HABITAT SELECTION AND REPRODUCTIVE SUCCESS OF
LEWIS'S WOODPECKER
IN THE SOUTH OKANAGAN VALLEY

By

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Abstract

Lewis's Woodpecker (*Melanerpes lewis*) has been listed as a species of
special concern due to its range-wide decline in population numbers, possibly as
a result of habitat loss and degradation. Management plans for this species need
information on habitat requirements. However, little is understood about how
habitat features affect nest site selection and reproductive success. I conducted
the first study of the species in Canada, in the South Okanagan Valley, British
Columbia, during 2004-2005 in an effort to fill this gap. I examined the habitat
features influencing nest site selection using multiple logistic regression models. I
also evaluated effects of habitat features and clutch initiation date on nest
success using multiple Weibull regression models. Nest tree decay class and
total basal area of large trees (DBH≥50cm)/ha were the most important factors
for nest site selection. Of the 57 nests monitored, 34 were located in snags, 22 in
dead-top trees, and only one in a live tree. Despite the importance of large,
decayed trees and newly-burned forest for nest site selection, these factors were
unrelated to the subsequent nest success. The Mayfield estimate of overall nest
success was 0.52 ± 0.08 (mean±S.E. n=57 nests). Early and late clutch
initiations had higher nest success than intermediate clutch initiations, possibly
due to seasonal variation in nest predation and cavity competition. But early
clutch initiations were more likely to produce large clutches and fledged broods
than late clutch initiations. Deep cavities with small entrances were able to
effectively lower predation risk especially during the peak of nest predation.
Overall, my results suggest that: (1) the habitat features related to nest site

selection were not correlated with nest success; (2) early clutch initiations allowed the bird to gain the highest annual production rate; and (3) nest predation and cavity competition appeared to be important limiting factors to the species in the South Okanagan Valley.

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Chapter 1: General Introduction

Habitat Selection

Habitat selection refers to a hierarchical set of behaviours that result in the disproportionate use of certain habitats that influence survival and fitness of individuals (Block and Brennan 1993; Cody 1985; Hutto 1985; Jones 2001; Rolstad et al. 2000). Habitat selection is a complex process that may involve multiple mechanisms (Hutto 1985). In general, animals are not distributed randomly within their distribution ranges (Cody 1985; Karr and Freemark 1983; Orians and Wittenberger 1991). The nonrandom distribution patterns are assumed to result from natural selection in relation to niche partitioning driven by inter- and intra-specific competition (Clark and Shutler 1999; Martin 1998).

Often, an animal first chooses a general area to live and then makes subsequent decisions about the use of different local habitats (Orians and Wittenberger 1991). Hutto (1985) suggested that individuals may explore possible habitats and settle according to habitat ranking. In this process, habitat features act as important cues for habitat selection (Cody 1981; Fretwell and Lucas 1970; Jones 2001; Kristan 2003; Muller et al. 1997; Roos 2004; Stamps 1988). Although habitat selection in birds has been studied in more detail than in most other animal taxa, it remains a poorly understood ecological process (Rolstad et al. 2000).

Several studies (Belthoff and Ritchison 1990; Clark and Shutler 1999; Li and Martin 1991; Martin 1993; Martin 1998; Martin and Roper 1988) have shown that

habitat features at different spatial scales affect not only foraging conditions of nesting birds but also risk of nest predation. As a result, individuals that are able to obtain optimal habitats will have more opportunity to produce more offspring. Sometime birds may be attracted to a poor habitat (an ecological "trap") by misleading cues (Kristan 2003). In this case, habitat selection may not correctly reflect habitat fitness. To distinguish these mechanisms, one needs to compare habitat selection vs. habitat-specific fitness. Thus to understand the habitat requirements of a species, it is important to understand how fitness components (reproductive success) vary between preferred and non-preferred habitats.

Conservation Concerns

Understanding habitat selection is a crucial step for species recovery planning in conservation (Hoekstra et al. 2002). As human activities increase, more and more species become threatened or go extinct. Habitat loss and degradation are the most pervasive causes of endangerment, affecting 86% of all threatened birds and mammals, and 88% of threatened amphibians (IUCN 2004). For instance, the decline of Lewis's Woodpecker (*Melanerpes lewis*) has been attributed to loss of suitable habitats due to fire suppression, forest cutting, agricultural development, water management practice and urbanization (Cooper et al. 1998; Tobalske 1997). Habitat protection has proven one of the most effective measures to rescue and recover threatened and endangered species (IUCN 2004). However, successful implementation of management plans depends on our knowledge of habitat requirements of target species, which may vary geographically.

Populations of many North American grassland birds have been declining for at least the last 30 years (Peterjohn and Sauer 1999; Vickery et al. 1999). These widespread and consistent declines appear to be primarily the result of loss and degradation of grassland habitats. Research on the habitat requirements of grassland birds is therefore particularly important to helping land managers and planners to mitigate or reverse some of these declines (Vickery et al. 1999).

Lewis's Woodpeckers have declined both locally and regionally since the 1960s (Tashiro-Vierling 1994). Like many other grassland birds, Lewis's Woodpeckers are sensitive to alteration of grassland habitats, especially the change of wildfire regime (Bock 1970; Saab et al. 2004; Saab and Vierling 2001). Periodic fires can maintain the openness of grassland habitats, which is crucial for most grassland species. Vickery et al (1999) suggested that management of grassland areas be directed toward the creation of a mosaic of grassland habitats to meet habitat requirements of grassland birds. Lewis's Woodpeckers can be viewed as an umbrella species because its habitats show a mosaic landscape structure (i.e. nesting in decayed trees and foraging in open mixed forest and grassland). Research on habitat requirements of Lewis's Woodpeckers is of a broader significance to the conservation of grassland avian communities as a whole.

Objectives

My objectives include: (1) to quantitatively evaluate the relative importance of habitat features to nest site selection of Lewis's Woodpeckers; (2) to quantify the potential effects of habitat features important in nest site selection on

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reproductive success; and (3) to provide detailed reproductive parameters of the Lewis's Woodpecker populations in the South Okanagan Valley.

Hypotheses

My hypotheses are: (1) Lewis's Woodpeckers actively select nest sites based on several key habitat features; and (2) these key habitat features determine the reproductive success of Lewis's Woodpeckers.

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Chapter 2: Habitat Selection and Reproductive Success of Lewis's Woodpecker in the South Okanagan Valley

Introduction

Lewis's Woodpecker has been listed as a species of special concern in Canada and United States because of steady declines in population numbers and distribution range (COSEWIC 2001; Tobalske 1997). Historically, the species had a wide distribution in western North America, ranging from northwestern Mexico north to southwestern Canada and from eastern Colorado to the California coast (Bock 1970). Since the 1960s, its range in Canada has contracted east from the southeastern Vancouver Island and the lower Fraser Valley to the southern interior B.C. with extirpation of the coastal sub-population. In British Columbia it now breeds only in the area from the Similkameen Valley east to the East Kootenay Trench with the center of abundance in the Okanagan Valley (Campbell et al. 1990; Cannings et al. 1987; Cooper et al. 1998). Estimates based on the Breeding Bird Survey and the Christmas Bird Count indicated that the species had experienced range-wide population declines by approximately 60% between 1966 and 1991 in western North America (Tashiro-Vierling 1994). During the past century, the population in British Columbia had declined by more than 50% to 350-600 breeding pairs in 1990 (Cooper et al. 1998; DeSante and George 1994). Population declines in this species have been attributed to habitat loss and degradation due to fire suppression, forest cutting,

over grazing, agricultural development, water management practices and urbanization (Cooper et al. 1998; Saab and Vierling 2001; Tobalske 1997).

Lewis's Woodpecker, a short distance migratory bird, tends to form long-term pair bonds (Bock 1970). Pairs produce one brood annually and may renest if the first attempt fails. Both sexes participate in incubating and nestling care, which lasts 13-15 days and 28-34 days respectively. The entire breeding cycle, plus laying period, lasts 52-58 days (Bock 1970). In British Columbia, clutch sizes range from 2-8 eggs (Campbell et al. 1990). Lewis's Woodpecker is a weak primary cavity excavator; it often nests in existing cavities initially excavated by strong cavity excavators such as the Northern Flicker (*Colaptes auratus*), and tends to return to the same nest sites in subsequent years (Bock 1970). The cavity reuse rate ranges from 54-100% (Wiebe et al. 2006). In the breeding season, the bird mainly feeds on flying insects with fruit as a secondary part of its diet depending on local availability (Bock 1970; Cannings et al. 1987).

Lewis's Woodpecker prefers open ponderosa pine (*Pinus ponderosa*) forest, riparian woodland dominated by black cottonwood (*Populus balsamifera*), and partially logged or burned pine forest (Bock 1970; Janos 1991). These habitats, which used to be maintained by periodic wildfires, provide the species with abundant nesting sites and good visibility for catching insects in the air (Bock 1970; Linder and Anderson 1998; Tobalske 1997; Vierling 1997). Wildfires may also reduce risk of nest predation through altering nest predator communities during the early post-fire period thus providing additional benefits to Lewis's Woodpeckers (Saab et al. 2004; Saab and Vierling 2001).

Previous studies focused on describing geographic distribution, habitat characteristics, population trends and general ecology of the species (Bock 1970; Cooper et al. 1998; Raphael and White 1984; Sousa 1982; Tashiro-Vierling 1994; Tobalske 1997). A few have additionally addressed microhabitat selection (Block and Brennan 1987; Linder and Anderson 1998; Saab et al. 2004; Vierling 1997) and reproductive success in burned pine and riparian cottonwood forests (Saab and Vierling 2001). No studies have quantitatively analyzed the effects of habitat features on nest site selection and individual fitness, or provided detailed reproductive success data for the species in relation to cavity features and timing of breeding. Thus, although habitat selection by Lewis's Woodpeckers has been studied in several areas, the underlying mechanisms remain unclear. This makes it challenging to determine the true habitat requirements of the species.

In this thesis I investigated nest site selection and habitat-specific reproductive success of the Lewis's Woodpeckers in the South Okanagan Valley in order to fill a gap in our understanding of habitat requirements and reproductive ecology of the species at the northern range of its distribution. I incorporated habitat features, cavity features, and timing of breeding into models to evaluate their relative importance to nest success. This approach allowed me to gain insight into broader ecological processes related to reproduction of the species in its northern range limit. I monitored nests at six sites and addressed two major questions: (1) what habitat features are important in determining nest site selection of Lewis's Woodpeckers in the South Okanagan Valley? (2) Do habitat features that determine nest site selection further influence nest success, clutch

size and fledgling production? To answer the first question, I compared the differences in habitat features between used and random sites. To answer the second question, I compared the differences in habitat features between successful nests and failed nests. Finally I presented detailed reproductive parameters of the species in the South Okanagan Valley. Based on the results from previous studies, I predicted that tree cover and composition, shrub cover, grass cover, elevation, distance from nest sites to the nearest orchards, density of large decayed trees, nest tree decay class, availability of suitable cavities and forest fires, were the most important factors in determining nest site selection, and that these factors plus clutch initiation date would influence annual fecundity of Lewis's Woodpeckers in the South Okanagan Valley.

Methods

Study Areas

The study was conducted during 2004-2005 in the South Okanagan Valley of interior BC, Canada (W119º20'- 119º45', N49º- 49º30'; Fig. 1). This area lies between the southeastern edge of the Thompson Plateau and the Okanagan highlands to the east. The valley bottom has a semi-arid steppe vegetation. With increasing elevation, the average temperature drops and precipitation increases, giving the surrounding hills a more humid continental climate (Cannings et al. 1987). Mean temperature for the valley ranges from -7° to -2°C in January and from 12° to 22°C in July. Annual rainfall ranges from 250-350 mm in the valleys to about 600 mm at the tree line (Cannings et al. 1987). Typical vegetation types include semi-arid grassland, shrub steppe, marsh, riparian woodland, Douglas fir

(*Pseudotsuga menziesii*) forest, open ponderosa pine forest, and Engelmann

spruce (*Picea engelmanni*)-sub-alpine fir (*Abies lasiocarpa*) forest (Cannings et

al. 1987). In the valley bottom, extensive development of agriculture has resulted

in decreased coverage of riparian cottonwood forest, one of the preferred

habitats for Lewis's Woodpeckers (Cannings et al. 1987; Cooper et al. 1998).
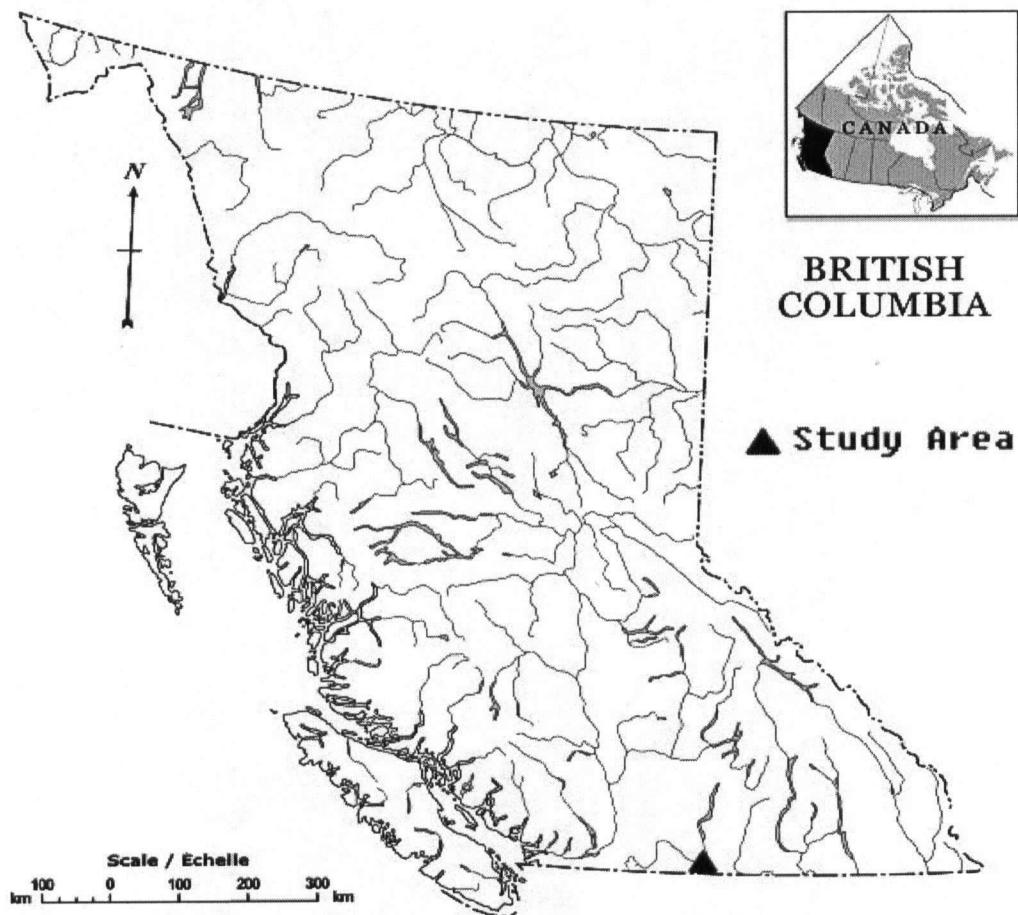
Figure 1. Location of the Lewis's Woodpecker study area in the South
Okanagan Valley, BC. Canada.

I established five study areas at elevations of 320-1100m, which included

Chopaka Grassland Protected Area (500ha, el. 500-800m); Spotted Lake

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Grassland Protected Area (430ha, el. 640-700m); Vaseux Lake Ecological Reserve (2430ha, el 320-900m); Kilpoola Grassland Protected Area (800ha, el. 800-1100m); and SunOka Provincial Park (40ha, el. 350m). The first two areas represented a typical open ponderosa pine and grassland habitat, while Vaseux Lake represented a low elevation, and newly burned, ponderosa pine habitat (burned in 2003 after breeding season). Kilpoola represented a high elevation, and less recently burned, Douglas fir and grassland habitat (burned in 1994), and SunOka Provincial Park consists of old riparian cottonwood habitat. The five areas were all on public lands with substantial protection. In addition, surveys for breeding pairs were conducted in surrounding areas, which covered an area of approximately 1500 ha.

Nest location and monitoring

I conducted four rounds of intensive surveys during each breeding season (early May to late August), searching each area thoroughly for nests and individuals with consistent effort. I used behaviour of Lewis's Woodpeckers as cues to locate their nests and to assign nest status to one of four stages: pre-laying, egg-laying, incubating and nestling. The freshness of woodchips found at the nest tree bottom was examined to identify if the cavity was old or newly excavated. Each nest was visited at 3-4 day intervals from discovery until either fledging or failure. If a nest failed prior to the nestling stage, it was regularly monitored until the end of breeding season to determine possible renesting. During each visit, I conducted one hour of behavioural observation, recording time spent on activities such as roosting, courtship, copulation, incubating,

provisioning, alarm calling, and cavity and territory defense. This information was helpful in determining nest status, especially during the incubating and nestling stages. To obtain more accurate information on clutch initiation, nest age, clutch size and number of fledglings, I also checked the contents of all accessible nests after behavioural observations, using a miniature digital camera. To minimize disturbance, I did not check nests during incubation unless unusual behaviours were observed. In my study, 81% of 57 nests were accessible, using a climbing rope. The accessible nests were located in a variety of habitats and varied from 5 to 21m in height. I was able to estimate nest age for most nests through comparison of the photographs taken over time, plus behavioural observations.

Vegetation Surveys

Vegetation surveys were conducted at 50 used sites and 28 random sites after the breeding seasons to minimize disturbance to nesting birds. The 50 used sites involved 57 nests, seven of which were located in the same cavities in both years. The 28 random sites were located using randomly-generated coordinates. At each site, I centered a 50m-radius plot on the nest tree or a randomly-selected large tree with diameter at breast height (DBH) $\geq$ 50cm (minimum used by Lewis's Woodpeckers in this study) for tree level measurements. If there was no tree with DBH $\geq$ 50cm at the centre of the random site, the plot centre was moved to the nearest suitable tree. A plot size of 50m radius (0.79ha) better represented habitat characteristics of Lewis's Woodpecker home range in contrast to 0.04 ha plot sizes used in previous studies for microhabitat selection (Linder and Anderson 1998; Saab et al. 2004). On each plot, five subplots of

10m-radius were positioned separately at north, east, south and west extremes, as well as the center of the plot, for shrub level measurements. At the center of each subplot, a 5m-radius small plot was added for grass/forb level measurements (see Fig. 2).

Northern subplot

NW   NE

Western subplot   50m   Eastern subplot

Central subplot

SW   NW

Southern subplot

10m

5m
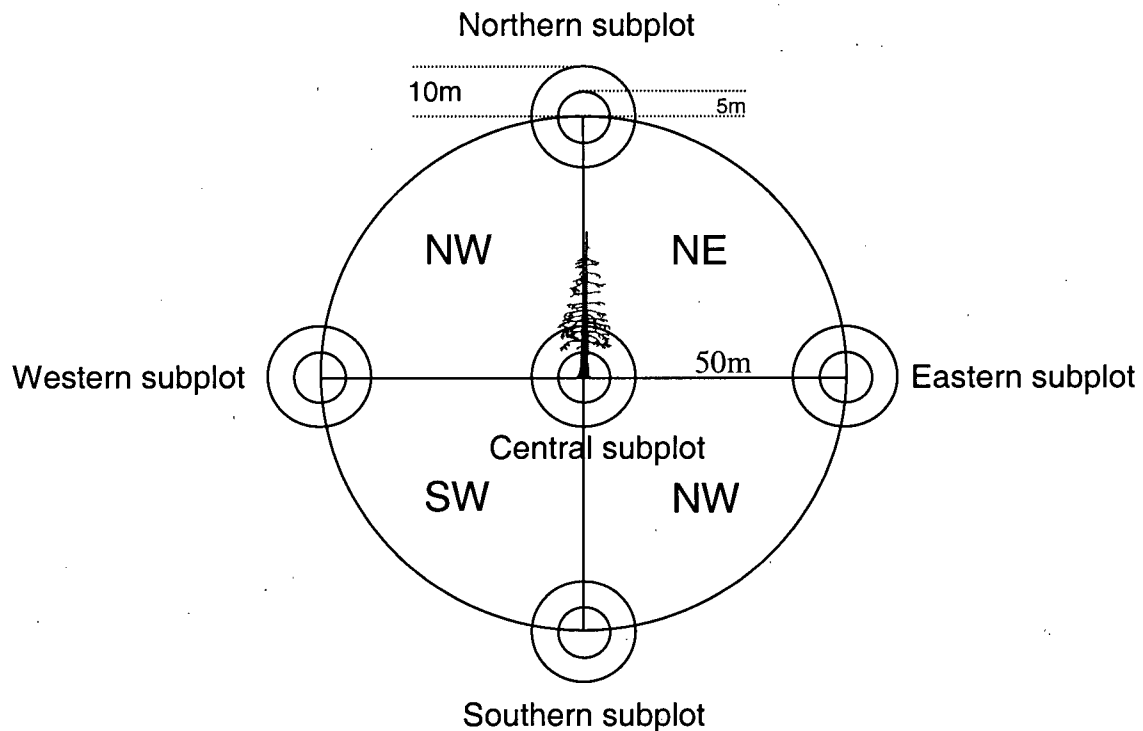
Figure 2. Layout for vegetation survey plots for nest and random sites.

On each plot a total of 23 habitat variables, plus three extra cavity features only applicable to used sites or accessible nests, were measured. Tree attributes measured at the scale of the 50m plot included species composition, live tree canopy cover, numbers of large trees (DBH ≥ 50cm), medium trees (30 ≤ DBH < 50 cm), small trees (DBH < 30 cm), snags, dead-top trees and live trees, number of suitable cavities, as well as tree height, DBH and decay class of large trees (DBH ≥ 50cm). Suitable cavities were identified according to visual estimation of

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the entrance size. Decay class was classified according to a modification of the scale published by the BC Wildlife Tree Conservation Committee (2001): i.e. 1 for live trees, 2 for dead-top trees, 3 for snags with all branches present and 4 for rotten snags with more than half of the branches missing. For shrubs (in 10m subplots) and grasses and forbs (in 5m small plots) I recorded species composition, and height and coverage of each species. For plot-centre trees, I recorded species, DBH, height, decay class, as well as nest height for used sites. For accessible nests I also measured diameter at cavity level, cavity depth and entrance size (i.e. product of hole width and hole height to the nearest 0.1 cm). I defined the ratio of cavity depth to entrance size as the cavity security index, assuming that a deep cavity with small entrance is better than a shallow cavity with large entrance in terms of avoiding nest predation (Martin et al. 2004). At the landscape level I recorded elevation, distance to the nearest orchard and fire history.

Data analysis and modeling

I did two types of analyses. The first compared overall habitat features of used sites with random sites, and for used sites, of successful with failed nests by using analysis of similarity (ANOSIM) and analysis of variance (ANOVA). The second analysis explored specific effects of habitat features on nest site selection and reproductive success by using multiple logistic (Menard 2002) and Weibull regressions (Hosmer and Lemeshow 1999; Murthy et al. 2004; Nur et al. 2004). Multiple Weibull regression has some advantages in analyzing nest survival data (see Appendix). For univariate comparisons, I arcsine-transformed all percentage

and proportion data, and square-root transformed all count data. Where data transformation did not result in a normal distribution, a nonparametric Wilcoxon test was used (Zar 1999).

In order to examine the correlation among variables and to reduce variable components, I conducted principle component analysis. Since PC1 and PC2 together only accounted for 45.8% of variance, instead of using the PCA axes, I first eliminated highly correlated variables, and then selected variables that were significant in the univariate logistic regression with $\alpha=0.25$, for multiple regression analysis.

In regression analyses, I first proposed two general hypotheses in the form of global models: (1) nest site selection was determined by several important habitat variables; (2) these variables plus clutch initiation date and cavity features further influenced reproductive success. Within the framework of each global model, I further established a series of candidate models. Since the overdispersion parameters of the global models were close to one, Akaike information criterion with correction for small sample size (AICc) was used for model ranking (Burnham and Anderson 2002). I evaluated relative likelihood of each model using model weight (Wi), a normalized Akaike weight that indicates relative support for different models in the candidate model set. I used a model-averaging method for final parameter estimations if the best model did not receive overwhelming support (i.e. AICc weight < 0.9; Johnson and Omland 2004). I evaluated relative importance of each variable according to the sum of AICc weight for all models containing that variable (Burnham and Anderson 2001;

Johnson and Omland 2003). Lewis's Woodpeckers are often thought to reuse the same cavities in the consecutive years and exhibit strong site fidelity. To avoid psuedoreplication, nest sites used in both years were included only once in nest site selection analysis.

Although the nest sites were spatially clustered within each of six study areas, each area was large enough to contain substantial variation in measured habitat variables and nest survival probability. Preliminary analysis found the block effect to be trivial, and thus it is not include in further analysis.

I estimated nest survival rates using Mayfield's (1961; 1975) method with variances calculated according to Johnson (1979). The Mayfield method can overcome positive bias in nest success, an inherent problem with the apparent nest success estimation, by estimating nest success based on observation days. I compared nest survival patterns between years using the Kaplan-Meier method (Hosmer and Lemeshow 1999; Kaplan and Meier 1958). The Kaplan-Meier method (survival time analysis) estimates nest success by calculating the probability for a nest to survive from the first egg to fledging. It assumes that the survival time of a nest follows a Weibull distribution. Because there was no significant difference in nest survival patterns between 2004 and 2005, the data were pooled for further analysis. To model nest success, I assumed that a successful nest was one that survived for 54 days (the mean nesting cycle in our study was 54.22 days, S.E. = 0.75, n=18 nests). I used the Mayfield midpoint method to estimate number of observation days for known-fate nests and used

the last active day to determine number of observation days for unknown-fate nests (Manolis et al. 2000).

I defined annual production rate as average female fledglings produced per nest annually and assumed that the sex ratio of fledglings was 50:50.

JMP 6 (SAS Institute, Inc, 2005) and PRIMER 5 (PRIMER-E Ltd, 2000) were used for all statistical analyses. All tests were two-tailed with significance levels of $\alpha = 0.05$, unless otherwise indicated.

Results

In total, 57 nests were found in all study areas, 21 in 2004 and 36 in 2005. Considering the equivalent search efforts conducted in the six areas (five study areas plus one surrounding area) in both years, the increase in nest number was significant (paired t-test: z = 2.61, df = 5, P = 0.048). In the Vaseux Lake area, the number of nests increased from four in 2004 to nine in 2005 after the 2003 wildfire. Annual differences in nest density were not accompanied by significant year effects on overall nest success, daily nest survival, average clutch size, fledged brood per successful nest or annual production rate (Table 1).

The overall nest success based on pooled data was estimated to be 0.52 ± 0.08 (mean±S.E.). Of the failed nests, 15 were predated, three were deserted, and two nests were destroyed by weather (one nest tree was blown down and a second nest filled with rainwater, drowning the nestlings). Nest success did not differ significantly among study areas (Wilcoxon test, $\chi_5^2 = 9.03$, P=0.11; Table 2).

Two nests were found located in newly excavated cavities in 2005 while the other 55 nests were in old cavities, giving the overall cavity reuse rate of 96.5%.

Table 1. Year effects in nest fates and reproductive success of Lewis's Woodpeckers. Daily nest survival and nest success were estimated using the Mayfield method. Production rate was equal to the half product of nest success and fledglings produced per successful nest. The standard error of production rate was calculated using moments estimator of a product of independent variables (Mood et al. 1974).

Item	2004		2005		Pooled		P-value
	(Mean±S.E.)	n	(Mean±S.E.)	n	(Mean±S.E.)	n	
Failed/total nests	8/21(3)[a]	-	12/36(1)	-	20/57(4)	-	**0.048***
Daily nest survival	0.987 ± 0.004	21	0.988 ± 0.004	36	0.988 ± 0.003	57	0.90*
Nest success	0.50 ± 0.12	21	0.53 ± 0.10	36	0.52 ± 0.08	57	0.89*
Clutch size	4.90 ± 0.23	10	5.05 ± 0.18	21	5.00 ± 0.14	31	0.64
F. brood/s. nest	2.50 ± 0.46	8	2.67 ± 0.25	21	2.62 ± 0.22	29	0.72
Production rate	0.63 ± 0.19	-	0.71 ± 0.15	-	0.68 ± 0.12	-	0.79*

* Denoted t-tests, otherwise Wilcoxon tests. P-values<0.05 are in bold.

a. Numbers in the parentheses stand for nests with uncertain fate.

Table 2. Total number of nests and failed nests by study area and year, and Mayfield estimate of nest success (mean ± S.E.).

Study Area	2004	2005	Pooled	Nest Success (Pooled data)
	Failed/Total	Failed/Total	Failed/Total	
Chopaka	0/1	4/4	4/5	0.12 ± 0.13
Kilpoola	4/7	2/9	6/16	0.49 ± 0.14
Spotted Lake	2/3	0/2	2/5	0.47 ± 0.25
SunOka	0/2	1/3	1/5	0.71 ± 0.24
Vaseux Lake	2/4	3/9	5/13	0.49 ± 0.16
Surrounding areas	0/4	2/9	2/13	0.77 ± 0.14

Habitat selection

When all 23 habitat variables were considered together, there was a significant overall difference between used sites and random sites (ANOSIM, $R=0.11$, $P=0.02$) but no overall difference between successful nests and failed nests (ANOSIM, $R=-0.026$, $P=0.63$), suggesting that although Lewis's Woodpeckers actively selected sites for nesting, their nest success was not predicted by these habitat attributes. Used sites differed significantly from random sites in nine of the 23 habitat variables (Table 3) but, as predicted by the ANOSIM, successful nests did not differ from failed nests in any of the 23 habitat variable plus three extra cavity features (Table 4). Used sites had significantly higher densities of large decayed trees and suitable cavities, and higher grass cover than random sites. Most nest trees were decayed and short with a dead top while randomly-selected large trees were usually healthy and tall with a live top.

Table 3. Comparison of habitat features between used sites and randomly chosen sites (plot size=0.79ha).

Habitat features	Used Mean ± S.E.	Random Mean ± S.E.	P-value
Elevation (m)	687 ± 40	737 ± 33	0.232
Distance to nearest orchard (m)	2528 ± 403	2625 ± 418	0.125
Ponderosa pine tree ratio %	54.9 ± 6.5	43.2 ± 7.4	0.444
Live tree canopy cover %	9.1 ± 1.4	14.2 ± 2.9	0.254
Grass height (cm)	68.2 ± 2.8	62.3 ± 3.0	0.122
Grass cover %	**41.4 ± 1.9**	**34.3 ± 2.3**	**0.024***
Shrub height (cm)	123.7 ± 17.7	126.6 ± 16.1	0.226
Shrub cover %	18.6 ± 2.1	18.55 ± 2.3	0.944
Simpson index[a]	0.84 ± 0.01	0.86 ± 0.01	0.319
No. large trees ha^{-1}	**9.4 ± 1.3**	**5.2 ± 1.0**	**0.042**
No. medium trees ha^{-1}	17.2 ± 2.1	19.1 ± 3.3	0.817
No. small trees ha^{-1}	68.3 ± 15.1	153.6 ± 44.4	0.568
No. snags ha^{-1}	39.5 ± 13.3	40.4 ± 17.8	0.921
No. top dead trees ha^{-1}	1.4 ± 0.3	1.8 ± 0.4	0.308
No. live trees ha^{-1}	54.6 ± 10.3	135.8 ± 41.4	0.153
Total basal area of large trees (m^2/ha)	**3.3 ± 0.4**	**1.6 ± 0.3**	**0.013**
Total volume of large trees (m^3/ha)	**67.1 ± 9.4**	**36.1 ± 8.6**	**0.038**
Nest tree decay class	**3.13 ± 0.14**	**1.93 ± 0.22**	**<0.0001**
Total decay index of large trees	**26.24 ± 3.85**	**9.78 ± 1.89**	**0.017**
Nest tree DBH (cm)	66.0 ± 2.7	65.6 ± 2.9	0.909*
Nest tree height (m)	**16.0 ± 0.8**	**21.9 ± 1.3**	**0.0005***
No. cavities in nest trees	**2.4 ± 0.9**	**0 ± 0**	**<0.0001**
No. suitable cavities ha^{-1}	**2.4 ± 0.5**	**0.5 ± 0.3**	**<0.0007**

* Indicates t -tests, otherwise Wilcoxon tests. P-values <0.05 are in bold;

a. Simpson index = $1 - \sum_{i}^{N} d_i^2$, where d_i = percentage cover of ith species and N = total number of species on a given plot.

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Table 4. Comparison of habitat features between successful nests and failed nests.

Habitat features	Successful Mean ± S.E.	Failed Mean ± S.E.	P-value*
Elevation (m)	638 ± 48	726 ± 57	0.139
Distance to nearest orchard (m)	3228 ± 546	2554 ± 624	0.610
Ponderosa pine tree ratio	58.7 ± 7.5	53.6 ± 9.6	0.646
Live tree canopy cover %	9.4 ± 1.9	8.5 ± 1.9	0.923
Grass height (cm)	68.7 ± 3.5	67.3 ± 4.9	0.714
Grass cover %	43.8 ± 2.3	36.9 ± 3.4	0.097*
Shrub height (cm)	142.8 ± 26.2	88.8 ± 11.7	0.106
Shrub cover %	19.2 ± 2.7	17.6 ± 3.3	0.846
Simpson index[a]	0.86 ± 0.01	0.82 ± 0.02	0.050
No. large trees ha^{-1}	9.1 ± 1.8	9.9 ± 2.0	0.552
No. medium trees ha^{-1}	16.3 ± 2.8	18.9 ± 2.9	0.270
No. small trees ha^{-1}	59.6 ± 15.7	84.26 ± 32.0	0.612
No. snags ha^{-1}	34.9 ± 14.4	47.9 ± 27.4	0.956
No. top dead trees ha^{-1}	1.2 ± 0.4	1.7 ± 0.4	0.087
No. live trees ha^{-1}	49.9 ± 11.2	63.4 ± 20.9	0.567
Total basal area of large trees (m^2/ha)	3.2 ± 0.6	3.4 ± 0.6	0.463
Total volume of large trees (m^3/ha)	63.9 ± 12.1	72.9 ± 15.3	0.490
Nest tree decay class	2.92 ± 0.16	3.25 ± 0.23	0.242
Total decay index of large trees	26.04 ± 4.98	26.61 ± 6.16	0.545
Nest tree DBH (cm)	68.2 ± 3.4	62.9 ± 3.1	0.251*
Nest tree height (m)	16.6 ± 0.8	15.7 ± 1.5	0.316*
No. cavities in nest trees	2.7 ± 0.2	2.4 ± 0.3	0.631
No. suitable cavities ha^{-1}	2.8 ± 0.8	1.7 ± 0.5	0.774
Nest height (m) [b]	11.3 ± 0.6	10.5 ± 1.3	0.571
Cavity level diameter (cm) [c]	38.4 ± 2.2	42.0 ± 2.2	0.070
Hole depth/entrance ratio (mm) [c]	0.69 ± 0.03	0.62 ± 0.03	0.117

* Indicates t -tests, otherwise Wilcoxon tests. P-values <0.05 are in bold.

a. For definition, see Table 3; b. only applicable to used sites; c. only applicable to accessible nests.

After elimination of highly-correlated habitat variables, five variables that influenced nest site selection with P-value ≤ 0.25 in univariate logistic regressions were selected for multiple logistic regressions. These included live tree canopy cover, grass cover, total basal area of large trees, nest tree decay class, and density of suitable cavities. The global model containing the five variables fitted the data well with P-values for lack-of-fit >0.35. To evaluate the relative importance of each of the five variables, I generated five reduced models by removing the variable being evaluated from the global model, and then summed the AICc weight of all models that retained the selected variable (Table 5a). Each reduced model thus represents a hypothesis that the removed variable does not significantly influence nest site selection. Nest tree decay class was the top-ranked variable (relative importance scored 0.99, positively correlated), followed by total basal area of large trees (0.97, positively correlated), grass cover (0.81, positively correlated), live tree canopy cover (0.71, negatively correlated) and density of suitable cavities (0.69, positively correlated). The best model contained all variables except density of suitable cavities and received slightly higher support than did the second model (Table 5a).

Since the best model did not receive overwhelming support, model averaging was adopted for parameter estimation for the final model (Table 6a). The confidence intervals of the coefficients for live tree canopy cover, grass cover and density of suitable cavities included zero. Thus, their effects on nest site selection were uncertain compared to nest tree decay class and total basal area of large trees.

Table 5. Model ranking for Lewis's Woodpecker's (a) nest site selection and (b) nest survival. n = sample size; K = number of parameters in the model; -2LN(L) = maximum likelihood of the model; AICc = Akaike's Information Criterion for small samples; ΔAICc = adjusted AICc relative to the top model; wi = AICc weight; ND = nest tree decay class; BA =total basal area of large trees (m^2/ha); TC = live tree canopy cover (%); GC = grass cover (%); SD = density of suitable cavities; CI = clutch initiation day; CS = cavity security index; NH = nest height; + indicates an additive effect of the variable.

a) Nest site selection models

Model	n	K	-2LN(L)	AICc	ΔAICc	Wi
ND+BA+TC+GC	78	5	68.90	79.73	0.00	0.31
ND+BA+GC+SD	78	5	69.00	79.83	0.10	0.29
ND+BA+TC+SD	78	5	69.83	80.66	0.93	0.19
ND+BA+TC+GC+SD	78	6	67.76	80.95	1.21	0.17
ND+TC+GC+SD	78	5	73.73	84.56	4.83	0.03
BA+TC+GC+SD	78	5	76.87	87.70	7.97	0.01
Constant	78	1	100.03	102.09	22.35	0.00

b) Nest survival models

Model	n	K	-2LN(L)	AICc	ΔAICc	Wi
CI+CI^2+CS	44	5	69.44	81.02	0.00	0.47
CI+CI^2+CS+ND	44	6	68.65	82.92	1.90	0.18
CI+CI^2+CS+BA	44	6	68.78	83.05	2.03	0.17
CI+CI^2+CS+NH	44	6	68.94	83.21	2.19	0.16
CI+CI^2+CS+NH+ND+BA	44	8	67.30	87.42	6.39	0.02
Constant	44	2	98.68	102.97	21.95	0.00

Table 6. Parameter estimates for the final models for Lewis's Woodpeckers' (a) nest site selection and (b) nest survival, using model averaging.

a) Final model for nest site selection

Parameter	Estimate	Lower 95% C.I.	Upper 95% C.I.	Odds Ratio
Intercept	-3.201	-6.921	0.520	0.041
*Live tree canopy cover (%)	-0.017	-0.067	0.032	0.983
*Grass cover (%)	0.017	-0.047	0.082	1.018
Total basal area of large trees (m^2/ha)	0.655	0.115	1.195	1.925
Nest tree decay class	0.820	0.238	1.402	2.271
*No. suitable cavities ha^{-1}	0.107	-0.176	0.390	1.113

b) Final model for nest survival

Parameter	Estimate	Lower 95% C.I.	Upper 95% C.I.
Intercept	2.639	0.066	5.212
*Total basal area of large trees (m^2/ha)	-0.016	-0.107	0.074
*Nest tree decay class	-0.039	-0.243	0.165
Clutch initiation date	-0.080	-0.154	-0.007
(Clutch initiation date)^2	0.008	0.002	0.015
Cavity security index	3.922	0.153	7.691
*Nest height (m)	0.006	-0.034	0.046
δ	0.810	0.401	1.219
β=1/ δ	1.235	0.066	5.212

* indicates that 95% confidence intervals include zero.

Nest survival

To compare nest survival patterns, I generated Kaplan-Meier nest survival curves for 2004 and 2005 that described the probability that a nest survives from the first egg laid until or beyond a given nest age (Fig. 3). In both years the birds experienced similar temporal patterns in nest survival in which nest survival rate

steadily declined between 8 and 30 days of age and then stabilized after 30 days. The data were pooled and fitted to the two-parameter Weibull distribution. The shape parameter (β) was estimated to be 0.996, indicating that the daily nest survival slowly increases with nest age when habitat variables were not taken into account (see Appendix).
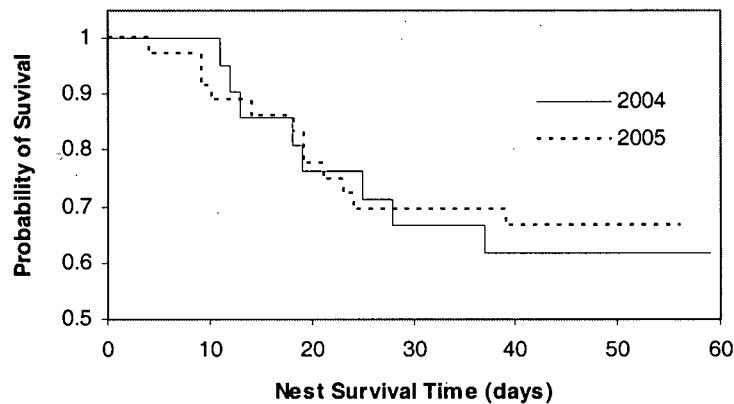
Figure 3. Annual nest survival patterns for Lewis's Woodpecker. The nest survival time refers to nest age, indicating the probability for a nest to survive from laying the first egg through to or beyond a given age.

Using nest survival models I tested my second hypothesis that habitat variables that determine nest site selection further influence nest survival. I first generated a global Weibull regression model that incorporated the two variables shown to have significant effects on nest site selection (i.e. total basal area of large trees and nest tree decay class) as well as clutch initiation date, nest height and cavity security index. I then proposed four reduced models of special interest for model ranking (Table 5b). The best model contained a linear and a

quadratic effect of clutch initiation date as well as a linear effect of cavity security index. This model was substantially better than the other candidate models (AICc weight = 0.47, equivalent to >2.6 times as much support as other models). Since the best model did not receive overwhelming support, model averaging method was used for parameter estimation (Table 6b). Effects of clutch initiation date (both linear and quadratic) and cavity security index were significant, while effects of total basal area of large trees, nest tree decay class and nest height were not significant. The model predicts that birds that begin laying around mid June are more likely to suffer failure compared to those laying earlier or later, and as cavity security index increases, so does survival probability (Fig. 4).
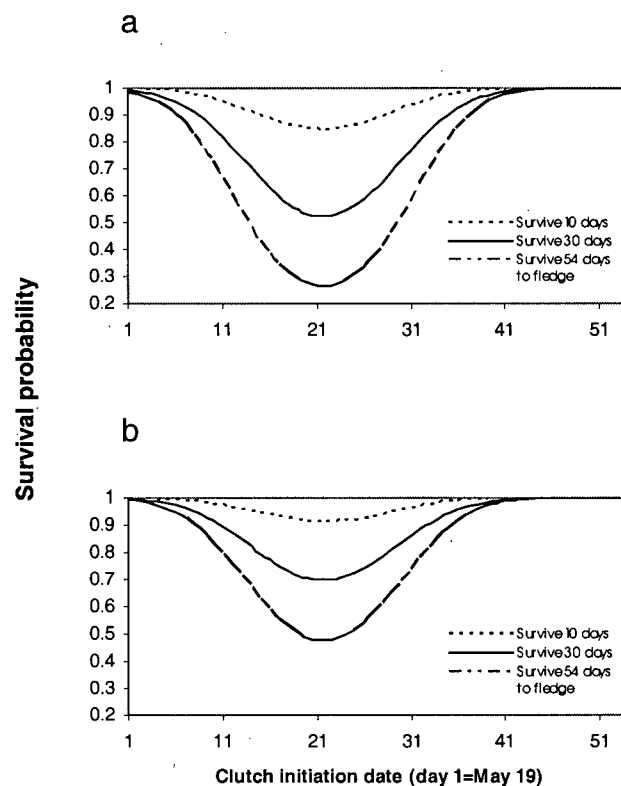

Figure 4. Lewis's Woodpeckers' predicted nest survival in relation to clutch initiation date and cavity security index (CS); (a) when CS=0.68 (=average); (b) when CS=0.8 (>average).

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Production rate

Clutch size and fledged brood size varied with clutch initiation date (Fig. 5). Given limited sample size, I examined influence of clutch initiation date and habitat variables on clutch size and fledgling production using univariate ordinal logistic regression models without considering combined effects of habitat variables. If the birds started laying late, the probability of producing a large clutch was significantly reduced (R^2=0.22, df=1, p=0.0001, n=31 nests), and also a large brood (R^2=0.05, df=1, p=0.04, n=28 nests). No habitat variables except elevation influenced clutch size or fledged brood size. Elevation and fecundity interacted: Lewis's Woodpeckers nesting at higher elevations started laying later (R^2 =0.39, P=0.01), and thus had smaller clutch sizes (R^2=-0.43, P=0.02).

Finally, I estimated annual production rate of Lewis's Woodpeckers in relation to clutch initiation date and cavity security index by multiplying nest success by average number of female fledglings produced per successful nest (Fig. 6). Since the nest success can be predicted from clutch initiation date and cavity security index (Fig. 4), and similarly, the female fledglings produced per successful nest can be predicted from clutch initiation date (Fig. 5), the two functions can be combined to predict the relationship between production rate and clutch initiation date in relation to cavity security index. This relationship suggested that early breeding (before June) allowed Lewis's Woodpeckers to gain substantially higher fitness than later breeding, and that cavity security index was particularly important to birds initiating clutches in the mid-season (ca. June 10).
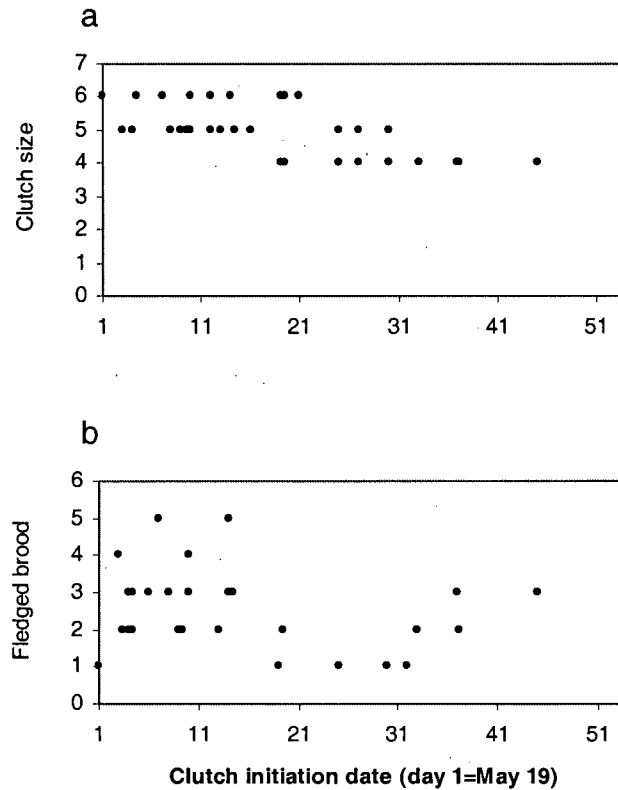
Figure 5. Patterns of (a) clutch size and (b) fledged brood size per successful nest in relation to clutch initiation date.

Clutch initiation date (day 1=May 19)
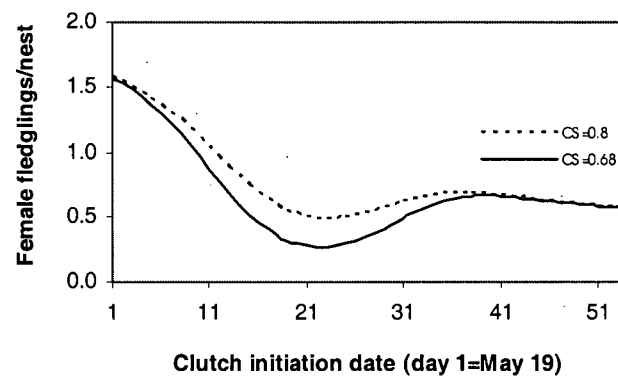
Figure 6. Predicted production rate in relation to clutch initiation date and cavity security index, calculated by multiplying predicted nest success by predicted average female fledglings produced per successful nest. The solid line and broken line denote predicted production rates when cavity security index (CS) equals 0.68 (average) and 0.8 (>average) respectively.

Discussion

Breeding habitat

In the South Okanagan Valley, Lewis's Woodpeckers bred at elevations from 330 to 1100m, in habitats including, at the valley bottom, open riparian cottonwood forests, mixed coniferous-broadleaved woodlands, open ponderosa pine, and mixed ponderosa pine-Douglas fir grassland; on the upper parts of surrounding hills, pure Douglas fir grassland. Live tree canopy cover at used sites ranged from zero in heavily burned areas up to 36% in old growth riparian cottonwood and mixed coniferous-broadleaved woodlands. With increasing elevation, clutch initiation tended to be later and clutch sizes lower.

Although variation of nest success among my study areas was not significant (Table 2), the nest success in the old growth riparian cottonwood and mixed woodlands (e.g. SunOka and surrounding areas) with relatively dense undergrowth and canopy cover tended to be higher than in dry open ponderosa pine and Douglas fir grassland habitats (e.g. Chopaka). The old growth riparian habitats provided the species with abundant suitable cavities and also plenty of flying insects and fruits. Unfortunately, this type of habitat accounts for only a small fraction of habitats available to Lewis's Woodpeckers and continues to disappear in the South Okanagan Valley (Cooper et al. 1998).

Factors determining nest site selection

A suite of habitat features appeared to be correlated with nest site selection in univariate analyses. However, only two of these features, i.e. nest tree decay class and total basal area of large trees (associated with density of large

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decayed trees), were important in determining nest site selection in multiple logistic regression analysis. Decayed trees were preferred nesting substrates for Lewis's Woodpeckers. Of the total of 57 nests, 22 were located in top-dead trees (decay class 2), 34 in snags (decay classes 3 and 4) and only one in a live tree (decay class 1). If a tree increases one level in decay class, I predicted that it would be 2.3 times more likely to be used. Decayed trees with heart rot are important habitat components for most cavity nesting species (Raphael and White 1984), especially weak excavators, such as Lewis's Woodpeckers (Bock 1970), chickadees (*Poecile sp.*) and nuthatches (*Sitta sp.*; Martin et al. 2004). For Lewis's Woodpeckers, advanced decay status can make cavity excavation easier, provide nest-lining materials, allow for food caching and increase drumming volume.

Total basal area of large trees was also important for nest site selection. If total basal area of large trees ha^{-1} increases by one square meter, my model predicted that the site would be 1.9 times more likely to be used. Snag size, especially diameter, and to a lesser extent height, are thought to be important characteristics for cavity nesting birds. Generally, larger diameter snags are used in preference to smaller diameter snags (Mannan et al. 1980; Raphael and White 1984). I detected a significant correlation between number of suitable cavities and density of large trees ($R^2=0.33$, $P<0.0001$), suggesting that large trees were more likely to have developed the heart rot that enables larger cavity nesting birds to excavate suitable cavities.

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Density of suitable cavities at used sites was much higher than at random sites and mostly concentrated in the nest trees. However, this variable was not a reliable predictor of nest site selection in the multiple logistic regression models, probably because high density of suitable cavities may attract not only Lewis's Woodpeckers but also cavity competitors and nest predators. Lewis's Woodpeckers often (ca. 48% of cases) shared the same nest trees with European Starling (*Sturnus vulgaris*), Northern Flicker and American Kestrel (*Falco sparverius*). The presence of multiple cavities and coexistence of different cavity nesters on the same nest trees may reflect limited numbers of suitable trees for excavation, or alternatively, the balance between benefits in lowering nest predation efficiency and negative effects of interaction among coexisting species (Martin 1988; Martin 1993).

Burned forests have been described as ephemeral source habitats for some cavity nesting species because early post-fire habitats provide an increase in nesting and foraging opportunities and a reduced risk of nest predation compared to unburned habitats (Saab et al. 2004; Saab and Vierling 2001). Intensity of fires and number of years post-fire strongly influence occupancy of nest cavities for both strong and weak excavators. Wildfires are an important ecological factor for Lewis's Woodpeckers, characterized as "burn specialists" due to their preference for nesting within burned forests (Bock 1970; Saab and Vierling 2001). Although I was unable to directly study the effects of wildfires on habitat selection of Lewis's Woodpeckers, I recorded a substantial increase in breeding pairs in the Vaseux Lake area in 2005 after the 2003 wildfire. When

comparing with the 10 year old burn in Kipoola, I found that the newly burned habitat did not have higher nest success, possibly due to the relatively low fire intensity in the Vaseux Lake area and heterogeneity other than fires between the two areas. Alternatively, the fires only enhanced some aspects of nesting conditions but did not substantially alter the nest predator community, which formed the major cause of nest failures in this study.

Other factors were also correlated with nest site selection in the univariate analysis but did not have high predictive power in the multivariate analysis. For example, shrub and grass cover were thought to be important components of breeding habitats of Lewis's Woodpeckers, providing substrates for arthropod prey (Bock 1970; Linder and Anderson 1998; Saab and Vierling 2001; Vierling 1997). My results showed that grass cover was significantly higher at used sites than at random sites but its effect on nest site selection in the multiple logistic regressions was not significant.

Factors affecting reproductive success

I found no evidence that the habitat features that affect nest site selection were correlated with nest success. This appears to contradict the theoretical expectation that birds select nest sites that maximize their reproductive success. Many other studies also report a lack of correlation between nest site selection and reproductive success (Davis 2005; Hooge et al. 1999; Nguyen et al. 2003; Pribill 1998). A reasonable explanation for Lewis's Woodpeckers is that some habitat features may act as prerequisites for breeding but are not further associated with nest success. In other words, Lewis's Woodpeckers may

experience different limitations to nest site selection and nest success. Nest site selection appeared to be based on both plot and tree-level habitat features (e.g. total basal area of large trees and nest tree decay class) all correlated with locating a limiting resource: nest cavities. Once a nest was initiated, nest success was primarily affected by clutch initiation date (i.e. individual behaviours), cavity security index (i.e. cavity features) and/or other unmeasured ecological factors (e.g. competition, weather, food abundance and functional response of nest predators to variation in food availability). These stochastic factors may substantially influence nest success and thus mask the potential effects of nest site selection on nest success under some situations.

Cavity dimensions were important as nests with higher cavity security index experienced higher daily nest survival. Since I did not compare cavity security index of used cavities vs. random cavities, it was unclear whether birds evaluated this feature at the nest site selection stage or whether some individuals were forced to occupy risky suboptimal cavities. I found the optimal cavity was deep with a small entrance, presumably a shape that excludes large-bodied nest predators (Martin et al. 2004). The occupancy of suboptimal cavities may demonstrate the opportunistic characteristics of Lewis's Woodpeckers in reproduction as a weak cavity excavator.

Clutch initiation date was found to significantly influence nest success of Lewis's Woodpeckers. Early and late clutch initiations had higher nest success than intermediate initiation dates. This pattern may result from seasonal variation in nest predation (Dinsmore et al. 2002). However, late clutch initiations may

result in poor conditions of both juveniles and adults due to limited time for migration preparation. To deal with this issue, the later breeders may shorten their breeding cycle by reducing clutch sizes. As expected, in my study, late breeders were less likely to produce a large clutch than early breeders. Taking together the nest success and fledged brood size, I found that early clutch initiations allowed Lewis's Woodpeckers to gain the highest fitness in terms of production rate, similar to Northern Flickers (Wiebe 2003).

Compared to the Idaho population (Saab and Vierling 2001), the South Okanagan Valley population had a lower overall nest success (Mayfield estimates: 0.52 ± 0.08 S.E in the South Okanagan Valley vs. 0.78 ± 0.06 S.E. in Idaho) but more fledglings per successful nest (2.62 ± 0.22 S.E. in the South Okanagan Valley vs. 1.78 ± 0.05 S.E. in Idaho). Consequently, both populations had similar annual production rates (0.68 ± 0.12 S.E. female fledglings per nest in the South Okanagan Valley vs. 0.69 ± 0.06 S.E. in Idaho). The Idaho population was considered as a source population because of its high annual production vs. assumed adult and juvenile mortality (Saab and Vierling 2001). If their assumptions regarding adult and juvenile mortality are plausible and apply to my study areas, the South Okanagan Valley population would currently be a source population. To clarify this conclusion, a priority for further research should be to obtain information on adult and juvenile mortality.

Cavity competition

Limited availability of suitable cavities in the South Okanagan Valley may limit Lewis's Woodpecker populations due to cavity competition and natural reduction

of snags. Lewis's Woodpeckers are weak excavators and often rely on old cavities initially excavated by other primary cavity nesters, such as Northern Flickers, in the South Okanagan Valley. Therefore, Lewis's Woodpeckers' nest sites are often associated with Northern Flickers and constrained by competition from other secondary cavity nesters such as American Kestrel (*Falco sparverius*), Bluebird (*Sialia sp.*) and European Starling. In 2005, 43% of cavities used by Lewis's Woodpeckers in 2004 were occupied by European Starlings that started breeding earlier than Lewis's Woodpeckers, especially at low elevation. Thus cavity availability may be a key limiting factor for Lewis's Woodpeckers at low elevations. In 2005 in Chopaka study area, I observed a Lewis's Woodpecker trying to usurp a cavity from a European Starling by ejecting its eggs. However, the European Starling won the cavity by effectively defending it from inside. I also observed a Lewis's Woodpecker cleaning a cavity after a brood of European Starlings had fledged, trying to reuse it. In this case, the Lewis's Woodpecker later abandoned the cavity. On several occasions, I observed that Northern Flickers competed for cavities with Lewis's Woodpeckers. Northern Flickers, though frequently excavating new cavities for breeding, may generate substantial competition pressure to Lewis's Woodpeckers under some situations (the cavity reuse rate for Northern Flickers ranges for 5%-65%; Wiebe 2006).

Management recommendations

Based on this study, conservation efforts for this species should focus on increasing or retaining suitable cavities close to good foraging areas. To increase suitable cavities, some proposals suggest increasing wildlife trees and cavities

artificially. Lewis's Woodpeckers are unlikely to accept artificial cavities unless the cavities contain a rotten interior from which to dig woodchips as nest materials (X. Zhu, pers obs.). Thus, preserving natural cavities and suitable nest trees should be a priority in the management plan of the species. The density of snags can be increased through girdling the bottom of or blasting the top of large trees. However, the manmade snag resources may not be directly usable by Lewis's Woodpeckers without participation of other primary cavity excavators, such as Northern Flicker (Martin et al. 2004), since Lewis's Woodpeckers rarely initiate new cavities. Thus, conservation of Lewis's Woodpeckers must also consider the larger cavity nester community in the grassland habitats. Even if Lewis's Woodpeckers can not directly use artificial cavities or fresh snags, increasing artificial cavities and fresh snags may indirectly benefit Lewis's Woodpeckers by increasing search costs of nest predators (Martin 1993) or reducing inter-specific competition for nest sites.

Finally, this study shows that cavity security index substantially impacts nest success of Lewis's Woodpeckers especially during the peak of nest predation and that foraging conditions (e.g. the distance from nest trees to good foraging areas) are important to nest success. Management actions and habitat assessment should therefore also consider the importance of cavity features and the spatial pattern of foraging patches and nesting patches.

This study is the first comprehensive study of the vital rates and habitat requirements of Lewis's Woodpeckers in the South Okanagan Valley. I have shown that nest site selection can readily be predicted by a number of easily-

measured habitat variables whereas nest success largely depends on complicated ecological interactions among nest predators, cavity competitors, primary cavity excavators, breeding behaviours and cavity features. It is hoped that these results will aid in habitat assessment and management leading to recovery of this species.

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Chapter 3: General Discussion and Conclusions

Nest site selection and reproductive success

I found that Lewis's Woodpeckers actively selected nest sites based on several important habitat features. In general, they nested in or adjacent to open habitats with live tree canopy cover ranging from zero to 36%. Total basal area of large trees (m^2/ha) and nest tree decay class were the most important factors determining nest site selection, i.e., the more decayed large trees the more likely the site would be used. This conclusion is consistent with previous studies (Bock 1970; Linder and Anderson 1998; Sousa 1982; Vierling 1997). Decayed trees provide the species with suitable cavities for nesting and roosting, perches for flycatching, and desiccated cracks for storing food (Bock 1970). Snag size (DBH), and to a lesser extent height, are also thought to be important characteristics related to bird usage. Generally, larger diameter snags are used in preference to smaller diameter snags (Mannan et al. 1980; Milne and Hejl 1989; Raphael and White 1984).

Because Lewis's Woodpecker is a weak cavity excavator and rarely initiates a new cavity even in fairly decayed trees, its preference of decayed trees is perhaps associated with cavities excavated by woodpeckers such as Northern Flickers. Northern Flickers are important primary excavators and thus a keystone species in the cavity nester community in British Columbia (Martin et al. 2004). The abundance of Northern Flickers increases the number of cavities available to Lewis's Woodpeckers and allows co-existence of a large number of secondary cavity nester species (Aitken and Martin 2004).

Habitat features that attract nest site selection of Lewis's Woodpeckers may not guarantee the high nest success. In fact, some factors positively associated with nest site selection may affect nest success negatively. These factors produce misleading cues (ecological "trap") for nest site selection under some circumstances. In this study, nest tree decay class and total basal area of large tree were perhaps such factors, though not statistically significant. These factors attract Lewis's Woodpeckers and may also attract nest predators and cavity competitors that potentially increase the risk of nest failures for Lewis's Woodpeckers when suitable nest trees and cavities are in low density. With suitable nest trees and cavities increasing to a certain level, the rate of nest predation may decrease and nest success may become positively correlated with nest site selection. In order to avoid misleading conclusions about habitat fitness, habitat selection studies must investigate both occurrence (i.e. nest site selection) and consequence (i.e. reproductive success; Jones 2001; Van Horne 1983) across a habitat gradient.

Clutch initiation date and cavity security index were key factors determining nest success of Lewis's Woodpeckers. Early and late clutch initiations allowed the species to have higher nest success than intermediate clutch initiations. Yet, late clutch initiations resulted in smaller clutches and less opportunity to renest if failed, given the relatively short breeding season in the northern range of its distribution and long breeding cycle of Lewis's Woodpeckers. Late clutch initiations may also impact conditions of both adults and juveniles and their post-breeding survival rates, especially if food availability is lower later in the season.

Deep cavities with a small entrance were able to lower predation risk, especially during the peak of nest predation in June. Cavity competition may force some individuals to occupy suboptimal nest sites or to miss the best time for breeding, resulting in lower nest success and production rate. Considering the pattern of nest success and the fact that early clutch initiations were most likely to produce large clutches, I conclude that individuals that start breeding early will gain higher fitness than late breeders.

Recent wildfires appeared to attract breeding pairs but not to significantly improve nest success and production rate in this study. There are two possible explanations that can be considered: first, the fire was not big enough to actually alter the nest predator communities, although it opened up habitats for Lewis's Woodpeckers to use. Secondly, my comparison was made between two different sites but not between pre-fire and post-fire on the same site because the fire happened before my study commenced.

Significance and limitations

My study is of great significance to the conservation of the species. I conducted the first study of the relationship between nest site selection and nest success, and documented nest survival curves for the Lewis's Woodpecker population in the South Okanagan Valley. Secondly, I provided detailed reproductive parameters which can be used for population dynamics and population viability analysis (PVA) for the species. Thirdly, the nest site selection models and nest survival models that I established can be readily used to predict

habitat use and evaluate habitat quality for recovery and management of the species.

On the other hand, my study had some limitations. First, because Lewis's Woodpecker is a rare species, the number of nests found was limited. As is always the case, my sample of nests in the reduced area of distribution may represent a special case for this rare species. Secondly, habitat selection is a complex process, which involves many factors: environmental, behavioural and combined. In my study, I could only consider the simple additive effects of habitat variables due to limitation of sample size. Thirdly, although Weibull-distribution-based survival time analysis has some advantages over Mayfield logistic regression (see Appendix), it can not model quadratic effect of nest age on daily nest survival.

Future research directions:

This study demonstrates the need to consider effects of habitat selection on population dynamics. Habitat selection can influence population dynamics by changing BIDE parameters (birth, immigration, death and emigration). In general, for highly mobile species, the distribution of individuals among different habitats may be determined largely by habitat selection. When a habitat is disturbed, the individuals may redistribute themselves among the remaining habitats, thereby affecting demographic rates in each habitat and population dynamics as a whole (Holt 1987; Kristan 2003; Pulliam and Danielson 1991). In this study, I only considered habitat selection and reproductive success. Many other aspects

regarding population dynamics (i.e. dispersal and mortality) are unclear, which should be addressed in the future study.

A more specific avenue of future research concerns the interaction between Lewis's Woodpeckers and other cavity competitors, especially European Starlings, in relation to habitat features. European Starlings are major cavity competitors of some woodpeckers, including Red-bellied Woodpeckers (*Melanerpesc atolinus*, Ingold 1989), Red-head Woodpeckers (*M. ythrocephalus*, Ingold 1989), Acorn Woodpeckers (*M. formicivorus*, Troetschler 1976), and Gila Woodpeckers (*M. opygialis,* Kerpez and Smith 1990). Nevertheless, it is unclear whether European Starlings represent a substantial threat to Lewis's Woodpeckers. There exists an argument that European Starlings do not constitute a threat to Lewis's Woodpeckers, because the data of the Breeding Bird Surveys and the Christmas Bird Count did not show correlation between Lewis's Woodpeckers' declines and European Starlings' invasion (Koenig 2003). Vierling (1998) suggested that European Starlings were not major nest cavity competitors of Lewis's Woodpeckers in southeastern Colorado because he observed that the latter were dominant in over 90% of the inter-specific interactions with the former and their nesting phenologies did not overlap. He believed that Lewis's Woodpeckers may compensate nest cavity loss by usurping nest cavities from Northern Flickers, Hairy Woodpeckers (*Picoides villosus*), Western Bluebirds (*Sialia mexicana*), and Mountain Bluebirds (*Sialia currucoides*). These reports might have ignored the possibility that cavity occupancy by European Starlings prior to the onset of breeding of Lewis's

Woodpeckers may actually reduce the cavity availability to Lewis's Woodpeckers (in community assembly models this phenomenon is referred to as a "priority effect") and the increased cost for Lewis's Woodpeckers to usurp nest cavities from other species. I observed that Lewis's Woodpeckers appeared to be reluctant to clean up cavities stuffed with nesting material from European Starlings for their own use immediately after European Starlings finished breeding in that cavity. In addition, the Lewis's Woodpeckers' dominance over European Starlings in the inter-specific interaction may not mean that they can successfully usurp nest cavities already occupied by European Starlings. I observed that the apparently subordinate European Starlings were very aggressive and successfully chased away Lewis's Woodpeckers close to their nest cavities during the incubation and nestling stages.

Finally, the ecological role of Lewis's Woodpeckers in the cavity nester community and the natural processes that create suitable habitats for all cavity-nesting birds in the grassland forest ecosystem are important directions for future research. Forest management practices intended to conserve a diverse wildlife community, and the processes that shape this community, must be based on quantitative assessments of these complex ecological interactions and processes. Research in these aspects will enable insights into ecological functions of different components of the cavity nester community and expand the scientific basis for conservation of Lewis's Woodpeckers in an integrated ecosystem.

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Appendix

Logistic regression has frequently been used to analyze the effect of habitat features on nest survival (Shaffer 2004). One of the important assumptions for logistic regression is that all nests sampled are independent of one another so that a binomial distribution can be used for parameter estimation. Such nest-based method has two major limitations. First, it can not include nests with uncertain fate. Secondly it can not make full use of information obtained from repeated nest visits to estimate daily nest survival. Dinsmore (2002) and Hazler (2004) integrated Mayfield method into logistic regression to develop so-called Mayfield logistic regression. This method takes observation days as sample units and assumes that the result of each observation day at a nest is an independent event as in the Mayfield method. Thus, nests with uncertain fate can be included and daily nest survival can be estimated as a function of various factors. However, this assumption is unwarranted because it may result in pseudoreplication. To avoid this fundamental mistake of the Mayfield logistic regression and the limitations of logistic regression, I applied Weibull regression, which takes nests as independent sample units, for nest survival modeling. Unlike logistic regression and Mayfield logistic regression, Weibull regression takes the probability function of nest survival time as the dependent variable and uses a Weibull distribution for parameter estimation. Therefore, information obtained from repeated nest visits for all nests can be included. This was particularly appropriate for me to model the conditional probability that a nest survives a given time with respect to various factors. Specifically, I fitted my data with a two-parameter Weibull distribution that takes the form of: $S(t) = e^{(-(t/\alpha)^{\beta})}$,

where t stands for nest age (days), α and β stand for scale parameter and shape parameter respectively (Pinder et al. 1978). I assumed that each nest follows an independent Weibull distribution, the scale parameter (α) of which can be determined by habitat features, year and laying day via a link function: $\alpha = e^{(b0+b_i X_i)}$. Since S(t) was interpreted as the conditional probability that a nest survives from onset of breeding (date of laying the first egg) to a given nest age under certain conditions determined by α, we could estimate daily nest survival rate (DSR) at any given nest age as DSR(t)=S(t+1)/S(t), and daily nest mortality rate (DMR) at any given nest age as DMR(t)=1-DSR(t)=1-S(t+1)/S(t). In this way, I actually relaxed two assumptions as in the Mayfield method: (1) daily nest survival rate is constant over breeding season or certain nesting stages; and (2) all nests are homogenous; i.e. all nests are subject to the same rate of mortality (Mayfield 1975).