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Habitat selection and use by the Dusky Flycatcher (Empidonax oberholseri) at multiple scales: Implications for habitat-based methods for population viability analysis

Andrew James Kroll
The University of Montana

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HABITAT SELECTION AND USE BY THE DUSKY FLYCATCHER (*EMPIDONAX OBERHOLSERI*) AT MULTIPLE SCALES: IMPLICATIONS FOR HABITAT-BASED METHODS FOR POPULATION VIABILITY ANALYSIS

by

Andrew James Kroll

B.A. St. John's College, Annapolis, MD. 1994

M.S. New Mexico State University, Las Cruces, NM. 2001

presented in partial fulfillment of the requirements

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Approved by:

Jack Ward Thomas

Chairperson

Dean, Graduate School

11-8-04

Date

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Habitat selection and use by the Dusky Flycatcher (*Empidonax oberholseri*) at multiple scales: implications for habitat-based methods for population viability analysis (179 pp.)

Committee Chair: Jack Ward Thomas JWT

Species viability is a primary component in the maintenance and enhancement of populations and a critical component of ecological sustainability. While species viability is a readily defined concept, the tools used to assess species viability are less certain and subject to significant controversy.

Viability may be analyzed through either demographic or habitat-based methods, but habitat-based methods are potentially more valuable because the interaction of a species with its habitat is recognized as underlying all efforts to maintain and enhance viability. In addition, operational planning for most land management agencies is conducted with respect to habitat alteration and mitigation and not through direct assessments of demographic changes.

I evaluated the assumptions of a habitat-based framework for the assessment of species viability. Specifically, I addressed the relationships between measures of habitat quality, territory size, density, and vegetation structure using the Dusky Flycatcher (*Empidonax oberholseri*) as a test species. I modeled habitat selection and use at four different spatial scales. Patterns of habitat selection and use were evaluated with respect to density and measures of reproductive success at all four spatial scales.

My results indicated that a habitat-based framework is tenable for species viability planning. However, I stress that patterns of habitat selection and use must be examined with respect to those fitness attributes–primarily reproduction and survival–that contribute significantly to individual fitness and population growth. I stress that all inferences and implications drawn from habitat-based frameworks must be made with reference to specific spatial scales of habitat selection and use, as my results indicate that differential effects may occur at different scales.

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Table of Contents

Abstract....ii
Acknowledgements....iii
Table of Contents....iv
List of Tables....v
List of Illustrations....vii

Chapter One: Introduction....1

Chapter Two: Evaluating habitat quality for the Dusky Flycatcher (*Empidonax oberholseri)* at the site scale: the relationships among nesting success, productivity, clutch size, egg weight, territory density, and vegetation structure....9

Chapter Three: Habitat selection and use, territory size, and consequences for reproductive success in the Dusky Flycatcher (*Empidonax oberholseri*)....46

Chapter Four: Model selection for Dusky Flycatcher (*Empidonax oberholseri)* nesting success at the nest-site and nest-patch scales....99

Chapter Five: Development and testing of habitat models for the Dusky Flycatcher (*Empidonax oberholseri*)....135

Chapter Six: Conclusion....164

Appendices....179

List of Tables

Chapter Two

Table 1: Pearson's correlation coefficients (r) for measures of reproductive success and vegetation structure for eight sites, central Idaho, 2002 and 2003....23

Chapter Three

Table 1: Candidate models for Dusky Flycatcher territory selection, central Idaho, 2002 and 2003....64
Table 2: Candidate models for Dusky Flycatcher territory success, central Idaho, 2002 and 2003....65
Table 3: Summary of information-theoretic model selection results for Dusky Flycatcher territory selection, central Idaho, 2002 and 2003....68
Table 4: Summary of cross-validation results for Dusky Flycatcher territory selection, central Idaho, 2002 and 2003....69
Table 5: Summary of information-theoretic model selection results for Dusky Flycatcher territory success, central Idaho, 2002 and 2003....70
Table 6: Parameter estimates from the best-supported territory success model (Model 17a) for Dusky Flycatchers, central Idaho, 2002 and 2003....71
Table 7: Parameter estimates for a model with year and density effects for Dusky Flycatchers, central Idaho, 2002 and 2003....71
Table 8: Means, standard errors, and 95% confidence intervals for six vegetation variables by territory success for Dusky Flycatchers, central Idaho, 2002 and 2003....72
Table 9: Summary of cross-validation results for Dusky Flycatcher territory success, central Idaho, 2002 and 2003....73
Table 10: Pearson's correlations (r) between mean territory size, variance in territory size, measures of reproductive success, vegetation structure, and density for Dusky Flycatchers, central Idaho, 2002 and 2003. Ninety-five percent confidence intervals were calculated for all correlations >|0.50|....75
Table 11: Mean and 95% confidence interval (back-transformed) for size (ha) of unsuccessful and successful Dusky Flycatcher territories, central Idaho, 2002 and 2003....76

Chapter Four

Table 1: Models for Dusky Flycatcher nesting success at the nest-site scale, central Idaho, 2002 and 2003....111
Table 2: Models for Dusky Flycatcher nesting success at the nest-patch scale, central Idaho, 2002 and 2003....112
Table 3: Summary of information-theoretic results for Dusky Flycatcher nesting success at the nest-site scale, central Idaho, 2002 and 2003....115
Table 4: Summary of information-theoretic results for Dusky Flycatcher nesting success at the nest-patch scale, central Idaho, 2002 and 2003....117

Table 5: Parameter estimates from the best three nest-patch models for nesting success in Dusky Flycatchers, central Idaho, 2002 and 2003..........118
Table 6: Summary of cross-validation results for Dusky Flycatcher nesting success at the nest-site scale, central Idaho, 2002 and 2003..........119
Table 7: Summary of cross-validation results for Dusky Flycatcher nesting success at the nest-patch scale, central Idaho, 2002 and 2003.......120

Chapter Five

Table 1: Candidate Dusky Flycatcher territory scale habitat models based on data from central Idaho, 2002 and 2003....................................148
Table 2: Candidate Dusky Flycatcher nest-patch habitat models based on data from central Idaho, 2002 and 2003..148
Table 3: Pearson's correlation coefficients (r) with 95% confidence intervals for site HSI scores (eight sites by two years), measures of reproductive success, and density for Dusky Flycatchers, central Idaho, 2002 and 2003...151
Table 4: Summary of cross-validation results for Dusky Flycatcher territory selection habitat models, central Idaho, 2002 and 2003..................152
Table 5: Summary of cross-validation results for Dusky Flycatcher nest-patch use habitat models, central Idaho, 2002 and 2003.......................153

List of Illustrations

Chapter Two

Figure 1: Nesting success (Mayfield estimator) and 95% confidence intervals for Dusky Flycatchers by site and year, central Idaho, 2002 and 2003 (sample sizes are above error bars)....20
Figure 2: Annual reproductive success (Murray 1992,2002) and 95% confidence intervals for Dusky Flycatchers by site and year, central Idaho, 2002 and 2003 (sample sizes are above error bars)....21
Figure 3: Fledglings per hectare (95% confidence intervals for means by year) for Dusky Flycatchers by site and year, central Idaho, 2002 and 2003 (total number of fledglings is above each site by year)....22
Figure 4: Mean clutch size with 95% confidence intervals for Dusky Flycatchers by site and year, central Idaho, 2002 and 2003 (sample sizes are above each site by year)....24
Figure 5: Mean egg weight with 95% confidence intervals for Dusky Flycatchers by site and year, central Idaho, 2002 and 2003 (sample sizes are above each site by year and for totals)....25
Figure 6: Territories per hectare (with 95% confidence intervals for means by year) for Dusky Flycatchers by site and year, central Idaho, 2002 and 2003 (total number of territories is above each site and for totals)...26
Figure 7: The number of fledglings per hectare vs. the number of territories per hectare on eight sites for two years, central Idaho, 2002 and 2003...27

Chapter Three

Figure 1: Mean length of nestling stage and 95% confidence intervals for Dusky Flycatchers by site and year, central Idaho, 2002 and 2003 (sample sizes are above each error bar)....52
Figure 2: Histogram of territory size (ha) for 107 Dusky Flycatcher territories, central Idaho, 2002 and 2003....74
Figure 3: Mean log territory size (ha) total, total by year, and by site and year for Dusky Flycatchers, central Idaho, 2002 and 2003....75
Figure 4: Mean territory size (ha; back-transformed) by number of nestlings and number of fledglings for Dusky Flycatchers, central Idaho, 2002 and 2003 (sample sizes above error bars)....77

Chapter Four

Figure 1: Mean length of nestling stage and 95% confidence intervals for Dusky Flycatchers by site and year, central Idaho, 2002 and 2003 (sample sizes are above error bars)....123

Chapter Five

Figure 1: Histogram of HSI territory scores from initial Dusky Flycatcher HSI model validated with data from central Idaho, 2002 and 2003........151

Chapter One: Introduction

The maintenance and enhancement of species populations is a primary component of ecological sustainability. Species viability is a critical concept in the maintenance and enhancement of populations. A viable species was defined by the December 2002 draft version of the USDA Forest Service planning regulations as "a species consisting of self-sustaining and interacting populations that are well distributed through the species' range. Self-sustaining populations are those that are sufficiently abundant and have sufficient diversity to display the array of life history strategies and forms to provide for their long-term persistence and adaptability over multiple generations."

However, scientifically-rigorous methods for the assessment of species viability are not so readily defined. Genetic analyses, demographic evaluations, and habitat assessments have all been utilized. Demographic evaluations serve as the foundation for population viability analysis (PVA), a technique that has received much recent attention (Boyce 1992, Beissinger and Westphal 1998, McCarthy et al. 2000, Beissinger and McCullough 2002). However, the appropriateness of demographic evaluations–those that require data on parameters such as birth, death, survival, and dispersal rates–for land management planning efforts, which often focus on the spatial and temporal configuration of habitat, is questionable (Gilpin and Soulé 1986, Boyce 1992, Boyce et al. 1994, Raphael and Marcot 1994, Samson 2002). Additional questions have been raised concerning the large confidence intervals of PVA risk metrics (Fieberg and Ellner 2000), the accuracy of model parameters as a result of sampling error (Ludwig 1999), and the difficulty of forecasting population dynamics over even brief time scales (Belovsky et al. 1999). In addition, studies that validate model parameters with large data sets over extended time periods have not been conducted (Holmes and Fagan 2002). Others have argued that PVA is a robust technique and that the problems associated with PVA result from application in inappropriate circumstances (Reed et al. 2002).

The interaction of a species and its habitat is recognized as underlying all efforts to maintain species viability. As a result, the need exists for linking the assessment of viability to estimates of present and projected habitat requirements (Rodenhouse et al. 1997, Dreschler and Wissel 1998, Franklin et al. 2000). The importance of habitat-based PVA was discussed by Noon et al. (1999), who stated that "the deterministic processes leading to habitat loss and fragmentation may dominate stochastic demographic effects in influencing population persistence." As land management agencies focus on future landscape use and habitat conditions, methods of projecting future habitat conditions related to species viability may become requisite tools. Habitat-based PVAs (Noon et al. 1999) and spatially-explicit PVAs (Akçacaya et al. 1995, McCarthy et al. 2000) relate species demographic parameters to habitat conditions. However, they are limited by the logistical and technical data requirements of PVAs. Habitat-based approaches to species viability are needed for the designation of critical habitat and for determining how habitat alteration will influence a species' viability (Thomas 1982, Roloff and Haufler 2002).

Roloff and Haufler (1997, 2002) described a method for assessing home range distributions and qualities for a species in a planning landscape in which a habitat-based, spatially-explicit approach to species viability may be applied. The framework developed by Roloff and Haufler (1997) involves (1) conducting a habitat assessment for the planning landscape to determine the contribution of each mapping unit to the quality and quantity of habitat for a species of interest; (2) establishing the relationship between habitat quality and the size of individual or pair home ranges; (3) evaluating the resulting habitat map to determine the size and configuration of home ranges; and (4) evaluating the number, quality, and distribution of home ranges relative to species viability needs. As a critical component of this framework, Roloff and Haufler (1997) suggested examining individual home ranges to determine if a relationship exists between habitat quality (defined by a priori criteria), home range size, and observed fitness parameters (e.g., number of offspring, adult survival, etc.). This method has not received empirical testing.

Objectives

This project was initiated to evaluate the assumptions used in the habitat-based approach to species viability described by Roloff and Haufler (1997, 2002). These general assumptions are that (1) habitat quality can be defined a priori (e.g., habitat quality is a direct function of vegetation composition and structure); (2) territory sizes are distributed along a habitat quality gradient, with the smallest territories occurring in the highest quality habitat; and (3) individuals with similarly sized territories will exhibit similar fitness attributes, with the smallest territories exhibiting the highest reproductive and survival rates. The Dusky Flycatcher (*Empidonax oberholseri*) was selected as an appropriate species to investigate these assumptions. The general objectives of this project were to:

(1) examine the relationship between territory size, vegetation composition and structure, density, and fitness correlates such as clutch size, egg mass, and the number of fledglings produced per breeding female;
(2) examine patterns of habitat selection and use at the nest-site, nest-patch, and territory scales;
(3) test and refine a habitat model for the Dusky Flycatcher in central Idaho.

Specific objectives were to (1) locate and monitor nests of Dusky Flycatchers at 8 different study sites to determine nesting success, average clutch weight, and adult survival; (2) determine the territory size of nesting pairs; (3) determine if vegetation variables were associated with nesting success at the nest site, nest patch, territory, and study site scales; (4) determine if vegetation variables differed between use vs. non-use areas; (5) determine if territory size was associated with vegetation variables at the territory scale; (6) determine if the number of fledglings was associated with vegetation variables at the territory scale; and (7) determine if associations existed between territory size, clutch size, and other fitness attributes.

In this report, I present the results of research efforts that address these objectives. Chapter 2 examines the relationship between vegetation structure and measures of habitat quality (general Objective 1). Chapter 3 examines patterns of habitat selection at the territory-scale and the relationships between vegetation structure, the density of breeding pairs, territory size, and reproductive success (general Objectives 1 and 2). Chapter 4 examines patterns of habitat use at the nest-site and nest-patch scales and their associations with reproductive success (general Objective 2). Chapter 5 tests a habitat model that was developed for the Dusky Flycatcher based on information from other studies, presents and tests additional habitat models, and suggests how these models may be used in management programs (general Objective 2). I conclude the report by discussing these results in the context of the habitat-based viability framework.

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Chapter Two: Evaluating habitat quality for Dusky Flycatchers (*Empidonax oberholseri*) at the site scale: the relationships among nesting success, productivity, clutch size, egg weight, territory density, and vegetation structure

ABSTRACT

The evaluation of habitat quality is a principal component of effective wildlife management. Areas of high quality habitat are expected to support higher densities and promote greater reproductive success and survival than areas of lower quality habitat. I examined the relationships between vegetation structure, density of breeding conspecifics, and reproductive success for the Dusky Flycatcher (*Empidonax oberholseri*) at eight forest sites in central Idaho in 2002 and 2003. Nesting success, annual reproductive success, and the number of fledglings per hectare were positively associated with greater understory diversity, an important habitat attribute for the Dusky Flycatcher. The number of breeding territories and the number of fledglings per hectare were positively associated, suggesting that density determined the reproductive success of the Dusky Flycatcher when expressed as young per unit area. Reproductive success expressed as young produced per breeding pair or young produced per nesting attempt did not differ significantly across sites. Mean clutch size and mean egg weight did not differ among sites and were not associated with measures of reproductive success or vegetation structure. Nest predation was the principal cause of reproductive failure in the study, and I suggest that high quality habitat for the Dusky Flycatcher provides an abundance of nest sites to either deter predators or to reduce their rate of success. I reiterate the need to

define habitat quality with respect to the habitat use and the fitness attributes of a species, and to determine how the density of breeding territories is related to and influences these relationships.

INTRODUCTION

The habitat used by a species may be ranked from low to high quality, with the best habitat conferring the combination of survival and reproduction that maximizes an individual's fitness (Van Horne 1983). Management activities may change habitat quality by modifying those features associated with the fitness attributes of a particular species (Martin 1992, Morrison et al. 1992). Treatments (e.g., timber harvests) may leave certain vegetative or structural components in place or purposefully alter components to create desired habitat conditions and qualities (Thomas 1979). These activities assume that the survival and fecundity of a species are associated with vegetation structure and composition and that directed changes in the vegetation structure and composition can positively influence reproductive success and survival (Holmes et al. 1996, Hunt 1996, Franklin et al. 2000, Donovan and Thompson 2001, Gram et al. 2003). In this report, we follow Morrison et al (1992) to define habitat as the combination of resources and conditions that prompt usage by a species and allow for reproduction and survival.

Successful management must also consider the scales at which a species is utilizing habitat (Orians and Wittenberger 1991, Donovan and Thompson 2001, Jones and Robertson 2001) and the features that a species uses to meet its life history requirements (Martin 1992, 1998). Although management treatments often occur at the stand-level (Thomas 1979), a species' survival and fecundity may be affected at different scales (e.g., the nest-site, territory, or landscape) or as a result of behavioral differences (Woodard and Murphy 1999, Martin et al. 2000). Stand-level analyses may not detect the causes of differences associated with the other scales, and stand treatments may not yield the desired management outcomes. Stands may contain heterogeneous vegetation structure and composition as a result of natural or human disturbances. However, an organism is most likely to use those patches that promote its individual survival and reproductive success (Petit and Petit 1996, Braden et al. 1997, Rodenhouse et al. 1997, Morse and Robinson 1999, Easton and Martin 2002). Habitat use (e.g., habitat incorporated within home ranges) may then differ markedly from what is available at the stand-level.

The evaluation of a species' performance at the territory scale may demonstrate which features are associated with reproductive success and survival (Alatalo et al. 1986, Matsuoka et al. 1997, Sockman 1997, Bowyer et al. 1999). However, density-dependent factors, such as competition for nest sites and food (Fretwell and Lucas 1970, Martin 1988b, 1995, Holmes et al. 1996, Both and Visser 2003), may operate at scales beyond the territory and influence habitat quality and use. For example, competition with conspecifics may influence where an individual establishes a territory by forcing an individual from preferred high quality habitat into habitat of lower quality (Fretwell and Lucas 1970, Stamps 1990, Petit and Petit 1996).

The evidence for the influence of density on fitness attributes is mixed and varies markedly by taxa. While a low density of active breeding territories at a site may indicate poor habitat quality (Petit and Petit 1996), high quality habitat may remain vacant at low population densities because individuals chose to settle near conspecifics even if they reside in low quality habitat (Saether et al. 1996, Courchamp et al. 1999). Conversely, high densities of territory holders does not necessarily equate with high quality habitat (Van Horne 1983, Bollinger and Gavin 1992). A high density of conspecifics may lead to reduced survival and reproductive success by attracting predators (Martin 1988a, Messier 1994, Tewksbury et al. 1998, Roos 2002) or by interference competition for resources (Dhondt et al. 1992, Holmes et al. 1996, Both 1998b, Zanette et al. 2000). Other studies have found that breeding territory density did not affect reproductive success and survival (Alatalo and Lundberg 1984, Both and Visser 2000).

An additional consideration for management plans is the type of metric used to define productivity in a population or sub-population. Productivity is often defined in terms of clutch size or fledglings per mated pair. Although mean clutch size can vary as a result of both habitat (Dhondt et al. 1992) and density (Both 1998b), mean clutch size is not an appropriate measure of productivity if reproductive success also varies and is related inversely to mean clutch size. Also, if individuals settle preferentially in high quality habitat and move into lower quality habitat as the population size increases, mean productivity may decline at the population level even though productivity remains high in high quality habitat (Dhondt et al. 1992, Ferrer and Donazar 1996, Both and Visser 2003).

In summation, the effect of density on survival and productivity (and thus considerations of habitat quality) is likely to vary along a habitat quality gradient, among sub-populations and populations (Greene and Stamps 2001), and be scale dependent. The definition of habitat quality for a species must be made with reference to scales of habitat use and to the measures of reproduction and survival that have the greatest influence on population demographics.

I studied the Dusky Flycatcher (*Empidonax oberholseri*) on eight sites within the moist grand fir (*Abies grandis*) habitat type (Daubenmire 1966). I selected sites to represent a diversity of understory and overstory features and structure. Previous studies have determined that the Dusky Flycatcher responds positively to increases in shrub density and the number of vegetation height classes and negatively to increases in overstory conifer density (Kelly 1993, Sedgwick 1993). I evaluated the relationships between vegetation structure (a determinant of habitat quality for the Dusky Flycatcher) and nesting success, productivity per female, study site productivity, average clutch size, average egg weight, and density of breeding territories. My objectives were to determine if variation in habitat quality among the sites was associated with measures of reproductive success and density and if these measures were associated with one another. I suggest which measures provide the best information for management programs.

METHODS

Study Sites

I studied Dusky Flycatcher nesting success at eight different sites in central Idaho, USA, during 2002 and 2003. The sites were chosen to provide a range of vegetative and structural features believed to influence Dusky Flycatcher habitat use and reproductive performance (Kelly 1993, Sedgwick 1993). Study sites ranged in size from 8.1 to 22.8 ha. All sites were located in the moist grand fir habitat type (Steele et al. 1981). Ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotzuga menziesii*), and grand fir (*Abies grandis*) were the dominant overstory trees. Scouler's willow (*Salix scouleriana*), Rocky Mountain maple (*Acer glabrum*), mallow ninebark (*Physocarpus malvaceus*), thinleaf alder (*Alnus sinuata*), buckthorn (*Ceanothus velutina*), and twinberry (*Lonicera utahensis*) were the dominant shrubs on all sites. The topography of the sites varied from flat benches to steep (> 35 degree) slopes. Elevations ranged from 1470 m to 1800 m. No perennial water was present at any site. Distances between sites ranged from 0.63-11.9 km. Understory shrub densities at each site varied as a result of past disturbance events (logging and fire) that reduced the overstory canopy and changed soil conditions, suppressing or encouraging understory growth. Shrub development and coverage on the sites ranged from extremely patchy to relatively continuous shrub cover greater than 2 m in height.

Nest Searching, Nest Monitoring, and Territory Mapping

I located nests by spot-mapping singing males (Bibby et al. 1992) and searching for nesting females throughout the breeding season. Nests were visited every one or two days, depending on the stage of the nesting cycle, to determine nest fate. Nests were checked daily during the laying phase and near the estimated fledging date to obtain accurate estimates of nesting survival. Observers approached nests from different routes on each visit and binoculars were used to observe nests from a distance when possible (Martin and Geupel 1993). The number of eggs, nestlings, and fledglings were recorded during each visit. The beginning of incubation was determined by the presence of warm eggs in the nest and incubation behavior by the female. Most females began incubation within 3 days after completing a clutch. As a result, I assumed that the incubation date began 2 days after the completion of egg laying for those nests that were too high to reach. The Dusky Flycatcher is single-brooded (Sedgwick 1993), although I did observe one female who reared two successful broods.

All clutches were weighed 2-3 days after the completion of the clutch to standardize measurements. All eggs in the clutch were weighed simultaneously with an AccuLab PP-2060D (readability .01/.001 g; AccuLab, Newtown, PA). Every clutch that could be reached by field personnel was weighed. However, some clutches could not be weighed as they were either destroyed before clutch completion, or were too high for field personnel to remove from the nest.

Territory boundaries were delineated during spot-mapping sessions. I returned to individual territories and mapped them by marking singing and counter-singing points, preferred foraging perches, and aggressive interactions with other males (Martin and Geupel 1993). Males were not color-banded, but I felt confident that I could identify individual territory holders by their recurrent use of singing perches and foraging sites and by simultaneous identification of nearby territory holders. I included those territories that went beyond the site boundaries, but which had the majority of their area within the site, in the calculations of site size. I chose non-habitat for the Dusky Flycatcher (e.g., logging roads, meadows or recent clearcuts) for site boundaries, and the majority of the territories fell within the sites.

Vegetation Measurements

Vegetation structure on the eight sites was measured from the third week of July until the third week of August in 2002 and 2003. Line-intercept transects 20 m in length were placed randomly throughout each of the eight sites. Starting points and direction for each transect were generated randomly using ArcView (v. 3.3). Vegetation was measured continuously on each transect for five understory height strata (0-1, 1-2, 2-3, 3-4, >4 m). I used two extendable poles to determine coverage in the upper strata. Overstory conifer coverage was determined using the stick method (Gysel and Lyons 1980). Percent coverage and species were recorded for each height stratum. Sampling was done proportionally to the size of each site (Thompson 2002). I added additional transects at each site as time allowed.

Statistical Analyses

I estimated nesting success using the Mayfield method (Mayfield 1975). The Mayfield method determines the probability of a nest fledging one or more young. We included the incubation and nestling stages and the hatching rate in the estimates of nesting success. I examined nesting success among sites and across years. I calculated standard errors for estimators with a bootstrapping method (Efron 1982). Bootstrapping allows for the calculation of a standard error of an estimator when no close-formed expression exists for the variance of that estimator. In this case, the bootstrap standard error is the standard deviation of the sampling distribution (Quinn and Keough 2002).

The Mayfield estimator may be biased significantly in certain situations (e.g., when observer effects are present (Rotella et al. 2000) or when mortality rates are periodic across the nesting season (Johnson and Shaffer 1990)). However, I felt that its use was appropriate to compare rates of nesting success because I also calculated measures of productivity to compare to the Mayfield estimator.

I calculated annual reproductive success following Murray (1992, 2000). Annual reproductive success (ARS(k)) is the number of young fledged per female per year in a study population (Murray 2000), and is the demographic parameter of most significance to a population. I calculated ARS(k) as: (the number of nesting attempts at a site/the number of first nesting attempts at a site) * (the number of successful broods at a site/the number of nesting attempts at a site) * (the total number of fledglings at a site/the number of successful broods at a site). This equation reduces to the number of fledglings at a site divided by the number of first nesting attempts. I calculated ARS(k) by site and year and for yearly totals. I calculated standard errors and 95% confidence intervals by bootstrapping.

We calculated both territories per hectare and fledglings per hectare by dividing the total counts of those variables by individual site size for each site. Both territories per hectare and fledglings per hectare were total counts and not point estimates, and I did not calculate a measure of variance for the total from each site. Yearly averages with standard errors were calculated.

Mean clutch size was calculated by dividing the total number of eggs produced in each completed clutch by the number of nesting attempts that resulted in completed clutches at the site. Standard errors for 95% confidence intervals were calculated with bootstrapping.

All eggs in a clutch were weighed together and mean egg weight was calculated as the average of all mean egg weights measured on a site. Standard errors for 95% confidence intervals were calculated with the standard statistical method. I considered non-overlapping 95% confidence intervals as indicators of significant relationships between test variables.

Vegetation and structural variables were tested for normality and homogeneity of variances. Many transects did not have vegetation in the higher strata, resulting in non-normal distributions for certain variables. To meet the normality assumption, the data were transformed with ln(variable+1). Standard errors for each average were calculated using the standard statistical method.

I used Pearson's correlation coefficients (r) (Quinn and Keough 2002) to examine relationships between the measures of reproductive success and the habitat variables. Pearson's correlation coefficients are measures of the linear association between variables. Pearson's correlation coefficients were used because I assumed general linear associations between the variables of interest. I considered any correlation coefficient that was greater than 0.5 to merit closer scrutiny. I calculated 95% confidence intervals by bootstrapping for any correlation coefficient greater than 0.75.

RESULTS

Nesting success differed significantly for only two sites within a given year, NB102 and NB202 (Figure 1). All other sites did not differ significantly across sites within years, nor did they differ by site across years (Figure 1). In 2002, the average nesting success for eight sites was 0.453 (range: 0.203-0.709). In 2003, the average nesting success was 0.368 (range: 0.159-0.595).

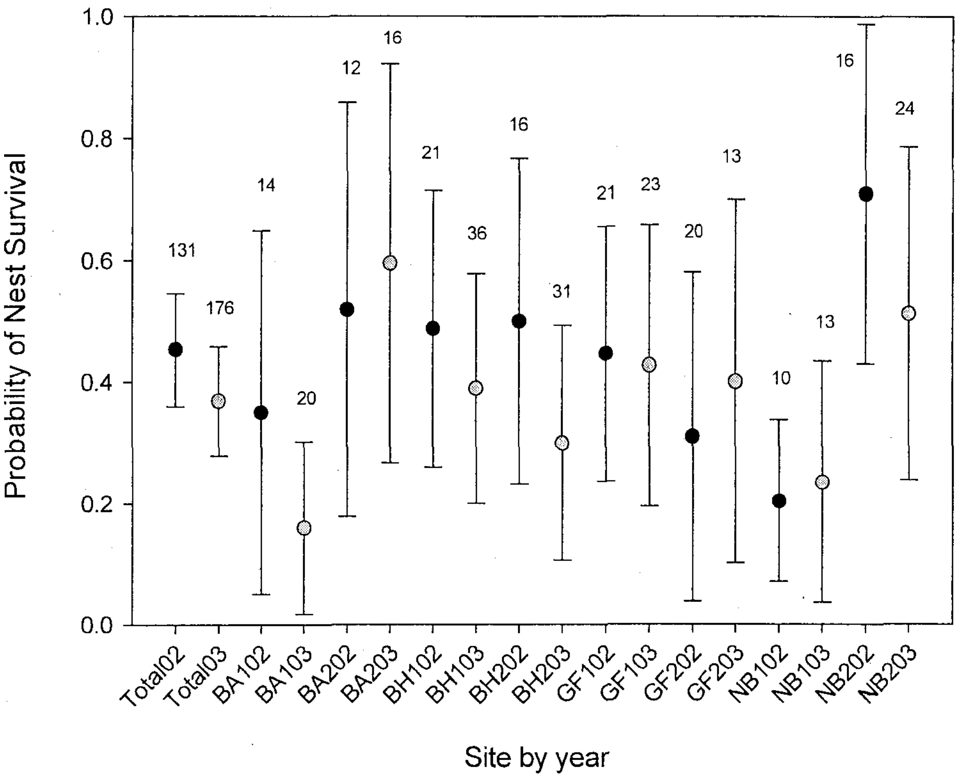

Figure 1: Nesting success (Mayfield estimator) and 95% confidence intervals for Dusky Flycatchers by site and year, central Idaho, 2002 and 2003 (sample sizes are above error bars).

Annual reproductive success did not differ significantly among sites within or between years (Figure 2). The average annual reproductive success for all sites in 2002 was 1.81 (range: 0.958-3.406). The average annual reproductive success for all sites in 2003 was 1.93 (range: 1.21-2.96).

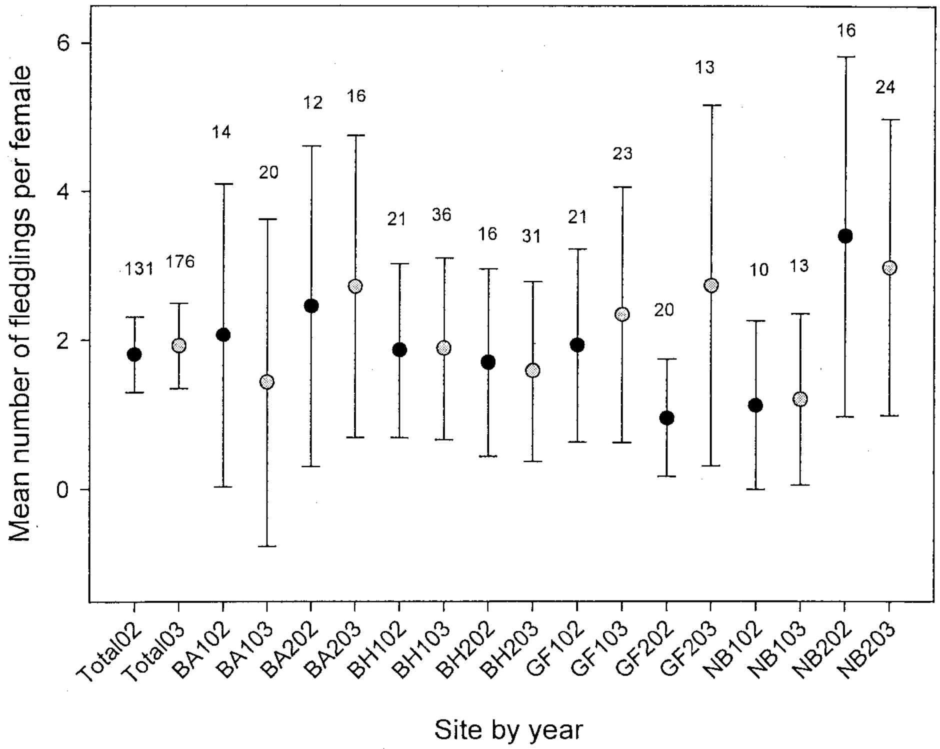

Figure 2: Annual reproductive success (Murray 1992, 2000) and 95% confidence intervals for Dusky Flycatchers by site and year, central Idaho, 2002 and 2003 (sample sizes are above error bars).

The number of fledglings per hectare differed by site in both 2002 and 2003 (Figure 3). The average number of fledglings per hectare in 2002 was 1.38 (range: 0.34-3.09). The average number of fledglings per hectare in 2003 was 1.65 (range: 0.79-3.82). BA2 had 60% more fledglings per hectare in 2003 than 2002 (1.98 to 1.19). NB1 had three times as many fledglings per hectare in 2003 than 2002 (1.02 to 0.34). The number of fledglings per hectare did not differ greatly between years for the other six sites.

Summary statistics (mean, standard error, 95% confidence interval) for six vegetation variables are in Appendix 1. Nesting success, annual reproductive success, and fledglings per hectare were all associated with elements of vegetation structure (Table 1). Nesting success was positively associated with understory vegetation in Strata B and C and overstory conifer coverage in Stratum E. Annual reproductive success was positively associated with Strata B, C, and D. The number of fledglings per hectare was positively associated with Strata B, C, and D.

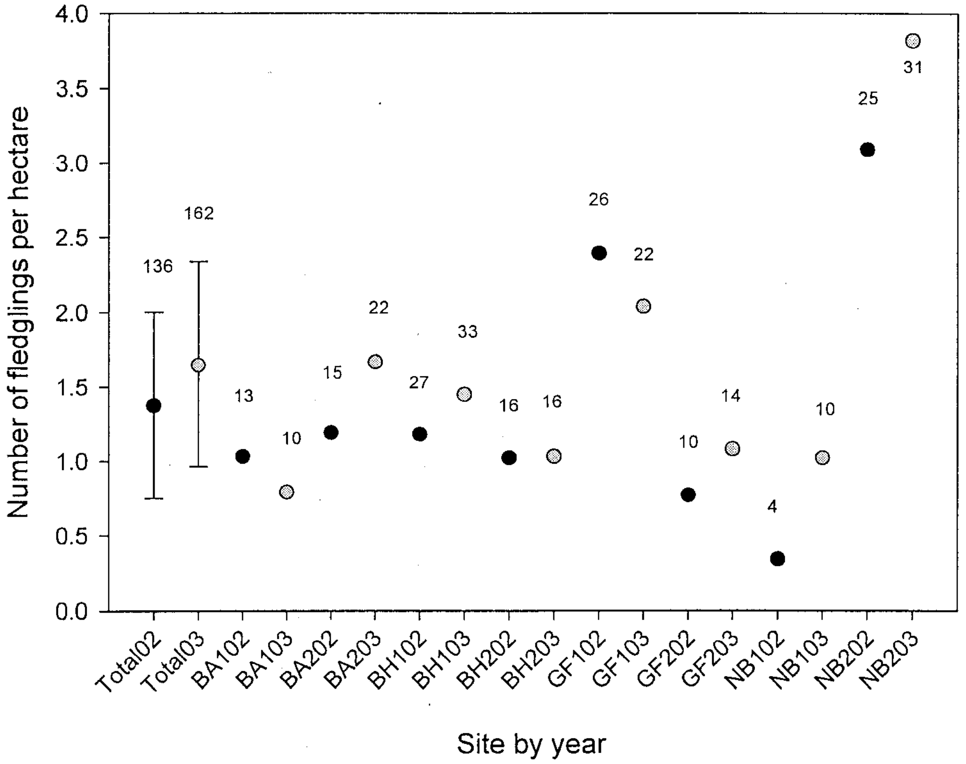

Figure 3: Fledglings per hectare (95% confidence intervals for means by year) for Dusky Flycatchers by site and year, central Idaho, 2002 and 2003 (total number of fledglings is above each site by year).

Table 1: Pearson's correlation coefficients (r) for measures of reproductive success and vegetation structure for eight sites, central Idaho, 2002 and 2003.

Variable	Nesting Success[a]	Annual reproductive success[b]	Fledglings per hectare	Mean clutch size	Mean egg weight	Territories per hectare	Site Size
% A (1-2 m)	0.392	0.342	0.276	0.213	-0.449	0.222	-0.490
% B (2-3 m)	0.564	0.671	0.664	0.378	-0.352	0.536	-0.395
% C (3-4 m)	0.558	0.572	0.707	0.355	-0.355	0.572	-0.306
% D (>4 m)	0.497	0.581	0.734	0.335	-0.176	0.628	-0.324
% E (canopy)	0.547	0.391	0.397	-0.013	-0.273	0.346	-0.134
% F (0-1 m)	0.289	0.310	0.326	0.449	-0.175	0.369	-0.417
Nesting success	1	0.821	0.686	0.161	-0.404	0.326	0.10
Annual reproductive success	0.821	1	0.761	0.042	-0.24	0.486	-0.328
Fledglings per hectare	0.686	0.761	1	0.129	-0.21	0.898	-0.448
Mean clutch size	-0.127	-0.266	-0.063	1	-0.234	0.063	0.286
Mean egg weight	-0.405	-0.241	-0.21	-0.138	1	-0.11	0.076
Territories per hectare	0.326	0.486	0.898	0.20	-0.110	1	-0.595

a. Probability of a nest producing one young or more (Mayfield 1975)
b. Mean number of fledglings per female (Murray 1992,2000)

Mean clutch size did not differ by site between years (Figure 4). The average mean clutch size was 3.19 in 2002 (range: 2.80-3.50. The average mean clutch size was 3.27 in 2002 (range: 3.0-3.46). Mean clutch size did not differ across sites in either 2002 or 2003.

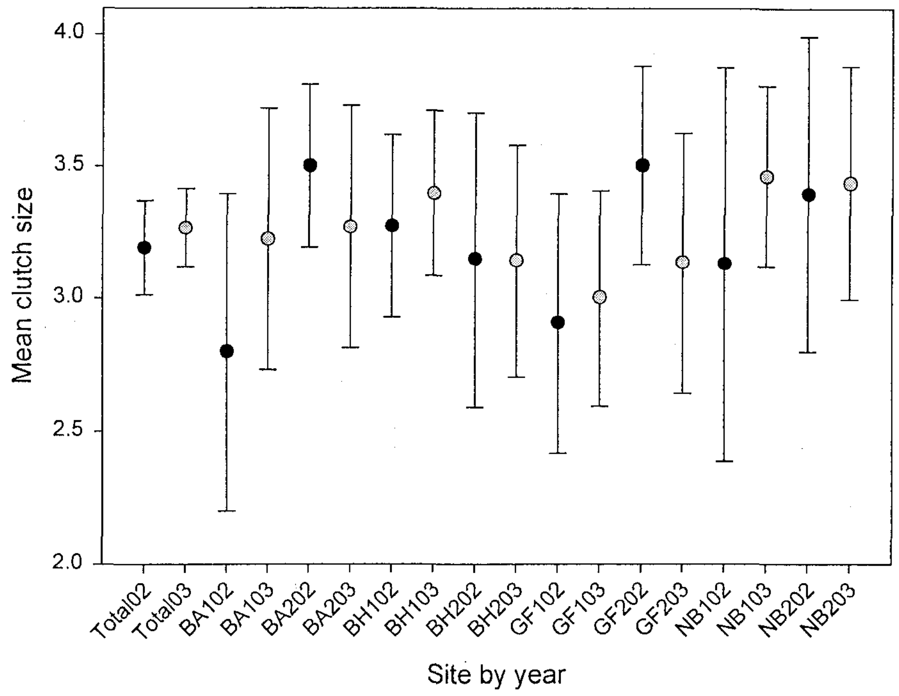

Figure 4: Mean clutch size with 95% confidence intervals for Dusky Flycatchers by site and year, central Idaho, 2002 and 2003 (sample sizes are above each site by year).

Mean egg weight differed by site between years (Figure 5). The average mean egg weight in 2002 was 1.55 gm (range: 1.33-1.62 gm). The average mean egg weight in 2003 was 1.60 gm (range: 1.55-1.73 gm). BA1, BA2, and NB2 all had significantly greater mean egg weights in 2003 than in 2002, although only 1 clutch was weighed at NB2 in 2002. None of the sites differed significantly in 2002. In 2003, both BA2 and GF2 were significantly greater than BH2, GF1, and NB1.

Mean clutch size and mean egg weight were not associated with vegetation structure (Table 1). A weak negative association existed between Strata A and mean egg weight (-0.449).

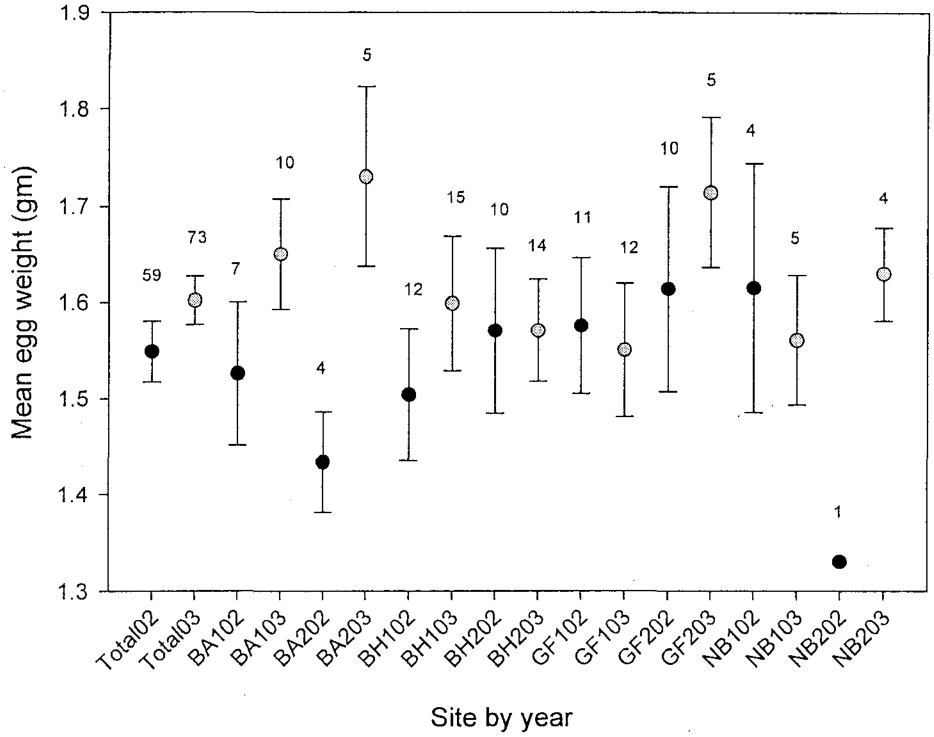

Figure 5: Mean egg weight with 95% confidence intervals for Dusky Flycatchers by site and year, central Idaho 2002 and 2003 (sample sizes are above each site by year and for totals).

Mean clutch size and mean egg weight were not associated with other measures of productivity (Table 1). Nesting success was associated positively with annual reproductive success (r=0.82) and fledglings per hectare (r=0.69). Annual reproductive success was positively associated with fledglings per hectare (r=0.76).

Territory density differed across sites within years (Figure 6). The mean territory density in 2002 was 0.88 territories per hectare (range: 0.57-1.61). The mean territory density in 2003 was 1.08 territories per hectare (range: 0.71-1.85). Territory density also differed within sites between years. Territory density was greater in 2003 than 2002 for all sites except GF2.

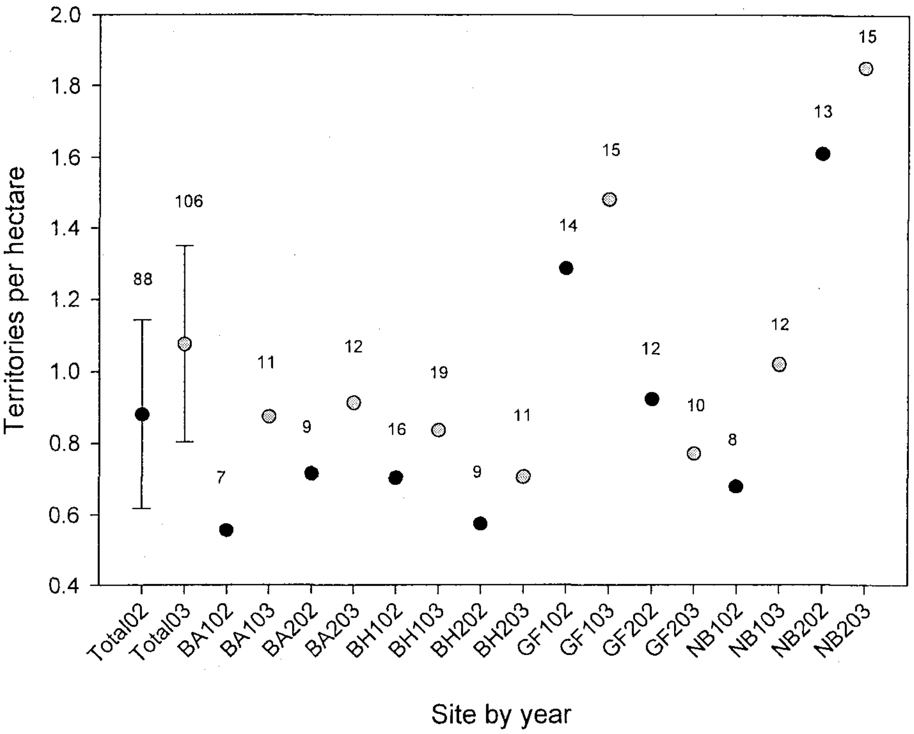

Figure 6: Territories per hectare (with 95% confidence intervals for means by year) for Dusky Flycatchers by site and year, central Idaho, 2002 and 2003 (total number of territories is above each site and for totals).

The number of territories per hectare was positively associated with Strata B, C, and D (r=0.536, 0.573, and 0.628 respectively), although the relationships were not strong (Table 1). The number of territories was negatively associated with site size (r=-0.595).

The number of territories per hectare was not strongly associated with nesting success (r=0.326) or annual reproductive success (r=0.486). The number of territories per hectare had a strong positive association with fledglings per hectare (r=0.898, 95% c.i. 0.672, 0.971)(Figure 7).

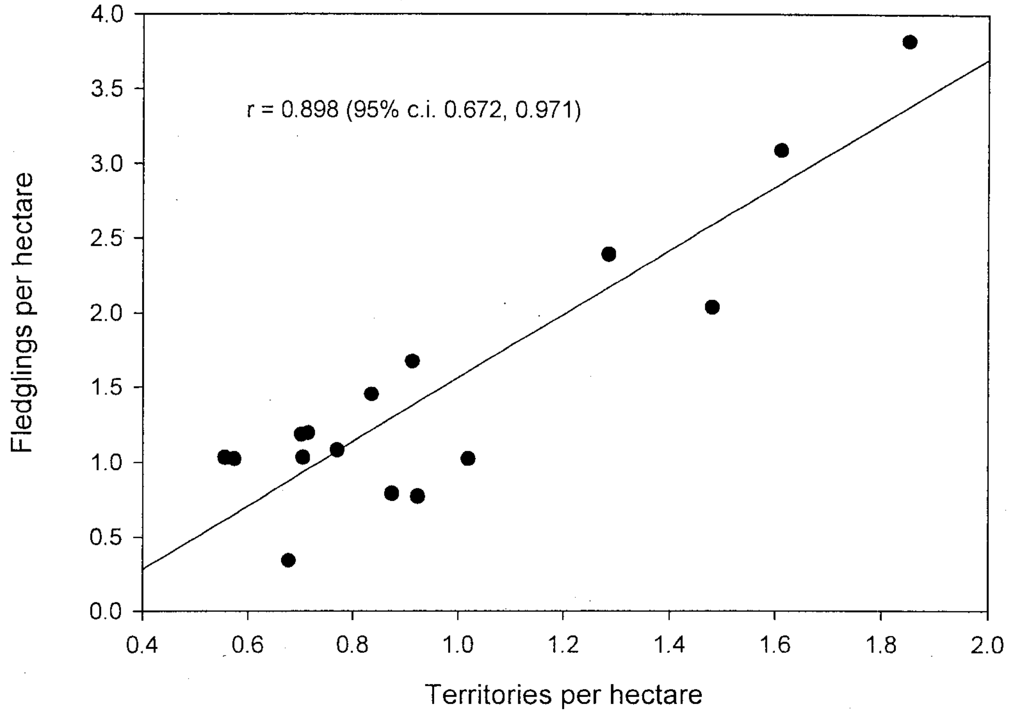

Figure 7: The number of fledglings per hectare vs. the number of territories per hectare on eight sites for two years, central Idaho, 2002 and 2003.

Territory density was not associated with mean clutch size (r=0.062) or mean egg weight (r=-0.109) (Table 1). I did not state a specific prediction for these variables, and will discuss the kind of relationships found in other studies in the next section.

DISCUSSION

Variation in reproductive success as a result of differences in habitat has been demonstrated for birds (Siikamäki 1995, Holmes et al. 1996, Morse and Robinson 1999) and other taxa (Whitham 1980, Morris 1989). Many of these studies have identified clear differences in habitat (e.g., sites with different vegetation types and structure). I demonstrated differences for nesting success, annual reproductive success, and fledglings per hectare across eight sites. Also, I demonstrated positive associations among these measures and with vegetation structure measured at the site-scale for eight sites. Understory shrub cover was positively associated with higher breeding territory densities and higher nesting success, annual reproductive success, and number of fledglings per hectare. In the following discussion, I consider how differences in vegetation structure could account for the observed associations, with specific reference to the predictions made in the first section of the report.

Nest predation is the primary cause of reduced reproductive success in open-cup nesting passerines (Martin 1995). In the two years of the study, I observed only two cases of nest failure for Dusky Flycatchers that were not related to nest predation. While other studies have documented reduced reproductive success as a result of food limitation (Martin 1987, Holmes et al. 1992), I did not observe any instances of nestling starvation. Food limitation can also constrain nestling growth, thereby increasing the number of exposure days and increasing the probability of predation. However, mean number of nestling days did not differ among the sites (Kroll, unpub. data). Finally, food limitation can continue into the post-fledgling stage, an aspect of reproductive success that I did not measure.

My results indicate that reproductive success in Dusky Flycatchers was associated with increased amounts of cover in the shrub understory. Although the differences in reproductive success among the eight sites were not statistically significant, the size of the effect between sites (Figs. 1, 2, and 3) suggests that meaningful biological differences existed and that these differences were tied to vegetation structure. I did not predict a positive association between nesting success and overstory canopy coverage (Table 1). However, three of the dominant shrub species (*Acer glabrum*, *Alnus sinuata*, and *Physocarpus malvaceus*) grow well on moderately-shaded sites in central Idaho (Steele et al. 1981). Moderate amounts of canopy cover may promote shrub growth and thus use by Dusky Flycatchers.

The most likely explanation for this pattern is that diverse vegetation structure and composition provided an abundance of potential nest sites that served to reduce predation and provided opportunities for renesting attempts upon nest failure. While none of the associations between reproductive success and understory cover were particularly strong, it is important to note that I measured habitat availability at each site and not habitat use.

An alternative explanation is that predator abundance and density decreased on the sites with greater understory coverage. I did not estimate predator densities, and cannot address this explanation directly. However, the higher quality sites (as defined by fledglings per hectare) had moderate canopy coverage and higher amounts of litter and woody debris, and it seems unlikely that red squirrel (*Tamiasciurus hudsonicus*) and least chipmunk (*Eutamias minimus*) densities would be reduced on these sites. Also, given the relatively small size of the sites, it is unlikely that more than one or two pairs of Steller's

Jays (*Cyanocitta stelleri*) could have been present, regardless of vegetation structure.

Mean clutch size and mean egg weight did not differ among sites. Mean clutch size was significantly different for only one site within year, NB1 in 2003 (Fig. 4). This was clearly an artifact of sampling, as none of the nests located on the site in 2003 were depredated during the building or laying phases, allowing for a larger mean clutch size. Although I may have underestimated mean clutch size (see Methods section), our estimator is an accurate reflection of reproductive output per unit of effort: a nest that fails before it reaches the laying stage still represents an investment by the female.

Mean egg weight differed significantly among sites in 2003 (Fig. 5), but not in 2002. Egg mass in birds is characterized by large intraspecific variation, and individuals of most species can produce eggs that differ in weight by as much as 50% (Christians 2002). Although egg weight can be an indicator of individual quality, the evidence for the relationship between egg weight and important traits such as nestling growth and survival is mixed (Williams 1994, Christians 2002). Egg quality, which we did not measure in this study, may be a more relevant biological factor and one that should be considered in tandem with egg mass (Both et al. 1998). However, any biological advantage of increased egg mass is negated if it is not associated with increased rates of nesting success (see Prediction 3). Finally, it is unlikely that significant differences in mean egg weight would exist in the absence of food limitation (reviewed in Martin 1987, Christians 2002), which did not appear to be a factor in this study.

Mean clutch size and mean egg weight were not associated with habitat structure (Table 1), the most clearly defined aspect of habitat quality for Dusky Flycatchers. The results for mean clutch size are in contrast to those of Hogstedt (1980) and Siikamäki (1995), both of whom found increased clutch sizes in high quality habitats. However, the experimental evidence for clutch size optimization to fit local circumstances is mixed (Both et al. 2000) and many of the experimental studies have been conducted in situations where nest predation is not a significant factor, limiting application to our results. Christians (2002) considered egg size to be an individual trait, and the proximate determinants of egg size, including food availability, female mass and female age, to be confounded with one another. Differences in mean egg mass and mean clutch size may be more closely tied to habitat use at finer scales (e.g., the territory, nest patch, and nest site).

Mean clutch size and mean egg weight were not associated with any measures of reproductive success (Table 1). Given the discussion in Prediction 2, this result is not entirely unexpected. Again, these measures may be more closely associated with inherent variability among individuals or habitat use at finer scales than the site and so unlikely to be sensitive to site-level differences.

Nesting success, mean number of fledglings per female, and the number of fledglings per hectare were all positively associated with one another. This result is expected as all three estimators are calculated from the same data (with some adjustments). However, nesting success is the probability that a nest fledges one or more young, a less informative statistic than mean number of fledglings per female or the number of fledglings per hectare. A site could possess a high nesting success and be lower in productivity if the mean clutch size was low or if productivity was constrained by food limitation.

Breeding territory density differed by site and between years (Fig. 6). I could not calculate a measure of variance for the individual site estimates between years, and thus it is impossible to determine if significant statistical differences exist between the yearly estimators for each site. Relevant biological differences across the sites for these estimators are discussed under Prediction 5.

The number of territories per hectare at each site was positively associated with vegetation in three different height strata, although examination of individual scatterplots shows that this trend is influenced by one site, NB2, which had a high density of territories and diverse vegetation structure in both 2002 and 2003. The other seven sites had relatively low amounts of cover in the upper strata (B, C, and D) making inferences about the relationship between vegetation structure and territory density difficult. Given this result, I would expect that habitat selection at the territory-scale on the other seven sites would show particularly strong differences between habitat use and availability. This prediction is assessed in Chapter 2.

Site size was negatively associated with breeding territory density. Site selection was based on the amount of vegetation cover and structure, and sites that had dense vegetation structure were kept small so that field workers could monitor breeding territories adequately. Site size was not associated with any measures of productivity (Table 1) and appears to have been an artifact of study design.

Nesting success and annual reproductive success were not positively associated (Table 1). However, both of these estimators are functions of the number of nesting attempts at a site and will be positively associated with territory density only if a density-dependence influence on reproduction is not acting and if the number of nesting attempts and the number of fledglings at a site are related inversely.

The number of fledglings per hectare and territory density had a strong positive relationship (Fig. 7). This relationship is intuitive only if predators do not exert a functional response to increased densities of breeding territories (Roos 2002). My results indicate that Dusky Flycatcher breeding territories tended to be more dense on the sites with greater vegetation coverage and that they produced more fledglings on those sites. Increased production on the sites with greater vegetation coverage was not a result of double-brooding (Holmes et al. 1996), but derived from a higher nesting success for first clutches (which tend to have either 3 or 4 eggs; Kroll, unpub. data).

While the results support the hypothesis that rates of nest predation are influenced by the amount of available nest sites, I stress that the results are descriptive and do not identify a specific mechanism. I cannot determine if predators are deterred by increased amounts of vegetation cover or if nests represent only an ephemeral resource (sensú Schmidt and Whelan 1998) and thus a small component of predator diets.

Mean clutch size and mean egg weight were not associated with territory density (Table 1). Patterns concerning the relationship between clutch size and density are not consistent (Both 2000) and evidence suggests that different mechanisms may be operating at the population and sub-population levels (Tinbergen and Both 1999, Both and Visser 2000). Evidence in support of clutch size optimization is mixed (Both 1998a, Both et al. 2000), but suggests that clutch size may be adjusted as a response to food resources available during the nestling period (Both et al. 2000). Again, I found no evidence for food limitation in our study and no significant differences across sites for mean clutch size, suggesting that this trait may be fairly constant for Dusky Flycatchers nesting in the study area. If egg weight is an individual trait that does not often vary as a result of proximate factors, then it is unreasonable to expect significant variation at the site-scale as a result of increased densities of conspecifics.

Appropriate Indicators of Habitat Quality

The definition of habitat quality must consider how survival and fecundity vary within and across the habitat used by a species (Holmes et al. 1996, Franklin et al. 2000), the proximate factors (e.g., vegetation structure, quantity of nest and foraging sites) that are associated with these parameters (Martin 1992, 1995, Petit and Petit 1996), and how density affects resource use (Fretwell and Lucas 1970) and a species' reproduction and survival (Van Horne 1983, Both et al. 2000). I demonstrated that habitat quality for the Dusky Flycatcher, as expressed by nesting success, annual reproductive success, and the number of fledglings per hectare, was associated with vegetation structure measured at the site-scale and that reproductive success and density were highest on those sites with greater amounts of vegetation coverage. Although the measurements of vegetation structure were made at a broad scale (i.e, greater than the territory), the results indicate that the Dusky Flycatcher chose to settle on sites with greater amounts of vegetation coverage and that reproductive success was enhanced on those sites.

The relationship between density and habitat quality (Van Horne 1983) is not clearly defined for most organisms. Our results demonstrated that density was positively correlated with the number of fledglings per hectare and thus an adequate measure of habitat quality for the Dusky Flycatcher. However, other purported measures of habitat quality (e.g., nesting success and annual reproductive success) were not associated with density. I reiterate the need for researchers to evaluate the nature of the relationships between habitat quality, density, reproductive success, and survival for species of interest. Although I did not estimate adult survival in the study, I have evidence that adult survival in the Dusky Flycatcher was high. Only 2 nests were abandoned after the laying cycle began (2/290; 0.7%) and both males and females were observed feeding on all nests that fledged young (95/331; 28.7%). Other studies (Sillett and Holmes 2002) have demonstrated similarly high rates of adult survival on the breeding grounds of Neotropical migrant passerines. Taken together, this evidence indicates that the most critical measure of habitat quality for the Dusky Flycatcher may be reproductive success, specifically the number of fledglings produced per breeding territory and juvenile survival (Anders et al. 1997). Future studies of habitat quality should include these estimates when possible and be certain to document the relationship between nesting success and productivity, regardless of the estimators used.

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Chapter Three: Habitat selection and use and consequences for territory size and reproductive success in the Dusky Flycatcher (*Empidonax oberholseri*)

ABSTRACT

I examined habitat selection and use and how habitat use was associated with territory size and reproductive success for the Dusky Flycatcher (*Empidonax oberholseri*) in central Idaho for two breeding seasons (2002-2003). I developed models for habitat selection and for the association between habitat use and reproductive success. Models were evaluated with information-theoretic and cross-validation methods. Habitat included within territories was characterized by greater cover of deciduous vegetation in two different height strata (0-1 and 2-3 m), reduced cover of conifers less than 4 cm dbh, and steeper slopes. I detected no differences in vegetation structure between successful (at least one fledgling) and unsuccessful territories. Territory success was positively associated with the density of conspecifics and both positively and negatively associated with specific study sites. Mean territory size did not differ significantly between years for all but one site. Mean territory size did not differ significantly for successful and unsuccessful territories in either year. Territory size was not associated with measures of reproductive success or vegetation structure at either the individual or site level. The variance in mean territory size was negatively associated with nesting success, annual reproductive success, the number of fledglings per hectare, and the density of conspecifics at each site. This latter result suggests that individuals on sites of poor habitat quality (as

expressed by measures of reproductive success) had either to extend territory boundaries to include sufficient resources or established territories based on what resources were available. Our results suggest that the Dusky Flycatcher optimized territory size to include sufficient resources to reproduce successfully. However, the success of both small and large territories suggests that other scales of habitat use (e.g., nest-site and nest-patch scales) may be important for the reproductive success of the Dusky Flycatcher.

INTRODUCTION

Habitat selection is a behavioral process that leads to the disproportionate use of those environmental conditions and resources that maximize reproductive success and survival (Block and Brennan 1993, Morris 2003). In order to maximize lifetime reproductive output (Fryxell 1997), an individual must rely on proximate cues to select habitat in which reproductive success and survival are enhanced (Fretwell and Lucas 1970, Williams and Nichols 1984). Habitat selection should be adaptive over time (Jaenike and Holt 1991, Orians and Wittenberger 1991, Fryxell 1997) and lead to the preference for certain vegetation types, structural features, and climate regimes that maximize individual fitness (Whitham 1980, Hayworth and Weathers 1984, Martin 1998, Weathers and Greene 1998, Clark and Shutler 1999, Spencer et al. 2002). In this report, I follow Morrison et al. (1992) to define habitat as the combination of resources and conditions that prompt use by a species and that allows for reproduction and survival.

Habitat selection occurs across a hierarchy of spatial scales (Johnson 1980, Morris 1987). Different features may be chosen at different scales (Hutto 1985, Morris 1987, Kotliar and Wiens 1990) and the evaluation of these features may yield differential effects on reproductive success and survival (Morrison et al. 1992). The habitat selection process results in the vegetative and structural components that are used by an organism (Johnson 1980, Orians and Wittenberger 1991) to meet its life history requirements (Block and Brennan 1993). Although habitat may be selected at broad spatial scales (Hutto 1985, Orians and Wittenberger 1991), the home range or territory defended by an organism defines the extent of the habitat that is available–in most cases–for use once the selection process is completed (Johnson 1980, Gates and Evans 1998).

A number of factors may constrain the size of the territory (or home range) besides the acquisition of sufficient amounts of resources to promote reproduction and survival. The primary determinant of home range size for large mammals is body mass, with carnivorous mammals having larger home ranges than herbivorous mammals (Harestad and Bunnell 1979). Body size, diet composition, and the habitat type in which the home range is located explained most of the variation in home range size (after correcting for phylogenetic effects) for lizards (Perry and Garland 2002). In both of these groups, habitat use and home range size are governed by physiological factors, including metabolic rates (Kelt and Van Vuren 2001), daily energy expenditure (Mace and Harvey 1983), and thermoregulation within specific temperature ranges (Perry and Garland 2002).

Territory size in other taxa is often correlated with the abundance of food resources across vegetation types (reviewed in Adams 2001). Experimental evidence suggests that territory size may decrease with increased food abundance, although it is difficult to determine if this is a result of an individual's increased foraging efficiency or the attraction of conspecifics that increase competition (Myers et al. 1979). The spatial aggregation and temporal availability of food resources is likely to exert a profound effect on territory size as well as shape (Adams 2001). Finally, food abundance and territory size were found either to be unrelated (Franzblau and Collins 1980, Askenmo et al. 1994, Dunk and Cooper 1994) or to have a negative relationship (Temeles 1987, Tricas 1989) in those studies where the effects of competition were controlled.

Avian territory size appears to be governed by two proximate factors: (1) the amount of food necessary for successful breeding and reproduction and (2) structural cues that serve as indirect indicators of habitat quality (food abundance, structural components and their influence on the abundance of nest sites) (Smith and Shugart 1987, Petit and Petit 1996, Marshall and Cooper 2004). Birds may monitor food resources directly or rely on structural aspects of the habitat to serve as indirect indicators of food abundance (the structural cues hypothesis, Seastedt and MacLean 1979, Smith and Shugart 1987). Although vegetation structure may predict food resources reliably (Smith and Shugart 1987, Petit and Petit 1996), a direct test of this hypothesis is not available. To determine if habitat selection is being driven by food resources or vegetation structure, one would have to establish plots that are similar in vegetation structure and composition, augment food resources on treatment plots, and see if individuals settle preferentially on those plots with greater food resources. Alternatively, one could reduce the abundance of food resources that are present on treatment plots. However, because many species arrive on the breeding grounds and establish territories before critical food resources are available (Morse 1976, Seastedt and MacLean 1979), it is likely that the evaluation of structural cues contributes in some part to habitat selection decisions (Pärt 2001).

Different constraints may influence a species' response to vegetation and structural cues. While food limitation can influence avian reproductive success (reviewed in Martin 1987), nest predation is the primary constraint on reproduction for many species, especially passerines (Ricklefs 1969, Martin 1992). Numerous studies have demonstrated that nest predation plays a substantial role in avian habitat selection (Martin and Roper 1988, Marzluff 1988, Martin 1998, Clark and Shutler 1999). For those species under intense predation pressure, habitat selection should be driven by the availability of suitable nesting sites and not food abundance, although both of these constraints may exist for certain species (Rodenhouse and Holmes 1992, Bull and Holthausen 1993, Holmes et al. 1996, Pasinelli 2000).

Nesting success is often positively associated with increases in understory density and structure for species that nest in the shrub understory (Martin and Roper 1988, Holmes et al. 1996, Howlett and Stutchbury 1996), but not all studies reach this conclusion (Holway 1991, Filliater et al. 1994, see discussion in Schmidt and Whelan 1999a). If nest predation is a limiting factor, shrub-nesting individuals should exhibit habitat selection at the territory, nest patch, and nest site scales. Individuals should select those areas with higher shrub densities for inclusion within a territory, and select nest-patches and nest-sites with greater vegetation coverage and more complex structure than what is available within the territory (Martin 1992, 1993). If a species' response to predation risk is adaptive, then territory size should be a function of the number and quality of suitable nest sites (Alatalo et al. 1986, Martin 1992). Thus, structural attributes of vegetation may be important for food and predation reasons (Martin 1988).

Intraspecific competition (or density effects) (Morse 1976; Wiens et al. 1985) is a constraint that may influence territory size. The effect of the density of conspecific territory holders on territory size and the reproductive performance of individuals has received extensive treatment in the avian literature (Morse 1976, Wiens et al. 1985, references in Adams 2001, Both and Visser 2003, Breininger and Oddy 2004). Generally, the impact of territoriality on reproductive success can follow one of two distributions (Fretwell and Lucas 1970). In the ideal free distribution, individuals distribute themselves without restriction and the fitness of all individuals across all occupied habitats is equivalent. In the ideal despotic distribution, territoriality serves to restrict the number of territory holders in the habitat of highest quality, and the fitness of individuals remains highest in the habitats of highest quality.

Researchers have argued that territory size should be optimized at a specific size or a range of sizes (Stamps and Krishnan 1999) and that these sizes will not be the smallest in the observed distribution (Knapton 1979, MacLean and Seastedt 1979). An optimal territory size represents a trade-off between sufficient resources and the energetic constraints of defending a territory against conspecifics and utilizing the resources in the territory efficiently (e.g., foraging costs) (Hixon 1980, Petit and Petit 1996)

Determining optimal territory size for a species poses a number of difficulties (MacLean and Seastedt 1979). First, one would need to observe territory holders across habitat of varying quality, and evaluate how territory size varied in relation to reproductive success and vegetation type and structure. Additionally, the effect of behavioral factors on habitat use needs to be controlled. For example, older individuals may settle preferentially in the best territories (Pärt 2001), confounding the effects of age (Nyström 1997, Lozano and Lemon 1999), habitat quality, and territory size on reproductive success (Badyaev and Faust 1996, Holmes et al. 1996, Petit and Petit 1996). To segregate these factors, one would have to force older birds (who presumably possess more experience in foraging and selecting suitable nest sites) (Forslund and Pärt 1995) to establish territories in habitat of poorer quality (a difficult task in field situations) or to manipulate habitat features after individuals have settled (Pärt 2001).

I examined habitat selection and use in Dusky Flycatchers (*Empidonax oberholseri*). My objectives were to determine which factors were associated with territory selection, territory success, and territory size, and how habitat use was associated with reproductive success.

A Priori Hypotheses and Predictions

I believed that the availability of food resources and suitable nest sites were the two main factors that could influence habitat selection, territory success, and territory size in Dusky Flycatchers. I did not measure food abundance in this study, and food did not appear to be a limiting factor for reproductive success (Chapter 2). Two lines of evidence support this contention. First, I observed no instances of nest abandonment during any stages of the nesting cycle and no instances of nestling starvation. Second, I examined the mean duration of the nestling stage for all successful nests by site and year (Figure 1). If food limitation was a factor, the mean length of the nestling stage should differ significantly among sites, with nestlings on poorer quality sites remaining in the nest for longer periods than nestlings on higher quality sites (reviewed in (Martin 1987). The mean length of the nestling stage for all sites was 15.11 days (s.e., 0.172) in 2002 (range: 14.89-15.25 days) and 14.9 days (s.e., 0.120) in 2003 (range: 13.86-16 days). The mean length of the nestling stage differed significantly for only one site (BA2) between years (based on the comparison of 95% confidence intervals).

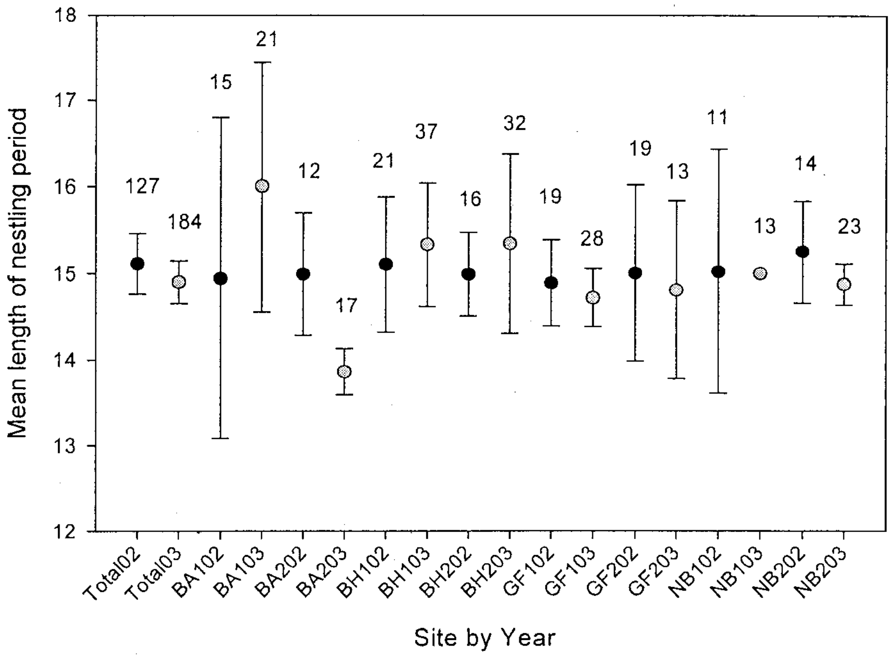

Figure 1: Mean length of nestling stage and 95% confidence intervals for Dusky Flycatchers by site and year, central Idaho, 2002 and 2003 (sample sizes are above each error bar).

As a result, I framed general biological hypotheses for the selection of appropriate nesting cover and structure and used them to develop models to explain variation in territory selection and territory success for Dusky Flycatchers. I included four sources of variation in these models:

1.) Year. Based on prior analyses, I knew that annual variation in nesting success existed between the two years of the study. Annual variation is common in avian populations and can result from factors such as local and/or regional weather patterns (Eckhardt 1975, Franklin et al. 2000), changes in predator density and abundance (Schmidt and Whelan 1999b), or fluctuations in food resources (Rodenhouse and Holmes 1992). While including the year in a model did not permit me to determine what factor (or factors) is responsible for the variation, it did allow me to reduce unexplained variation not accounted for by other variables.

2.) Site. I designed the study to examine how variation in vegetation structure influenced habitat use and reproductive performance in Dusky Flycatchers. While I felt that these differences in reproductive performance would result from variation in vegetation composition and structure, variation among the sites may be a result of other unmeasured factors such as predator density and abundance and/or food resources (although the latter seems unlikely).

3.) Vegetation. The Dusky Flycatcher is known to respond positively to increases in understory coverage and decreases in the overstory canopy (Kelly 1993, Sedgwick 1993a, Easton and Martin 2002, Liebezeit and George 2002). In My study area, Dusky Flycatchers place their nests primarily in deciduous shrubs and restrict their use of conifers to foraging and singing perches. Increases in conifer density and coverage may be associated with an increased abundance of red squirrels (*Tamiasciurus hudsonicus*), least chipmunks (*Eutamias minimus*), and Steller's Jays (*Cyanocitta stelleri)*, the primary nest predators in the study area. Also, high overstory canopy coverage suppresses understory coverage in the grand fir vegetation type (see *Study Sites*).

4.) Density. The presence of conspecific territory holders can influence territory size (Fretwell and Lucas 1970, references in Stamps 1990, Both and Visser 2000) and measures of reproductive success (Dhondt et al. 1992, Both 1998a). High densities may invoke a functional response by predators (Mitchell and Brown 1990, Schmidt and Whelan 1999b, Roos 2002) or lead to interference competition by conspecifics for resources (Both 1998b).

METHODS

Study Sites

I studied Dusky Flycatchers at eight different sites in central Idaho, USA, during 2002 and 2003. The sites were chosen to provide a range of vegetative and structural features thought to influence Dusky Flycatcher habitat selection, use, and reproductive performance (Kelly 1993, Sedgwick 1993b). Study sites ranged in size from 8.1 to 22.8 ha. All of the study sites were located in the moist grand fir habitat type (Steele et al. 1981). Ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotzuga menziesii*), and grand fir (*Abies grandis*) were the dominant overstory trees. Scouler's willow (*Salix scouleriana*), Rocky Mountain maple (*Acer glabrum*), mallow ninebark (*Physocarpus malvaceus*), thinleaf alder (*Alnus sinuata*), buckthorn (*Ceanothus velutina*), and twinberry (*Lonicera utahensis*) dominated the understory on all of the sites. The topography of the sites varied from flat benches to steep (> 35 degree) slopes. Elevations ranged from 1470 m to 1800 m. No perennial water was present at any of the sites. Distances between sites ranged from 0.63-11.9 km. Shrub densities varied at each site as a result of past disturbance events (logging and fire) that reduced the overstory canopy and altered soil conditions. Shrub development and coverage on the sites ranged from extremely patchy to relatively continuous shrub cover > 2 m in height.

Nest Searching and Nest Monitoring

I located nests by spot-mapping singing males (Bibby et al. 1992) and searching for nesting females throughout the breeding season. Nests were visited every one or two days, depending on the stage of the nesting cycle, to determine nest fate. Nests were checked daily during the laying phase and near the estimated fledging date to obtain accurate estimates of nesting survival. Observers approached nests from different routes on each visit and binoculars were used to observe nests from a distance when possible (Martin and Geupel 1993).

Territory Mapping

Initial territory boundaries were delineated during weekly spot-mapping sessions that were conducted from the first week of May until the last week of June in each year. I randomly selected territories for mapping from the total number of active territories at each site. I returned to individual territories and mapped them by marking singing and counter-singing points, preferred foraging perches, and aggressive interactions with other males (Martin and Geupel 1993). No unpaired males maintained territories on any of the eight sites in either year. To standardize measurements across territories and sites, the actual delineation of a male's defended territory was begun after a female had completed a nest and was incubating eggs. Territories were delineated during three visits to the sites (over five days). Males were not color-banded, but I felt confident that I could identify individual territory holders by their recurrent use of singing perches and foraging sites and by simultaneous identification of nearby territory holders. Males were observed from a distance when conditions permitted; in denser vegetation, males were followed more closely. Colored flagging was placed to indicate singing and/or foraging perches and points of aggressive encounters with other males. I recorded at least 15 points for each male with a GPS unit. I included those territories that went beyond the site boundaries, but which had the majority of their area within the site, in the calculations of site size. I chose non-habitat for Dusky Flycatchers (e.g., logging roads, meadows, or recent clearcuts) for site boundaries, and the majority of the territories fell within the sites.

Territory size was calculated using ArcView (v. 3.3). I examined the territory outlines visually and removed all points that were in the interior of the territory. Exterior points were connected and the area of the resulting figure was calculated. I measured the area defended by the male territory holder, and felt that connecting boundary points and calculating the total area was more appropriate than using a home range estimator such as the adaptive kernel.

Vegetation Measurements

Line-intercept transects 20 m in length were placed randomly throughout each of the eight study sites to sample vegetation and structural variables. Starting point and direction for each transect were generated randomly using ArcView (v. 3.3). The species and percent coverage of all understory vegetation in five strata (0-1 m, 1-2 m, 2-3 m, 3-4 m, > 4 m) were measured. Two extendable fiberglass poles were used to measure the placement of vegetation features in the individual stratum classes. Overstory canopy coverage was measured using the stick method (Gysel and Lyons 1980). Percent slope was determined by having two observers stand at either end of a line bisecting the patch and one observer viewing a marker at eye level through a clinometer. The results of spot-mapping allowed us to determine if a transect was in or out of a territory (use or non-use). At least five transects were sampled within the subset of territories that had their boundaries mapped by field personnel. Definitions for abbreviations of vegetation and other variables are in Appendix 2.

Modeling Habitat Selection and Territory Success for Dusky Flycatchers

The use of a particular model selection framework is contingent upon the objectives of the analysis (Chatfield 1995). Model selection may be viewed generally in the context of either description or prediction (Nichols 2001, Ginzburg and Jensen 2004). In the former case, independent variables may be added to the model to achieve a better fit and reduce the amount of unexplained variance in the data. This decision may lead to an over-specified model that has little predictive power when applied to external data. One alternative is to use a method that selects the best model based on its ability to classify individual cases correctly. In either case, model selection uncertainty will exist and perhaps influence the type of inference made about questions of interest. To address these issues, I evaluated candidate models with two different frameworks.

Information-theoretic method–Akaike's Information Criterion provides an estimate of the relative distance between a model fitted to sample data and the "true" model (which is unknown in most situations) (Burnham and Anderson 2002). The value of the estimator is: AIC = -2 log (L (θhat|y)) + 2K, where log (L (θhat|y)) is equal to the log-likelihood of the model estimating θ and K is equal to the number of estimable parameters in the model. The second term in the equation is a penalty for overfitting a model, and raises the AIC estimate for those models with extra parameters. The first term is multiplied by -2 in order to remain consistent with other uses of the log-likelihood (Burnham and Anderson 2002). However, it is important to note that model selection with AIC would not change if the first term was multiplied by other factors: only the relative values would change and not the order of ranking. I used AICc, a small sample criterion that is appropriate when n/K < 40 (Burnham and Anderson 2002). Once the models have been fit, AIC_c values are calculated for all models in the candidate set and the models are ranked relative to the model with the lowest AIC value (AIC_{cmin}). The relative distances (Δ AIC_c) between the best approximating model (AIC_{cmin}) and the other models are calculated as Δ AIC_{ci} = AIC_{ci} - AIC_{cmin}. Normalized Akaike weights (w_i) are computed for each of the R models as w_i = exp[-0.5 * (Δ AIC_{ci})] / [sum for all models of exp[-0.5 * (Δ AIC_{ci})]. The weights are used to evaluate the strength of evidence for each model and may be viewed as a way to incorporate model selection uncertainty into the analysis (Chatfield 1995, Burnham and Anderson 2002). In addition, the weights may be used to calculate model-averaged parameter estimates for prediction of external data cases.

The use of AIC to select models has been proposed as a way to minimize problems associated with traditional null hypothesis testing, p values, and arbitrary measures of significance (Johnson 1999, Guthery et al. 2001, Anderson and Burnham 2002). Information-theoretic approaches do not provide a test of the hypotheses being considered and the best models are not considered to be significant in any way (Burnham and Anderson 2002). Instead, models within a candidate set are compared to one another relative to the strength of evidence (the model "weights") that they contain given the sample data that were used to estimate model parameters. The best model based on AIC is only the best model in the candidate set. A better model may exist but it cannot be evaluated if it is not included in the candidate set (Burnham and Anderson 2002). Finally, as with any model selection procedure, a different "best" model could be selected given a second data sample from the same population (Burnham and Anderson 2002).

Cross-validation method–Cross-validation selects the best models from a candidate set based on their ability to classify data cases correctly (Shao 1993). The model that has the best overall prediction rate (given the nature of the dependent variable) is considered the best model. Cross-validation avoids the bias inherent in assessing models with the same data that was used to parameterize the models (Efron 1983).

The simplest form of cross-validation is the holdout method, in which the dataset is split into training and testing segments. The training segment is used to parameterize candidate models and the testing segment is used to evaluate the predictive ability (or error rate) of the candidate models. Although a data set can be split in numerous ways, cross-validation is most often accomplished with a leave-one-out method. In this method, one case is removed from the data set, the model is fitted with the remaining cases, and the value of the excluded case is predicted. While the leave-one-out method is commonly implemented (Shao 1993, Zhang 1993), it is known to be conservative and to select over-fitted models (Shao 1993).

K-folds cross-validation is preferred to the leave-one-out method (Shao 1993, Zhang 1993). In k-fold cross-validation, the data set is divided into k subsets. The model is parameterized with the remaining k-1 subsets, and the data cases in the withdrawn testing set are evaluated with the resulting model. This process is repeated k times and the average prediction error across k trials is computed. The value of each data case is predicted once and each data case is included in a training set k-1 times. Efron (1983) determined that k-folds cross-validation gave a nearly unbiased estimate of the apparent error rate (the proportion of observed errors made by the prediction rule on its training set), but this estimate could be highly variable for small datasets.

Cross-validation is a computer-intensive technique and few software programs offer it as an analysis option. This may account for the rarity of its application in wildlife and ecology studies (Burnham and Anderson 2002).

However, the goal of any modeling effort should be to develop a "purposeful representation" (Starfield 1997) that will explore various questions with regards to a data set and guide additional research efforts. While models do not have to be validated to be useful (Starfield 1997), validation provides a relatively unambiguous measure of a model's performance and its potential utility for guiding management programs.

Statistical Analyses

I conducted separate multiple logistic regression analyses to determine 1.) if vegetation and structural features differed between use and non-use transects and 2.) if vegetation and structural features and density were associated with territory success. I developed candidate model sets for both the use/non-use and territory success analyses (Tables 1 and 2). I limited the number of models to be considered in each set to < 20. Year was included as a covariate in all territory selection and success models. Site was included as covariate in the best models for territory selection and success. Density was included as a covariate in the best territory success models. Definitions for variables are in Appendix 2. I considered only those variables that occurred on > 50% of the transects for inclusion in models. I examined scatterplot matrices to determine which independent variables were correlated. Correlated independent variables were not entered into the same model to prevent problems in model parameterization as a result of multicollinearity (Christensen 1996, Graham 2003).

I examined the fit of the global models to assess the degree of overdispersion in the data (Burnham and Anderson 2002, Dinsmore et al. 2002). Overdispersion of count data may occur if sampling units are not independent of one another (e.g., nesting attempts of colonial birds are likely to be spatially correlated). I had no reason to think that individual nesting attempts of Dusky Flycatchers were not independent, but I examined the estimate of *c* (the overdispersion parameter) to be certain. To assess model structure in the best models, I examined confidence intervals for parameter estimates and checked for linearity in the logit as a function of the independent variables (Hosmer and Lemeshow 2000).

To examine the relationship between territory size and measures of reproductive success, I calculated nesting success, annual reproductive success, and the number of fledglings per hectare at each site. I estimated nesting success using the Mayfield method (Mayfield 1975). I included the incubation and nestling stages and the hatching rate in the estimates of nesting success. I calculated nesting success by site. I calculated standard errors for estimators by bootstrapping (Efron 1982). Bootstrapping calculates the standard error of an estimator when no close-formed expression exists for the variance of that estimator. The bootstrap standard error is the standard deviation of the sampling distribution (Quinn and Keough 2002).

The Mayfield estimator may be biased significantly in certain situations (e.g., when observer effects are present (Rotella et al. 2000) or when mortality rates are periodic across the nesting season (Johnson and Shaffer 1990)).

However, I felt that its use was appropriate because I calculated measures of productivity and determined how they were associated with territory size.

I calculated annual reproductive success following Murray (1992, 2000). Annual reproductive success (ARS(k)) is the number of young fledged per female per year in a study population (Murray 2000), and is the demographic parameter of most significance to a population. I calculated ARS(k) as: (the number of nesting attempts at a site/the number of first nesting attempts at a site) * (the number of successful broods at a site/the number of nesting attempts at a site) * (the total number of fledglings at a site/the number of successful broods at a site). This equation reduces to the number of fledglings at a site divided by the number of first nesting attempts. I calculated ARS(k) by site and year and for yearly totals. I calculated standard errors and 95% confidence intervals by bootstrapping.

I calculated the number of fledglings per hectare by dividing the total count of fledglings by individual site size for each site. The number of fledglings per hectare was a total count and not a point estimate, and I did not calculate a measure of variance for the total from each site.

I examined the relationship between mean territory size per site and measures of reproductive success (nesting success, annual reproductive success, fledglings per hectare) using Pearson's correlation coefficients (r) (Quinn and Keough 2002). Pearson's correlation coefficients are measures of the linear association between variables. Pearson's correlation coefficients were used because I expected general linear associations between the variables of interest. I calculated 95% confidence intervals by bootstrapping for any correlation coefficient that was greater than 0.50.

I used a subset size of 20 for the k-folds cross-validation. This partitioned the dataset randomly into 20 subsets. However, the number of cases in the k subset had fewer cases than the other nineteen because the data were not equally divisible by 20.

Table 1. Candidate models for Dusky Flycatcher territory selection, central Idaho, 2002 and 2003.

Model	Variables in model	Hypothesis
1	Year, Site, Slope, PerA, PerB, PerC, PerD, PerE, PerF, AGA, AGB, AGC, AGF, ASA, ASB, ASC, ASF, SSA, SSB, SSC, SSF, CVA, CVF, PMA, PMF, RPA, RPF, LDA, LDF, ConA	Global
2	Year, PerA, PerC	General cover
3	Year, PerF, PerB	General cover
4	Year, PerA, PerC, PerE	General cover
5	Year, PerF, PerB, PerE	General cover
6	Year, PerA, PerC, PerD, PerE	General cover
7	Year, PerF, PerB, PerD, PerE	General cover
8	Year, ASF, ASB, ASD	Substrate selection
9	Year, ASA, ASC, ASD	Substrate selection
10	Year, AGA, AGC, ASA, ASC, SSA, SSC, CVA, PMA	Substrate selection
11	Year, AGF, AGB, ASF, ASB, SSF, SSB, CVF, PMF	Substrate selection
12	Year, PMA, RPA, LDA	Ground cover
13	Year, ConA, PerF, PerB	General cover
14	Year, ConA, PerF, PerB, Site	13 with Site
15	Year, ConA, PerF, PerB, Slope **(15a with site)**	13 with Slope
16	Year, ConA, PerA, PerC, Slope	Habitat
17	Year, Site	General

Table 2. Candidate models for Dusky Flycatcher territory success, central Idaho, 2002 and 2003.

Model	Variables in model	Hypothesis
1	Year, Slope, PerA, PerB, PerC, PerD, PerE, PerF, AGA, AGB, AGC, ASA, ASB, ASC, ASD, ASF, SSA, SSB, SSC, SSF, CVA, CVF, PMA, PMF, RPA, LDA, ConA	Global
2	Year, PerA, PerC	General cover
3	Year, PerF, PerB	General cover
4	Year, PerA, PerC, PerE **(4a with Site)**	General cover
5	Year, PerF, PerB, PerE **(5a with Site)**	General cover
6	Year, PerA, PerC, PerD, PerE	Habitat
7	Year, PerF, PerB, PerD, PerE **(7a with Site)**	Habitat
8	Year, ASF, ASB, ASD	Substrate selection
9	Year, ASA, ASC, ASD	Substrate selection
10	Year, AGA, AGC, ASA, ASC, SSA, SSC, CVA, PMA	Specific substrates
11	Year, AGB, ASF, ASB, SSF, SSB, CVF, PMF	Specific substrates
12	Year, PMA, RPA, LDA	Ground cover
13	Year, ConA, PerF, PerB	Habitat
14	Year, ConA, PerA, PerC	Habitat
15	Year, ConA, PerF, PerB, Slope	13 with Slope
16	Year, ConA, PerA, PerC, Slope	Habitat
17	Year, Site **(17a with Density)**	General

RESULTS

I mapped 107 Dusky Flycatcher territories in 2002 and 2003. I mapped 51 territories in 2002 (21 unsuccessful and 30 successful) and 56 territories in 2003 (27 unsuccessful and 29 successful). Territories were monitored for the length of the breeding season and fated. I sampled 309 non-use transects and 337 use transects in 2002 and 263 non-use transects and 318 use transects in 2003. Of the territories that I mapped and fated, 109 transects were in unsuccessful territories and 111 transects were in successful territories in 2002. One hundred and nineteen transects were in unsuccessful territories and 146 were in successful territories in 2003.

Territory Selection

Information-theoretic method–Territory selection was a function of percent coverage of all conifer species < 4 cm dbh in Stratum A, percent cover of shrub species in Stratum F, percent cover of shrub species in Stratum B, slope, and year (Table 3). The estimate from the best model for the effect of percent coverage of all conifer species < 4 cm dbh in Stratum A was $\beta_{ConA} = -3.205$ (1 standard error = 1.036, 95% confidence interval = -5.236, -1.174) on a logit scale. This estimate was negative in all models with the percent coverage of conifer species < 4 cm dbh in Stratum A effect. The estimate from the best model for the effect of percent coverage of shrub species in Stratum F was $\beta_{PerF} = 2.356$ (1 standard error 0.271, 95% confidence interval = 1.825, 2.887). This estimate was positive in all models with the percent coverage in Stratum F effect. The estimate from the best model for the effect of percent coverage of shrub species in Stratum B was $\beta_{PerB} = 3.311$ (1 standard error 0.35, 95% confidence interval = 2.625, 3.997). This estimate was positive in all models with the percent coverage in Stratum B effect. The estimate from the best model for the effect of slope was $\beta_{Slope} = 0.102$ (1 standard error 0.025, 95% confidence interval = 0.053, 0.151). This estimate was positive in all models with the percent coverage in Slope effect. The estimate from the best model for the effect of Year was $\beta_{Year} = 0.224$ (1 standard error 0.125, 95% confidence interval = -0.021, 0.469). Other models received almost no support. The global model fit adequately and the estimate of $c = 1.18$ indicated that the model variances are not underestimated. I used AIC_c as the model selection criteria.

The addition of site to the best model did not improve the model substantially (Model 15a, Δ AIC$_c$ = 4.10, Table 3).

The logistic regression equation (one standard error for each β_i are in parentheses with variable names) for the best model (Model 16) was

$$\text{logit}(\hat{S}_i) = -1.108\ (0.185) + 0.224\ (\text{Year},\ 0.125) - 3.205\ (\text{ConA},\ 1.036)$$
$$+ 2.356\ (\text{PerF},\ 0.271) + 3.311\ (\text{PerB},\ 0.350) + 0.102\ (\text{Slope},\ 0.025)$$

To evaluate the effects of percent coverage of all conifer species < 4 cm dbh in Stratum A, percent coverage of shrub species in Stratum F, and percent coverage of shrub species in Stratum B, I consider three examples. First, a transect that had 50% coverage of conifer species > 4 cm dbh in Stratum A was 2.6 times less likely to be included in a territory than a transect that had 20% coverage (exp(-3.205*(0.5-0.2))). Second, a transect that had 50% coverage of shrub species in Stratum F was 2 times as likely to be included in a territory than a transect that had 20% coverage (exp(2.356*(0.5-0.2))). Finally, a transect that had 50% coverage of shrub species in Stratum B was 2.7 times as likely to be included in a territory than a transect that had 20% coverage (exp(3.311*(0.5-0.2))). Ninety-five percent confidence intervals for the estimates of year (-0.021,0.469) and slope (0.014,0.190) indicate that the effect sizes are minimal.

Table 3. Summary of information-theoretic model selection results for Dusky Flycatcher territory selection, central Idaho, 2002 and 2003.

Model	-2 Log likelihood	K	AIC_c	ΔAIC_c	w_i
15	1567.71	6	1579.78	0.00	0.80
15a	1557.58	13	1583.88	4.10	0.10
13	1575.57	5	1585.62	5.84	0.04
1	1510.95	37	1587.31	7.54	0.02
16	1576.06	6	1588.13	8.35	0.01
5	1579.25	5	1589.30	9.52	0.01
7	1577.44	6	1589.51	9.73	0.01
3	1581.57	4	1589.60	9.83	0.01
14	1566.28	12	1590.54	10.76	0.00
4	1591.65	5	1601.70	21.92	0.00
2	1595.19	4	1603.22	23.45	0.00
6	1591.30	6	1603.37	23.60	0.00
10	1584.88	10	1605.06	25.28	0.00
11	1607.47	10	1627.65	47.87	0.00
9	1658.43	5	1668.48	88.70	0.00
8	1664.30	5	1674.35	94.57	0.00
12	1676.64	5	1686.69	106.91	0.00

Cross-validation method–Models 6 and 16 were better able to predict habitat selection than the other models in the candidate set (Table 4). The average combined prediction rate (use and non-use; range 0.501-0.688), the average use prediction rate (range 0.522-0.713), and the average non-use prediction rate (non-use only; range 0.421-0.664) varied widely across the candidate models. Models 6 and 16 were able to predict all three categories with an accuracy of 65% or higher.

Table 4. Summary of cross-validation results for Dusky Flycatcher territory selection, central Idaho, 2002 and 2003.

Model	k	Total Correct	Use Correct	Non-use Correct
6	6	0.688	0.713	0.664
16	6	0.679	0.695	0.655
2	4	0.643	0.681	0.607
5	5	0.638	0.672	0.605
4	5	0.637	0.673	0.601
13	5	0.635	0.672	0.599
7	6	0.635	0.668	0.601
14	12	0.633	0.673	0.596
15a	13	0.632	0.672	0.595
15	6	0.630	0.668	0.594
3	4	0.623	0.659	0.587
10	10	0.583	0.591	0.579
11	10	0.576	0.680	0.564
12	5	0.563	0.594	0.532
9	5	0.546	0.565	0.516
8	5	0.501	0.522	0.421
1	na	na	na	na

Territory Success

Information-theoretic method–Territory success was a function of year, site, and density (Table 5). Parameter estimates for the best model (Model 17a) are included in Table 6. The addition of density to Model 17 increased support for the model significantly. The addition of site to Models 5, 4, and 7 increased the support for those models significantly, but they did not have as much support as Model 17. Other models received little support in the analysis. The global model fit adequately and My estimate of c = 1.21 indicated that model variances were not underestimated. I used AIC_c as the model selection criteria.

Model 17a had a strong negative effect of density on territory size (Table 6). The intercept estimate was inflated because it included the estimate for one site (NB2) where all of the measured territories were successful and where the density of territories was the highest. The effect of density on territory success was negative in all models with both density and site parameters. The effect of density was positive in all models that did not include site parameters. For example, the model with only year and density effects had a positive effect for density on territory success (Table 7).

Table 5. Summary of model selection results for Dusky Flycatcher territory success, central Idaho, 2002 and 2003.

Model	-2 Log likelihood	K	AIC$_c$	Δ AIC$_c$	w_i
17a	662.373	10	682.78	0.00	0.73
4a	659.802	13	686.49	3.70	0.11
5a	659.869	13	686.55	3.77	0.11
7a	659.599	14	688.39	5.61	0.04
17	675.513	9	693.85	11.07	0.00
5	730.293	5	740.40	57.62	0.00
4	731.292	5	741.40	58.62	0.00
7	730.079	6	742.23	59.45	0.00
11	724.714	9	743.05	60.27	0.00
6	731.291	6	743.45	60.66	0.00
3	736.422	4	744.50	61.71	0.00
2	736.556	4	744.63	61.85	0.00
8	735.303	5	745.41	62.63	0.00
1	652.317	43	745.85	63.07	0.00
12	736.307	5	746.42	63.63	0.00
13	736.373	5	746.48	63.70	0.00
14	736.476	5	746.59	63.80	0.00
15	734.841	6	747.00	64.21	0.00
16	734.932	6	747.09	64.30	0.00
10	727.138	10	747.55	64.77	0.00
9	739.381	5	749.49	66.71	0.00

Table 6. Parameter estimates from the best-supported territory success model (Model 17a) for Dusky Flycatchers, central Idaho, 2002 and 2003.

Variable	Estimate of ß	Standard error	95% confidence interval
Intercept	4.434	1.161	2.158, 6.710
Year	0.189	0.049	0.093, 0.285
Density	-4.169	1.131	-6.386, -1.952
BA1	1.119	0.211	0.705, 1.533
BA2	0.330	0.108	0.118, 0.542
BH1	-0.202	0.075	-0.349, -0.055
BH2	0.497	0.124	0.254, 0.740
GF1	0.0002	0.047	-0.092, 0.092
GF2	-0.018	0.040	-0.096, 0.060
NB1	0.658	0.116	0.431, 0.885

Table 7. Parameter estimates for a model with year and density effects for Dusky Flycatchers, central Idaho, 2002 and 2003.

Variable	Estimate of ß	Standard error	95% confidence interval
Intercept	-0.326	0.114	-0.549, -0.052
Year	-0.199	0.065	-0.326, -0.072
Density	0.702	0.198	0.319, 1.09

Models with only habitat feature effects received little support in the analysis (Table 5). I calculated summary statistics (mean, standard error and 95% confidence interval) for six vegetation variables for successful and unsuccessful territories (Table 8). Ninety-five percent confidence intervals overlap for all vegetation coverage estimates, indicating that significant differences did not exist between successful and unsuccessful territories for prominent habitat features. Standard errors for all estimates were not inflated when compared to the size of the respective variable means.

Table 8. Means, standard errors, and 95% confidence intervals for six vegetation variables by territory success for Dusky Flycatchers, central Idaho, 2002 and 2003.

	Unsuccessful (n=228)			**Successful (n=257)**		
Variable	**Mean**	**Standard error**	**95% confidence interval**	**Mean**	**Standard error**	**95% confidence interval**
PerA	0.197	0.015	0.166, 0.227	0.223	0.015	0.193, 0.252
PerB	0.076	0.011	0.054, 0.098	0.102	0.012	0.078, 0.126
PerC	0.033	0.008	0.016, 0.049	0.051	0.008	0.034, 0.067
PerD	0.017	0.006	0.005, 0.030	0.025	0.006	0.013, 0.037
PerF	0.455	0.022	0.411, 0.498	0.498	0.018	0.461, 0.535
PerE	0.177	0.017	0.143, 0.212	0.205	0.021	0.163, 0.246

Cross-validation method–Models 17a, 7a, 5a, and 4a were better able to predict territory success than the other models in the candidate set (Table 9). The average combined prediction rate (successful and unsuccessful; range 0.479-0.670), the average successful prediction rate (range 0.581-0.698), and the average unsuccessful prediction rate (range 0.286-621) varied widely across the candidate models. The addition of site and density to Models 4, 5, and 7 significantly improved their predictive ability for unsuccessful territories.

Table 9: Summary of cross-validation results for Dusky Flycatcher territory success, central Idaho, 2002 and 2003.

Model	k	Total Correct	Successful	Unsuccessful
17a	10	0.670	0.698	0.621
7a	14	0.665	0.695	0.613
5a	13	0.658	0.690	0.602
4a	13	0.652	0.685	0.595
17	9	0.630	0.659	0.571
7	6	0.582	0.594	0.500
15	6	0.582	0.589	0.500
4	5	0.579	0.592	0.485
10	10	0.579	0.586	0.472
16	6	0.577	0.583	0.440
12	5	0.577	0.581	0.286
9	5	0.575	0.582	0.409
8	5	0.575	0.581	0.375
5	5	0.573	0.589	0.464
13	5	0.573	0.580	0.333
3	4	0.571	0.580	0.350
6	6	0.566	0.585	0.435
11	9	0.555	0.587	0.436
14	5	0.485	0.582	0.399
2	4	0.479	0.581	0.365
1	na	na	na	na

As a result of the discrepancy between the number of transects in successful and unsuccessful territories (318 failed, 58%; 228 successful, 42%), the average total prediction rate did not increase noticeably even when the average unsuccessful prediction rate increased (Table 9).

Territory Size–The distribution of territory sizes (n=107) followed a log-normal distribution (Figure 2) and I used a log-based transformation to normalize the data and to calculate summary statistics.

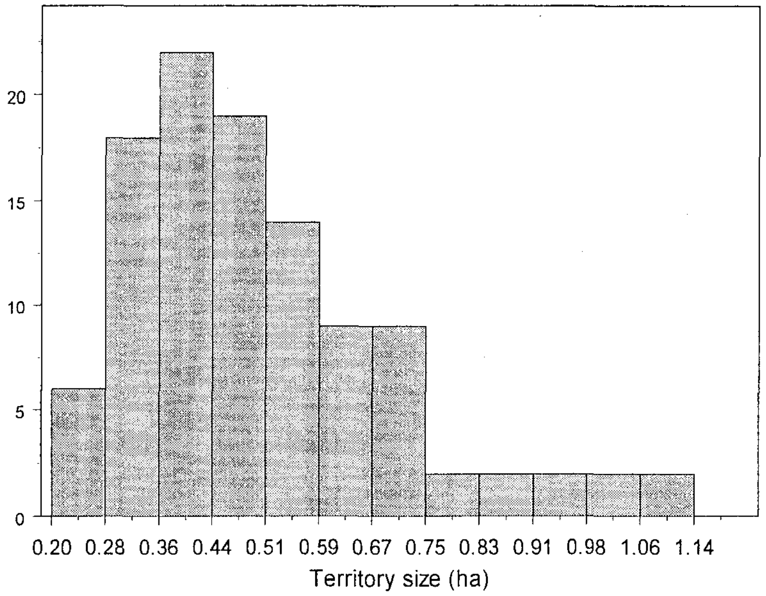

Figure 2: Histogram of territory size (ha) for 107 Dusky Flycatcher territories, central Idaho, 2002 and 2003.

Mean log territory size per site was not associated with measures of reproductive success or habitat structure (Table 10). The variance of the mean log territory size per site was negatively associated with nesting success, annual reproductive success, the number of fledglings per hectare, the density of territories (territories per hectare), and the percent overstory canopy coverage at each site (Table 10). However, bootstrapped 95% confidence intervals were large, indicating that the relationship was highly variable.

Mean log territory size for all sites did not differ significantly between years (Figure 3). The mean log territory size differed significantly for NB2 between years (Figure 3). All other sites did not differ significantly between years. The mean log territory site differed significantly for GF2 and NB2 in 2002. The mean log territory size on GF1 differed significantly from BH1, BH2, GF2, and NB2 in

2003. The large amount of variation in territory size among territories at individual sites precluded the use of more formal statistical tests.

Table 10. Pearson's correlations (r) between mean territory size, variance in territory size, measures of reproductive success, vegetation structure, and density for Dusky Flycatchers, central Idaho, 2002 and 2003. Ninety-five percent confidence intervals were calculated for all correlations > |0.50|.

	Nesting success	**ARS(k)**	**Fledglings per hectare**	**Territories per hectare**	**PerA**
Mean log territory size	0.13	-0.05	-0.20	-0.38	0.31
Variance of log territory size	-0.63 -0.85, -0.36	-0.58 -0.88, -0.37	-0.58 -0.75, -0.39	-0.51 -0.74, -0.31	-0.15
	PerB	**PerC**	**PerD**	**PerE**	**PerF**
Mean log territory size	0.13	0.10	0.12	0.12	-0.03
Variance of log territory size	-0.41	-0.37	-0.47	-0.64 -0.83, -0.27	-0.09

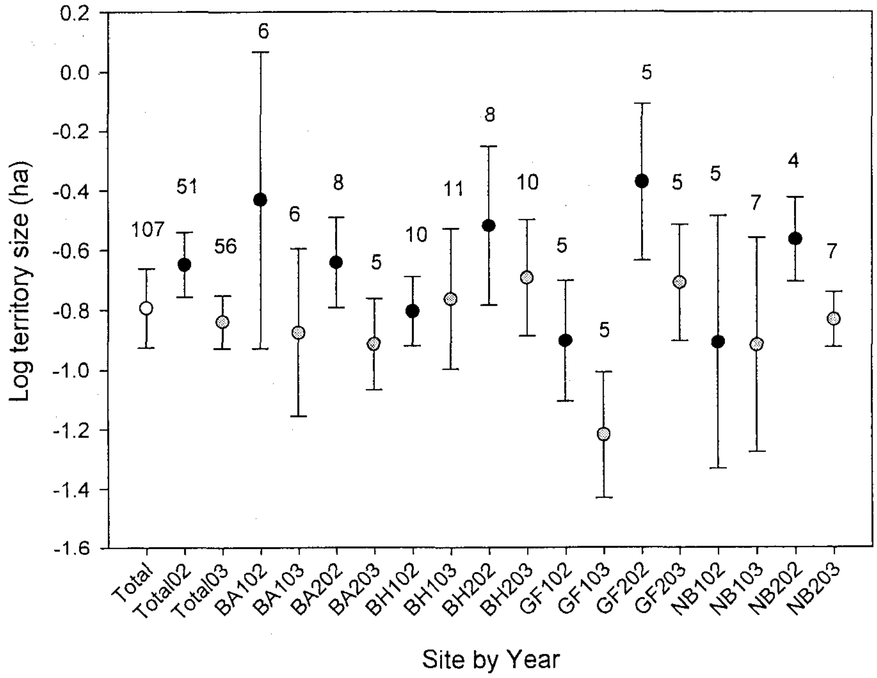

Figure 3: Mean log territory size (ha) total, total by year, and by site and year for Dusky Flycatchers, central Idaho, 2002 and 2003.

Significant differences did not exist between the mean log territory size for successful and unsuccessful territories by year (Table 11). I did not calculate the mean log territory size for unsuccessful and successful territories by site because of low sample sizes at each site.

Table 11. Mean and 95% confidence interval (back-transformed) for size (ha) of unsuccessful and successful Dusky Flycatcher territories, central Idaho, 2002 and 2003.

	Unsuccessful		**Successful**	
Year	**Mean**	**95% Confidence interval**	**Mean**	**95% Confidence interval**
2002	0.519	0.422, 0.637	0.526	0.469, 0.588
2003	0.411	0.364, 0.463	0.452	0.395, 0.518

Finally, I calculated the mean territory size by both the number of nestlings and the number of fledglings produced by the territory (Figure 4). Ninety-five percent confidence interval coverage was good for all estimators except those with low sample sizes. The average territory size for territories that produced three or four fledglings was 20% larger than for unsuccessful territories. A significant biological effect was present, although 95% confidence intervals overlapped for these estimators.

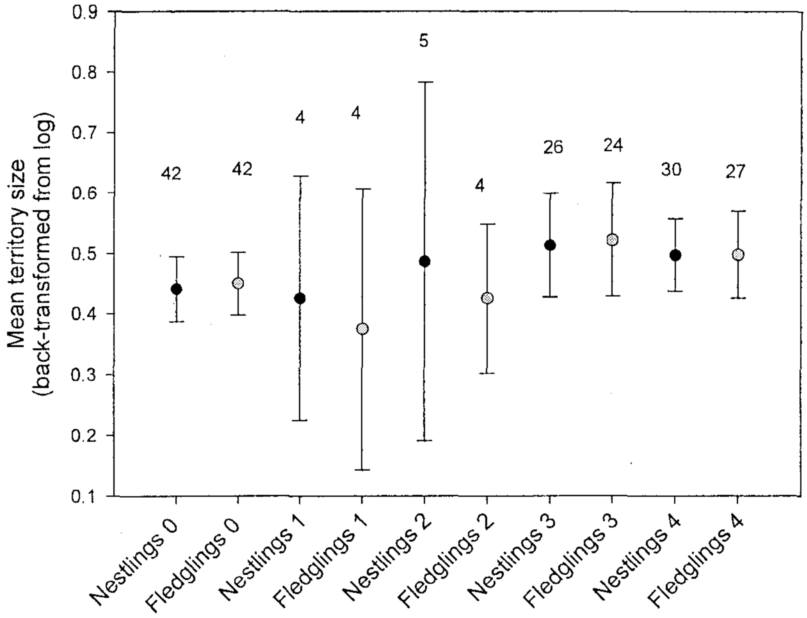

Figure 4: Mean territory size (ha; back-transformed) by number of nestlings and number of fledglings for Dusky Flycatchers, central Idaho, 2002 and 2003 (sample sizes are above error bars).

DISCUSSION

Territory selection by Dusky Flycatchers was associated primarily with vegetation composition and structure, slope, and year. The results of the information-theoretic analysis provided strong support for a single model (Table 3). However, this model was not the best predictor of territory selection in an independent data set (Table 4) and three models with fewer parameters were better able to predict territory selection for Dusky Flycatchers. My results are in contrast with the findings of Kelly (1993), who concluded that Dusky Flycatcher habitat selection was only detectable at small scales of habitat use. The data supported simple models that fit the data adequately and were able to predict independent cases with a relatively high rate of accuracy.

Nest predation was the primary constraint on reproductive success for Dusky Flycatchers during My study (see *A Priori Hypotheses and Predictions*). Dusky Flycatcher nests were located primarily in deciduous shrubs and habitat selection was strongly associated with vegetation features in the understory strata. Dusky Flycatchers may have selected habitat for inclusion within territory boundaries based on the availability of suitable nest-sites that reduced predation risk and provided additional nest-sites for renesting attempts (Martin 1992, Kelly 1993, Martin 1993, Liebezeit and George 2002).

An alternative hypothesis is that Dusky Flycatchers selected territories based on the abundance and/or quality of food resources (MacLean and Seastedt 1979, Franzblau and Collins 1980, Martin 1987). Dusky Flycatchers use the shrub understory for both nesting and foraging (Kelly 1993, Sedgwick 1993b, a), and I cannot reject the hypothesis that Dusky Flycatchers selected territories based on the availability of food resources. Both of these factors share the same proximate cue (vegetation composition and structure) and I cannot determine with certainty how individuals responded to this cue and made a selection decision. However, evidence suggested that the availability of food was not a limiting factor for Dusky Flycatchers (see *A Priori Hypotheses and Predictions*).

I did not detect significant differences in vegetation composition and structure between successful and unsuccessful territories (Table 5). The best model from the information-theoretic analysis contained year, site, and density effects, although confidence intervals for several estimates were close to 0, indicating small effect sizes. Model 17a was the only model to have a negative parameter estimate for density and the intercept estimate for Model 17a was much larger than the intercepts for other models. In all other models, the effect of density on territory size was positive. As a result, inference should be made with caution. Model 17a was the best predictor of territory success (Table 9), although the differences between the best three predictive models were slight. Models that did not include site effects were generally poor predictors of successful and unsuccessful territories. These results are in agreement with Kelly (1993), who found no significant differences in habitat composition and structure between successful and unsuccessful Dusky Flycatcher territories.

Evidence supporting the relationship between territory-scale habitat features and reproductive success in passerines is scant. For example, Braden et al. (1997) found significant correlations between territory vegetation and measures of reproductive success such as the number of successful nests and the number of nestlings. Both Matusoka et al. (1997) and Jones and Robertson (2001) found differences between territory and non-use habitat, but neither one of these studies determined if habitat features differed between successful and unsuccessful territories. Smith and Shugart (1987) found that habitat features measured at the territory-scale were associated with food abundance, but did not examine how habitat features or food abundance influenced reproductive success. Finally, Seastedt and MacLean (1979) concluded that vegetation composition within territories was not related to reproductive success in Lapland Longspurs (*Calcarius lapponicus*).

Territory success may be a function of either smaller scales of habitat use (Martin 1992, Murphy et al. 1997) or individual characteristics (Daunt et al. 1999). For example, vegetation features measured at the territory-scale may serve as an index of the general availability of nest-sites, but the actual placement and use of nest-sites may determine whether individuals reproduce successfully or not. Also, if variation in parental activity has a strong effect on nest predation rates (Martin 1998, Martin and Ghalambor 1999), then it is unlikely that territory-scale features would differ between successful and unsuccessful territories. Finally, first-time breeders may select appropriate habitat features at the territory-scale, but be less likely to select appropriate nest-patches and nest-sites (Forslund and Pärt 1995) and experience reduced reproductive success (Lozano and Lemon 1999, Woodard and Murphy 1999, Hoover 2003).

The effect of density on avian reproduction may vary by both species and study system. A high density of conspecifics may lead to reduced survival and reproductive success by attracting predators (Roos 2002) or by interference competition for resources (Dhondt et al. 1992, Holmes et al. 1996, Both 1998b, Zanette et al. 2000). Other studies have found that breeding territory density did not affect reproductive success and survival (Alatalo and Lundberg 1984, Both and Visser 2000).

The density of breeding territories in my study was associated positively with the number of fledglings per hectare (Chapter 2), a result that was reflected in all of the territory success models that included density but not site parameters (Tables 5, 6, and 7). Individual site effects confounded the relationship between density and reproductive success because many of the measured territories failed on certain sites where measures of reproductive success were high. Similarly, 9 of 11 territories measured on NB2 were successful, resulting in a large estimate for the intercept in models that included site as a parameter. Future workers should interpret density effects on reproductive success with caution and be certain to examine how parameter estimates may change as a result of unbalanced samples.

The mean territory size for a site was not associated with vegetation composition and structure or density (Table 10). My estimates for mean territory size for Dusky Flycatchers are less than what other workers have reported. Liebezeit and George (2002) found a mean territory size of 0.80 ha (se = 0.04) for Dusky Flycatchers in northern California. Eckhardt (1975) found a mean territory size of 0.73 ha (se = 0.23) in Colorado. Although both of these estimates are larger than what I report here, estimated densities reported in Sedgwick (1993a) suggest that the mean territory size for Dusky Flycatchers in moist grand fir forests in central Idaho was below the average derived across all habitat types.

The variance of mean territory size was negatively associated with overstory canopy coverage. This result contrasts with known patterns of habitat selection and use for the Dusky Flycatcher (Kelly 1993, Sedgwick 1993a, Easton and Martin 2002), which is thought to prefer areas with open canopies. However, the shrub understory in the moist grand fir habitat type increases with moderate amounts of overstory coverage (see *Study Sites*). Also, sites with small variances for territory sizes had not been harvested recently and had more continuous overstory coverage.

Evidence is mixed regarding the relationship between vegetation features and territory size in passerines. Marshall and Cooper (2004) found no correlations between territory volume and foliage density, a composite measure of vegetation structure. Territory volume was negatively correlated with foliage density, although the relationship was highly variable and the sample size very small. Braden et al. (1997) found no relationship between territory size and vegetation features for California Gnatcatchers (*Polioptila californica californica*). Knapton (1979) determined that the largest territories for Clay-colored Sparrows (*Spizella pallida*) had a lower proportion of their area covered by a preferred nesting substrate, suggesting that individuals were trying to incorporate sufficient nesting cover within territory boundaries. Porneluzi and Faaborg (1999) found no difference between Ovenbird (*Seiurus aurocapillus*) territory size on fragmented and unfragmented sites within the same habitat type. Jones et al. (2001) described significant differences in Cerulean Warbler (*Dendroica cerulea*) territory size following a natural disturbance that affected vegetation structure within one habitat type, suggesting that individuals compensated by increasing territories to include sufficient amounts of resources (e.g., nest-sites).

The relationship between vegetation features and territory size can be confounded by several factors. Petit and Petit (1996) found that territory size for Prothonotary Warblers (*Protonotaria citrea*) increased in lower quality habitat (as defined by vegetation structure and reproductive success). Also, Hunt (1996) found that American Redstarts (*Setophaga ruticilla*) had smaller territories and experienced increased reproductive success in preferred early successional vegetation. Interpretation of the results from these last two studies is problematic because the gradient of habitat quality was assessed in habitat types that differed by composition and structure. Differences in territory size may be associated with structural or compositional differences across the habitat types or by differences inherent in the various vegetation types (e.g., food abundance and/or quality and predation risk). I controlled for this latter issue by selecting study sites that were in the moist grand fir habitat type and that varied based on vegetation composition and structure.

Finally, the way in which I defined the territory of a breeding pair may have influenced my results. I mapped territories only during the incubation period (see *Methods*). I did not map territories during the nestling period because the majority of male Dusky Flycatchers were occupied with provisioning nestlings and not singing or defending territory boundaries (Kroll, pers. obs.). I could not calculate the total utilized territory (Stenger and Falls 1959), which is the combined estimate of the area mapped during the incubation and nestling periods. Although I may have underestimated the actual territory used by a breeding pair, this bias was uniform across all territories that were measured.

The mean territory size for a site was not associated with measures of reproductive success (Table 10). Post hoc examination of scatterplots of mean territory size against measures of reproductive success did not reveal discernible relationships. However, post hoc examination of scatterplots suggested negative relationships between the variance of territory size and nesting success, annual reproductive success, and the number of fledglings per hectare at a site (Table 10). Previous analyses indicated that significant biological differences existed for measures of reproductive success across sites (Chapter 2). Individuals on higher quality sites (as expressed by fledglings per hectare) maintained territories of similar size to individuals on lower quality sites.

Avian territory size and reproductive success do not appear to be associated in a consistent manner. Although Bédard and LaPointe (1984), Knapton (1979), Porneluzi and Faaborg (1999), and Seastedt and MacLean (1979) found no relationship between territory size and reproductive success, Petit and Petit (1996) and Hunt (1996) found that territory size was negatively associated with reproductive success. Braden et al. (1997) suggested that territory size is associated with reproductive success but did not present evidence to support their contention.

The variance in territory size on lower quality sites may result from several factors. Individual territory size may be an optimized characteristic that varies based on local conditions, including vegetation structure, individual condition (Petit and Petit 1996), individual experience (Woodard and Murphy 1999, Pärt 2001), settlement time (Lanyon and Thompson 1986), and the density of conspecifics (Both and Visser 2000). Territories should be of similar size on sites that have relatively uniform vegetation composition and that support individuals of relatively equal competitive ability. On sites where vegetation cover is less uniform, individuals may have to extend their territory boundaries to include the resources that are necessary for successful reproduction. Conversely, individuals who settle later than conspecifics may only have access to small patches of low quality habitat and be forced to defend territories that are smaller in size than what is optimal. Both very small and very large territories were successful, suggesting that individuals can make required adjustments under sub-optimal conditions

CONCLUSION

Territory size has been proposed as a good surrogate measure of avian habitat quality (Smith and Shugart 1987, Hunt 1996, Petit and Petit 1996). If food is a limiting constraint, evidence indicates that territory size may decrease in habitat where food resources are aggregated and easily acquired (references in Martin 1987, Holmes et al. 1996). In these cases, territory size should be negatively correlated with both the abundance of food resources and reproductive success. I reiterate that territory size should only be used as a measure of habitat quality when a strong relationship between territory size and reproductive success has been demonstrated. Studies that suggest a close tie between habitat quality and territory size without examining how reproductive success varies as a result of these factors should be viewed cautiously (e.g., Smith and Shugart 1987, Marshall and Cooper 2004).

My results suggest that constraints imposed by nest predation select for an optimal territory size in Dusky Flycatchers. Dusky Flycatchers selected territories with higher diversity in the shrub understory than non-use areas. Although I was unable to detect differences in territory scale vegetation measurements between successful and unsuccessful territories, additional evidence suggests that significant differences exist in vegetation composition and structure between successful and unsuccessful nest-sites and nest-patches (Chapter 3). Individuals may select territories that provide adequate nest-sites and the size of the territory may result from the spatial distribution of these nest-sites (references in Martin 1992, Braden et al. 1997). On those sites that support relatively continuous understory cover, individuals may maintain a territory at a size that balances the trade-offs between nest predation, territory defense, and the efficient acquisition of food resources. On those sites where vegetation cover is discontinuous, individuals may have to extend the size of the territory to include sufficient nest-sites and nest-patches. On sites of poorer habitat quality, younger individuals (e.g., juveniles) or birds that arrived later in the season may be forced to settle in whatever habitat remained available and be forced to defend smaller territories.

I did not detect strong evidence suggesting that density influenced territory size in Dusky Flycatchers. An experiment that tests the response of individuals to the removal of conspecific territory-holders is the only way to assess the effect of density on territory size with certainty (Fretwell and Lucas 1970, Both and Visser 2000). However, I have presented evidence elsewhere (Chapter 2) indicating that a measure of reproductive success was positively associated with density. Also, we have presented evidence in this chapter that suggests that the variance in territory size was negatively associated with density. Taken together, these suggest that individuals that settle on the highest quality sites are able to acquire and maintain territories of equivalent quality and size and experience higher reproductive success than individuals on low quality sites.

Finally, although I was able to develop and validate simple models for Dusky Flycatcher territory selection, those models that incorporated the effects of vegetation composition and structure and density on reproductive success were not supported. I stress that my approach of model formulation and testing is not equivalent to experimental tests of various hypotheses concerning how vegetation features and structure and/or density may influence reproductive success. Models evaluated in this study are approximations of biological phenomena. Future efforts should develop models that address how habitat selection and use at multiple scales influences reproductive success and survival. Models should be tested experimentally and validated across the range of environmental conditions utilized by a species in order to draw inference from general patterns of habitat selection, habitat use, and fitness attributes.

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Chapter Four: Model selection for Dusky Flycatcher (*Empidonax oberholseri*) nesting success at the nest-site and nest-patch scales

ABSTRACT

I modeled breeding habitat use by the Dusky Flycatcher (*Empidonax oberholseri*) at the nest-site and nest-patch scales in central Idaho for two breeding seasons (2002-2003). I used information-theoretic and cross-validation methods to select the models with the most support from the two candidate sets. Successful nest-sites were characterized by greater concealment from above the nest and a greater distance to the edge of the substrate in which the nest was located. Successful nest-patches had fewer conifers less than 4 cm in diameter, less percent cover of conifers less than 4 cm in diameter, less percent cover of green ground cover, and greater percent coverage of deciduous shrubs than unsuccessful nest-patches. The probability of a nest succeeding was associated with study year at both scales. The nest-site models that received the most support from the information-theoretic method were able to predict successful and unsuccessful nests with high accuracy rates. Two of the three nest-patch models that received support from the information-theoretic method were able to predict successful and unsuccessful nests well, although the third model was unable to predict successful nests with reasonable accuracy. My results provide support for the hypothesis that habitat use by the Dusky Flycatcher at the nest-site and nest-patch scales is associated with predation risk. I stress that model selection criteria should be based on both the evaluation of biological hypotheses

and the development of models that may be used to examine general patterns of habitat use by a species across its geographic distribution.

INTRODUCTION

Habitat features that promote survival and reproductive success should be selected over time and lead to non-random patterns of habitat selection and use (Southwood 1977, Rosenzweig 1991, Martin 1996, Clark and Shutler 1999). Habitat selection and use in many organisms is a hierarchical process (Johnson 1980, Orians and Wittenberger 1991). However, the finer scales of habitat use may have a profound influence on an individual's performance (Whitham 1980, Kolbe and Janzen 2002). Nest-site placement can have direct effects on both maternal survival (Spencer 2002) and reproductive success (Martin 1988a, Bowyer et al. 1999, Clark and Shutler 1999, Spencer et al. 2002). For open-cup nesting passerines in temperate regions, nest predation is the primary constraint on reproductive success (Ricklefs 1969, Martin 1988b) and it may exert a strong selective pressure on individuals to use those habitat features that maximize reproductive success by reducing predation risk (Martin 1998, Clark and Shutler 1999).

Nest placement by birds is the result of a nest-site process that occurs across various spatial scales (Johnson 1980, Morris 1987). The nest-site (the substrate in which the nest is constructed) and the nest-patch (the general area surrounding the nest substrate) are embedded in a territory. Vegetation features at both scales may reduce predation risk by concealing the nest and parental movements to and from the nest and/or by increasing predator search times and reducing foraging efficiency (Martin and Roper 1988, Schmidt and Whelan 1999b). The regulation of the thermal environment (Walsberg 1985, With and Webb 1993) to maximize nestling growth (Calder 1973, Zerba and Morton 1983) or to reduce metabolic costs (Ricklefs and Hainsworth 1969, Shutler et al. 1998) and the proximity to foraging substrates (Bekoff et al. 1987, Steele 1993) are additional hypotheses for non-random nest placement. The latter hypothesis is tied closely to predation as parental activity can increase predation rates (Martin and Ghalambor 1999, Martin et al. 2000). Parents may be able to reduce provisioning trips if the nest is placed in a patch with abundant food resources. However, Holway (1991) found little support for this hypothesis in a study of the Black-throated Blue Warbler (*Dendroica caerulescens*), a species that prefers dense shrub patches for nest placement.

While numerous workers have examined the influence of vegetation characteristics on nest predation (Knopf and Sedgwick 1992, Filliater et al. 1994, Murphy et al. 1997, Sockman 1997, Martin 1998, Kershner et al. 2001), a limited number of studies have examined nest-site and nest-patch use simultaneously and determined if the same features are being used at both scales. Also, many studies have compared used nest-sites to random nest-sites (Steele 1993, Matsuoka et al. 1997, Dearborn and Sanchez 2001, Jones and Robertson 2001, Liebezeit and George 2002), despite exhortations (Martin 1992) to examine nest-site use with specific reference to its influence on fitness attributes (e.g., by comparing successful and unsuccessful nests). The identification of the scales at which habitat use occurs and of the influence of habitat use on fitness attributes is required to determine how proximate factors shape ultimate responses (Martin 1998, Clark and Shutler 1999).

I developed candidate models to evaluate habitat use and its influence on nesting success of the Dusky Flycatcher (*Empidonax oberholseri*) at the nest-site and nest-patch scales. I formulated models based on other studies of the Dusky Flycatcher (Kelly 1993, Sedgwick 1993b, Liebezeit and George 2002) as well as those factors that I thought were important in my study system. In addition, I considered models that represented alternative hypotheses concerning nest placement in open-cup nesting passerines (e.g., thermal regulation of the nest environment and proximity to foraging substrates). For the nest-site, I considered only predation and thermal regulation models; for the nest-patch, I considered predation, thermal regulation, and proximity to foraging substrates models.

Finally, I used two different model selection frameworks to evaluate the candidate models. I discuss which models had the most support based on the respective selection methods and the interpretation of the biological mechanisms represented by the models. I address how the choice of a particular framework may influence both those models considered for inference and the validity of inference gained from modeling efforts.

A Priori Hypotheses and Predictions

I considered several biological hypotheses for nest placement in open-cup nesting passerines and used them to develop specific models to explain variation in the nesting success of the Dusky Flycatcher. I included three sources of variation in the models:

1.) Year. Based on prior analyses, I knew that annual variation existed between the two years of the study. Annual variation is common in bird populations and can result from factors such as local and/or regional weather patterns (Eckhardt 1975, Franklin et al. 2000), changes in predator density and abundance (Schmidt and Whelan 1999b), or fluctuations in food resources (Rodenhouse and Holmes 1992). While including year in a model would not permit us to determine what factor (or factors) is responsible for the variation, it does allow us to reduce unexplained variation not accounted for by vegetation variables that may not display significant variation between years.

2.) Site. I designed the study to examine how variation in vegetation composition and structure influenced habitat use and reproductive performance in Dusky Flycatchers. While I felt that differences in nesting success would result from variation in vegetation features, variation among the sites may result from other factors such as predator type and/or density and the availability of food resources.

3.) Vegetation. Dusky Flycatchers have been reported to respond positively to increases in understory coverage and decreases in the overstory canopy (Kelly 1993, Sedgwick 1993a, Liebezeit and George 2002). In my study area, Dusky Flycatchers placed their nests primarily in deciduous shrubs and restricted their use of conifers to foraging and singing perches. Increases in conifer density and coverage may be associated with increased abundance of red squirrels (*Tamiasciurus hudsonicus*), least chipmunks (*Eutamias minimus*), and Steller's Jays (*Cyanocitta stelleri*), the primary nest predators in the study area. Also, high overstory canopy coverage suppresses understory coverage in the moist grand fir habitat type (Steele et al. 1981)(see *Study Sites*).

I developed models that described how vegetation structure influenced nesting success through three mechanisms: 1.) predation, 2.) thermal regulation; and 3.) proximity to foraging substrates.

At the nest-site scale, I expected nesting success to be positively associated with increases in substrate height, nest height, the number of stems of the substrate, distance to the edge of the nesting substrate, and measures of nest concealment. I expected nesting success to be negatively associated with distance to the nearest suitable nesting substrate and with south-facing orientations. I did not expect nesting success to vary among the five principal substrates used as nest-sites.

At the nest-patch scale, I expected nesting success to be positively associated with increases in the number and percent cover of the five principal nesting substrates (*Acer glabrum*, *Alnus sinuata*, *Ceanothus velutina*, *Physocarpus malvaceus*, *Salix scouleriana*) and the number and percent cover of all shrub species. I expected nesting success to be negatively associated with increases in percent litter cover, the number and percent cover of conifer species

< 4 cm, the percent cover of overstory conifer species, and the number of conifer species > 4 cm dbh. I felt these four variables would be associated with the presence of least chipmunks and red squirrels, both of which are known nest predators of the Dusky Flycatcher (Sedgwick 1993a, Liebezeit and George 2002). I had no specific predictions for the effect that the number of snags would have on nesting success.

METHODS

Study Sites

I studied Dusky Flycatcher nesting success at eight different study sites in central Idaho, USA, during 2002 and 2003. The sites were chosen to provide a range of vegetative and structural features believed to influence Dusky Flycatcher habitat use and reproductive performance (Kelly 1993, Sedgwick 1993a). Study sites ranged in size from 8.1 to 22.8 ha. All of the study sites were located in the moist grand fir habitat type (Steele et al. 1981). Ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotzuga menziesii*), and grand fir (*Abies grandis*) were the dominant overstory trees. Scouler's willow (*Salix scouleriana*), Rocky Mountain maple (*Acer glabrum*), mallow ninebark (*Physocarpus malvaceus*), thinleaf alder (*Alnus sinuata*), buckthorn (*Ceanothus velutina*), and twinberry (*Lonicera utahensis*) were the dominant understory plants on all sites. Site topography varied from flat benches to steep (> 35 degrees) slopes. Elevations ranged from 1470 m to 1800 m. Distances between sites ranged from 0.63-11.9 km. No perennial water was present at any site.

Shrub densities varied at each site as a result of past disturbance events (logging and fire) that reduced the overstory canopy and altered soil conditions. Shrub development and coverage on the sites ranged from extremely patchy to relatively continuous shrub cover greater than 2 m in height.

Red squirrels (*Tamiasciurus hudsonicus*), least chipmunks (*Eutamias minimus*), Steller's Jays (*Cyanocitta stelleri*), and Gray Jays (*Perisoreus canadensis)* were the dominant nest predators of the Dusky Flycatcher on all study sites (Kroll, pers. obs.). Mice (*Peromyscus* spp.) may have been occasional nest predators. I observed one incident of a Columbian ground squirrel (*Citellus columbianus*) destroying a nest.

Nest Searching and Nest Monitoring

I located nests by spot-mapping singing males (Bibby et al. 1992) and searching for nesting females throughout the breeding season. Nests were visited either every one or two days, depending on the stage of the nesting cycle, to determine nest fate. Nests were checked daily during the laying phase and near the estimated fledging date to obtain accurate estimates of nesting survival. Observers approached nests from different routes on each visit and binoculars were used to observe nests from a distance when possible (Martin and Geupel 1993).

Vegetation Measurements

Independent variables characterized habitat features at the nest-site and the nest-patch scales. The nest-site scale was associated with the actual substrate in which a nest was located. The nest-patch scale measured the vegetation structure within a 5 m radius plot (0.008 ha) centered on the nest substrate (Martin et al. 1997). Vegetation at the nest-site and nest-patch scales was measured within 10 days after a nest with eggs or young failed or fledged. Nests that were destroyed or abandoned before eggs were present were measured within 14 days of failure. Definitions for abbreviations of habitat descriptors are in Appendix 3.

Nest-site scale–The species of the nesting substrate, the height of the substrate, the height of the nest, the number of stems of the substrate, the nest orientation in the substrate, the distance from the nest to the nearest edge of the substrate, and the distance from the nest to the outer edge of the closest suitable substrate were recorded. The closest suitable substrate was defined as the nearest shrub that most closely resembled the nesting substrate. The degree of concealment from a distance of 1 m in each cardinal direction and from above and below the nest was measured by an ocular estimate. The degree of concealment from above for nests greater than 3 m in height could not be measured accurately.

Nest-patch scale–The slope, aspect, percent green ground cover (all green vegetation < 0.25 m in height), percent bare ground, percent woody debris (stumps, downed logs, slash), and percent other (road surfaces, rocks) were measured within the 5 m radius patch. Percent slope was determined with two observers standing at either end of a line bisecting the patch, and one observer viewing a marker at eye level through a clinometer. Overstory canopy coverage was measured with the stick method (Gysel and Lyons 1980) along a continuous line-intercept that bisected the nest-patch. The species and percent coverage of all understory vegetation in five strata (0-1 m, 1-2 m, 2-3 m, 3-4 m, > 4 m) were measured along the same transect. Two extendable fiberglass poles were used to measure the placement of vegetation features in the individual stratum classes. For shrub cover, the species, number of individual plants, and the percent cover were recorded. For conifer species, the species, number, and percent cover for all species < 4 cm dbh were recorded. For species > 4 cm dbh, the dbh was recorded. The dbh of all snags > 4 cm was also measured.

Modeling Nesting Success for Dusky Flycatchers

The use of a particular model selection framework is contingent upon the objectives of the analysis (Chatfield 1995). Model selection may be viewed generally in the context of either description or prediction (Nichols 2001, Ginzburg and Jensen 2004). In the former case, independent variables may be added to the model to achieve a better fit and reduce the amount of unexplained variance in the data. This decision may lead to an over-specified model that has little predictive power when applied to external data. An alternative is to use a method that selects the best model based on its ability to classify individual cases correctly. In either case, model selection uncertainty will exist and perhaps influence the type of inference made about questions of interest (Chatfield 1995, Burnham and Anderson 2002). To address these issues, I evaluated candidate models with two different frameworks.

Information-theoretic method–Akaike's Information Criterion provides an estimate of the relative distance between a model fitted to sample data and the "true" model (which is unknown in most situations) (Burnham and Anderson 2002). The value of the estimator is: AIC = -2 log (*L* (θhat|y)) + 2K, where log (*L* (θhat|y)) is equal to the log-likelihood of the model estimating θ and K is equal to the number of estimable parameters in the model. The second term in the equation is a penalty for overfitting a model, and raises the AIC estimate for those models with extra parameters. The first term is multiplied by -2 in order to remain consistent with other uses of the log-likelihood (Burnham and Anderson 2002). However, it is important to note that model selection with AIC would not change if the first term was multiplied by other factors: only the relative values would change and not the order of ranking. I used AICc, a small sample criterion that is appropriate when n/K < 40 (Burnham and Anderson 2002).

Once the models have been built, AIC_c values are calculated for all models in the candidate set and the models are ranked relative to the model with the lowest AIC value (AIC_{cmin}). The relative distances (Δ AIC_c) between the best approximating model (AIC_{cmin}) and the other models are calculated as $\Delta AIC_{ci} = AIC_{ci} - AIC_{cmin}$. Normalized Akaike weights (w_i) are computed for each of the R models as $w_i = \exp[-0.5 * (\Delta AIC_{ci})]$ / [sum for all models of $\exp[-0.5 * (\Delta AIC_{ci})]$. The weights are used to evaluate the strength of evidence for each model and may be viewed as a way to incorporate model selection uncertainty into the analysis (Chatfield 1995, Burnham and Anderson 2002). In addition, the weights may be used to calculate model-averaged parameter estimates for prediction of external data cases.

Cross-validation method–Cross-validation selects the best models from a candidate set based on their ability to classify data cases correctly (Shao 1993). The model that has the best overall prediction rate (given the nature of the dependent variable) is considered the best model. Cross-validation avoids the bias inherent in assessing models with the same data that was used to parameterize the models (Efron 1983).

I used k-folds cross-validation to assess candidate models. K-folds cross-validation is preferred to the leave-one-out method (Shao 1993, Zhang 1993). In k-folds cross-validation, the data set is divided into k subsets. The model is parameterized with the remaining k-1 subsets, and the data cases in the k testing set are evaluated with the resulting model. This process is repeated k times and the average prediction error across k trials is computed. Each data case is used once for prediction and each data case is in a training set k-1 times. Efron (1983) determined that k-folds cross-validation gave a nearly unbiased estimate of the apparent error rate (the proportion of observed errors made by the prediction rule on its training set), but this estimate could be highly variable for small datasets.

I conducted separate multiple logistic regression analyses to determine 1.) if vegetation features measured at the nest-site scale were associated with the probability of nest success and 2.) if vegetation features measured at the nest-patch scale were associated with the probability of nest success. For nesting success analyses, nests were classified as either predated/ abandoned or successful (produced at least 1 fledgling).

Table 1: Models for Dusky Flycatcher nesting success at the nest-site scale, central Idaho, 2002 and 2003.

Model	Variables in model	Hypothesis
1	All variables from other models	Global model
2	Species	Predation
3	Abcon, Becon, Mecon, NestOr, DistEdge, NeHeight	Predation (Kelly 1993)
4	#Stems, DistEdge, DistNear, NeHeight	Predation
5	Height, NeHeight, Height by Nest Height	Predation (Sedgwick 1993a)
6	Species, Height, NeHeight, Height by Nest Height	Predation
7	NeHeight, #Stems, DistEdge, DistNear, NestOr	Predation
8	DistEdge, AbCon (Model 8a with Site)	Predation
9	Species, #Stems, NestOr, DistEdge, NorthCon, SouthCon, EastCon, WestCon, AbCon, BeCon	Thermal regulation
10	NestOr, NorthCon, SouthCon, EastCon, WestCon, AbCon,	Thermal regulation
11	#Stems, NestOr, DistEdge, NorthCon, SouthCon, EastCon, WestCon, AbCon,	Thermal regulation
12	Species, NestOr, DistEdge	Thermal regulation
13	NorthCon, SouthCon, EastCon, WestCon, AbCon, BeCon, MeanCon	Thermal regulation

Table 2: Models for Dusky Flycatcher nesting success at the nest-patch scale, central Idaho, 2002 and 2003.

Model	Variables in model	Hypothesis
1	All variables from other models	Global
2	Year and Site	General
3	PerA, PerB, PerC, PerD, PerF	Predation
4	Pergreen, Perlitter, Aspect (habitat)	Predation
5	PerA, PerB, PerC, PerF	Predation
6	#Snags, PerA, PerB, PerC, PerD, PerCon	Predation (Kelly 1993)
7	SSA, SSB, AGA, AGB, ASA, ASB, CVA, CVB, PMA, PMB	Predation (Multiple nest-sites)
8	PerGreen, NumShrubs, PerShrubs	Predation
9	SSA, AGA, ASA, CVA, PMA	Predation
10	PerGreen, NumCS, PerAG, PerSS, NumCV **(Model 10a with Site)**	Predation
11	NumRP, PerRP, NumLD, PerLD	Predation
12	NumCon, PerCon, NumSS, PerSS, NumSnag, SnagDbh, NumCon, ConDbh	Predation
13	NumAG, %AG, NumAS, %AS, NumSS, %SS	Foraging substrates
14	NumCon, NumAG, %AG, NumAS, %AS, NumSS, %SS	Foraging substrates
15	Aspect, Slope	Thermal
16	NumShrubs, Pershrubs, Aspect, Slope	Thermal
17	PerA, PerB, PerC, PerD, PerOS, Aspect, Slope	Thermal
18	NumShrubs, Pershrubs, NumCS, PerCS (Model 18a with Site)	Thermal
19	Same as 6 with PerF	Predation

I developed candidate model sets for both the nest-site (Table 1) and nest-patch scales (Table 2). I limited the number of models to be considered in each set to < 25. Year was included as a covariate in all models. Site was included as a covariate in the most supported models. I considered only those vegetation variables that occurred on > 50% of the nest-site and nest-patch plots in order to limit the number of parameters available for consideration in models. I considered interaction of terms in specific cases (e.g., when modeling a result from a different study). Definitions for variables are in Appendix 3.

I examined the fit of the global models to assess the degree of overdispersion in the data (Burnham and Anderson 2002, Dinsmore et al. 2002).

Overdispersion of count data may occur if sampling units are not independent of one another (e.g., nesting attempts of colonial birds are likely to be spatially correlated). I had no reason to think that individual nesting attempts of the Dusky Flycatcher were not independent, but examined the estimate of *c* (the overdispersion parameter) to be certain. To assess model structure in the most supported models, I examined confidence intervals for parameter estimates and checked for linearity in the logit as a function of the independent variables (Hosmer and Lemeshow 2000).

I used a subset size of 20 for the k-folds cross-validation. This partitioned the dataset randomly into 20 subsets. However, the number of cases in the k subset will have fewer cases than the other nineteen because the data were not equally divisible by 20.

RESULTS

I found 324 Dusky Flycatchers nests in 2002 and 2003. Three hundred and eleven nests had the requisite data to be included in the analysis. Nests excluded from the analysis were either too high in a substrate to sample accurately, destroyed by human activity (e.g., logging), or had their exact locations recorded incorrectly and could not be relocated to sample. I sampled 127 nests in 2002 (47 successful nests, 37%) and 184 nests in 2003 (49 successful nests, 27%).

Information-theoretic method

Nesting success at the nest-site scale–Nesting success at the nest-site scale was a function of concealment from above the nest, the distance from the nest to the edge of the substrate, and year (Table 3). The estimate from the best model for the effect of concealment from above on nesting success was $\beta_{AbCon} = 1.908$ (1 standard error = 0.442, 95% confidence interval = 1.041, 2.774) on a logit scale. This estimate was positive in all models with the concealment from above effect. The estimate from the best model for the effect of the distance from the nest to the edge of the substrate on nesting success was $\beta_{DistEdge} = 0.448$ (1 standard error = 0.110, 95% confidence interval = 0.232, 0.664). The effect of distance to the edge of the substrate on nesting success was positive in all models. The estimate from the best model for the effect of year on nesting success was $\beta_{Year} = 0.749$ (1 standard error = 0.271, 95% confidence interval = 0.218, 1.280). The logit was a linear function of all model parameter estimates. Other models received almost no support. The global model fit adequately and my estimate of $c = 1.158$ indicated that the model variances were not underestimated. I used AIC_c as the model selection criteria.

The addition of site to the best model did not improve the model substantially (Model 8a, $\Delta AIC_c = 1.31$, Table 3). However, some evidence exists for an effect of site on nesting success and this model should be considered for inference.

Table 3: Summary of information-theoretic results for Dusky Flycatcher nesting success at the nest-site scale, central Idaho, 2002 and 2003.

Model	-2 Log likelihood	K	AIC_c	ΔAIC_c	w_i
8	355.14	4	363.27	0.00	0.66
8a	341.70	11	364.59	1.31	0.34
13	358.96	8	375.43	12.16	0.00
3	347.70	15	379.33	16.05	0.00
10	352.96	15	384.58	21.31	0.00
5	376.56	5	386.76	23.49	0.00
11	347.94	18	386.28	23.01	0.00
4	376.68	6	388.95	25.68	0.00
2	376.37	7	390.74	27.46	0.00
6	372.17	10	392.90	29.63	0.00
9	345.88	23	395.72	32.45	0.00
7	370.85	14	400.27	37.00	0.00
12	367.04	16	400.89	37.62	0.00
1	323.24	34	399.87	36.59	0.00

The logistic regression equation (one standard error for each β_i are in parentheses with variable names) for the best model (Model 8) was

$$\text{logit}(\hat{S}_i) = -2.855\ (0.459) + 0.448\ (\text{DistEdge}, 0.091) + 1.908\ (\text{AbCon}, 0.342) - 0.749\ (\text{Year}, 0.271)$$

To evaluate the effects of distance to the edge of the substrate, nest concealment, and year on nesting success, I consider three examples. First, a nest that was 85% concealed from above was 2.6 times as likely to be successful as a nest that was 35% concealed from above (exp(1.908*(0.85-0.35))). Second, a nest that was 1.75 meters from the edge of its substrate was 1.57 times as likely to be successful as a nest that was 0.75 meters from the edge of its substrate (exp(0.448*(1.75-0.75))). Finally, nests built in 2002 were twice as likely to be successful as those in 2003 (exp(0.749)).

Nesting success at the nest-patch scale–Three models received substantial support for nesting success at the nest-patch scale and the best two models had nearly identical amounts of support (Table 4). In the best two models, nesting success at the patch scale was positively related to the percent cover of shrubs and the percent cover of *Salix scouleriana* and negatively related to the number of conifer species < 4 cm dbh and percent green ground cover. The effects of percent shrub cover and percent cover of *Salix scouleriana* were positive in all models, while the effects of the number of conifer species < 4 cm dbh and percent green ground cover were negative in all models (Table 5). The addition of site to the best models did not improve the models (Δ AIC$_c$ = 7.65, 6.15, and 6.78 for Models 18a, 10a and 8a, Table 4). The logit was a linear function of the model parameter estimates in the three best models. The global model fit adequately and my estimate of c = 1.09. I used AIC$_c$ as the model selection criteria.

To evaluate the effects of model parameter estimates, I consider four examples. First, a nest in a patch that had 75% shrub cover was 1.55 times as likely to be successful than a nest in a patch with 25% shrub cover (exp(0.884*(0.75-0.25))) (Model 18). Second, a nest in a patch with 50 conifers < 4 cm dbh was 0.548 times as likely to succeed as a nest in a patch with 25 conifers < 4 cm dbh (exp(-0.024(50-25))) (Model 18). Third, a nest in a patch with 75% percent cover of *Salix scouleriana* was 2 times as likely to be successful as a nest in a patch with 25% cover of *Salix scouleriana* (exp(1.388*(.75-.25))) (Model 10). Finally, a nest in a patch with 75% green ground cover was 0.60 times as likely to succeed as a nest in a patch with 25% green ground cover (exp(-1.00*(.75-.25))) (Model 10).

Table 4: Summary of information-theoretic results for Dusky Flycatcher nesting success at the nest-patch scale, central Idaho, 2002 and 2003.

Model	-2 Log likelihood	K	AIC_c	ΔAIC_c	w_i
18	368.64	6	380.92	0.00	0.48
10	366.66	7	381.03	0.12	0.45
8	371.87	5	382.07	1.15	0.27
7	359.57	12	384.62	3.70	0.08
9	370.92	7	385.28	4.37	0.05
19	367.36	9	385.96	5.04	0.04
10a	357.65	14	387.07	6.15	0.02
2	368.94	9	387.53	6.62	0.02
8a	362.66	12	387.70	6.78	0.02
5	369.21	9	387.81	6.89	0.02
18a	361.34	13	388.57	7.65	0.01
11	376.73	6	389.01	8.09	0.01
3	377.70	6	389.98	9.06	0.01
12	373.52	8	390.00	9.08	0.01
13	372.26	9	390.86	9.94	0.00
14	376.80	7	391.17	10.25	0.00
6	375.89	8	392.37	11.45	0.00
16	370.04	12	395.08	14.17	0.00
4	373.05	11	395.94	15.02	0.00
15	375.67	10	396.41	15.49	0.00
17	371.04	15	402.66	21.75	0.00
1	296.14	47	407.30	26.38	0.00

Table 5: Parameter estimates for the best three nest-patch models for nesting success in Dusky Flycatchers, central Idaho, 2002 and 2003.

Model	Parameter estimates with 1 standard error	Hypothesis
18	logit ($\hat{S}_i$) = -1.575 (0.424) - 0.024 (NumCS, 0.0012) - 0.045 (PerCS, 0.0112) + 0 (NumShrub, 0.003) + 0.884 (PerShrub, 0.25) + 0.88 (Year, 0.325)	Thermal
10	logit ($\hat{S}_i$) = -0.643 (0.33) - 0.028 (NumCS, 0.0012) -1.001 (PerGreen, 0.325) – 0.47 (PerAG, 0.936) + 1.388 (PerSS, 0.923) + 0.048 (NumCV, 0.036) + 0.707 (Year, 0.278)	Predation
8	logit ($\hat{S}_i$) = -1.597 (0.457) – 0.816 (PerGreen, 0.369) + 0.002 (NumShrub, 0.003) + 0.947 (PerShrub, 0.148) + 1.025 (Year, 0.342)	Predation

Cross-validation method

Nesting success at the nest-site scale-Models 8 and 8a were better able to predict nesting success at the site scale than the other models in the candidate set (Table 6). Both the average total prediction rate (failed and successful nests; range 0.617-0.731) and the average failed prediction rate (failed nests only; range 0.654-0.753) were reasonably good for all models. However, the best two models were able to predict successful nests at a higher average rate. Finally, the addition of site to Model 8 did not increase its predictive power.

As a result of the large discrepancy between the number of failed and successful nests (215 failed, 69%; 96 successful, 31%), the average total prediction rate did not increase noticeably even when the average successful prediction rate increased (Table 6). For example, if two cases out of the twenty in a subset were successful nests, they are likely to have little effect on the overall average prediction rate for that subset even if both were predicted correctly. Selection of cases for each subset is random, and it is unlikely that more than forty percent of the cases in a subset were successful nests.

Table 6: Summary of cross-validation results for Dusky Flycatcher nesting success at the nest-site scale, central Idaho, 2002 and 2003.

Model	k	Percent Correct	Percent Successful Correct	Percent Failed Correct
8	3	0.731	0.667	0.753
8a	10	0.714	0.658	0.735
3	14	0.695	0.514	0.717
11	16	0.672	0.500	0.718
12	15	0.669	0.333	0.693
13	8	0.655	0.400	0.699
9	22	0.652	0.425	0.708
7	13	0.651	0.385	0.695
10	14	0.649	0.406	0.703
2	6	0.641	0.333	0.692
6	9	0.636	0.333	0.654
5	4	0.625	0.400	0.664
4	5	0.617	0.167	0.689
1	34	na	na	na

Nesting success at the nest-patch scale-Models 10 and 8 were the best predictors of nesting success at the patch scale (Table 7). Both the average total prediction rate (range 0.61-0.71) and the average failed prediction rate (range 0.642-0.714) were reasonably good for all models. However, models 8, 10, 11, and 13 were able to predict successful nests at a much higher rate than the other candidate models (range 0.667-0.706). Models 18 (average successful = 0.272), 7 (average successful = 0.333), and 9 (average successful = 0.333) were not able to predict successful nests reliably. These three models were among the five best-supported models in the information-theoretic analysis (Table 4). Finally, the addition of site to the best models lowered their predictive ability.

Table 7: Summary of cross-validation results for Dusky Flycatcher nesting success at the nest-patch scale, central Idaho, 2002 and 2003.

Model	k	Percent Correct	Percent Successful Correct	Percent Failed Correct
10	7	0.714	0.706	0.714
8	5	0.704	0.70	0.704
11	6	0.695	0.667	0.695
13	8	0.694	0.667	0.695
12	9	0.690	0.50	0.695
15	10	0.689	0.174	0.690
14	9	0.687	0.455	0.697
16	12	0.681	0.455	0.697
6	8	0.681	0.286	0.691
17	15	0.681	0.286	0.691
10a	14	0.694	0.517	0.713
4	11	0.694	0.556	0.699
9	7	0.681	0.333	0.692
5	6	0.682	0.364	0.693
19	9	0.683	0.40	0.696
8a	12	0.682	0.44	0.703
18	6	0.675	0.273	0.690
3	7	0.675	0.333	0.693
7	12	0.672	0.333	0.693
2	9	0.610	0.333	0.642
18a	13	0.649	0.217	0.684
1	na	na	Na	na

DISCUSSION

Model predictions and the evaluation of biological hypotheses

Nesting success in the Dusky Flycatcher was primarily influenced by year and vegetation composition and structure. The effect of study site received some support in the nest-site models, but little support in the nest-patch models. Nesting success was influenced by total vegetation coverage and not by the coverage of certain shrub species. The data did not support my predictions concerning the distance to the nearest suitable nesting substrate, the height of the substrate, the height of the nest, and the number of stems of the nest substrate. At the nest-patch scale, the data did not support my predictions concerning the orientation of the nest-patch, percent litter cover in the nest-patch, and the amount of overstory canopy coverage. The results from the two model selection methods were generally concurrent and suggest that certain habitat features measured at the nest-site and nest-patch scales were associated with the nesting success of the Dusky Flycatcher.

My results support findings from two other studies of Dusky Flycatcher habitat use. Liebezeit and George (2002) found that the percent foliage concealment and the distance to the edge of the nest substrate differed significantly between successful and unsuccessful nests (although they entered variables from both the nest-site and nest-patch scales in the same models). In addition, my results provide some support for their finding that nest success was negatively associated with the number of seedlings and saplings in the nest-patch (Models 18 and 10, Table 5). However, I note that Model 18 did not classify successful nests with a reasonable rate of accuracy. Models (Model 3 at the nest-site scale and Model 6 at the nest-patch scale) based on the results presented in Kelly (1993) received little support in the information-theoretic analysis (Tables 3 and 4). Model 3 was a good predictor of nesting success at the nest-site scale (Table 6), although the model had a large number of parameters (k=14). Model 6 did a poor job of predicting successful nests correctly (Table 7). Finally, I note that Kelly (1993) and Liebezeit and George (2002) studied the Dusky Flycatcher in different habitat types and that my models represent approximations of their results and do not model their findings directly.

I found little support for alternative models that represented hypotheses concerning thermal regulation and proximity to foraging substrates. However, my models represented generalizations of how I thought that vegetation and structural features would influence biological mechanisms. Although the selection and use of certain habitat features could serve to reduce predation risk by providing cover for parental movements or by concealing the nest from predators, I cannot reject the hypotheses that Dusky Flycatchers select nest-sites and nest-patches in order to regulate the immediate thermal environment around the nest or to more readily access food resources. I did not measure ambient temperature or moisture levels at individual nests, and cannot address whether nests could be distinguished by thermal characteristics. Also, I did not measure the abundance and/or quality of food resources within nest-patches and cannot address whether food resources could differentiate nests. However, if the availability and/or quality of food were limiting factors for breeding Dusky Flycatchers, significant differences would have existed in the mean nestling period across study sites, as both food limitation and thermal costs may constrain nestling growth and influence the duration of the nestling period (reviewed in Martin 1987).

Two lines of evidence suggest that neither of these mechanisms influenced nest-site and nest-patch selection by Dusky Flycatchers. First, I observed no instances of nest abandonment during any stages of the nesting cycle and no instances of nestling starvation. Second, I examined the mean duration of the nestling stage for all successful nests by site and year (Figure 1).

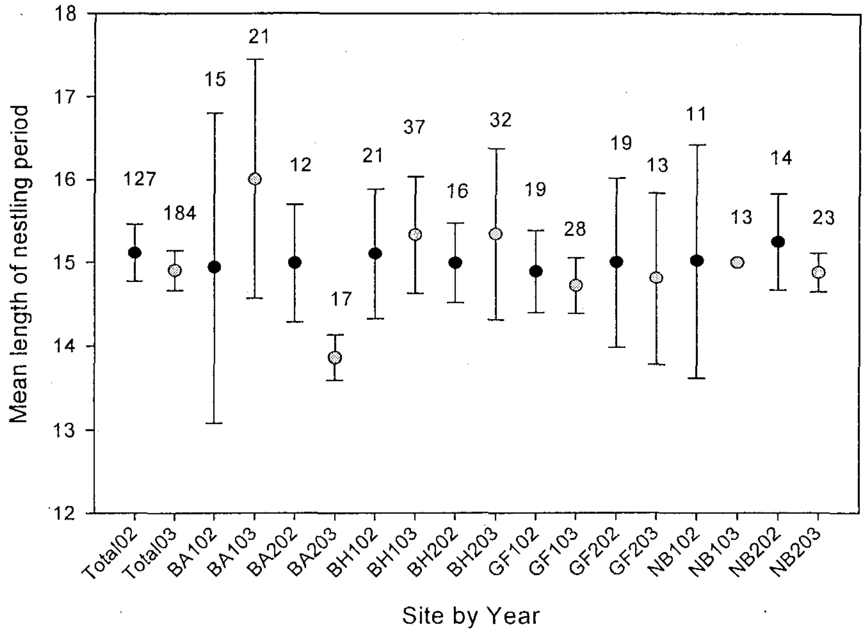

Figure 1: Mean length of nestling stage and 95% confidence intervals for Dusky Flycatchers by site and year, central Idaho, 2002 and 2003 (samples sizes are above error bars).

The mean length of the nestling stage for all sites was 15.11 days (s.e., 0.172) in 2002 (range: 14.89-15.25 days) and 14.9 days (s.e., 0.120) in 2003 (range: 13.86-16 days). The mean length of the nestling stage differed significantly for only one site (BA2) between years. Despite the large variance in the length of the nestling period for some sites, the effect size across sites is fairly uniform. This result indicates either that food availability and/or quality did not constrain nestling growth or that it did so in a uniform manner across sites.

Model selection and the validity of inference

Information-theoretic methods have been proposed as an alleged panacea for problems involved with traditional statistical hypothesis testing

(Anderson et al. 2000, Johnson and Omland 2004). However, all statistical methods can be abused and information-theoretic methods are not immune to misapplication (Anderson and Burnham 2002, for an example, see Budnik et al. 2002). Models selected by information-theoretic approaches may be over-specified (Shao 1993, Zhang 1993) and have little predictive power when applied to external datasets. My results indicate that some models with a strong degree of support from information-theoretic criteria may have little predictive power and thus be of little use for drawing general conclusions about breeding habitat use by the Dusky Flycatcher or for guiding management applications.

The averaging of parameters from the best models has been proposed as a remedy to this problem (Burnham and Anderson 2002). However, other methods such as cross-validation and bootstrapping need to be explored by researchers in the context of specific questions. Objectives may vary across studies and one method is unlikely to be of equal utility in all cases (Starfield 1997). Information-theoretic methods may not be useful if managers are interested in models that can predict external cases at a stated level of accuracy. At the very least, researchers should evaluate models with two or more distinct criteria and compare how inferences may or may not differ between methods. Neither information-theoretic nor cross-validation methods represent tests of observed data (Anderson et al. 2001). These methods are not equivalent to experimental tests that evaluate alternative hypotheses (Platt 1964) and partition sources of variation in a controlled manner (Guthery et al. 2001). Multiple methods should be employed when descriptive data are being evaluated.

Nest predation and scale

Numerous studies have concluded that nest predation is an important determinant of nest-site and nest-patch selection for birds (e.g., Martin and Roper 1988, Murphy et al. 1997, Clark and Shutler 1999) and that habitat features can differentiate successful and unsuccessful nests. However, these findings are not unanimous (Filliater et al. 1994, Howlett and Stutchbury 1996, Wilson and Cooper 1998, Braden 1999, Dearborn and Sanchez 2001, Jones and Robertson 2001). Existing discrepancies may be attributable to differences among the various study systems (e.g., predation rates may differ significantly by species, habitat type, and landscape context Martin 1995, Sockman 1997, Schmidt and Whelan 1999b, Chalfoun et al. 2002). Also, study design (Schmidt and Whelan 1998, Dearborn and Sanchez 2001) and the use of a particular method of analysis (Schmidt and Whelan 1999a) may influence the detection of meaningful relationships and the kind of inference that is derived from a study. For example, univariate tests of habitat and other variables rarely examine questions of biological interest in a unified manner (Morrison 2001). These approaches may have questionable statistical or biological validity and provide only limited insight into the phenomena being investigated.

The realization that biological phenomena operate at multiple scales is not new (Johnson 1980, Morris 1987, Orians and Wittenberger 1991), yet many studies do not examine habitat selection and use at scales that are relevant to an organism's ecology. The results from this chapter and Chapters 2 and 3 indicate that factors associated with habitat selection, habitat use, and reproductive success may vary across scales. Attempts to alter these patterns through management efforts would be misguided and potentially deleterious if the close association between scale and process became confused. Future studies of nesting success in passerines must examine reproductive success and survival at multiple scales and determine how biological processes such as nest predation, food limitation, and competition mediate patterns of habitat selection and use.

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Chapter Five: Development and testing of habitat models for Dusky Flycatchers (*Empidonax oberholseri*)

ABSTRACT

I evaluated breeding habitat use models for the Dusky Flycatcher (*Empidonax oberholseri*) at the site, territory and nest-patch scales. I validated an existing HSI model for the Dusky Flycatcher with data from a study of Dusky Flycatcher breeding ecology in central Idaho (2002-2003). I developed models to predict habitat selection at the territory scale and to predict reproductive success at the nest-patch scale with data from the same study. The HSI model performed well, showing significant association with habitat occupancy, nesting success, and the number of fledglings per hectare at the site scale. It also predicted habitat occupancy at the territory scale for the majority of territories sampled. The models that I developed for the territory and nest-patch scales were able to predict territory selection and nest-patch success reasonably well. I suggest ways in which the models may be used and validated in other geographic areas. I discuss how these models may be incorporated into a habitat-based viability framework.

INTRODUCTION

Wildlife habitat models that evaluate the relationships between organisms and their habitat are integral components of wildlife management and conservation planning (Thomas 1982, Verner et al. 1986, Morrison et al. 1992, Beutel et al. 1999, Scott et al. 2002). Models may predict species distributions

(Edwards et al. 1996, Dettmers and Bart 1999, Gutzwiller and Barrow 2001), habitat occupancy (Wiens et al. 1987, Karl et al. 2000, Pearce and Ferrier 2000), and habitat suitability and/or quality (U.S.F.W.S. 1981, Maurer 1986, Riitters et al. 1997). We define habitat as the combination of resources and conditions that prompt usage by a species and that allows for reproduction and survival (Morrison et al. 1992, Block and Brennan 1993). Habitat selection is the set of innate and learned responses used by an individual to distinguish various environmental components. Habitat use occurs after habitat has been selected and refers to the acquisition and utilization of resources. Habitat quality is the relative ability of a specific area to provide conditions that sustain individual performance and population persistence.

Model performance and utility should be evaluated with reference to the objectives and context of a particular study (Starfield 1997, Johnson 2001). However, all useful wildlife habitat models share basic features. Wildlife habitat models should be based on realistic biological functions and criteria, general enough for application to a range of situations (e.g., not be over-specified for a certain habitat type), and have relatively modest data requirements in order to derive reliable predictions (Van Horne and Wiens 1991, Starfield 1997). Models that have numerous parameters and are difficult and/or expensive to validate are less likely to see widespread application, especially by those not involved in model development (Johnson 2001).

The quality of information derived from habitat modeling can vary widely (Starfield 1997, Karl et al. 2000, Tyre et al. 2001). For example, modeling efforts often seek to predict habitat occupancy by an individual, or several, species (Scott et al. 2002). However, the presence or absence of a species in a particular site is not always a reliable indicator of the habitat quality of the site (Van Horne 1983, Maurer 1986, Zanette 2000, Woodward et al. 2001, Kristan 2003), although habitat occupancy rates can provide valuable data for monitoring population trends as a function of habitat change. In many cases, habitat occupancy cannot provide insight into how reproductive success and survival (the primary determinants of habitat quality) vary across the habitat conditions used by a species (Tyre et al. 2001). Life history traits (e.g., age at first reproduction, mean fecundity, juvenile survival) cannot be calculated to explain the variance in observed population growth rates and to assess species viability (Beissinger and Westphal 1998, Akçacaya 2000, Franklin et al. 2000, Van Horne 2002) without demographic and survival information. However, in those circumstances where the habitat requirements and patterns of use, density effects, and limiting factors of a species are well-studied, habitat occupancy rates may be used to set planning objectives.

Models that predict habitat selection and use by an organism and demonstrate how habitat use is associated with the reproductive success and survival of individuals in specific habitat types (and that allow for the evaluation of habitat quality as a continuous metric) are more difficult to develop (Conroy et al. 1995) and validate (Verbyla and Litvaitis 1989, Pearce and Ferrier 2000). Also, the data requirements of these models may prohibit their use in many instances. However, these models are essential both for understanding patterns of habitat selection and use and for determining how these patterns influence reproductive success and survival. In addition, models that predict components of reproductive success are required for the designation of critical habitat and for determining how habitat alteration will influence a species' viability (Thomas 1982, Roloff and Haufler 2002).

Several factors need to be considered when developing habitat models. Habitat use for most organisms is scale-dependent (Johnson 1980, Morris 1987, Orians and Wittenberger 1991) and wildlife habitat models should be developed and tested at scales relevant to an organism's ecology (Boone and Krohn 1999, Roloff and Kernohan 1999, Karl et al. 2000). Also, the modeling of specific interactions and/or mechanisms should be done with reference to the natural and life-history characteristics of the study species (Warwick and Cade 1988, Martin 1995, Clark and Shutler 1999, Van Horne 2002). Finally, wildlife habitat models may examine reproduction and survival with specific reference to individuals (Martin 1986, DeAngelis et al. 2001, Railsback and Harvey 2002) and/or to sub-populations and populations (Conroy et al. 1995, Maurer 2002). Researchers need to be explicit about the levels at which they are modeling relationships and how model results and/or inferences may change if they are extrapolated to different levels (Van Horne 2002).

I modeled habitat selection and habitat use by the Dusky Flycatcher (*Empidonax oberholseri*) as part of a broader effort to examine habitat-based viability procedures. The Dusky Flycatcher is a Neotropical migrant passerine that nests in the deciduous understory of western coniferous forests and appears to benefit from forestry practices or other disturbances that reduce overstory coverage (Sedgwick 1993). I monitored Dusky Flycatcher reproductive success on eight sites across two years in central Idaho and used the results to guide the development of individual-based habitat models that predict habitat selection and reproductive performance.

My objectives were to 1.) evaluate at two different scales an existing habitat model that was developed from a literature review of past studies; 2.) refine and/or develop scale-sensitive, individual-based habitat models with a limited number of parameters from data from my study of Dusky Flycatcher habitat use and reproductive performance in central Idaho; and 3.) cross-validate these models. Finally, I discuss how these models may be applied in a habitat-based viability framework.

METHODS

Study Sites

I studied the Dusky Flycatcher at eight different sites in central Idaho, USA, during 2002 and 2003. The sites were chosen to provide a range of vegetative structural features thought to influence Dusky Flycatcher habitat use and reproductive performance (Kelly 1993, Sedgwick 1993). Study sites ranged in size from 8.1 to 22.8 ha. All sites were located in moist grand fir habitat type (Steele et al. 1981). Ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotzuga menziesii*), and grand fir (*Abies grandis*) were the dominant overstory trees. Scouler's willow (*Salix scouleriana*), Rocky Mountain maple

(*Acer glabrum*), mallow ninebark (*Physocarpus malvaceus*), thinleaf alder (*Alnus sinuata*), buckthorn (*Ceanothus velutina*), and twinberry (*Lonicera utahensis*) were the dominant shrubs on all sites. The topography of the sites varied from flat benches to steep (> 35 degree) slopes. Elevations ranged from 1470 m to 1800 m. Distances between sites ranged from 0.63-11.9 km. No perennial water was present at any site. Understory shrub densities at each site varied as a result of past disturbance events (logging and fire) that reduced the overstory canopy and changed soil conditions, suppressing or encouraging understory growth. Shrub development and coverage on the sites ranged from extremely patchy to relatively continuous shrub cover greater than 2 m in height.

Nest Searching, Nest Monitoring, and Territory Mapping

I located nests by spot-mapping singing males (Bibby et al. 1992) and searching for nesting females throughout the breeding season. Nests were visited every one or two days, depending on the stage of the nesting cycle, to determine nest fate. Nests were checked daily during the laying phase and near the estimated fledging date to obtain accurate estimates of nesting survival. Observers approached nests from different routes on each visit and binoculars were used to observe nests from a distance when possible. The number of eggs, nestlings, and fledglings were recorded at each visit. The beginning of incubation was determined by the presence of warm eggs in the nest and incubation behavior by the female. For those nests that could not be reached, incubation date was assumed to begin 2 days after the completion of egg laying.

Dusky Flycatchers are single-brooded (Sedgwick 1993), although I did observe one female who reared two successful broods in 2002.

Territory boundaries were delineated during spot-mapping sessions. I returned to individual territories and mapped them by marking singing and counter-singing points, preferred foraging perches, and aggressive interactions with other males (Martin and Geupel 1993). All territory mapping was conducted during the incubation period. Males were not color-banded, but I felt confident that I could identify individual territory holders by their recurrent use of singing perches and foraging sites and by simultaneous identification of nearby territory holders. I included those territories that went beyond the site boundaries, but which had the majority of their area within the site, in the calculations of site size. I chose non-habitat for the Dusky Flycatcher (e.g., logging roads, meadows or recent clearcuts) for site boundaries, and the majority of the territories fell within the sites.

Vegetation Measurements

Territory selection and use–Vegetation structure on the eight sites was measured from the third week of July until the third week of August in 2002 and 2003. Line-intercept transects 20 m in length were placed randomly throughout each of the eight study sites to sample vegetation and structural variables. Starting points and direction for each transect were generated randomly using ArcView (v. 3.3). If transects fell across territory boundaries, the transect was moved so that the entire length fell either within the territory or outside of the territory. The species and percent coverage of all understory vegetation in five stratum (0-1 m, 1-2 m, 2-3 m, 3-4 m, > 4 m) were measured. Two extendable fiberglass poles were used to measure the placement of vegetation features in the individual stratum classes. Overstory canopy coverage was measured using the stick method (Gysel and Lyons 1980). Percent slope was determined by having two observers stand at either end of a line bisecting the patch and one observer viewing a marker at eye level through a clinometer. The results of spot-mapping allowed us to determine if a transect was in or out of a territory (use or non-use). At least five transects were sampled within the subset of territories that had their boundaries mapped by field personnel. Definitions for abbreviations of vegetation and other variables are in Appendix 4.

Nest-patch scale–Independent variables characterized habitat features at the nest-patch scale. The nest-patch scale measured the vegetation structure within a 5 m radius plot (0.008 ha) centered on the nest substrate. Vegetation at nest-patch scale was measured within 10 days after a nest with eggs or young failed or fledged. Nests that were destroyed or abandoned before eggs were present were measured within 14 days of failure. Definitions for abbreviations of habitat descriptors are in Appendix 5.

The slope, aspect, percent green ground cover (all green vegetation < 0.25 m in height), percent bare ground, percent woody debris (stumps, downed logs, slash), and percent other (road surfaces, rocks) were measured within the 5 m radius patch. Percent slope was determined with two observers standing at either end of a line bisecting the patch, and one observer viewing a marker at eye level through a clinometer. Overstory canopy coverage was measured with the stick method (Gysel and Lyons 1980) along a continuous line-intercept that bisected the nest patch. The species and percent coverage of all understory vegetation in five strata (0-1 m, 1-2 m, 2-3 m, 3-4 m, > 4 m) were measured along the same transect. Two extendable fiberglass poles were used to measure the placement of vegetation features in the individual stratum classes. For shrub cover, the species, number of individual plants, and the percent cover were recorded. For conifer species, the species, number, and percent cover for all species < 4 cm dbh were recorded. For species > 4 cm dbh, the dbh was recorded. The dbh of all snags > 4 cm was also measured.

Statistical Analysis

Model testing

A Habitat Suitability Index (HSI) framework (Van Horne and Wiens 1991) was used by Roloff (2001) to develop the initial model. The output of HSI models is an index of habitat suitability (or quality) scaled from 0 to 1. Individual variables receive a habitat suitability score from 0 to 1 based on the proposed relationship between the variable and habitat suitability. The resulting scores are combined in a final formula and can be weighted based on their proposed importance (U.S.F.W.S. 1981). At the site scale, I examined the association between the HSI score for the study site and measures of reproductive success and density. At the territory scale, I considered the habitat suitability score as a probability of habitat occupancy, as none of the studies that were used to develop the model provided information on reproductive success and/or survival at the territory scale.

The variables considered for the model were derived from a review of available literature on Dusky Flycatcher habitat use and general bird/habitat studies (Roloff 2001). The model quantifies habitat suitability in terms of the contribution of any specific area towards Dusky Flycatcher habitat at the territory-scale (although none of the studies included in the review examined habitat use at the territory-scale). Also, recent studies that documented the relationship between habitat use and reproductive success in the Dusky Flycatcher were either not used (Kelly 1993) or unavailable at the time of model development (Easton and Martin 2002, Liebezeit and George 2002).

Optimum habitat conditions for the Dusky Flycatcher were assumed to occur in forests with well-developed understory layers and low to moderate overstory coverage. Four variables were considered in the model: canopy cover (percent overstory canopy cover), presence of trees (presence or absence of coniferous trees), understory coverage (all deciduous understory vegetation < 5 m in height), and ground cover (all vegetation < 1 m in height). If canopy cover at a site was 0 and at least one tree per hectare ≥10 cm dbh was present, a value of 0.10 was entered into the model for canopy cover. The relationship between canopy coverage and habitat suitability followed a binomial curve, with optimum canopy coverage for the Dusky Flycatcher occurring between 20 and 40%. The relationship between understory coverage and habitat suitability followed a positive exponential function. The relationship between ground cover and habitat suitability also followed a binomial curve, with optimum ground cover occurring between 30 and 70%. Understory coverage and canopy cover were considered to be more important variables than ground cover and were weighted more heavily in the final HSI. The habitat suitability index was calculated as

$$\text{Final HSI} = \{[2^*(\text{Understory Coverage} + \text{Canopy Cover})] + \text{Ground Cover}\}/5$$

The model was validated with two years of data from the current study in central Idaho. I used the canopy coverage estimate for the Canopy Cover variable. I combined variables PerA, PerB, PerC, and PerD for the Understory Coverage variable. I used PerF for the Ground Cover variable. I had no territories where the mean canopy cover was 0 and did not need to use the Tree Presence variable.

Territory scale

I decided a priori that classifying HSI model scores at the territory scale to have them correspond with observed reproductive success (e.g., a score of 0-0.25 equates to a failed territory, a score of 0.251-0.50 equates to a territory that produced 1 nestling, etc.) was too fine of a distinction. Instead, I considered a score of 0-0.50 to equate with a low quality area that had a high probability of being unoccupied and a score > 0.50 to equate with an occupied territory (a territory that supported one or more breeding attempts). I tallied the number of territories that were classified correctly by the HSI model.

I calculated the mean values for model variables from all of the transects that were sampled within a specific territory.

Site scale

I examined the relationship between site HSI scores, estimators of reproductive success, and density of breeding territories. I used Pearson's correlation coefficients (r) (Quinn and Keough 2002) to determine the degree of association between site HSI scores and nesting success, annual reproductive success (ARS(k)), the number of fledglings produced per hectare, and density of breeding territories at each site (for detailed descriptions of these estimators, see Chapter 1). Pearson's correlation coefficients are measures of the linear association between variables. Pearson's correlation coefficients were used because I expected general linear associations between the variables of interest. I calculated 95% confidence intervals for each correlation coefficient by bootstrapping.

I calculated the mean values for model variables from all of the transects that were sampled at a specific site. As a result, both use and non-use transects were used to calculate the HSI score for a site.

Territory model development

I used relevant biological hypotheses to guide the development of candidate models for habitat selection and use at the territory scale and for habitat use at the nest-patch scale (Chapters 2 and 3). I evaluated candidate models with two criteria: information-theoretic (which selects the model that has the most support from the data) and cross-validation (which selects the model with the best ability to classify cases correctly).

The development of alternative Dusky Flycatcher habitat models was based on the results presented in Chapters 2, 3,and 4. My objective in this chapter was to develop a model that predicted Dusky Flycatcher habitat use and described those habitat features associated with reproductive success. I was not interested in modeling habitat use with regards to a particular hypothesis (e.g., vegetation composition and structure to reduce nest predation or to provide sufficient food resources; see Chapters 3 and 4 for specific discussion). Instead, I focused on the variables that were the best predictors of habitat use and reproductive success. In addition, I considered those variables that could be sampled efficiently by potential model users.

I used logistic regression to model habitat relationships for the Dusky Flycatcher. Logistic regression is a generalized linear model that calculates the mean of a response variable as a function of both categorical and continuous predictor variables (Hosmer and Lemeshow 2000). The response variable is bounded by 0 and 1. Individual parameter estimates in the model may be examined to determine how the odds of the response being 1 either increase or decrease as a function of a specific variable. I used logistic regression because of the ease of interpretation of parameter estimates and because the response variable for the habitat models was either 0 or 1 (i.e., habitat was either selected for inclusion within a territory or not selected and a nest-patch was either successful or unsuccessful).

Previous analyses indicated that territory success was related to habitat composition at the site scale (Chapter 1), but not the territory scale (Chapter 2). As a result, I modeled habitat features at the territory scale that were associated with territory selection (occupancy) and not territory success. Nest-patch models were developed to predict reproductive success at the nest-patch scale. Models for the two respective scales are in Tables 1 and 2.

Table 1: Candidate Dusky Flycatcher territory scale habitat models based on data from central Idaho, 2002 and 2003.

Model	**Variables in model**
1	PerF, PerB, PerD, PerE, ConA, Slope
2	PerA, PerC, PerE, ConA, Slope
3	PerF, PerB, ConA, Slope
4	PerA, PerC, ConA, Slope
5	PerF, PerA, PerB, PerC, PerD, PerE, ConA, Slope

Table 2: Candidate Dusky Flycatcher nest-patch habitat models based on data from central Idaho, 2002 and 2003.

Model	**Variables in model**
1	NumShrubs, PerShrubs, NumCS, PerCS, PerGreen, NumSnags, PerCon
2	NumShrubs, PerShrubs, PerGreen, PerCon, NumSnags
3	PerAG, PerSS, PerAS, PerPM, PerCV (specific shrubs), PerGreen
4	PerF, PerA, PerB, PerC, PerD, PerE, NumCS, PerCS
5	PerF, PerB, PerGreen, NumCS, PerCS
6	PerGreen, NumShrubs, PerShrubs
7	PerGreen, NumCS, PerAG, PerSS, NumCV
8	NumRP, PerRP, NumLD, PerLD

Territory model validation

I used a cross-validation method to evaluate the territory Dusky Flycatcher habitat models. Cross-validation selects the best models from a candidate set based on their ability to classify data cases correctly (Shao 1993). The model that has the best overall prediction rate (given the nature of the dependent variable) is considered the best model. Cross-validation avoids the bias inherent in assessing models with the same data that were used to parameterize the models (Efron 1983).

I used k-folds cross-validation in preference to the leave-one-out method (Shao 1993, Zhang 1993). In k-fold cross-validation, the data set is divided into k subsets. The model is parameterized with the remaining k-1 subsets, and the data cases in the withdrawn testing set are evaluated with the resulting model. This process is repeated k times and the average prediction error across k trials is computed. The value of each data case is predicted once and each data case is included in a training set k-1 times. Efron (1983) determined that k-folds cross-validation gave a nearly unbiased estimate of the apparent error rate (the proportion of observed errors made by the prediction rule on its training set), but this estimate could be highly variable for small datasets. I used a k = 20 for all cross-validation runs.

RESULTS

Model testing

I sampled 646 vegetation transects in 2002 (309 were not in territories and 337 were within territories). I sampled 581 vegetation transects in 2003 (263 were not in territories and 318 were in territories).

I mapped 107 Dusky Flycatcher territories in 2002 and 2003. I mapped 51 territories in 2002 (21 unsuccessful and 30 successful) and 56 territories in 2003 (27 unsuccessful and 29 successful). I sampled 337 use transects in 2002 and 318 use transects in 2003. For the territories that I mapped and fated, 109 transects were in unsuccessful territories and 111 transects were in successful territories in 2002. One hundred and nineteen transects were in unsuccessful territories and 146 were in successful territories in 2003.

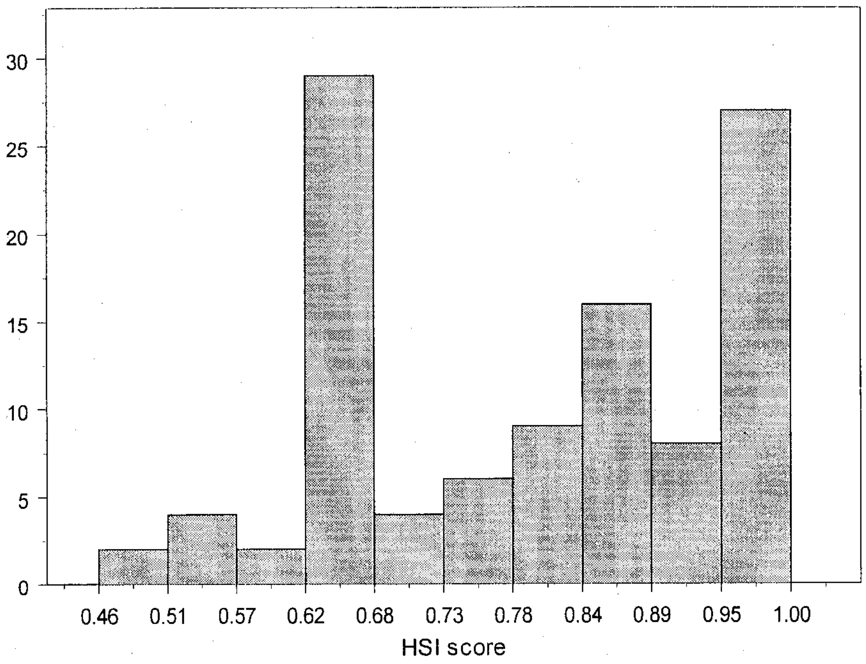
HSI site scores ranged from 0.35-1.0. The HSI site score had moderate positive associations with nesting success and fledglings per hectare (Table 3). HSI site score had weak positive associations with annual reproductive success and density of breeding territories had a mild positive association. The 95% confidence intervals were not symmetric for all four coefficients as a result of slightly skewed bootstrap sampling distributions (the sample bootstrap correlation coefficient tended to underestimate the parameter value). The 95% confidence intervals were adjusted to account for this bias.

Table 3. Pearson's correlation coefficients (r) with 95% confidence intervals for site HSI scores (eight sites by two years), measures of reproductive success, and density for Dusky Flycatchers, central ID, 2002 and 2003.

	Site HSI score	95% confidence interval
Nesting success	0.608	0.266, 0.855
Annual reproductive success	0.477	0.184, 0.752
Fledglings per hectare	0.542	0.224, 0.803
Density (territories per hectare)	0.404	0.181, 0.714

The HSI model (Roloff 2001) also performed well at the territory scale. The model correctly predicted habitat occupancy for 105/107 territories (98%). The scores ranged from 0.46-1.0 (Figure 1). Territories were binned in either the 0.0-0.5 or 0.51-1.00 categories.

Figure 1. Histogram of HSI territory scores from initial Dusky Flycatcher HSI model validated with data from central Idaho, 2002 and 2003.



Model cross-validation

Territory selection–All models in the candidate set predicted territory selection reasonably well (Table 4). The overall prediction rate ranged from 0.635-0.654. The used prediction rate ranged from 0.672-0.691. The non-used prediction rate ranged from 0.604-0.622.

The performance of the two models is not directly comparable. The model developed by Roloff (2001) uses all transects within a given territory to calculate an HSI score for that territory. The cross-validation approach assesses each transect and determines the probability that the transect would be included within a territory. The model developed by Roloff (2001) could be used to score each transect individually. However, I did not score the non-use transects.

Table 4: Summary of cross-validation results for Dusky Flycatcher territory selection habitat models, central Idaho, 2002 and 2003.

Model	k	Total Correct	Used Correct	Non-used Correct
1	7	0.641	0.672	0.608
2	6	0.654	0.691	0.619
3	5	0.635	0.671	0.600
4	5	0.643	0.683	0.606
5	8	0.654	0.687	0.622
6	4	0.638	0.672	0.604
7	5	0.650	0.688	0.614

Nest-patch use–The overall prediction rate for the nest-patch models was good for all models in the candidate set (Table 5). The overall prediction rate ranged from 0.682-0.714. The prediction rate for successful patches ranged from 0.333-0.714. The prediction rate for unsuccessful patches ranged from 0.692-0.715.

Table 5: Summary of cross-validation results for Dusky Flycatcher nest-patch use habitat models, central Idaho, 2002 and 2003.

Model	k	Total Correct	Successful Correct	Unsuccessful Correct
1	8	0.714	0.706	0.715
2	7	0.698	0.583	0.702
3	8	0.682	0.333	0.692
4	9	0.682	0.412	0.697
5	7	0.698	0.556	0.706
6	5	0.698	0.583	0.702
7	7	0.711	0.714	0.710
8	6	0.695	0.667	0.695

DISCUSSION

Model testing

The HSI model performed well on test data at both the site and territory levels. HSI site scores were strongly associated with nesting success and the number of fledgling per hectare and mildly associated with annual reproductive success and the density of breeding territories. The variables included in the models were able to predict habitat occupancy with a high rate of accuracy. Models performed well despite their general forms (models were additive and did not include higher order terms) and despite the tentative relationship that model variables had with habitat quality for the Dusky Flycatcher (e.g., the abundance of the Dusky Flycatcher was used as an indicator of habitat quality in some of the studies used in model development).

The results presented in Chapter 1 indicated that broad measures of vegetation structure (e.g., percent cover in Stratum A) were associated with measures of reproductive success at the site scale (Chapter 1), but not with territory success when comparing successful and unsuccessful occupied territories (Chapter 2). Habitat quality was closely associated with vegetation and structural features measured at the nest-site and nest-patch scales (Chapter 3). As a result, models that predict territory occupancy may be more appropriate and reliable than models that attempt to predict territory success. For example, the models were able to predict what general habitat features the Dusky Flycatcher would include within breeding territories. However, at the territory scale, the model could not identify the fine scale features (e.g., at the nest-patch and nest-site scales) that were most strongly associated with territory success in this study. Finally, the strong associations between model outputs and nesting success and fledglings per hectare indicated that the variables in the model were associated with reproductive performance, and not simply occupancy.

Model cross-validation and validation

I did not cross-validate a model with specific parameter estimates. Instead, parameters were estimated for each of the 20 blocks in the k-folds cross-validation (these estimates should be close to one another as long as the data are not highly variable) for a specific combination of independent variables. Therefore, I did not evaluate a specific model, but only evaluated the ability of certain independent variables to predict territory selection and nest-patch use for the Dusky Flycatcher when entered into a logistic regression model.

I did not evaluate a specific model for several reasons. I found some support for site and year effects in previous chapters, a common result in studies of avian habitat use (Eckhardt 1975, Jones et al. 2001, Dinsmore et al. 2002). Researchers in other systems should determine if site and year effects influence habitat use and reproductive success by the Dusky Flycatcher. In those instances where non-habitat effects are biologically significant, researchers may want to parameterize specific models with data drawn from a particular system and not use external models to make predictions.

Also, the Dusky Flycatcher occurs across a range of habitat types and more extensive study would be required to determine if they select for certain vegetation components or for general vegetation structure per se. The Dusky Flycatcher in central Idaho places the majority of its nests in five shrub species. These species may not be available to the Dusky Flycatcher in other areas of its range, in which case substrate-specific models would be of little use. The extent to which the Dusky Flycatcher does select and use certain substrates is most likely a function of the nest predators that occur with them in specific areas. Nest predation can exert a strong selective effect on shrub-nesting birds (Martin 1998), resulting in patterns of habitat use that are adaptive for specific circumstances.

Both the territory selection and nest-patch success models had reasonably good prediction rates despite the exclusion of site and year as predictor variables. The nest-patch habitat models were better predictors than the territory selection models. This result follows from the evidence presented in Chapters 3 and 4 suggesting that habitat use at the nest-patch was more closely associated with reproductive success than habitat use at the territory scale.

Suggestions for model application

Potential users of these models have three options. First, they can formulate their own HSI model for the Dusky Flycatcher based on the results presented here and in Chapters 3 and 4 or use the Roloff (2001) model at the territory scale to identify use areas that have a good probability of having high reproductive success. Generally, the probability of a Dusky Flycatcher establishing a territory in a certain habitat type is 1.) associated positively with increases in understory shrub strata; 2.) negatively with increases in the number of seedling conifers; and 3.) increases with moderate amounts of overstory coverage and decreases with low or high amounts of overstory coverage. I suggest that these be considered as linear effects, as my results are descriptive and I cannot identify the mechanisms by which these features are associated with nesting success.

Second, they can use the most supported models (based on the two selection criterion) presented in Chapters 3 and 4. In this case, model users would have to sample the requisite variables, enter them into the model, and compare the resulting predictions with the known fate of territories and nest-patches. I stress the comparison of model predictions to the actual results observed in the field. The generality and utility of models in specific systems cannot be assessed without comparing predictions to field data.

If field data do not match well with model predictions, a third option is to use the results presented here to parameterize models based on what available data will support and cross-validate the resulting models. In so doing, researchers have to parameterize their own models and determine the relative size of effects that different variables have on the outcome of interest (e.g., habitat selection or nest-patch success). This is the least likely option, as most researchers will not have the resources to repeat this study for the Dusky Flycatcher at a particular location.

Finally, I stress that the relationship between habitat quality (as determined by reproductive success and/or survival) and density be well understood for a species of interest (Horne 1983, Morris 1989, Both and Visser 2003). This relationship must be defined if habitat occupancy rates are to be used as a measure of habitat quality. Results from the current study (Chapter 2) indicated that density was associated strongly with habitat quality (expressed as the number of fledglings produced per hectare) for the Dusky Flycatcher. However, site HSI scores were strongly associated with measures of reproductive success but not with density. Territory occupancy rates may be a valid means of defining habitat quality and establishing viability planning objectives for those species that do not exhibit differences in territory scale measurements between unsuccessful and successful territories but that do show a positive relationship between density and productivity. The relationships between model output and measures of reproductive success and density should be examined closely.

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Chapter Six: Conclusion

The results presented in this dissertation indicate that a habitat-based methodology is a tenable approach for assessing species viability within a formal planning framework. In this section, I review the major results presented in this report and suggest aspects of the habitat-based viability framework that require further investigation.

Chapter 2

Nesting success, annual reproductive success, and the number of fledglings per hectare were positively associated with vegetation structure for Dusky Flycatchers. The number of breeding territories and the number of fledglings per hectare were positively associated, suggesting that density determined the reproductive success of Dusky Flycatchers when expressed as young per unit of area. Reproductive success expressed as young produced per breeding pair or young produced per nesting attempt did not differ significantly across sites. Mean clutch size and mean egg weight did not differ among sites and were not associated with measures of reproductive success or vegetation structure.

The composition and structure of understory vegetation was the principal determinant of habitat quality for Dusky Flycatchers. I suggest that diverse vegetation structure provided an abundance of nest sites that served to deter predators. I reiterate the need to define habitat quality for any organism in regards to the habitat use and the fitness attributes of a species, and to determine how the density of breeding territories is related to and may influence these relationships.

Chapter 3

Dusky Flycatchers selected habitat at the territory scale with greater cover of understory vegetation in two height strata, reduced cover of conifer seedlings, and steeper slopes. I did not detect differences in vegetation structure between successful and unsuccessful territories. Territory success was positively associated with the density of conspecifics and both positively and negatively associated with specific study sites. Mean territory size did not differ significantly for all sites by year and differed significantly across years for only one study site. Mean territory size did not differ significantly for successful and unsuccessful territories by year. Territory size was not associated with measures of reproductive success or habitat structure at either the individual or site level. The variance in mean territory size was negatively associated with nesting success, annual reproductive success, the number of fledglings per hectare, and the density of conspecifics at each site.

This latter result suggests that individuals on sites of poor habitat quality had either to extend territory boundaries to include sufficient resources or established territories based on what resources were available. My results provided support for the hypothesis that Dusky Flycatchers optimize their territory size to include sufficient resources to reproduce successfully. However, the success of both small and large territories suggests that other scales of habitat use (e.g., nest-site and nest-patch scales) may be important for the reproductive success of Dusky Flycatchers.

The relationship between territory (or home-range) size variation and habitat quality is an important component of the habitat-based viability framework (Roloff and Haufler 1997, 2002). Roloff and Haufler (1997, 2002) assumed that the relationship between territory size and habitat quality would follow a negative exponential distribution, with the smallest territory sizes occurring in the highest quality habitat. I suggest that Dusky Flycatchers optimize their territory size in a certain range and that territory sizes both smaller and larger than the optimum size may occur in habitat of poor quality. However, if reproductive success and survival for certain organisms are associated with finer scales of habitat use within the territory or home-range (e.g., nest or natal sites), than territory size may not have a close association with habitat quality. For these organisms, territory sizes in the highest quality habitat should be close to the mean value of all territory sizes and territory sizes in poorer quality habitat should exhibit greater variation from the mean value. To incorporate this relationship, planning frameworks could model territory size in poorer quality habitats as a stochastic variable that varies around a stated mean value.

Finally, for those organisms that defend territories actively, the relationship between territory size and density of conspecifics needs to be specified. If density is positively associated with habitat quality, territory size may be constrained by conspecifics in the highest quality habitat. Conversely, territory size may exhibit greater variation in poor quality habitat if individuals have not saturated the habitat. However, available high quality habitat may not be occupied by a species that exists at low densities or that has suffered a severe population decline. In this case, a weak relationship between territory size and habitat quality may also be expected.

Chapter 4

The reproductive success of Dusky Flycatchers was most closely associated with habitat use at the nest-site and nest-patch scales. Vegetation structure and habitat features at both of these scales discriminated successful and unsuccessful nests with a relatively high rate of accuracy. The nest-site models that received the most support from the information-theoretic method were able to predict successful and unsuccessful nests with high accuracy rates. Two of the three nest-patch models that received support from the information-theoretic method were able to predict successful and unsuccessful nests well, although the third model was unable to predict successful nests with reasonable accuracy.

The habitat-based viability framework relies on mapping habitat use at the territory scale to make viability predictions. For this framework to be successful, a species' fitness attributes must be associated closely with habitat use at the territory scale. The ability to map habitat use (e.g., with remotely-sensed information) is also a prerequisite. Viability predictions may be difficult to make for those species whose fitness attributes are associated closely with fine scales of habitat use (e.g., nest or natal sites) that cannot be mapped with the information that is available currently. Finally, the habitat-based viability approach will be of little utility for those species in which fitness attributes are associated closely with behavioral patterns, e.g., when predation rates are associated with parental behavior or when habitat selection is maladaptive.

Chapter 5

The HSI model for Dusky Flycatchers developed by (Roloff 2001) performed well in predicting areas that were occupied and that had high reproductive success at the site level for the range of vegetation conditions in the habitat type we evaluated in Central Idaho. The HSI scores for each site were positively associated with measures of reproductive success and density of breeding territories. The model was also able to predict habitat occupancy at a high rate for the territories that we sampled. However, it could not effectively distinguish between successful and unsuccessful occupied territories. This determination required finer scale information on nest patch characteristics. The models that we developed with the data from the current study were able to predict territory selection and nest-patch success with reasonably high rates of accuracy. Both of these models could be used to assess habitat quality for Dusky Flycatchers in planning frameworks, although I stress the importance of validating these models with data on Dusky Flycatcher habitat selection and use from other geographic regions.

The habitat-based viability framework requires habitat models that can predict habitat selection and use with a reasonably high rate of accuracy. In addition, the amount and kind of data required to derive model predictions should be fairly modest. I was able to evaluate, develop, and validate fairly simple models for Dusky Flycatcher habitat selection and use and tie those models to reproductive performance. While obtaining accurate maps of the understory habitat components required by Dusky Flycatchers may be difficult, these results are encouraging. They provide empirical support to the use of habitat-based approaches to species viability. However, I note that habitat selection and use patterns in other organisms may not be associated in a similar way with the fitness attributes I noted for Dusky Flycatchers. For example, other factors (e.g., food availability) may influence fitness attributes and population dynamics in other species in different ways than we found. Habitat-based approaches will need to consider and evaluate these other relationships prior to assuming that viability predictions can be made for other species with a reasonable rate of accuracy.

Final Considerations

This study both refuted and supported components of the habitat-based approach to assessing species viability proposed by Roloff and Haufler (1997, 2002). I did not observe a direct relationship between habitat quality and territory size for Dusky Flycatchers, a critical relationship behind their approach. Reproductive success for Dusky Flycatchers was relatively constant across all observed territory sizes, although an increase in reproductive success was observed around the mean territory size. I suggest that Dusky Flycatchers have an optimal territory size that contains the sufficient amounts and diversity of nesting cover needed for successful reproduction. The species may expand territory sizes to obtain more of the necessary nesting cover where it is present in limited amounts, a relationship consistent with the assumption of Roloff and Haufler (1997, 2002). However, my evidence indicates that Dusky Flycatchers may attempt to subsist on a reduced amount of nesting cover occurring in a smaller territory and experience, on average, reduced reproductive success. These smaller territories are therefore of lower quality, rather than of higher quality as assumed by Roloff and Haufler (1997, 2002).

Using the HSI model of Roloff (2001) at the site scale, I found that sites with higher quality habitat (more nesting cover), as predicted by the model, supported higher densities of Dusky Flycatchers and demonstrated higher nesting success and reproductive success. At this scale, the model worked in a manner consistent with the approach of Roloff and Haufler (1997, 2002). This was due to the finding that in higher quality sites, territory sizes became more uniform with fewer larger territories, and more importantly, higher quality sites contained fewer areas that were unoccupied. However, if the GIS home range grower was used, it would have assigned a higher quality to smaller home ranges in lower quality sites. While the concept of identifying and mapping home ranges of varying quality is supported by the findings of this study, using the relationship of home range size to habitat quality was not supported. For Dusky

Flycatchers, home ranges at the mean size would need to be assigned the highest quality, while smaller and larger home ranges would be of lower quality.

Chapters 3 and 4 provided information on finer scales of habitat use that would allow more specific analyses to be conducted at the territory, nest-patch, and nest-site scales. Using this information, a more accurate description of habitat quality at the territory size could be developed. However, the complexity of the required information could make application of such models difficult.

The Dusky Flycatcher model from Roloff (2001) performed well. Minor modifications to the HSI model are recommended. Specifically, I suggest the close examination of model relationships to determine whether other model forms (e.g., linear or exponential) may be more appropriate for modeling the relationships between habitat variables.

Dusky Flycatchers did not show the type of association between territory size and habitat quality assumed by the habitat-based approach of Roloff and Haufler (1997, 2002). This does not mean that this relationship would not be correct for other species. The reproductive success of Dusky Flycatchers on their breeding territories appeared to be primarily controlled by nest predation. Home ranges with sufficient amounts and close or continuous patches of high quality shrub cover provided optimum conditions. Home ranges with more dispersed shrub patches or with smaller amounts or quality of shrub patches had reduced reproductive success. Other species, such as those limited by food resources, may show a consistent relationship between territory size and reproductive performance. Additional studies on other species would be needed to determine if consistent relationships exist, or if other species demonstrated the bimodal relationship of lower quality habitat noted for the Dusky Flycatcher.

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Appendices

Appendix 1: Summary statistics (mean, standard error, 95% confidence intervals) for six habitat variables at eight sites in central Idaho, 2002 and 2003 (sample sizes are in parentheses).

	2002 (n=646)								2003 (n=581)							
Variable	BA1	BA2	BH1	BH2	GF1	GF2	NB1	NB2	BA1	BA2	BH1	BH2	GF1	GF2	NB1	NB2
	(76)	(72)	(86)	(93)	(80)	(83)	(67)	(89)	(68)	(64)	(103)	(95)	(63)	(71)	(59)	(58)
%A	0.121	0.147	0.121	0.169	0.164	0.173	0.216	0.357	0.085	0.125	0.081	0.117	0.091	0.206	0.18	0.157
St.error	0.015	0.014	0.012	0.014	0.015	0.015	0.017	0.018	0.012	0.016	0.009	0.011	0.012	0.019	0.02	0.015
95% l.	0.09	0.118	0.097	0.141	0.133	0.142	0.18	0.319	0.059	0.092	0.063	0.095	0.064	0.169	0.14	0.125
95 % u.	0.15	0.176	0.145	0.198	0.194	0.204	0.252	0.394	0.109	0.157	0.10	0.137	0.117	0.243	0.22	0.187
%B	0.008	0.048	0.023	0.086	0.036	0.028	0.034	0.172	0.027	0.045	0.534	0.075	0.04	0.074	0.06	0.129
St.error	0.002	0.011	0.005	0.012	0.008	0.008	0.008	0.017	0.007	0.009	0.009	0.011	0.01	0.015	0.012	0.019
95%l.	0.002	0.026	0.012	0.062	0.018	0.013	0.019	0.136	0.012	0.026	0.035	0.052	0.019	0.044	0.04	0.09
95 % u.	0.014	0.068	0.034	0.11	0.054	0.043	0.05	0.207	0.04	0.064	0.07	0.098	0.061	0.10	0.09	0.169
%C	0.002	0.02	0.012	0.049	0.007	0.009	0.014	0.075	0.001	0.008	0.028	0.03	0.026	0.02	0.02	0.082
St.error	0.001	0.006	0.003	0.011	0.003	0.003	0.004	0.013	0.001	0.004	0.007	0.006	0.01	0.006	0.005	0.016
95% l.	0	0.008	0.005	0.027	0.002	0.002	0.005	0.048	0	0	0.015	0.018	0.005	0.007	0.007	0.05
95 % u.	0.004	0.033	0.019	0.071	0.013	0.015	0.022	0.10	0.002	0.017	0.042	0.042	0.047	0.032	0.03	0.114
%D	0.001	0.004	0.005	0.017	0.005	0.012	0.006	0.038	0.004	0.008	0.016	0.022	0.012	0.017	0.005	0.044
St.error	0.001	0.002	0.002	0.006	0.003	0.005	0.004	0.009	0.004	0.005	0.006	0.007	0.006	0.006	0.002	0.011
95% l.	*0*	*0*	*0.000*	*0.005*	*0.001*	*0.001*	*-0.003*	*0.019*	*-0.004*	*0*	*0.006*	*0.007*	*0.0002*	*0.004*	*0.001*	*0.022*
95 % u.	0.003	0.009	0.01	0.03	0.010	0.022	0.015	0.057	0.012	0.019	0.027	0.037	0.025	0.028	0.010	0.067
%E	0.125	0.202	0.164	0.164	0.246	0.251	0.08	0.238	0.103	0.152	0.165	0.162	0.255	0.201	0.076	0.153
St.error	0.015	0.02	0.018	0.02	0.022	0.017	0.013	0.022	0.016	0.022	0.017	0.018	0.028	0.02	0.013	0.023
95% l.	0.095	0.16	0.128	0.125	0.20	0.215	0.057	0.194	0.070	0.108	0.13	0.125	0.199	0.16	0.048	0.106
95 % u.	0.15	0.24	0.20	0.204	0.289	0.286	0.11	0.282	0.136	0.195	0.199	0.199	0.311	0.243	0.10	0.201
%F	0.253	0.30	0.277	0.319	0.30	0.324	0.37	0.47	0.257	0.336	0.317	0.217	0.292	0.382	0.447	0.363
St.error	0.019	0.017	0.014	0.014	0.018	0.015	0.013	0.012	0.016	0.021	0.017	0.011	0.020	0.017	0.024	0.017
95% l.	0.215	0.267	0.247	0.290	0.263	0.293	0.344	0.447	0.224	0.292	0.282	0.193	0.251	0.348	0.39	0.328
95 % u.	0.29	0.333	0.307	0.349	0.336	0.355	0.399	0.495	0.290	0.379	0.352	0.24	0.332	0.416	0.49	0.398

Appendix 2: Abbreviations for vegetation and structural variables included in territory selection and success models.

Variable	Definition
Slope	Percent slope
% A	Percent coverage in height stratum A (1-2 m.)
% B	Percent coverage in height stratum B (2-3 m.)
% C	Percent coverage in height stratum C (3-4 m.)
% D	Percent coverage in height stratum D (4-5 m.)
% F	Percent coverage in height stratum F (0-1 m.)
% E	Percent overstory canopy cover
AGA	Percent coverage of *Acer glabrum* in Stratum A
AGB	Percent coverage of *Acer glabrum* in Stratum B
ASA	Percent coverage of *Alnus sinuata* in Stratum A
ASB	Percent coverage of *Alnus sinuata* in Stratum B
SSA	Percent coverage of *Salix scouleriana* in Stratum A
SSB	Percent coverage of *Salix scouleriana* in Stratum B
SSC	Percent coverage of *Salix scouleriana* in Stratum C
CVA	Percent coverage of *Ceanothus velutina* in Stratum A
CVF	Percent coverage of *Ceanothus velutina* in Stratum F
PMA	Percent coverage of *Physocarpus malvaceus* in Stratum A
PMF	Percent coverage of *Physocarpus malvaceus* in Stratum F
PerAG	Percent cover of *Acer glabrum* in all stratum
PerSS	Percent cover of *Salix scouleriana* in all stratum
PerAS	Percent cover of *Alnus sinuata* in all stratum
PerPM	Percent cover of *Physocarpus malvaceus* in all stratum
PerCV	Percent cover of *Ceanothus velutina* in all stratum
ConA	Percent cover of all conifer species in Stratum A

Appendix 3: Abbreviations for vegetation and structural variables included in nest-site and nest-patch candidate models.

Variable	Scale	Definition
Species	Site	Substrate species in which the nest was located
Height	Site	Height of substrate
NeHeight	Site	Height of nest in substrate
#Stems	Site	Number of individual stems of the nest substrate
NestOr	Site	Nest orientation; cardinal direction of nest placement relative to substrate center
DistEdge	Site	Distance to edge of substrate; distance from nest to the nearest edge of the substrate
DistNear	Site	Distance to nearest substrate; distance from nest to the nearest suitable nesting substrate
NorthCon	Site	Percent concealment of the nest from the north
SouthCon	Site	Percent concealment of the nest from the south
EastCon	Site	Percent concealment of the nest from the east
WestCon	Site	Percent concealment of the nest from the west
AbCon	Site	Percent concealment of the nest from above
BeCon	Site	Percent concealment of the nest from below
MeanCon	Site	Average of the six concealment measures
Aspect	Patch	Aspect on which the nest substrate is growing
Slope	Patch	Percent slope of nest patch plot
PerGreen	Patch	Percent green ground cover in nest patch plot
PerBare	Patch	Percent bare ground in nest patch plot
PerOther	Patch	Percent ground cover not included in other three classes (e.g., road surface or rock)
PerOS	Patch	Percent overstory canopy cover for nest patch plot
%A	Patch	Percent coverage in height stratum A (1-2 m.) along plot transect
%B	Patch	Percent coverage in height stratum B (2-3 m.) along plot transect
%C	Patch	Percent coverage in height stratum C (3-4 m.) along plot transect
%D	Patch	Percent coverage in height stratum D (> 4 m.) along plot transect
%F	Patch	Percent coverage in height stratum F (0-1 m.) along plot transect
AGA	Patch	Percent coverage of *Acer glabrum* in Stratum A along plot transect
AGB	Patch	Percent coverage of *Acer glabrum* in Stratum B along plot transect
ASA	Patch	Percent coverage of *Alnus sinuata* in Stratum A along plot transect
ASB	Patch	Percent coverage of *Alnus sinuata* in Stratum B along plot transect
SSA	Patch	Percent coverage of *Salix scouleriana* in Stratum A along plot transect
SSB	Patch	Percent coverage of *Salix scouleriana* in Stratum B along plot transect
SSC	Patch	Percent coverage of *Salix scouleriana* in Stratum C along plot transect
CVA	Patch	Percent coverage of *Ceanothus velutina* in Stratum A along plot transect
PMA	Patch	Percent coverage of *Physocarpus malvaceus* in Stratum A along plot transect
NumCon	Patch	Number of conifers > 4 cm dbh on plot
ConDbh	Patch	Mean dbh for all conifers > 4 cm dbh on plot
NumSnags	Patch	Number of snags on plot
SnagDbh	Patch	Mean dbh for all snags on plot
NumCon	Patch	Number of conifers < 4 cm dbh, including seedlings on plot
PerCon	Patch	Percent cover of all conifers < 4 cm on plot
NumShrub	Patch	Number of shrubs on plot
PerShrub	Patch	Percent cover of shrubs on plot

Appendix 3 continued: Abbreviations for vegetation and structural variables included in nest-site and nest-patch candidate models.

Variable	Scale	Definition
NumAG	Patch	Number of *Acer glabrum* on plot
PerAG	Patch	Percent cover of *Acer glabrum* on plot
NumSS	Patch	Number of *Salix scouleriana* on plot
PerSS	Patch	Percent cover of *Salix scouleriana* on plot
NumPM	Patch	Number of *Physocarpus malvaceus* on plot
PerPM	Patch	Percent cover of *Physocarpus malvaceus* on plot
NumCV	Patch	Number of *Ceanothus velutina* on plot
PerCV	Patch	Percent cover of *Ceanothus velutina* on plot
NumRP	Patch	Number of *Rubus parviflorus* on plot
PerRP	Patch	Percent cover of *Rubus parviflorus* on plot
NumLD	Patch	Number of *Lonicera utahensis*
PerLD	Patch	Percent of *Lonicera utahensis* on plot

Appendix 4: Abbreviations for vegetation and structural variables included in territory selection models for Dusky Flycatchers.

Variable	Definition
Slope	Percent slope
% A	Percent coverage in height stratum A (1-2 m.)
% B	Percent coverage in height stratum B (2-3 m.)
% C	Percent coverage in height stratum C (3-4 m.)
% D	Percent coverage in height stratum D (4-5 m.)
% F	Percent coverage in height stratum F (0-1 m.)
% E	Percent overstory canopy cover
ConA	Percent cover of all conifer species in Stratum A

Appendix 5: Abbreviations for vegetation and structural variables included in nest-patch habitat models for Dusky Flycatchers.

Variable	Scale	Definition
PerGreen	Patch	Percent green ground cover in nest patch plot
PerOS	Patch	Percent overstory canopy cover for nest patch plot
%A	Patch	Percent coverage in height stratum A (1-2 m.) along plot transect
%B	Patch	Percent coverage in height stratum B (2-3 m.) along plot transect
%C	Patch	Percent coverage in height stratum C (3-4 m.) along plot transect
%D	Patch	Percent coverage in height stratum D (> 4 m.) along plot transect
%F	Patch	Percent coverage in height stratum F (0-1 m.) along plot transect
NumCon	Patch	Number of conifers > 4 cm dbh on plot
NumSnags	Patch	Number of snags on plot
NumCon	Patch	Number of conifers < 4 cm dbh, including seedlings on plot
PerCon	Patch	Percent cover of all conifers < 4 cm on plot
NumShrub	Patch	Number of shrubs on plot
PerShrub	Patch	Percent cover of shrubs on plot
PerAG	Patch	Percent cover of *Acer glabrum* on plot
PerSS	Patch	Percent cover of *Salix scouleriana* on plot
PerPM	Patch	Percent cover of *Physocarpus malvaceus* on plot
PerCV	Patch	Percent cover of *Ceanothus velutina* on plot
NumRP	Patch	Number of *Rubus parviflorus* on plot
PerRP	Patch	Percent cover of *Rubus parviflorus* on plot
NumLD	Patch	Number of *Lonicera utahensis*