breeding systems (Ed. by T. H. Clutton Brock), pp. 454–471. University of Chicago Press, Chicago, Illinois.

Gutiérrez, R. J. 1985. An overview of recent research on the Spotted Owl, p. 39–49. *In* R. J. Gutiérrez and A. B. Carey [TECH. COORDS] Ecology and management of the Spotted Owl in the Pacific northwest. USDA Forest Service General Technical Report PNW-GTR-185.

Iverson, W. F. 2004 Reproductive success of Spotted Owls sympatric with Barred Owls in Western Washington. Journal of Raptor Research 38(1):88–91.

Korpimäki, E. 1988. Effects of age on breeding performance of Tengmalm's Owl *Aegolius funereus* in western Finland. Ornis Scandinavica 19:21–26.

Korpimäki, E. 1992. Fluctuating food abundance determines the lifetime reproductive success of male Tengmalm's Owls. Journal of Animal Ecology 61:103–111.

Korpimäki and Hakkarainen 1991. Fluctuating food supply affects the clutch size of Tengmalm's Owl independent of laying date. Oecologis, 85:543–552.

Krüger, O. 2005. Age at first breeding and fitness in Goshawk *Accipiter gentilis*. Journal of Animal Ecology 74:266–273.

Krüger, O., and Lindstrom. 2001. Lifetime reproductive success in Common Buzzard, *Buteo buteo*: from individual variation to population demography. Oikos 93:260–273.

Laaksonen, T., E. Korpimäki, and H. Hakkarainen. 2002. Interactive effects of parental age and environmental variation on the breeding performance of Tengmalm's Owls. Journal of Animal Ecology. 71:23–31.

Laaksonen, T., H. Hakkarainen, and E. Korpimäki. 2004. Lifetime reproduction of a forest-dwelling owl increases with age and area of forests. Proceedings of the Royal Society of London. B 265:1521–1525.

Lack, D. 1947. The significance of clutch sizes. Ibis 89:302–352.

Lack, D. 1948. The significance of clutch size. Ibis 90:25–45.

LaHaye, W. S., R. J. Gutiérrez, and D. R. Call. 1997. Nest site selection and reproductive success of California Spotted Owls. Wilson Bulletin 109:42–51.

Lambrechts, M. M., J. Blondel, A. Caizergus, 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*). The Auk 114(2):288–290.

Linkhart, B. D., and R. T. Reynolds. 2004. Longevity of Flammulated Owls: additional records and comparisons to other North American strigiforms. Journal of Field Ornithology 75:192–195.

Linkhart, B. D., and R. T. Reynolds. 2006. Lifetime reproduction of Flammulated Owls in Colorado. Journal of Raptor Research. 40:29–37.

Lint, J., B. Noon, R. Anthony, E. Forsman, M. Raphael, M. Collopy, and E. Starkey. 1999. Northern Spotted Owl effectiveness monitoring plan for the Northwest Forest Plan. USDA Forest Service General Technical Report PNW-GTR-440.

Livezey, K. B. 2005. Letter: Iverson (2004) on Spotted Owls and Barred Owls: comments on methods and conclusions. Journal of Raptor Research 39(1):102–103.

Marti, C. D. 1997. Lifetime reproductive success of the Barn Owl near the limit of the species' range. Auk 114:581–592.

Martin, K. 1995. Patterns and mechanisms for age-dependent reproduction and survival in birds. American Zoologist 35:340–348.

McGraw, J. B., and H. Caswell. 1996. Estimation of individual fitness from life history data. American Naturalist 147:47–64.

Merilä, J. and B. C. Sheldon. 2000. Lifetime reproductive success and heritability in nature. The American Naturalist 155:301–310.

Moen, C. A., A. B. Franklin, and R. J. Gutiérrez. 1991. Age determination of subadult Northern Spotted Owls in northwest California. Wildlife Society Bulletin 19:489–493.

Newton, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, South Dakota.

Newton, I. 1985. Lifetime reproductive output of female Sparrowhawks. Journal of Animal Ecology 54:241–253.

Newton, I., [ED.]. 1989a. Lifetime reproduction in birds. Academic Press, San Diego, California.

Newton, I., [ED.]. 1989b. Sparrowhawk. In: Lifetime reproduction in birds (Ed. by I. Newton), pp. 279–296. Academic Press, San Diego, California.

Newton, I., and P. Rothery. 1997. Senescence and reproductive value in Sparrowhawks. Ecology 78:1000–1008.

Newton, I. 1998. Population limitation in birds. Academic Press, New York, NY.

Newton, I., and P. Rothery. 2002. Age related trends in different aspects of the breeding performance of individual female Eurasian Sparrowhawks (*Accipiter nisus*). Auk 119:735–748.

Nielsen, J. T., and J. Drachmann. 2003. Age-dependent reproductive performance in Northern Goshawks (*Accipiter gentilis*). Ibis 145:1–8.

Nisbet, I. C. T. 2001. Detecting and measuring senescence in wild birds: experience with long-lived seabirds. Experimental Gerontology 36:833–843.

Noon, B. R., and A. B. Franklin. 2002. Scientific research and the Spotted Owl: opportunities for major contributions to avian population ecology. Auk 119:311–320.

Oli, M. K., G. R. Hepp, and R. A. Kennamer. 2002. Fitness consequences of delayed maturity in female Wood Ducks. Evolutionary Ecology Research 4:563–576.

Olson, G. S., E. M. Glenn, R. G. Anthony, E. D. Forsman, J. A. Reid, P. J. Loschl, and W. J. Ripple. 2004. Modeling demographic performance of Northern Spotted Owls relative to forest habitat in Oregon. Journal of Wildlife Management 68:1039–1053.

Postupalsky, S. 1989. Osprey. In: Lifetime reproduction in birds (Ed. by I. Newton), pp. 297–313. Academic Press, San Diego, California.

Pyle, P., W. J. Sydeman, and M. Hester. 2001. Effects of age, breeding experience, mate fidelity and site fidelity on breeding performance in a declining population of Cassin's Auklets. Journal of Animal Ecology 70:1088–1097.

Ramsey, F. L., and D. W. Schafer. 2002. The Statistical Sleuth: a course in methods of data analysis. 2nd edition. Duxbury, Pacific Grove, California.

Rattiste, K. 2004. Reproductive success in presenescent Common Gulls (*Larus canus*): the importance of the last year of life. Proceedings of the Royal Society London B. 271:2059–2064.

Reid, J. A., R. B. Horn, and E. D. Forsman. 1999. Detection rates of Spotted Owls based on acoustic-lure and live-lure surveys. Wildlife Society Bulletin 27:986–990.

Rockwell, R. F., E. G. Cooch, C. B. Thompson, and F. Cooke. 1993. Age and reproductive success in female lesser Snow Geese: experience, senescence and the cost of philopatry. The Journal of Animal Ecology 62:323–333.

Rosenberg, D. K., K. A. Swindle, and R. G. Anthony. 2003. Influence of prey abundance on Northern Spotted Owl reproductive success in western Oregon. Canadian Journal of Zoology 81:1715–1725.

Ryder, J. P. 1981. The influence of age on the breeding biology of colonial nesting seabirds. *In*: J. Burger, B. L. Olla, and H. E. Winn. (EDS). Behavior of marine animals. Volume 4:Marine Birds. Plenum Press, New York, pp. 153–168.

SAS Institute Inc. 2004. Base SAS 9.1.3 procedures guide. Cary, NC: SAS Institute Inc.

Saether, E. B. 1987. The influence of body weight on the covariation between reproductive traits in European birds. Oikos 48: 79–88.

Saether, E. B. 1990. Age-specific variation in the reproductive performance of birds, p. 25l–283. *In* D. M. Power (ED.), Current ornithology. Plenum Press, New York.

Saurola, P. 1989. Ural Owl. In: Lifetime reproduction in birds (Ed. by I. Newton), pp. 327–345. Academic Press, San Diego, California.

Smith, R. B., M. Z. Peery, R. J. Gutiérrez, and W. S. LaHaye. 1999. The relationship between Spotted Owl diet and reproductive success in the San Bernardino Mountains, California. Wilson Bulletin 111:22–29.

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

Sydeman, W. J., H. R. Huber, S. D. Emslie, C. A. Ribic, and N. Nur. 1991. Age-specific reproductive success of northern elephant seals in relation to previous breeding experience. Ecology 72:2204–2217.

Thomas, J. W., E. D. Forsman, J. B. Lint, E.C. Meslow, B. R. Noon, and J. Verner. 1990. A conservation strategy for the Northern Spotted Owl. A report by the Interagency Scientific Committee to address the conservation of the Northern Spotted Owl. USDA, Forest Service, and U. S. Department of the Interior, Fish and Wildlife Service, Bureau of Land Management, and National Park Service. Portland, Oregon, USA.

USDA and USDI. 1994. Final supplemental environmental impact statement on management of habitat for late successional and old growth forest related species within the range of the Northern Spotted Owl, 2 volumes. U. S. Department of Agriculture Forest Service and U. S. Department of Interior Bureau of Land Management, Portland, Oregon, USA.

USDI. 1990. Endangered and threatened wildlife and plants: determination of threatened status for the Northern Spotted Owl. Federal Register 55:26114–26194.

Wagner, F. F., E. C. Meslow, G. M. Bennett, C. J. Larson, S. M. Small, and S. Destefano. 1996. Demography of Northern Spotted Owls in the southern Cascades and Siskiyou Mountains, Oregon. Studies in Avian Biology 17:67–76.

Ward, J. P. JR, R. J. Gutiérrez, and B. R. Noon. 1998. Habitat selection by Northern Spotted Owls: the consequences of prey selection and distribution. Condor 100:79–92.

White, G. C., and P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46 (Supplement):120–138.

Wiens, J. T., and R. T. Reynolds. 2005. Is fledging success a reliable index of fitness in Northern Goshawks? Journal of Raptor Research 39:210–221.

Wolfinger, R. 1993. Covariance structure selection in general mixed models. Communications in statistics—Simulation and computation 22:1079–1106.

Wooller, R. D., J. S. Bradley, I. J. Skira, and D. L. Serventy. 1989. Short-tailed Shearwater. In: Lifetime reproduction in birds (Ed. by I. Newton), pp. 405–417. Academic Press, San Diego, California.

Zimmerman, G. S., W. S. LaHaye, and R. J. Gutiérrez. 2003. Empirical support for a despotic distribution in a California Spotted Owl population. Behavioral Ecology 14:433–437.

APPENDICIES

Appendix A. Error model selection results. Structures marked in bold were selected
for use in the effects analysis.

Dataset	AIC*c*	Model	Covariance structure	K	Δ AIC*c*
TYE femlaes	1901.6	age age2 yr	local=exp(age)	3	0.0
TYE femlaes	**1902.3**	**age age2 yr**	**(ar(1))**	**3**	**0.8**
TYE femlaes	1902.6	age age2 yr	(toep(2))	3	1.1
TYE femlaes	1902.8	age age2 yr	(toep(3))	4	1.2
TYE femlaes	1903.0	age age2 yr	(toep(1))	2	1.4
TYE femlaes	1903.0	age age2 yr	(vc)	2	1.4
TYE femlaes	1903.0	age age2 yr	(cs)	2	1.4
TYE femlaes	1904.5	age age2 yr	(toeph(2))	18	3.0
TYE femlaes	1906.6	age age2 yr	(toeph(1))	17	5.0
TYE femlaes	1907.1	age age2 yr	local=exp(age yr)	18	5.5
OCR females	**1103.3**	**age age2 yr**	**local=exp(age yr)**	**17**	**0.0**
OCR females	1121.8	age age2 yr	(toeph(1))	16	18.4
OCR females	1123.5	age age2 yr	(toeph(2))	17	20.1
OCR females	1245.4	age age2 yr	local=exp(age)	3	142.0
OCR females	1253.9	age age2 yr	(toep(3))	4	150.6
OCR females	1254.8	age age2 yr	(vc)	2	151.4
OCR females	1254.8	age age2 yr	(cs)	2	151.4
OCR females	1254.8	age age2 yr	(toep(1))	2	151.4
OCR females	1254.8	age age2 yr	(ar(1))	3	151.5
OCR females	1255.1	age age2 yr	(toep(2))	3	151.8
HJA females	**1004.1**	**age age2 yr**	**(ar(1))**	**3**	**0.0**
HJA females	1005.4	age age2 yr	(toep(3))	4	1.3
HJA females	1005.4	age age2 yr	(toeph(1))	4	******
HJA females	1005.4	age age2 yr	(toeph(2))	4	******
HJA females	1007.2	age age2 yr	(toep(2))	3	3.0
HJA females	1022.3	age age2 yr	local=exp(age)	3	18.1
HJA females	1022.3	age age2 yr	local=exp(age yr)	3	*******
HJA females	1023.4	age age2 yr	(vc)	2	19.2
HJA females	1023.4	age age2 yr	(cs)	2	19.2
HJA females	1023.4	age age2 yr	(toep(1))	2	19.2
CLE females	644.1	age age2 yr	(vc)	2	0.0
CLE females	644.1	age age2 yr	(cs)	2	0.0
CLE females	644.1	age age2 yr	(toep(1))	2	0.0
CLE females	644.1	age age2 yr	(toep(3))	4	0.0
CLE females	644.4	age age2 yr	local=exp(age)	3	0.3
CLE females	**644.6**	**age age2 yr**	**(ar(1))**	**3**	**0.5**
CLE females	644.9	age age2 yr	(toep(2))	3	0.8
CLE females	646.8	age age2 yr	(toeph(1))	16	2.7
CLE females	648.5	age age2 yr	(toeph(2))	17	4.4
CLE females	648.7	age age2 yr	local=exp(age yr)	17	4.6

Appendix A. continued

Dataset	AICc	Model	Covariance structure	K	Δ AICc
TYE males	**1897.1**	**age age2 yr**	**local=exp(age yr)**	**18**	**0.0**
TYE males	1898.5	age age2 yr	(toep(3))	4	1.4
TYE males	1899.3	age age2 yr	local=exp(age)	3	2.3
TYE males	1900.3	age age2 yr	(toeph(2))	18	3.2
TYE males	1900.9	age age2 yr	(toeph(1))	17	3.8
TYE males	1905.3	age age2 yr	(ar(1))	3	8.2
TYE males	1905.8	age age2 yr	(toep(2))	3	8.7
TYE males	1905.9	age age2 yr	(vc)	2	8.8
TYE males	1905.9	age age2 yr	(toep(1))	2	8.8
TYE males	1905.9	age age2 yr	(cs)	2	8.8
ORC males	**1267.1**	**age age2 yr**	**(ar(1))**	**3**	**0.0**
ORC males	1268.3	age age2 yr	(toep(2))	3	1.3
ORC males	1268.4	age age2 yr	(toep(3))	4	1.4
ORC males	1268.4	age age2 yr	(toeph(1))	4	*******
ORC males	1268.4	age age2 yr	(toeph(2))	4	*******
ORC males	1276.9	age age2 yr	local=exp(age)	3	9.9
ORC males	1276.9	age age2 yr	local=exp(age yr)	3	*******
ORC males	1282.9	age age2 yr	(vc)	2	15.8
ORC males	1282.9	age age2 yr	(cs)	2	15.8
ORC males	1282.9	age age2 yr	(toep(1))	2	15.8
HJA males	884.2	age age2 yr	local=exp(age)	2	0.0
HJA males	884.2	age age2 yr	local=exp(age yr)	2	******
HJA males	886.9	age age2 yr	(toep(3))	3	2.7
HJA males	886.9	age age2 yr	(toeph(1))	3	******
HJA males	886.9	age age2 yr	(toeph(2))	3	******
HJA males	**887.5**	**age age2 yr**	**(ar(1))**	**3**	**3.3**
HJA males	889.0	age age2 yr	(toep(2))	3	4.8
HJA males	894.4	age age2 yr	(toep(1))	1	10.3
HJA males	894.4	age age2 yr	(vc)	1	10.3
HJA males	895.7	age age2 yr	(cs)	2	11.5
CLE males	**552.3**	**age age2 yr**	**(ar(1))**	**3**	**0.0**
CLE males	553.6	age age2 yr	(toep(2))	3	1.3
CLE males	553.8	age age2 yr	(toep(3))	4	1.5
CLE males	553.8	age age2 yr	(toeph(1))	4	*******
CLE males	553.8	age age2 yr	(toeph(2))	4	*******
CLE males	556.2	age age2 yr	local=exp(age)	3	3.9
CLE males	556.2	age age2 yr	local=exp(age yr)	3	*******
CLE males	557.3	age age2 yr	(vc)	2	4.9
CLE males	557.3	age age2 yr	(cs)	2	4.9
CLE males	557.3	age age2 yr	(toep(1))	2	4.9

****** Model failed to converge.
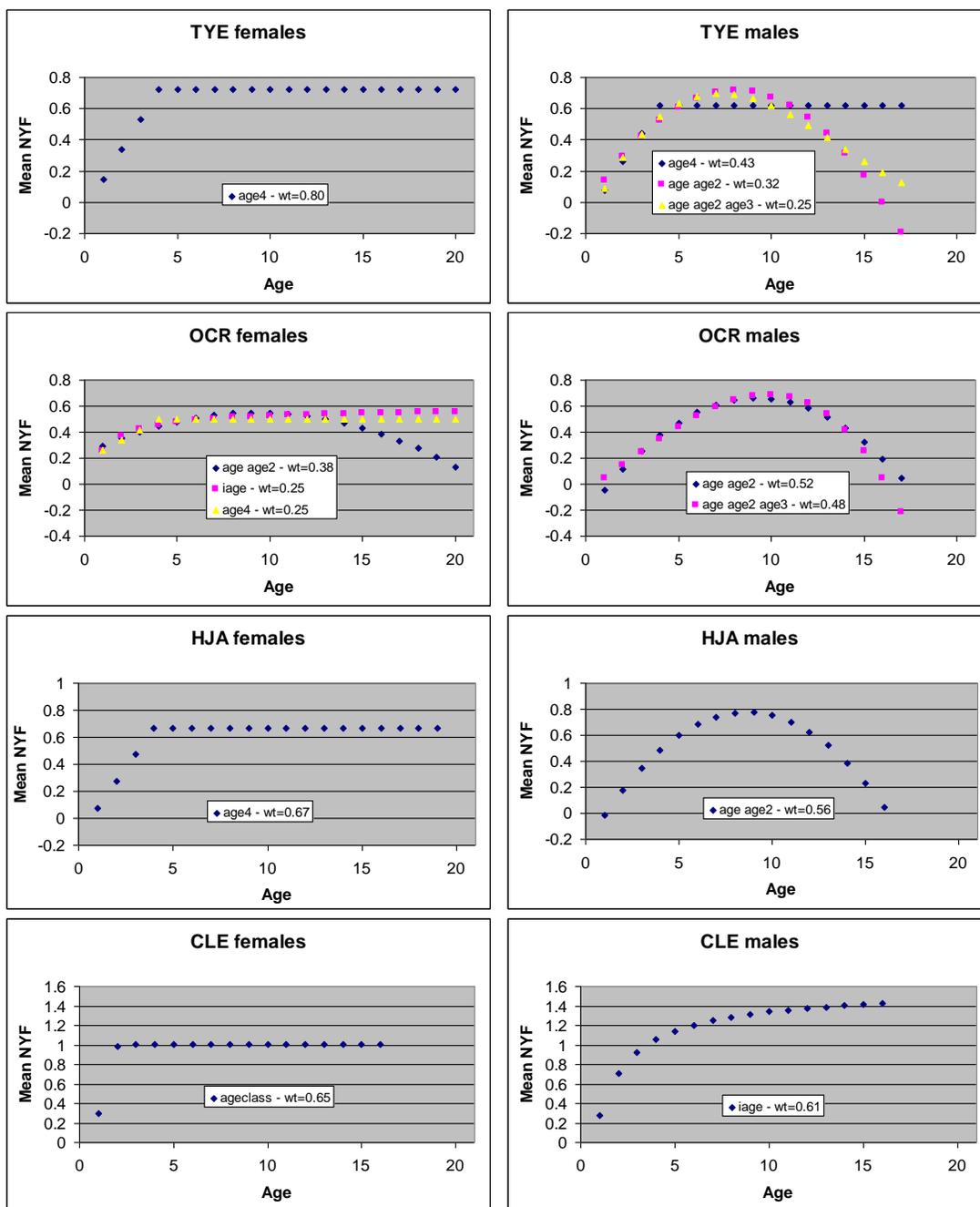
Appendix B. Top and competitive models that describe the relation of age and reproduction for known age female and male Northern Spotted Owls on four study areas in Oregon and Washington. Different symbols show the predictions from the top ranked (blue diamonds) and competing (red squares and yellow triangles; $\Delta AIC_c <$ 2) models. All models included year as a categorical fixed effect and legends indicate the additional additive fixed effects and the AIC weights from each model. A single plot per model representing an average over all years was graphed.

Appendix C. Comparison of the ranges of values for summary data from the 336 known age Northern Spotted Owls included in the analysis of LRS with those of the 1857 banded owls that were excluded on four study areas in Oregon and Washington.

Sex/Variables	Owls in LRS analysis			Excluded owls		
	N	Minimum	Maximum	N	Minimum	Maximum
Females						
Lifespan (years)	148	1	18	892	1	20
Lifetime fledglings	148	0	20	892	0	22
Lifetime recruits	148	0	6	892	0	7
Breeding attempts	148	0	15	892	0	14
Successful attempts	148	0	11	892	0	11
Mates	148	0	5	892	0	6
Breeding dispersal	148	0	6	892	0	5
Territories	148	1	4	892	1	5
Missed adult resights	148	0	2	892	0	10
Cohort (birth year)	148	1986	1992	318	1974	2004
Males						
Lifespan (years)	188	1	17	965	1	20
Lifetime fledglings	188	0	18	965	0	17
Lifetime recruits	188	0	7	965	0	7
Breeding attempts	188	0	13	965	0	11
Successful attempts	188	0	10	965	0	10
Mates	188	0	6	965	0	5
Breeding dispersal	188	0	5	965	0	5
Territories	188	1	4	965	1	5
Missed adult resights	188	0	2	965	0	12
Cohort (birth year)	188	1986	1992	330	1974	2004

Appendix D. Proportions of female and male Northern Spotted Owls that began breeding at different ages on four areas in Oregon and Washington. Data are for 371 owls from the 1986 to 1996 cohorts that bred at least once, never had a backpack radio, and were not missed in more than two adult years. Owls that were first observed breeding at age ≥9 are listed as 9+. Including cohorts through 1996 was justified since LRS was not the focus of this table and since owls still alive in 2005 would be ≥9 and few if any owls bred for the first time after age 8. $\sum$% is the proportion of the breeding male or female owls on each area that made their first nest attempt by each age.

| | CLE | | | | | | HJA | | | | | |
| | Females | | | Males | | | Females | | | Males | | |
Age first breeding	No.	%	$\sum$%	No.	%	$\sum$%	No.	%	$\sum$%	No.	%	$\sum$%
1	4	14.8	14.8	4	14.3	14.3	3	9.4	9.4			
2	15	55.6	70.4	11	39.3	53.6	3	9.4	18.8	5	12.8	12.8
3	6	22.2	92.6	7	25.0	78.6	8	25.0	43.8	12	30.8	43.6
4	2	7.4	100.0	3	10.7	89.3	11	34.4	78.1	9	23.1	66.7
5				3	10.7	100.0	2	6.3	84.4	7	18.0	84.6
6							3	9.4	93.8	3	7.7	92.3
7							0	0.0	93.8	1	2.6	94.9
8							2	6.3	100.0	1	2.6	97.4
9+										1	2.6	100.0

| | OCR | | | | | | TYE | | | | | |
| | Females | | | Males | | | Females | | | Males | | |
Age first breeding	No.	%	$\sum$%	No.	%	$\sum$%	No.	%	$\sum$%	No.	%	$\sum$%
1	1	2.1	2.1				2	3.0	3.0	1	1.3	1.3
2	15	31.3	33.3	6	10.7	10.7	20	30.3	33.3	10	13.3	14.7
3	6	12.5	45.8	9	16.1	26.8	13	19.7	53.0	17	22.7	37.3
4	14	29.2	75.0	16	28.6	55.4	17	25.8	78.8	22	29.3	66.7
5	6	12.5	87.5	6	10.7	66.1	8	12.1	90.9	19	25.3	92.0
6	4	8.3	95.8	7	12.5	78.6	6	9.1	100.0	4	5.3	97.3
7	1	2.1	97.9	3	5.4	83.9				2	2.7	100.0
8	1	2.1	100.0	6	10.7	94.6						
9+				3	5.4	100.0						

Appendix E. Maximum values of reproductive success and associated components of breeding observed from lifetime data recorded for Northern Spotted Owls on four study areas in Oregon and Washington, 1983–2005. Rows indicate data for individual males and females for which maximums were recorded. Maximum values for each gender are in bold. An asterisk after the territory name indicates owls that were fitted with a backpack radio at some point during the study.

Territory Name	Year of last resight	Study area	Sex[a]	Lifetime fledglings	Lifetime recruits	Lifespan[b]	Breeding attempts	Successful attempts[c]	Breeding experience[d]	Breeding lifespan[e]	Age at first breeding	Age at last breeding	Breeding dispersal events[f]	Different territories[g]	Mates[h]	Pair experience[i]	Consecutive years nesting[j]	Consecutive years fledging[k]	Missing adult resights[l]
Pedee Creek*	2005	OCR	F	0	0	**20**	2	0	5	5	16	**20**	4	3	4	-	-	-	7
Blachly East	2005	OCR	F	4	2	19+	7	2	11	14	6	16	1	2	1	**15**	-	-	2
Bear Creek BLM	2005	OCR	F	9	1	17	9	6	15	16	2	16	1	2	1	**15**	-	-	0
Bear Creek BLM	2005	OCR	M	9	1	18+	9	6	15	16	3	17	1	2	1	**15**	-	-	1
Blachly East	2005	OCR	M	4	2	17+	7	2	11	14	4	14	1	2	1	**15**	-	-	0
Table Mountain USFS	2005	OCR	M	5	2	17+	4	4	10	10	8	17	4	**5**	4	-	-	-	2
Turner Creek	1999	OCR	F	3	0	10+	3	2	5	6	5	9	4	**5**	3	-	-	-	0
East Fawn	2005	OCR	M	4	0	9	4	3	6	7	3	8	4	**5**	2	-	-	-	0
Flagler Creek	2005	TYE	F	14	**7**	19	11	9	12	12	8	19	1	2	2	-	-	-	4
Little Tom Folley	2005	TYE	F	7	2	**20+**	7	4	16	16	5	**20**	1	2	3	-	-	-	3
Gold Beach*	2005	TYE	F	6	2	19	8	5	**17**	**17**	3	19	1	2	2	-	-	-	1
Old Blue	2005	TYE	F	12	4	**20**	7	7	15	15	6	**20**	1	2	5	-	-	-	0
Brush Headwaters	2005	TYE	F	17	6	18	**15**	**11**	16	16	3	18	1	2	3	-	**12**	-	0
Umpqua Overlook	2005	TYE	M	**18**	6	17	**13**	**10**	14	16	2	15	0	1	3	-	-	-	0
Brush Headwaters	2005	TYE	M	13	5	15	12	9	14	14	2	15	1	2	3	-	**10**	-	0
Deadman Butte	2002	TYE	M	4	0	14+	6	3	12	12	3	14	**5**	2	3	-	-	-	0

Lower Little Canyon	2004	TYE	M	17	1	16+	11	**10**	14	14	3	16	0	1	5	-	-	**7**	0
Lower EF Rader Creek	2003	TYE	M	14	**7**	15+	9	8	12	12	4	15	1	2	2	-	-	-	0
Thistleburn Creek	2005	TYE	M	11	6	14	10	7	10	11	4	13	2	2	1	-	**10**	-	0
Squaw Creek	2005	TYE	F	5	2	13	5	3	11	12	2	12	**6**	4	2	-	-	-	0
Doe Creek	2005	TYE	M	9	**7**	13	7	5	10	11	3	12	1	2	4	-	-	-	0
Bear Ridge	2004	TYE	M	5	3	10	3	3	5	5	6	10	**5**	5	2	-	-	-	0
Lower Little Canyon	2002	TYE	F	13	1	11	8	8	9	10	2	10	0	1	2	-	-	**7**	0
Peterson Point	2005	TYE	F	2	0	9	4	1	5	5	5	9	4	**5**	3	-	-	-	1
Standup Cr	2004	CLE	F	17	2	15	10	10	12	13	3	14	0	1	3	-	-	**7**	1
Snowboulder*	2004	CLE	F	**22**	4	18+	14	**11**	16	16	3	18	0	1	5	-	-	-	0
Taneum S Fk	2005	CLE	F	13	1	16	9	7	15	15	2	16	4	2	**6**	-	-	-	3
Middle Mcrae Creek	1992	HJA	M	7	1	**20+**	4	4	**16**	18	3	18	0	1	2	-	-	-	11
Upper Delp*	2005	HJA	M	0	0	**20+**	1	0	1	2	19	**19**	1	2	2	-	-	-	12
West Mack Creek	2005	HJA	F	9	0	19	7	6	14	14	6	19	5	**5**	5	-	-	-	3
Upper Cook Creek	2005	HJA	M	5	0	17	4	3	8	12	6	13	4	3	**6**	-	-	-	2
Wildcat RNA	2003	HJA	M	1	0	12	1	1	1	1	12	12	**5**	4	2	-	-	-	1

[a] M = male and F = female.

[b] Age in years during the owl's last resight. Plus (+) indicates age is a minimum because the owls was an unbanded adult at its first resight.

[c] Number of breeding attempts that resulted in ≥1 fledgling.

[d] Span of years from first nest attempt to the last nest attempt.

[e] Span of years from first nest attempt to the last resight.

[f] Number of non-juvenile dispersal events based on a changes to territories occupied.

[g] Number of different territories occupied over the study period

[h] Number of mates an owl had based on the unique banded individuals with which they shared territories.

[i] Number of years two individuals were found together.

[j] The number of consecutive years an owl made nesting attempts.

[k] The number of consecutive years an owl produced in ≥1 fledgling.

[l] The number of years the owl was not resighted after age 2 based on gaps in its resight history.