5-2011

Behavioral Responses of Willow Flycatchers, *Empidonax traillii*, to a Heterogeneous Environment

Amanda V. Bakian
Utah State University

UtahState University
MERRILL-CAZIER LIBRARY

BEHAVIORAL RESPONSES OF WILLOW FLYCATCHERS, *EMPIDONAX TRAILLII*, TO A

HETEROGENEOUS ENVIRONMENT

by

Amanda V. Bakian

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Ecology

Approved:

_____   _____
Kimberly Sullivan   Thomas Edwards, Jr.
Major Professor   Committee Member

_____   _____
Ethan White   S. K. Morgan Ernest
Committee Member   Committee Member

_____   _____
D. Richard Cutler   Byron Burnham
Committee Member   Dean of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

2011

ABSTRACT

Behavioral Responses of Willow Flycatchers, *Empidonax traillii*, to a Heterogeneous

Environment

by

Amanda V. Bakian, Doctor of Philosophy

Utah State University, 2011

Major Professor: Dr. Kimberly A. Sullivan
Department: Biology

Spatial heterogeneity impacts population and community-level dynamics including

species-level dispersal patterns, the use and availability of refugia, predator/prey dynamics, and

reproductive fitness. Understanding how wild animal populations respond to environmental

heterogeneity is essential for their proper management and conservation. In this study, I examine

the responses of Willow Flycatchers to spatial heterogeneity in the distribution of their food and

habitat resources. Over the course of three breeding seasons, I radio- tracked Willow Flycatchers

at Fish Creek in Manti-La Sal National Forest in Utah, recorded detailed behavior data at each

radio location, and collected fecal, feather and insect samples. I formulated individual and

population-level Bayesian spatial resource selection functions to model Willow Flycatcher

foraging and vocalization behavior on multiple scales. These models indicate that vocalization

and foraging behavior are spatially segregated within the home ranges of Willow Flycatchers.

Further, Willow Flycatchers were found to use mature riparian habitat for vocalizing while they

used a variety of habitat types for foraging. The insect samples were used to identify distinct

carbon and nitrogen stable isotope signatures for the aquatic and terrestrial insect communities at

Fish Creek. In conjunction with the fecal samples, I used the stable isotope signatures to determine the contribution of aquatic versus terrestrial insects to the Willow Flycatcher diet. Aquatic insects comprised a larger proportion of the diet of adult than nestling Willow Flycatchers. This suggests that adult flycatchers consume a diet that is distinct from the one they feed to their nestlings. Finally, I compared space use characteristics in two populations of Willow Flycatchers: a population of the endangered Southwestern Willow Flycatcher at Roosevelt Lake, Arizona and another belonging to a non-endangered subspecies of Willow Flycatcher at Fish Creek, Utah. Differences in space use were found largely among breeding flycatchers while space use characteristics in non-breeding Willow Flycatchers did not differ across populations. This suggests that space use patterns in non-breeding Southwestern Willow Flycatchers may be generalizable to non-breeding flycatchers from non-endangered populations. This study expands our understanding of how Willow Flycatchers respond to spatial heterogeneity while its key findings have management and conservation implications for the species.

(137 pages)

DEDICATION

The writing of this dissertation has been the greatest challenge of my life thus far. The reason that this, and not some other event, has been my life's greatest challenge is because of my parents, Linda and Victor Bakian. Your parenting and guidance over the years have allowed for my greatest challenge to be of my own making. Therefore I want to dedicate my dissertation to you, Mom and Dad. Over the years, you have instilled a curiosity in me and a lack of fear, and your influence created the lenses through which I view and interpret the world. Although this curiosity has currently led me to ponder ecological processes and patterns, where it will lead me in the future remains to be seen. Wherever the road takes me, I am so grateful that your guidance, wisdom, support, and love have finally led me here.

ACKNOWLEDGMENTS

On my very first day of graduate school, I met Ian McAlexander who quickly became my best friend and eventually my husband. Ian, thank you for providing me with love, support, and empathy over the past eight years. My sister Marielle has served as my confidant, best friend, and personal stylist throughout graduate school, thanks sista! I am grateful for my parents and extended family for their constant encouragement. Finally, although it occasionally served as a hindrance, thank you Mother Nature for the epic snow!

Amanda V. Bakian

CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

Spatial heterogeneity is a common feature of the natural world. Understanding the spatial context of ecological patterns and processes continues to be an important goal in ecology. Animals respond to spatial heterogeneity on multiple scales (Wiens 1989) and individual level responses impact population and community-level dynamics (Kareiva 1990). Perhaps most importantly, it is environmental heterogeneity over space and time that creates niche space, promotes species diversity (MacArthur and MacArthur 1961, MacArthur 1964) and community stability (Huffaker 1958, May 1974), and enables the coexistence of species (Holt 1984, Levin 1992). Ecologists have assembled a considerable amount of empirical evidence establishing the link between spatial pattern and ecological process. For example, spatial heterogeneity has been found to impact species-level dispersal patterns (Morales and Ellner 2002, Bonte et al. 2006, Merckx and Van Dyck 2007), the use and availability of refugia (Gilinsky 1984, Kauffman et al. 2007), predator/prey dynamics (Oksanen and Henttonen 1996, Thies et al. 2003, Bonoit-Bird and Au 2003), reproductive fitness (Palmer 1995, Nilsen et al. 2004), and animal space use (Kie et al. 2002).

Although the ecological theory of spatial heterogeneity was well developed by the end of the 20th century, experimental tests of the theory were implemented at a slower pace (Legendre and Fortin 1989, Doak et al. 1992). For years, the spatial variation of natural populations and communities and the resources on which they depend were typically assumed to follow a uniform distribution over space and time (Pickett and Cadenasso 1995). Starting in the 1980's, the incorporation of space into applied ecology resulted in a number of key papers (e.g. Legendre and Fortin 1989, Turner 1989, Wiens 1989, Kareiva 1990). The ideas championed in these papers eventually lead to the development of landscape ecology as a sub-discipline of ecology (Turner 1989, Wiens 1989, Turner et al. 2001). Landscape ecology emphasizes the ecological causes and

consequences of spatial heterogeneity and the influence of scale on population and community-level interactions and dynamics (Forman 1983, Risser et al. 1984, Wiens et al. 1993, Turner et al. 2001).

At the same time that landscape ecologists were promoting the paradigm that spatial heterogeneity is a driver of ecological phenomenon, quantitative and statistical ecologists were making progress with incorporating spatial variation into statistical models. Legendre and Fortin (1989) was one of the first papers to address the general inferential problems that spatially autocorrelated data introduces to ecological analyses when it goes uncontrolled. Statistical models formulated from spatially autocorrelated data in which the spatial dependency in the data is ignored typically suffer from residual spatial autocorrelation leading to deflated parameter standard errors, increased type I errors, and erroneous inference (Lennon 2000, Aarts et al. 2008). In recent years, numerous analytical techniques have been introduced and used by researchers to satisfy statistical assumptions of independence of errors in the presence of spatial autocorrelation including wavelet-revised generalized linear regression (Carl and Kuhn 2008), conditional and simultaneous autoregressive models (Lichstein et al. 2002), lagged-predictor models (Florax and Folmer 1992), autologistic models (Augustin et al. 1996), generalized estimating equations (Carl and Kühn 2007), and generalized linear mixed models with spatial random effects or spatially dependent error covariance (Diggle et al. 1998). In addition, the increasing use of Geographic Information Science by ecologists has further facilitated the incorporation of spatial structure into ecological analysis. Despite progress in developing spatially-explicit statistical models, some debate remains over how vital consideration of spatial autocorrelation is in some statistical models (Diniz-Filho et al. 2003, Hawkins et al. 2007).

These two concepts, understanding the impact of spatial heterogeneity on ecological processes and appropriately modeling spatial structure, are growing increasingly important as the natural world undergoes widespread human-induced change resulting in greater numbers of wild

populations requiring active management for conservation. The Willow Flycatcher, *Empidonax traillii*, is one such species whose long-term population viability is challenged by habitat alteration. While spatial heterogeneity may impact many aspects of the Willow Flycatcher's ecology, I investigate the influence that spatial heterogeneity has on their individual and population-level dynamics. More specifically, I focused on exploring Willow Flycatcher's space use, resource selection and food web responses to spatial heterogeneity.

The Willow Flycatcher is a small, neo-tropical migrant that breeds in dense riparian habitat throughout the continental United States (Fig. 1.1). In the western United States, the species has experienced population declines due largely to habitat modification and destruction and due to nest parasitism by the Brown-headed Cowbird (Sedgwick 2000). The Southwestern Willow Flycatcher, *Empidonax trailli extimus*, is a federally listed endangered species (US Fish and Wildlife 1995). Other sub-species of Willow Flycatcher are facing similar declines in the western U.S. Understanding resource selection and space use in the Willow Flycatcher is important for its active management and conservation. In addition, Willow Flycatchers are conspicuous throughout their range and are easy to identify through sight and song making them an ideal model species for hypothesis testing.

In chapter 2 of my dissertation, I investigate Willow Flycatcher's foraging and vocalization resource selection using Bayesian spatial generalized linear models. Behavior is often overlooked in habitat selection studies (Lima and Zollner 1996) although the distribution of behavior on a landscape reflects the underlying spatial pattern of resources important to a species. I model foraging and vocalization behavior separately to test the hypothesis that behavior is spatially segregated in the home ranges of Willow Flycatchers. By doing so, I produced separate probability maps of foraging and vocalization behavior in Willow Flycatcher home ranges which may be viewed as "behavioral landscapes". The modeling approach presented in chapter 2 is novel yet amenable to most resource selection analyses. Another goal of chapter 2 is to

demonstrate the general utility of this modeling approach to analyzing behavioral animal resource selection.
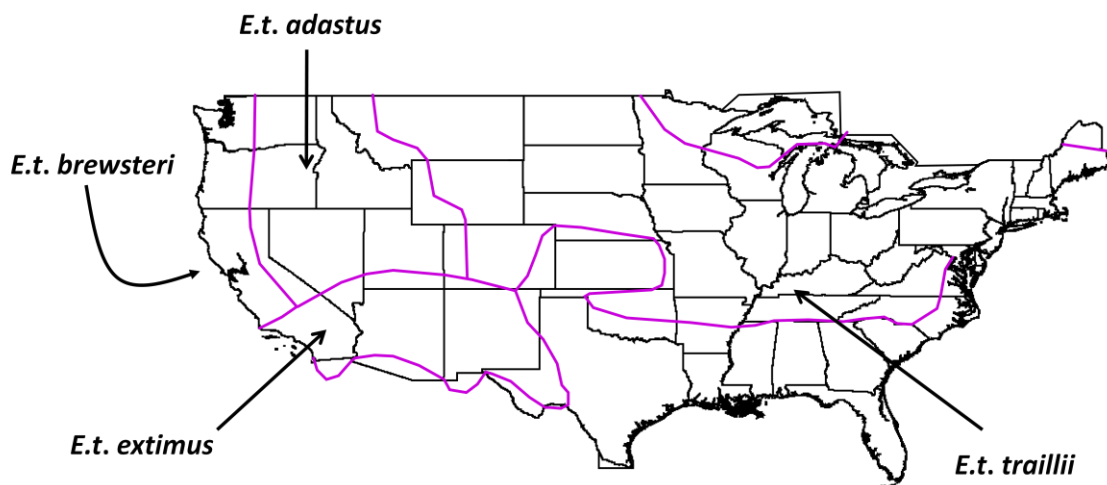
Fig.1.1. Breeding range of the four recognized Willow Flycatcher sub-species in the continental U.S.

In chapter 3, I test hypotheses concerning the use of aquatic versus terrestrial insects by the Willow Flycatcher. Food resources vary spatially and temporally over the course of the Willow Flycatcher's breeding season at Fish Creek. In addition, habitats vary in their insect productivity and arthropods emerging from more productive habitats may move into adjacent, less productive habitats. Willow Flycatchers inhabit the riparian zone that buffers open water and terrestrial environments. Past studies of the flycatcher diet indicate that flycatchers may require prey resources produced outside of the riparian zone during the breeding season (Wiesenborn and Heydon 2007). I measured the contribution of aquatic and terrestrial insects to the diet of Willow Flycatchers using carbon and nitrogen stable isotopes and fecal sample dissection. In addition, I

compared the diet of Willow Flycatchers at Fish Creek, Utah with the diet of Willow Flycatchers from previously published studies.

In chapter 4, I compare and contrast space use metrics in two populations of Willow Flycatcher, *E.t. extimus*, commonly known as the Southwestern Willow Flycatcher (SWFL), and *E.t. adastus*, commonly known as the Willow Flycatcher (WIFL). Although Willow Flycatchers appear to be in decline throughout much of their range in the western United States, the SWFL sub-species, a federally-listed endangered sub-species, has received most of the research attention and little is known about other populations of Willow Flycatchers. Information collected on the Southwestern Willow Flycatcher may be used to manage non-SWFL populations yet the suitability of SWFL ecology to WIFL populations is largely unknown. I hypothesized that flycatchers at Roosevelt Lake, Arizona maintain smaller home ranges and core areas than flycatchers at Fish Creek, Utah due to differences in the structure and composition of habitat patches between these two sites. In addition, I expected to find differences in space use metrics as a function of flycatcher breeding status and sex.

In the final chapter of my dissertation, I summarize the studies' major findings and discuss the implications of these findings on the conservation and management of the Willow Flycatcher, and on landscape and spatial ecological theory. In addition, I suggest future research needs based on this study's primary findings.

LITERATURE CITED

Aarts, G., M. MacKensie, B. McConnell, M. Fedak, and J. Matthiopoulos. 2008. Estimating space-use and habitat preference from wildlife telemetry data. Ecography 31: 140-160.

Augustin, N. H., M.A. Mugglestone, and S.T. Buckland. 1996. An autologistic model for the spatial distribution of wildlife. Journal of Applied Ecology 33: 339_347.

Benoit-Bird, K.J., and W.W.L. Au. 2003. Prey dynamics affect foraging by a pelagic predator (*Stenella longirostris*) over a range of spatial and temporal scales. Behavioural and Ecological Sociobiology 53: 364-373.

Bonte, D., J. Vanden Borre, L. Lens, and J.P. Maelfait. 2006. Geographical variation in wolf spider dispersal behaviour is related to landscape structure Animal Behaviour 72: 655-662.

Carl, G. and I. Kühn. 2007. Analyzing spatial autocorrelation in species distributions using Gaussian and logit models Ecological Modelling. 207: 159-170.

Carl, G., and I. Kühn. 2008. Analyzing spatial ecological data using linear regression and wavelet analysis. Stochastic and Environmental Research and Risk Assessment 22: 315-324.

Diggle, P.J., J.A. Tawn, and R.A. Moyeed. 1998. Model-based geostatistics. Journal of Applied Statistical Science 47: 299-350.

Diniz-Filho, J. A. F., L. M. Bini, and B.A. Hawkins. 2003. Spatial autocorrelation and red herrings in geographical ecology. Global Ecology and Biogeography 12: 53-64.

Doak, D.F., P.C. Marino, and P.M. Kareiva. 1992. Spatial scale mediates the influence of habitat fragmentation on dispersal success: Implications for conservation. Theoretical Population Biology 41: 315-336.

Florax, R., and H. Folmer. 1992. Specification and estimation of spatial linear regression models: Monte-Carlo evaluation of pretest estimators. Regional Science and Urban Economics 22:405–432.

Forman, R.T.T. 1983. Corridors in a landscape: their ecological structure and function. Ekol. CSSR 2: 375-387.

Gilinsky, E. 1984. The role of fish predation and spatial heterogeneity in determining benthic community structure. Ecology 65: 455-468.

Hawkins, B.A., J. A. F. Diniz-Filho, L. M. Bini, P. De Marco, and T.M. Blackburn. 2007. Red herrings revisited: spatial autocorrelation and parameter estimation in geographical ecology. Ecography 30: 375-384.

Holt, R.D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. The American Naturalist 124: 377-406.

Huffaker, C.B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. Hilgardia 27: 343-383.

Kareiva, P. 1990. Population dynamics in spatially complex environments: theory and data. Philosophical Transactions of the Royal Society of London 330: 175-190.

Kauffman, M.J., N. Varley, D.W. Smith, D.R. Stahler, D.R. MacNulty, and M.S. Boyce. 2007. Landscape heterogeneity shapes predation in a newly restored predator-prey system. Ecology Letters 10: 690-700.

Kie, J.G., R. T Bowyer, M.C. Nicholson, B.B Boroski, and E.R. Loft. 2002. Landscape heterogeneity at differing scales: Effects on spatial distribution of mule deer. Ecology 83: 530-544.

Legendre, P., and M.J. Fortin. 1989. Spatial pattern and ecological analysis. Vegetatio 80: 107-138.

Lennon, J.J. 2000. Red-shifts and red herrings in geographical ecology. Ecography 23: 101-113.

Levin, S.A. 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur Award Lecture. Ecology 73:1943-1967.

Lichstein, J.W., T.R. Simons, S.A. Shriner, and K.E. Franzreb. 2002. Spatial autocorrelation and autoregressive models in ecology. Ecological Monographs 72: 445-463.

Lima S.L., and P.A. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. Trends in Ecology and Evolution 11, 131-135.

MacArthur, R.H. 1964. Environmental factors affecting bird species diversity. American Naturalist 98: 387-397.

MacArthur, R.H., and J.W. MacArthur. 1961. On bird species diversity. Ecology 42: 594-598.

May, R.M. 1974. Stability and complexity in model ecosystems, 2nd ed. Princeton University Press, Princeton, NJ.

Merckx, T. and H. Van Dyck. 2007. Habitat fragmentation affects habitat-finding ability of the speckled wood butterfly, *Pararge aegeria* L. Animal Behaviour 74: 1029-1037.

Morales, J. M. and S.P. Ellner. 2002. Scaling up animal movements in heterogeneous landscapes: The importance of behavior. Ecology 83: 2240-2247.

Nilsen, E.B., J.D.C. Linnell, and R. Andersen. 2004. Individual access to preferred habitat affects fitness components in female roe deer *Capreolus capreolus*. Journal of Animal Ecology 73: 44-50.

Oksanen, T. and H. Henttonen. 1996. Dynamics of voles and small mustelids in the taiga landscape of northern Fennoscandia in relation to habitat quality. Ecography 19: 432-443.

Palmer, T.M. 1995. The influence of spatial heterogeneity on the behavior and growth of two herbivorous stream insects. Oecologia 104: 476-486.

Pickett, S.T.A., and M.L. Cadenasso. 1995. Landscape ecology: spatial heterogeneity in ecological systems. Science 269: 331-334.

Risser, P.G., J.R. Karr, and R.T. Forman. 1984. Landscape ecology-directions and approaches. Illinois Natural History Survey Special Publication No. 2 Champaign, IL.

Sedgwick, J. A. 2000. Willow Flycatcher (Empidonax traillii), The Birds of North America Online, A. Poole, [Ed.]. Ithaca, NY: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/533

Thies, C. I. Steffan-Dewenter, and T. Tscharntke. 2003. Effects of landscape context on herbivory and parasitism at different spatial scales. Oikos 101: 18-25.

Turner, M.G. 1989. Landscape ecology: the effect of pattern on process. Annual Review of Ecology and Systematics 20: 171-197.

Turner, M.G., R.H. Gardner, and R.V. O'Neill. 2001. Landscape ecology in theory and practice, pattern and process. Springer, 401 pps.

U.S. Fish and Wildlife Service. 1995. Final rule determining endangered status for the southwestern wil-low flycatcher. U.S. Federal Register 60: 10694-10715.

Wiens, J.A. 1989. Spatial Scaling in Ecology. Functional Ecology 3: 385-397.

Wiens, J. A., N. C. Stenseth, B. Van Horne, and R. A. Ims. 1993. Ecological mechanisms and landscape ecology. Oikos 66:369-380.

Wiesenborn, W.D., and S.L. Heydon. 2007. Diet of Southwestern Willow Flycatcher compared among breeding populations in different habitats. Wilson Journal of Ornithology 119: 547-557.

CHAPTER 2

IDENTIFYING SPATIAL PATTERNS OF BEHAVIOR IN WILLOW FLYCATCHERS,

EMPIDONAX TRAILLII, USING BAYESIAN RESOURCE SELECTION FUNCTIONS[1]

ABSTRACT

Animal resource selection is a complex, hierarchical decision-making process. Resource selection studies often focus on the presence and absence of an animal rather than the animal's behavior at resource use locations. In this study, we investigate foraging and vocalization resource selection in a population of Willow Flycatchers, *Empidonax traillii adastus*, using individual and population-level Bayesian spatial generalized linear models. Radio telemetry locations were collected from 35 adult Willow Flycatchers ($n = 14$ males, $n = 13$ females, and $n = 8$ unknown sex) over the 2003 and 2004 breeding seasons at Fish Creek, Utah. Results from the 2-stage modeling approach indicate that habitat type, perch position, and distance from the arithmetic mean of the home range (in males) or nest site (in females) were important factors influencing foraging and vocalization resource selection. Parameter estimates from the individual-level models indicated high intraspecific variation in the use of the various habitat types and perch heights for foraging and vocalization. Foraging was found to have a larger effective range of spatial dependency than vocalization based on the average estimated value of the individual-level model's spatial decay parameter. Male flycatchers were observed to have a larger effective range of spatial dependency than female flycatchers for foraging and vocalization. On the population level, Willow Flycatchers selected riparian habitat over other habitat types for vocalizing but used multiple habitat types for foraging including mountain shrub, young riparian and upland forest. Mapping of observed and predicted foraging and vocalization resource selection indicates that the behavior often occur in disparate areas of the home range. This

---

[1] Coauthored by Bakian, A.V., K.A. Sullivan, and E.H. Paxton

suggests that multiple core areas may exist in the home ranges of individual flycatchers. We discuss the management implications of individual-level heterogeneity versus population-level inference on Willow Flycatcher conservation and management.

1. Introduction

A paramount objective of ecology is to understand not only where organisms exist but also to understand why (Krebs, 1978). Despite increasingly sophisticated technology available to study animal resource selection and use, we remain largely ignorant about the motivations of animals when selecting resources. Inference based on studies of resource selection would greatly improve if resource selection incorporated behavior rather than mere presence (Lima and Zollner, 1996; Marzluff et al., 2001).

Closely aligned with animal resource selection is the field of animal space use. Identifying the home range, the area an organism uses to fulfill its breeding, foraging and survival needs (Burt, 1943), is often the focal point of animal space use studies. When an animal's daily activity is largely restricted to its home range, we may infer that the home range contains the majority of resources required by an animal for breeding and survival. Hence, the home range serves as the natural spatial boundary within which to examine resource selection (Marzluff et al., 2004).

Within the home range, space use patterns rarely follow a uniform distribution and animals typically show a tendency to use certain parts of their home ranges more frequently than other parts (Hayne, 1949). The disparate use of parts of the home range reflects the spatially segregated nature of the resources important to an organism. Areas of intensive use within the home range are known as core areas. Most space use studies focus on delineating a single core area within an individual's home range (Laver and Kelly, 2008) although multiple core areas may exist. If so, across these multiple core areas resource selection may vary as a function of behavior indicating that particular core areas are used for unique behavior. For example, Marzluff et al. (2001),

recommends constructing behavioral-specific kernel utilization distributions to look for differential space use for foraging, locomotion, perching and parental care behavior in the American Crow. Their analysis found that the most frequent behavior of crows' (ie, perching and foraging) was spatially segregated.

Resource selection is a complex, hierarchical decision-making process. Most studies of resource selection compare landscape and habitat attributes at used locations with attributes at either available or unused locations using popular resource selection function (RSF) modeling approaches such as categorical analysis (Neu et al., 1974), discrete choice models (Cooper and Millspaugh, 1999, 2001), compositional analysis (Aebischer et al., 1993), or logistic regression (Manly et al., 2002). In this study, we show how resource selection can be analyzed as a hierarchical process by formulating behaviorally and spatially-explicit Bayesian resource selection functions with random effects to investigate and predict vocalization and foraging behavior in Willow Flycatchers at individual (home range level) and population-levels. We chose to set our multi-level RSFs in a Bayesian framework for a number of reasons. First, hierarchical relationships are easily specified in Bayesian models and given the hierarchical nature of resource selection, the Bayesian framework naturally lends itself well to modeling RSFs. Second, Bayesian procedures also provide a straightforward way to include random effects in generalized linear models. Third, Bayesian inference is based on interval estimation and not on large-sample theory, and Bayesian inference is less sensitive to the influence of sample sizes than are frequentist significance tests.

The Willow Flycatcher, *Empidonax traillii*, is a small, neotropical migrant that selects riparian habitats for breeding throughout the continental United States. They are territorial and central place foragers (Orians and Pearson, 1979; Stephens and Krebs, 1986). Male flycatchers sing and defend territories from tall perches (McCabe, 1991). The majority of research on the Willow Flycatcher has focused on male flycatchers due to their easier detectability. Research

indicates however that male and female flycatchers show variation in their habitat preferences for breeding and nest site selection (Sedgwick and Knopf, 1992) suggesting that it is critical to incorporate both sexes into research studies aimed at deriving population-level inference. Willow Flycatchers are a riparian-habitat obligated species (Sedgwick, 2000), yet circumstantial evidence exists to suggest that they may rely on a diversity of habitat types to meet their resource needs during the breeding season. The degree to which Willow Flycatchers use non-riparian habitats during the breeding season remains largely unknown. By measuring resource selection as a function of specific behavior, we hope to gain an understanding of when and why Willow Flycatchers use alternative habitats.

Our study integrates statistical modeling and GIS to estimate home ranges, visualize flycatcher vocalization and foraging behavior, and produce images of spatial predictions of flycatcher resource selection. In addition, in response to the wide-spread use of arbitrary core area delineators such as the 50% kernel utilization distribution, we will demonstrate the utility of our modeling approach for delineating behaviorally specific core areas and for identifying spatially segregated behaviors within the home range. Our study's primary objectives are: 1) demonstrate the utility of modeling animal resource selection in a spatially and behaviorally explicit Bayesian RSF framework, 2) investigate differences in Willow Flycatcher foraging and vocalization resource selection between male and female flycatchers at the individual and population scale, 3) examine the degree of spatial segregation in foraging and vocalization behavior in the home ranges of Willow Flycatchers, and 4) elucidate differences in the use of various habitat types for foraging and vocalization.

2. Methods

2.1 Study site

This study was conducted along a three-mile stretch of the Fish Creek drainage in Manti-La Sal National Forest, Carbon County, Utah (Fig. 1; 39°77' N, 111°20' W). Fish Creek is a perennial high elevation (~2560 m) creek that drains the Wasatch Plateau from west to east into Scofield reservoir and contains the highest density of Willow Flycatchers in Utah (Frank Howe, personal communication). Within the floodplain, Fish Creek is composed primarily of young and mature riparian vegetation that is dominated by willow shrubs (*Salix* spp.), growing in a series of patches along the stream corridor. Herbaceous vegetation, open water (creek and beaver ponds) and upland habitat types border the riparian patches. Upland habitats with north facing aspects are composed of forests dominated by Englemann's spruce (*Picea engelmanni)*, White fir (Abies concolor), Douglas fir (*Pseudotsuga menziesii*), and Quaking aspen (Populus tremuloides) species. Upland habitats with south facing aspects are composed of a mixture of mountain shrub and desert shrub steppe vegetation dominated by big sagebrush (*Artemisia tridentate* sp.), Utah serviceberry (*Amelanchier utahensis*), chokecherry (*Prunus virginiana*), mountain snowberry (*Symphoricarpos oreophilus*) and various shrubsteppe grasses (Table 2.1).

2.2 Field data collection

Data was collected over the 2003 and 2004 breeding seasons during which the population size of flycatchers along the five mile stretch of Fish Creek studied was stable (n ~ 50; Bakian, unpublished data). From the approximately 25 territories established per year, fifteen territories were selected annually from which to sample flycatchers. Willow Flycatchers were trapped using mist-nets, and birds were captured using both passive netting and target netting techniques (Sogge et al., 2001). Captured Willow Flycatchers were banded with a red-color anodized Federal bird band on one leg, and a uniquely, colored metal band on the opposite leg. Age was determined by

examining plumage, molt patterns, and skull ossification. Sex was determined based on the

presence of a cloacal protuberance in males or brood patch in females, and in some cases based

on wing chord and tail length (Pyle, 1997). Occasionally, sex was challenging to determine and

for these individuals, their sex was recorded as unknown. After a flycatcher was banded and

measured, the Holohil LB-2N radio-transmitter, was attached to the lower back of the animal

using Skin-bond ®, a medical adhesive (Paxton et al., 2003).

Table 2.1. Habitat type definitions at Fish Creek, Utah.

Habitat type	Definition
Mature riparian	Stands of mature willow (*Salix spp.*; > 1 m tall) dominated vegetation found adjacent to standing water. An understory of mixed grasses and forbes is typically present. Breeding habitat for flycatchers.
Young riparian	Stands of shrubby, mixed vegetation found adjacent to standing water. Typically, comprised of immature willow (*Salix spp.*; < 1 m tall) that may grow as isolated clumps, or as individual plants. Willows may be interspersed with other shrub species including black twin-berry (*Lonicera involucrate*), choke cherry (*Prunus virginiana*), serviceberry (*Amelanchier alnifolia*), and various forbes and grasses. Vegetation may also be interspersed with areas of bare ground.
Bare ground	Areas void of vegetation and comprised of bare soil, rock or sand.
Upland forest	Continuous stands comprised of various tree species including White Fir (*Abies concolor*), Douglas Fir (*Pseudotsuga menziesii)*, Englemann's Spruce (*Picea engelmanni*, and Quaking Aspen (*Populus tremuloides*).
Mountain shrub steppe	Various shrubs including but not limited to big sagebrush (*Artemisia tridentate*), choke cherry, gooseberry (*Ribes spp.*), black twin-berry, service berry, and rabbitbrush (*Chrysothamnus spp.*). Shrubs are interspersed with various forbes and grasses.
Open water	Areas of flowing or standing water of measurable depth.

2.3 Radio tracking

Radio-tracking was conducted at least four times daily for each Willow Flycatcher,

within four established time periods: AM early (0600-0915), AM late (0916-1230), PM early

(1231-1545) and PM late (1546-1900). All tracking was randomly assigned within each time

interval, and for the most part, the tracking efforts were evenly distributed across all four intervals for each bird with a goal of collecting at least 30 radio locations per bird. Equipment used in tracking included R-1000 Telemetry receivers manufactured by Communications Specialists, Inc. and standard hand-held 3-element yagi antennas.

We used a homing-in method (Paxton et al., 2003) to pin-point the geographical position of radio-tagged flycatchers, and a radio-location was established as soon as the radio-tagged flycatcher became visible to the tracker. Occasionally, the technician caused the bird to move from its original position prior to acquiring an observation. In such cases, the tracker estimated the position of the bird before it was disturbed and used this estimate as the bird's location. On other occasions, the radio-tagged flycatcher was heard nearby but a visual confirmation was not possible due to thick vegetation. When this occurred, both the homing-in method and an estimate of the vocalization position were used to determine the position of the bird.

Following visual confirmation of a bird's location, the tracker recorded geographical and detailed behavioral information about the bird including the bird's perch substrate, the bird's position in the substrate, habitat type, and the flycatcher's behavior. Specific behavior recorded included vocalization, foraging, nest building, territorial defensive, feeding nestlings or fledglings, and thermoregulating. Detailed vocalization and foraging behavior recorded included vocalization type (song or call) and foraging type (e.g. sally or glean). The bird's perch height position in the vegetation was measured on a scale of low, medium or high. Six habitat types were considered at Fish Creek: mature riparian habitat (Willow Flycatcher nesting habitat), young or scrubby riparian habitat, mountain shrub, upland forest, bare ground and water (Table 2.1). The geographic location (in UTMs) and their associated accuracy measurements of each bird location were recorded using a global positioning system (GPS) device (Garmin Etrex Legend H GPS Navigator). Tracking was continued daily until the transmitter failed due to battery failure,

or the flycatcher became undetectable. All attempts were made to relocate a flycatcher when a signal was lost.

2.4 Landscape and home range analyses

We used the fixed-kernel UD with least squares cross validation for estimating individual flycatcher home ranges. Kernel UD home ranges were estimated in ArcView 3.3 using the ANIMAL MOVEMENT extension (Hooge and Eichenlaub, 1997). We limited our estimation of fixed-kernel UD home ranges to individuals for which at least 30 observations were collected to ensure accurate home range estimation (Seaman et al., 1999).

A population-level estimate of the total area used by the Willow Flycatchers over the 2003 and 2004 breeding seasons was calculated by simultaneously displaying all flycatcher home ranges and creating a polygon encompassing all home ranges while minimizing the inclusion of non-home range areas. A land cover map of Fish Creek was constructed for the landscape area encompassed by the 'total area used' polygon with habitat types delineated into six habitat types (listed in Table 2.1) based on a combination of field surveys and color aerial photographic images. The habitat composition of individual home ranges was determined by intersecting the home range polygons with the land cover map.

2.5 Statistical analyses

2.5.1 Conceptual model

Our analytical approach used a standard logistic regression model, with a spatial random effect added to the logistic regression model. This model was then set in a Bayesian hierarchical framework. The presence or absence of a specific behavior (e.g. vocalization or foraging) at each radio-telemetry location was treated as the response variable. The analysis was conducted at the individual and population-level in which the presence or absence of a behavior was grouped across individuals. Many of the parameters in the logistic regression models such as the

explanatory variable coefficients and the spatial random effect parameters were treated as
unknown variables and were represented by distributions with pre-specified means and variances.
A Metropolis-Hastings Markov chain Monte Carlo algorithm is used to produce distributions of
estimates of the unknown parameters, and individual and population-level inference such as the
use of mountain shrub habitat for foraging by female Willow Flycatchers is based on these
distributions.
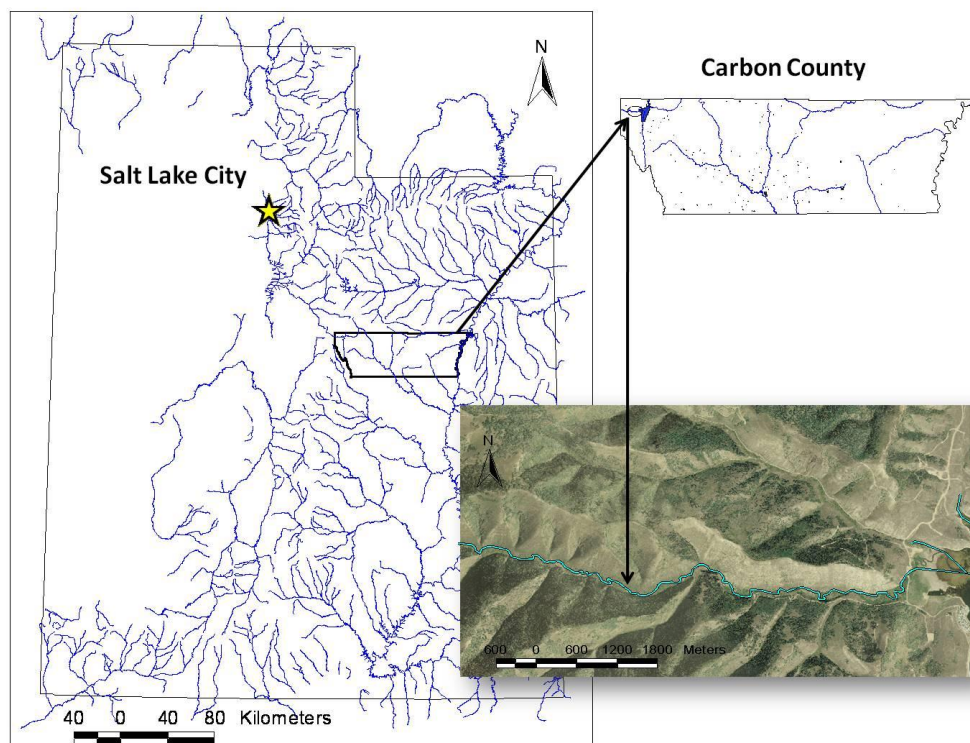
Fig. 2.1. Geographical location of the Fish Creek drainage in Carbon County, Utah.

2.5.2 *Exploratory data analysis*

Animal resource use locations are often autocorrelated in space and time. In many
selection studies, spatial autocorrelation is overlooked and invalidates assumptions of RSF model
independence and identically distributed data. In our individual-level models that investigate

vocalization and foraging selection behavior throughout the home range, we included a Gaussian

process to capture the spatial variance inherent in the response and explanatory data.

Spatial autocorrelation was confirmed visually by plotting a variogram to individual

flycatcher data. Variograms display the correlation in the deviations of the observations from the

mean response as a function of distance between locations assuming a stationary process (an

example is shown in Fig. 2.2). Variograms were fit to logistic regression models including

complete sets of covariates. Individual and population-level variograms were fit separately for

vocalization and foraging behaviors.

Exponential and spherical parametric spatial models without a nugget parameter were fit

to the variograms using weighted least squares. The spatial models were used to find estimates of

the partial sill (asymptotic point on the vertical axis) and range (asymptotic point on the

horizontal axis) parameters to apply as starting points for the spatial process models in the

Bayesian RSFs. The better fit spatial model (either spherical or exponential) was determined via

eye-balling and used in the spatial process component of the hierarchical model.

2.5.3 *Explanatory variables*

Three attributes were measured at each flycatcher observation location for inclusion in

the hierarchical models: 1) categorical habitat type, 2) distance of the radio-location from the

nest site (females) or arithmetic mean of the home range (males), and 3) vertical position of the

bird in the vegetation. The categorical habitat type was coded as a dummy variable. In the

individual-level models, the choice of reference habitat varied among models depending on the

habitat types selected by the individual; not all habitat types available were used. In general, an

effort was made to examine the use of mature riparian habitat (nesting habitat) for vocalization

and foraging behavior versus "alternative" habitat types including mountain shrub, forest or

young riparian habitats. In the individual-level models, riparian or mountain shrub habitats were

used as the reference habitats while riparian habitat served as the reference habitat in the population-level models.

The Euclidean distance (in meters) was measured from the observation to the nest site location (in the case of female flycatchers) or arithmetic mean of the home range (in the case of male flycatchers) to explore what influence central place fidelity may have on flycatcher foraging and vocalization. Finally, association between bird habitat perch position and behavioral activity were explored through the addition of habitat perch position as a model covariate. Perch position was coded as a dummy variable with three levels: low, medium or high. In the individual-level models, typically low or high served as the reference location while high served as the reference position in the population-level models.

2.6 Hierarchical Bayesian spatial model

Our hierarchical spatial model is composed of three conditional model components: a data or likelihood model$[data|process, data\ parameters]$, a process model$[process|process\ parameters]$, and a parameter model$[data\ and\ process\ parameters]$. The likelihood model is similar to the likelihood used in traditional maximum-likelihood estimation and specifies the distribution of the observed data conditioned on both the process of interest and the data model's parameters. The process model specifies the process of interest conditioned on its parameters, and the parameter model describes the distribution of the parameters in the data and process models. By applying Bayes' Theorem, the posterior or joint distribution of the hierarchical model is obtained:

$$[process, parameters|data] \propto$$
$$[data|process, parameters] \times [process|parameters][parameters]. \tag{1}$$

Alternatively, the joint posterior distribution can be represented as

$$p(\phi, \boldsymbol{\theta}|Data) \propto p(\phi, \boldsymbol{\theta})p(Data|\boldsymbol{\theta}), \tag{2}$$

where, ϕ represents the process model, and $\boldsymbol{\theta}$ represents the unknown parameter vector. The

unknown parameters in $\boldsymbol{\theta}$ and the data, **y**, are linked only through the process model, $\emptyset$.

2.6.1 Data and process models

Separate hierarchical models were fit to each behavior (vocalization and foraging) for

each individual resulting in two models per animal. One population-level model was fit to each

behavior for a total of 2 population-level models. The logistic link regression model serves as the

starting framework for both the individual and population-level hierarchical models. If we

sampled $i = 1, ..., n$ animals observing each animal at $j = 1, ..., m$ locations and considering

only one behavior at a time (either foraging or vocalization), then, $y_{ij} = 1$ indicates the presence

of behavior at location j by animal i and $y_{ij} = 0$ indicates the absence of that behavior. Given a

response that is conditional upon a set of covariates, such as $\mathbf{x}_{ij}$ for location j, we assume the y_{ij}'s

(the *data* model component) follow a Bernoulli distribution, $y_{ij} \sim Ber(p(\mathbf{x}_{ij}))$ with

$P(y_{ij} = 1|\boldsymbol{x}_{ij}) = p(\boldsymbol{x}_{ij})$. The relationship between the response data vector $\boldsymbol{y}_i = (y_{ij}, ..., y_{im})$,

and the $m \times k$ matrix of k predictor variables, $\boldsymbol{X}_i = [\boldsymbol{x}_{i1}^T, ..., \boldsymbol{x}_{im}^T]$, where each $\boldsymbol{x}_{i1}^T$ is the $1 \times k$

vector of covariates at the j-th location, the probability of use by animal i of location j (the

process model component) is modeled as a logistic link regression,

$$p(\mathbf{x}_{ij}) = \frac{\exp(\mathbf{x}_i^T \boldsymbol{\beta}_i)}{1 + \exp(\mathbf{x}_i^T \boldsymbol{\beta}_i)}, \tag{3}$$

where $\boldsymbol{\beta}_i = (\boldsymbol{\beta}_{i1}, ..., \boldsymbol{\beta}_{ik})$ is the k-dimensional vector of parameters for animal i.

2.6.2 Modeling spatial variation

There are a number of ways to treat spatial variability in linear models (see Littell et al., 2006, chapter 11; Diggle and Ribeiro, 2007). We start by considering the form of the general linear mixed model:

$$\mathbf{Y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Zu} + \mathbf{e}, \tag{4}$$

where, $\mathbf{Y}$ is the vector of observations, $\mathbf{X}$ is the matrix of explanatory variables or covariates, $\boldsymbol{\beta}$ is the vector of fixed effect parameters, $\mathbf{Z}$ is the matrix of covariates pertaining to the random factor, $\mathbf{u}$ is the vector of random effects, and $\mathbf{e}$ is the vector of independent and identically distributed Gaussian random errors. In the case of a generalized linear mixed model, the Gaussian model in (4) is adjusted to

$$h(\mathbf{Y}) = \mathbf{X}\boldsymbol{\beta} + \mathbf{Zu}, \tag{5}$$

where we now consider the expectation of $\mathbf{Y}$ (assumed to be generated from a distribution belonging to the exponential family) to be related to the mean conditional on $\mathbf{u}$ through a known link function $h(.)$. The variance of the model described in (5) is determined by the form of the conditional likelihood.

In our spatial generalized linear model, spatial variation is incorporated as a random effect. The radio-locations are regarded in a spatial context and each flycatcher observation is spatially referenced (a 2-dimensional Easting-Northing position in our case) as $S = \{\mathbf{s}_1, \ldots, \mathbf{s}_M\}$. Our response, the presence or absence of a behavior, $y(\mathbf{s}_{ij}) = 1$ or 0, now depends on spatially-associated covariates, $\mathbf{x}(\mathbf{s}_{ij})$ at location $\mathbf{s}_{ij}$. Our spatial generalized linear mixed model now takes on the form,

$$h\big(\mathbf{Y}(\mathbf{s})\big) = \mathbf{X}(\mathbf{s})\boldsymbol{\beta} + \mathbf{W}(\mathbf{s}), \tag{6}$$

where $\mathbf{W(s)}$ is a random effect capturing the spatial variance in the ecological process.

Combining the logistic regression model shown in (1) with the spatial generalized linear mixed

model displayed in (6) produces,

$$p(\mathbf{s}_{ij}) = \frac{\exp\left(\mathbf{x}(\mathbf{s}_{ij})^T \boldsymbol{\beta}_i + w(\mathbf{s}_{ij})\right)}{1 + \exp\left(\mathbf{x}(\mathbf{s}_{ij})^T \boldsymbol{\beta}_i + w(\mathbf{s}_{ij})\right)}. \tag{7}$$

As mentioned above, the spatial variation in the process model is captured by $\mathbf{W(s)}$ in (6)

and in (7), we find that for a collection of radio-locations, in our case, S, the realization of the

spatial process becomes $\mathbf{w}_i = \left(w(\mathbf{s}_{ij})\right)_{j=1}^{M}$. We used a Gaussian process to model spatial

variation, a popular choice for linear models due to their flexibility in characterizing spatial

correlation (see Cressie, 1993; Banerjee et al., 2004). We modeled $\mathbf{w}_i$ as a multivariate Gaussian

distribution, $MVN\left(\mathbf{0}, \sigma^2{}_i R(\phi_i)\right)$, where $R(\phi_i) = \left[\rho\left(s_j - s_k; \phi_i\right)\right]_{k,j=1}^{M}$ is the $M \times M$ spatial

correlation matrix, and the spatial dependence is modeled by $\rho(\mathbf{s} - \mathbf{s}'; \phi_i)$, a spatial correlation

function belonging to the Matérn family of spatial functions. In our individual models, we choose

between the spherical and exponential correlation functions. The exponential model takes the

form, $\rho\left(s_j - s_k; \phi_i\right) = \exp\left(-\phi_i \|\mathbf{s} - \mathbf{s}'\|\right)$ while the spherical model follows $\rho\left(s_j - s_k; \phi_i\right) =$

$\left(\frac{3}{2}\left\|\frac{\mathbf{s}-\mathbf{s}'}{\phi_i}\right\| - \frac{1}{2}\left\|\frac{\mathbf{s}-\mathbf{s}'}{\phi_i}\right\|^3\right)$. The effective spatial range, d_0, of the modeled behavior process was

calculated as $d_0 \approx 3/\phi_i$ (Finley et al., 2008) in the models using the exponential covariance

function, and $d_0 \approx 2\sqrt{3}/\phi$ in the models using the spherical covariance function. Two

parameters are required to model $\mathbf{w}_i$, the spatial decay parameter ϕ_i, and the spatial effect

variance, $\sigma^2{}_i$. Returning to equation (2), we have now fully specified the posterior distribution of

our individual-level hierarchical model (Table 2.2).

Table 2.2. Individual-level and population level Hierarchical model conditional model components.

Component	Specification
	Individual-level
Data model	$y_{ij} \sim Ber(p(\mathbf{s}_{ij}))$
Process model	$p(\mathbf{s}_{ij}) = \dfrac{\exp\left(\mathbf{x}(\mathbf{s}_{ij})^T \boldsymbol{\beta}_i + w(\mathbf{s}_{ij})\right)}{1 + \exp\left(\mathbf{x}(\mathbf{s}_{ij})^T \boldsymbol{\beta}_i + w(\mathbf{s}_{ij})\right)}.$
Parameters	$\boldsymbol{\Omega} = \left(\boldsymbol{\beta}_i, \sigma_i^2, \phi_i, \mathbf{w}_i\right)$
	Population-level
Data model	$y_{ij} \sim Ber(p(\mathbf{x}_{ij}))$
Process model	$p(x_{ij}) = \dfrac{\exp\left(\mathbf{x}_i^T \boldsymbol{\beta}_{il} + \boldsymbol{\gamma}_{0i}\right)}{1 + \exp\left(\mathbf{x}_i^T \boldsymbol{\beta}_{il} + \boldsymbol{\gamma}_{0i}\right)}$
Parameters	$\boldsymbol{\Omega} = \left(\boldsymbol{\beta}_{il}, \boldsymbol{\beta}_i^*, \sigma_i^2, \boldsymbol{\gamma}_{0i}, \varepsilon\right)$

2.6.3 Population-level model

On a population-level, the occupancy of discrete patches by flycatchers on the landscape introduces spatial correlation that is challenging to capture statistically. Also, this form of spatial covariance dominates the finer grain spatial covariance captured in the individual level models. For these reasons, spatial covariance was not included in the population level models. Instead, individual heterogeneity is captured by the population-level models with the addition of bird-level random-effects parameter to the process model.

The process model used for the population-level inference is equation (3). In addition, a probability model for the individual random effects is added to (3) to represent the sub-populations of flycatchers randomly selected in this study from the total population of flycatchers at Fish Creek. The random bird-effects parameter takes the form $\gamma_{0i} \sim N(0, G)$ where G is a covariance matrix, $G \sim W^{-1}(V, n)$. Residual error, ε, is assumed to follow a normal distribution

where $\varepsilon \sim N(0, R)$ and $R \sim W^{-1}(1, 1\mathrm{e}+6)$. The predictor coefficients, $\boldsymbol{\beta}_{il}$, are modeled as

$\boldsymbol{\beta}_{il} \sim N(\boldsymbol{\beta}_l^*, \sigma_l^2)$, for $l = 1, 2, \ldots, k$, where individual covariate estimates are calculated across all

animals using independent normal distributions with common coefficient $\boldsymbol{\beta}_l^*$ and variance σ_l^2.

2.6.4 Prior specification

Prior distributions must be specified for the parameters included in the models. In the

individual-level models, these parameters include $\boldsymbol{\Omega} = (\boldsymbol{\beta}_i, \boldsymbol{\sigma}_i^2, \phi_i, \mathbf{w}_i)$ with length m+2+k per

animal i. The actual length of $\boldsymbol{\beta}_i$, the k-dimensional vector of parameters for animal i, varies from

individual to individual but falls within the range $3 \leq k \leq 6$ when including the intercept. We

specified independent, normal distributions to the k fixed effect parameters so that

$\boldsymbol{\beta}_i \sim N\left(\beta_{j0}, \sigma_{\beta_j}^2\right)$, where $\beta_{j0} \sim N(0,10)$ and $\sigma_{\beta_j}^2 \sim \mathrm{Inv} - \chi^2(0.01, 0.01)$ (chosen such that the mean is

1). Our use of a large variance parameter in $\boldsymbol{\beta}_i$ indicates our vague knowledge regarding the

value of the prior. In the population-level model, the parameters were modeled similarly where

$\boldsymbol{\beta}_{il} \sim N(\boldsymbol{\beta}_l^*, \sigma_l^2)$, $\boldsymbol{\beta}_l^* \sim N(0, 10)$, $\sigma_l^2 \sim IG(0.01, 0.01)$, $\gamma_{0i} \sim N(0, G)$, $G \sim W^{-1}(1,0)$, $\varepsilon \sim N(0, R)$ and

$R \sim N(1, 1\mathrm{e}+6)$. The spatial parameter, $\boldsymbol{\sigma}_i^2$, received an inverse-Gamma distribution,

$\sigma_i^2 \sim IG(\mathrm{a}_\sigma, \mathrm{b}_\sigma)$, and we chose to fix $\mathrm{a}_\sigma = 2$ which gave the distribution an infinite variance with a

mean of b_σ. The spatial decay parameter was given a uniform distribution, $\phi \sim U(\mathrm{a}_\sigma, \mathrm{b}_\sigma)$ where

a_σ=3/2000 and b_σ=1. The posterior distribution for the individual-level models, given the

specification of the conditional model components, now takes on the form:

$$p(\boldsymbol{\Omega}|Data) \propto p(\phi)p(\boldsymbol{\beta})p(\sigma^2)p(\mathbf{w}|\sigma^2, \phi) \times L(\boldsymbol{\Omega}; Data), \tag{8}$$

where $L(\boldsymbol{\Omega}; Data)$ is the likelihood of the data given the parameter set.

2.6.5 Posterior sampling and convergence diagnostics

We used the 'spBayes' (Finley et al., 2009; http://cran.r-project.org/) and the

MCMCglmm (Hadfield, 2009; http://cran.r-project.org/) packages in R, for model specification,

posterior sample generation and posterior prediction. Marginal posterior distributions were

generated from a Metropolis-Hastings Markov chain Monte Carlo algorithm following model

specification. The coefficients calculated from a non-hierarchical fitted logistic regression model

served as the candidate values for the **β** parameters in the hierarchical models. In the individual-

level models, candidate values for the mean (b_σ) of the spatial parameter, $\boldsymbol{\sigma}_i^2$, and the spatial

decay parameter were taken as the sill and the range on the vertical and horizontal axes of the

empirical variogram, respectively. The parameter tuning values were adjusted to maintain healthy

acceptance rates between 23%-50% (Gelman et al., 2004). We generated multiple independent

chains for each model with 75,000 iterations discarding the initial 25,000 samples as burn-in. Of

the remaining 50,000 iterations, we thinned every 25th sample, and therefore posterior

distributions, parameter estimates and prediction are based on 2,000 iterations. Density estimate

and trace plots of the chains were produced by the Convergence Diagnostics and Output Analysis

for MCMC (CODA) package in R (Plummer et al., 2009). Only chains in which healthy

acceptance rates were maintained were used for inference.

2.6.6 Model selection

We used a multi-step approach for selecting individual-level behavior models as follows.

First, the simplest model was fit for each individual and for each behavioral response. The

Metropolis-Hastings algorithm was then used to generate the marginal posterior distributions for

each parameter in the model. Following successful model convergence, distributions of the

simulated marginal posterior distributions were inspected to ensure that marginal posterior

distributions were sensible and congruent with the prior distributions (Fig. 2.3).
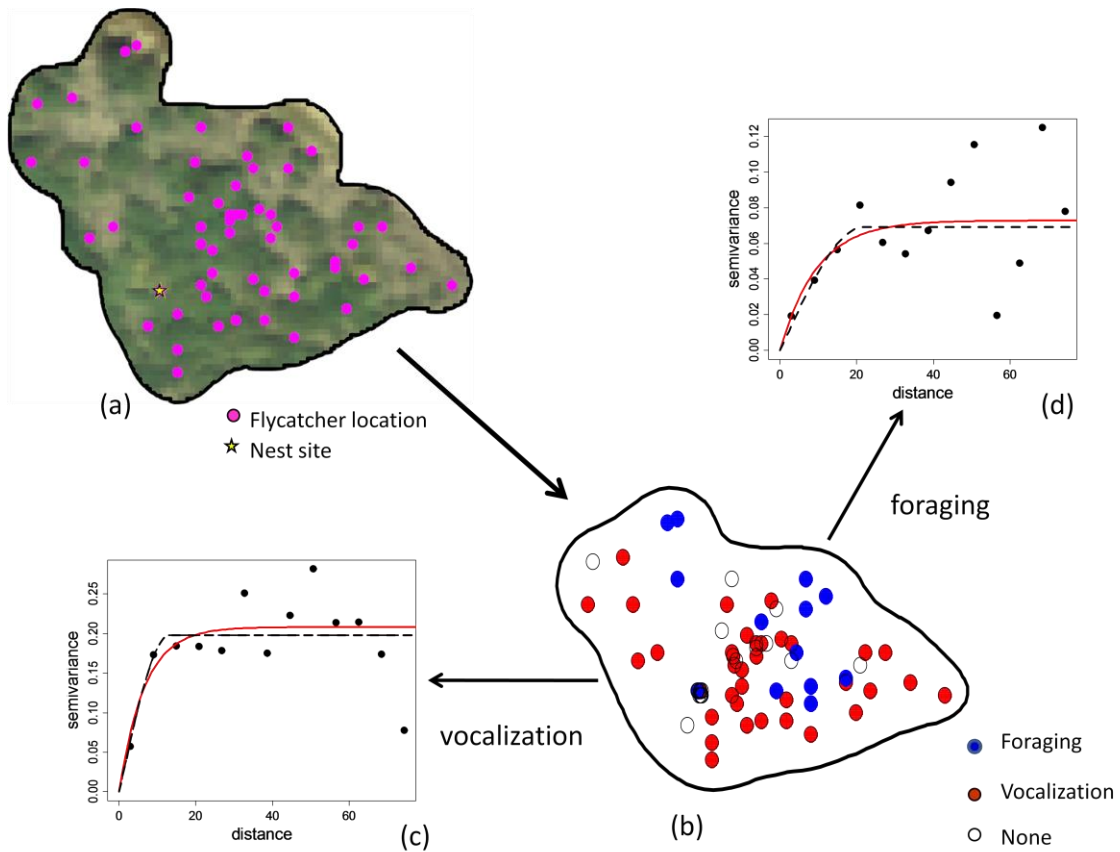
Fig, 2.2. Process used to observe and estimate the spatial autocorrelation present among a flycatcher's radio telemetry locations. First, radio-locations are projected on to aerial photographs (pink points) and the home range is estimated as a two-dimensional 95% utilization distribution (UD, black outline) using a fixed-kernel estimator (a). The distribution of vocalization and foraging behavior is clearly observed when viewing their locations separately; in this example, foraging behavior is represented by blue points, vocalization behavior is represented by red points, and the absence of either behavior is represented by transparent points (b). Spatial autocorrelation is observed by plotting behavioral response specific variograms for vocalization (c) and foraging (d) where the x-axis represents distance between radio locations and the y-axis represents semi-variance.

Next, marginal parameter distributions were used to produce images of the fitted

response to compare with images of the observed response to look for discrepancies between the

observed and simulated data thereby validating the model thru graphical posterior predictive

checks (Gelman et al., 2004, section 6.4). After visually examining the fit of the simplest models,

additional covariates were added to the model to try to improve the fit between the observed and

the posterior simulated data. Marginal posterior samples were re-simulated via the Metropolis-

Hastings algorithm, and the distribution of the posterior samples and images of the fitted response

versus the observed response were again examined. This process was repeated until graphical

posterior predictive checks were optimized. In other words, the models from which posterior

samples of the fitted response most closely resembled the observed response were selected as the

optimal individual models (see Fig. A.1 for example). The average individual selection parameter

estimates and the average individual selection parameter estimate standard errors were computed

and the average individual selection parameter estimate values standard errors were estimated by

$$\sqrt{\frac{\sum_{i=1}^{m}\left(\hat{\beta}_{il}-\overline{\hat{\beta}}_{il}\right)^2}{n(n-1)}} \tag{9}$$

where n is the number of animals.

2.7 Prediction

After satisfactory samples of the parameter's posterior distributions were acquired,

$p(\mathbf{\Omega}|Data)$, the presence or absence of behavior, $p\big(y_0(\mathbf{s}_0)\big)$ was predicted throughout an

individual's home range, where $\mathbf{s}_0$ represents locations with known covariate values and y_0

represents the unknown response. For prediction purposes, we pursue a posterior predictive

distribution with the specification:

$$p\big(y_i(\mathbf{s}_0) = 1|\mathbf{y}, \mathbf{x}, \mathbf{x}(\mathbf{s}_0)\big) = \int p\big(y_i(\mathbf{s}_0) = 1|\mathbf{\Omega}, \mathbf{y}, \mathbf{x}(\mathbf{s}_0)\big) p(\mathbf{\Omega}|\mathbf{y}, \mathbf{x})d\mathbf{\Omega}, \tag{10}$$

where $\mathbf{x}(\mathbf{s}_0)$ represents a known vector of covariates at locations $\mathbf{s}_0$. We created evenly spaced

point grids throughout an individual's home range and derived a vector of covariates associated

with each location in the grid. A predictive sample of use probabilities was then computed at

each grid location by composition sampling by $p\left(y_i(\mathbf{s}_0) = 1|\mathbf{\Omega}^j, \mathbf{y}, \mathbf{x}(s_0)\right)$ for $j = 1, ..., M$ (refer to Finley et al., 2008). The posterior mean and standard deviation values from the predictive distribution at each grid location were used to create home range habitat use probability maps for each individual and each behavior (see Appendix, Fig. 1 for example). Posterior prediction distributions were not generated for the population-level models.
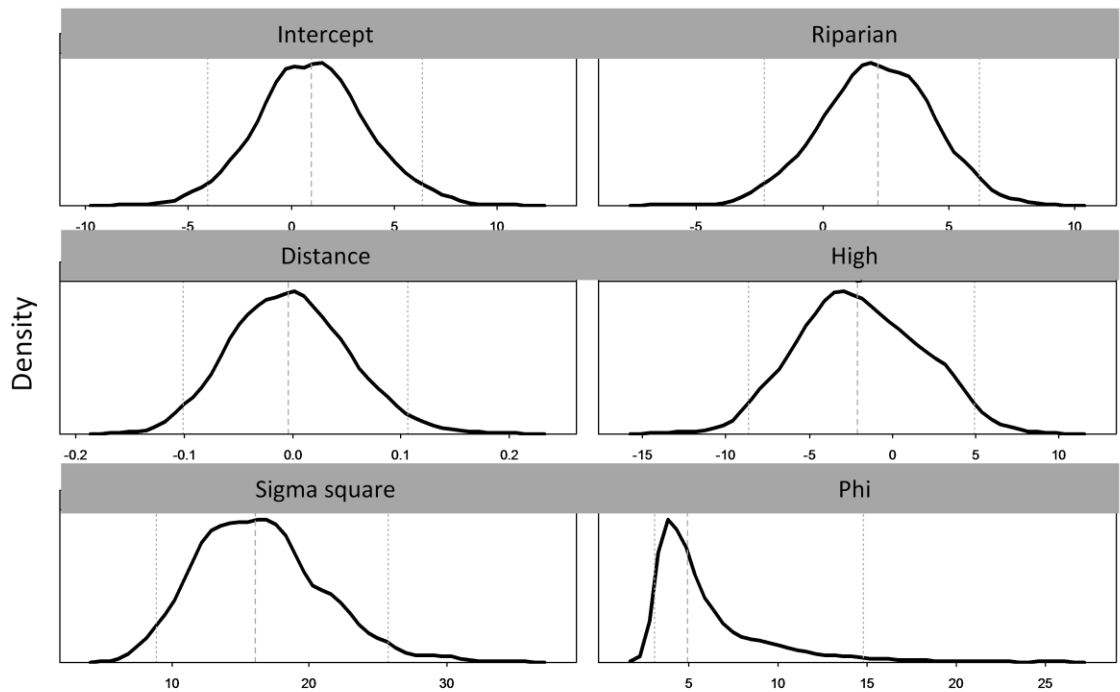
Fig. 2.3. Marginal posterior distributions of WIFL 1 vocalization behavior model parameters: intercept, riparian, distance, high, σ^2, and ϕ.

3. Results

3.1 Radio telemetry

For the 35 Willow Flycatchers (female $n= 13$, male $n =14$, and unknown sex $n =8$) radio-tagged and tracked over the 2002 and 2003 breeding seasons at Fish Creek, the total number of radio telemetry locations per individual ranged from 5-95 with an average of 39.5 locations/bird.

Individual home ranges were found to encompass different combinations and varying proportions of all six habitats (Table 2.3), with riparian and mountain shrub habitat types composing the majority of the home ranges. Home range size varied among individuals and the combined area of home ranges over the 2 years covered 63.4 hectares (Table 2.3). Male flycatcher's home ranges (mean = 2.6 ha, SD = 1.8) were slightly larger on average than female home ranges (mean = 2.2 ha, SD =2.6), however the differences are not statistically significant [$t(25)=0.430$, p = .67 (two-tailed)].

3.2 Individual-level models

Forty-seven individual-level Bayesian generalized linear spatial models were formulated for flycatchers with sample sizes ≥ 24 observations/individual: 24 vocalization and 23 foraging models. Parameter estimates from the individual-level vocalization models show variation across individuals in their sign and magnitude (Fig. 2.4). This, along with the relatively large size of the standard errors of the average individual selection parameter estimates (column 7, Table 2.4) indicates intraspecific variation in the use of habitat types and perch positions by flycatchers for vocalization. The distributions of the mountain shrub and low perch position parameter estimates indicate that the majority of flycatchers do not select mountain shrub habitat or low perch position for vocalization. Overall, the average value of the individual selection parameter estimates ($\hat{\beta}_{il}$) and the median value of the parameter estimates are in concordance (Fig. 2.4 and Table 2.4). The exception is the low perch position variable which has a negative median value but an average individual value just slightly above zero ($\hat{\beta}_{il} = 0.016$). This discrepancy does not impact inference because both the median and average individual low perch position values are essentially zero. The average values of the individual selection parameter estimates suggest that across the population flycatchers select riparian ($\hat{\beta}_{il} = 3.544$) and young riparian ($\hat{\beta}_{il} = 0.506$) habitats and mid ($\hat{\beta}_{il} = 3.183$) and high perch ($\hat{\beta}_{il} = 0.630$) positions for vocalization relative to

mountain shrub habitat ($\hat{\beta}_{il}$ = -1.274) and low perch position ($\hat{\beta}_{il}$ = 0.016). The average

individual selection parameter for distance indicates that the probability of vocalizing decreases

with increasing distance from center of the home range (males) or nest site location (females),

($\hat{\beta}_{il}$ = -0.001). Finer scale patterns emerge when resource selection is broken down by flycatcher

sex (Fig. 2.6). Intraspecfic variation in the use of young riparian habitat for vocalization appears

to be driven by male's, but not female flycatcher's, selection of young riparian habitat. Both

males and females select riparian habitat for vocalization, and female flycatchers show more

variation in their use of low perch positions for vocalizing than males. The average individual

selection distance parameter in the vocalization models is positive for females ($\hat{\beta}_{il}$ = 0.035) but

negative for males ($\hat{\beta}_{il}$ = -0.037).
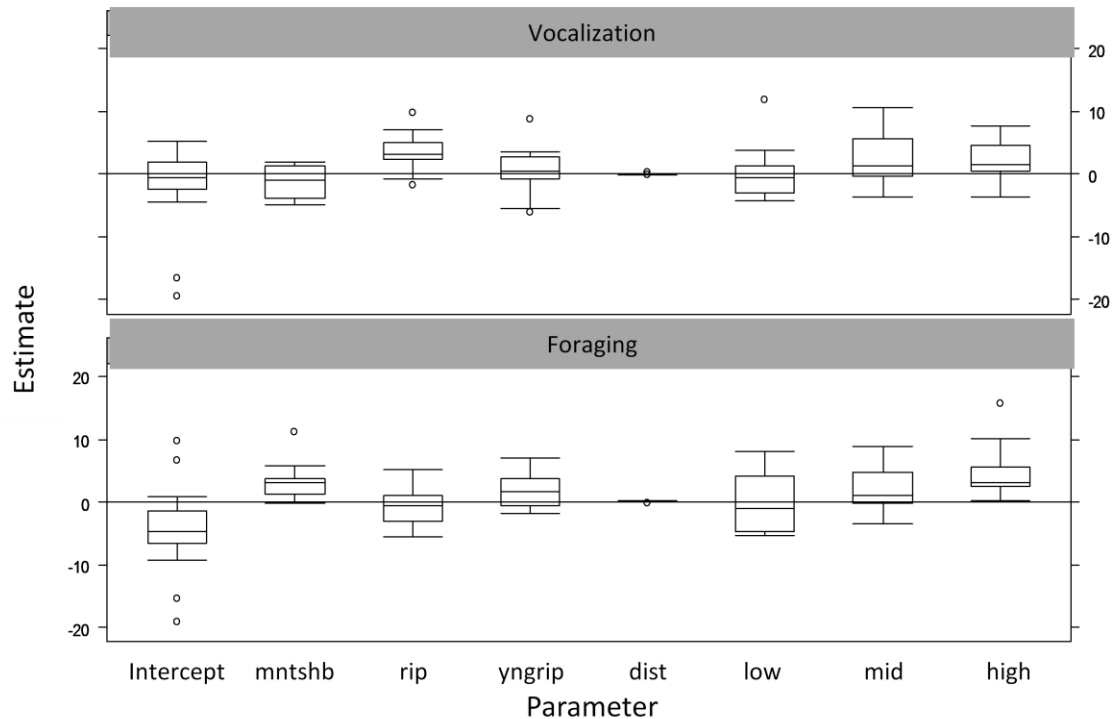
Fig. 2.4. Boxplots of individual parameter estimates for each model covariate (intercept, mountain shrub, riparian, young riparian, distance, low, mid and high) by behavior: vocalization (top panel) and foraging (bottom panel). Boxes indicate first and third quartiles with median shown as a line in the box. Dashed lines extend to ±1.5 times the interquartile range from first and third quartiles. Individual points represent outliers.

Table 2.3. Willow Flycatcher home range habitat availability (proportion of home range) and home range size.

Willow Flycatcher	Bare ground	Forest	Mountain shrub	Riparian	Open water	Young Riparian	Home range size (ha)
1	0	0	0.004	0.863	0	0.134	0.283
2	-	-	-	-	-	-	-
3	0.000	0.000	0.468	0.502	0	0.029	0.204
5	-	-	-	-	-	-	-
6	0.027	0.034	0.089	0.656	0.029	0.166	0.560
7	0	0	0.293	0.366	0.042	0.299	1.202
8	0.003	0.005	0.243	0.452	0.058	0.238	3.489
9	-	-	-	-	-	-	-
10	0.000	0.090	0.192	0.523	0.028	0.166	3.164
11	0.032	0.036	0.148	0.597	0.095	0.091	0.471
12	0	0	0	0.560	0.058	0.382	0.979
13	0.000	0.035	0	0.651	0.029	0.285	1.372
14	0.020	0.253	0.282	0.246	0.037	0.161	2.424
15	-	-	-	-	-	-	-
16	0.008	0	0.246	0.517	0.026	0.203	0.775
17	0.044	0.268	0.398	0.220	0.033	0.038	7.109
18	0.035	0.020	0.573	0.262	0.052	0.057	3.536
19	0	0	0.438	0.390	0.063	0.108	1.344
20	0	0	0.502	0.327	0.078	0.093	1.769
21	0.031	0.119	0.191	0.309	0.134	0.216	0.194
22	0.051	0.132	0.101	0.357	0.099	0.260	1.680
23	0.070	0.062	0.521	0.342	0	0.004	0.738
25	-	-	-	-	-	-	-
26	-	-	-	-	-	-	-
27	0.000	0.033	0.375	0.342	0.055	0.196	4.246
28	0.000	0.065	0.256	0.394	0.059	0.225	3.855
29	-	-	-	-	-	-	-
30	0.005	0.162	0.364	0.253	0.053	0.162	9.429
31	0.010	0.022	0.423	0.311	0.029	0.205	3.020
32	0.042	0	0.521	0.373	0.053	0.011	4.352
33	0.050	0	0.538	0.370	0.041	0.002	3.660
34	-	-	-	-	-	-	-
35	0.054	0.000	0.661	0.124	0.002	0.159	2.565
37	0.104	0.000	0.485	0.247	0.006	0.158	1.004
38	-	-	-	-	-	-	-
Total	0.013	0.265	0.432	0.137	0.051	0.102	63.424

Table 2.4. Population-selection parameter estimates and standard errors.

Covariate	β_l^*	SE	95% HPD interval lower bound	95% HPD interval upper bound	Average value of individual selection parameter estimate	SE of average individual selection parameter estimates
			Vocalization			
Intercept	0.696	0.007	0.289	1.127	-1.562	1.161
Forest	-1.634	0.021	-2.893	-0.458	NA	NA
Mountain shrub	-0.677	0.006	-1.137	-0.224	-1.274	1.584
Riparian	NA	NA	NA	NA	3.544	0.799
Young riparian	-0.531	0.006	-0.917	-0.140	0.506	1.012
Distance	NA	NA	NA	NA	-0.001	0.020
Low	-0.894	0.006	-1.251	-0.524	0.016	1.397
Mid	-0.513	0.006	-0.867	-0.161	3.183	1.900
High	NA	NA	NA	NA	0.630	1.048
			Foraging			
Intercept	-1.300	0.006	-1.678	-0.944	-4.160	1.257
Forest	1.415	0.017	0.277	2.534	NA	NA
Mountain shrub	2.121	0.007	1.663	2.567	3.389	1.027
Riparian	NA	NA	NA	NA	-0.712	1.235
Young riparian	1.408	0.006	1.002	1.817	1.939	0.665
Distance	NA	NA	NA	NA	0.024	0.017
Low	-0.900	0.006	-1.308	-0.484	-0.088	1.524
Mid	-0.542	0.005	-0.911	-0.169	1.826	0.944
High	NA	NA	NA	NA	4.819	1.354

Different patterns in resource selection are inferred from the individual-level foraging

models compared to the individual-vocalization models. The distributions of the individual-level

parameter estimates indicate that many flycatchers select mountain shrub and high perch

positions for foraging (Fig. 2.4). The distribution of riparian and young riparian habitat and low

and mid perch position parameter estimates around zero as well as the relatively large magnitudes

of the standard errors of the average individual selection parameter estimates (column 7, Table

2.4) suggests intraspecific variation in the use of these variables for foraging. The values of the

median and average individual-selection parameters agree across variables (Fig. 2.4 and Table

2.5). The average values of the individual selection parameter estimates suggest that across the

population, flycatchers select mountain shrub ($\hat{\beta}_{il}$ = 3.389) and young riparian habitat ($\hat{\beta}_{il}$ =

1.939) and mid ($\hat{\beta}_{il}$ = 1.826) and high perch ($\hat{\beta}_{il}$ = 4.819) positions for foraging relative to

riparian habitat ($\hat{\beta}_{il}$ = -0.712) and low perch position ($\hat{\beta}_{il}$ = -0.088) variables. The average

individual selection parameter for distance indicates that the probability of foraging increases

with increasing distance from the center of the home range (males) or nest site (females), ($\hat{\beta}_{il}$ =

0.024). Differences in selection patterns for foraging as a function of flycatcher sex also emerge.

Both males and females show intraspecific variation in the selection of mid perch position for

foraging while more females select low perch positions for foraging than males (Fig. 2.7).

Females show greater intraspecific variation in selecting riparian habitat for foraging while males

show greater intraspecific variation in selecting young riparian habitat for foraging. The average

individual selection distance parameter for both males ($\hat{\beta}_{il}$ = 0.028) and females ($\hat{\beta}_{il}$ = 0.021) is

positive.

Summaries of the spatial parameter estimates are displayed in Table 2.5 and Figure 2.5.

The average individual parameter estimates for the spatial decay parameter, ϕ, are similar for

vocalization and foraging (0.371 and 0.319, respectively). These estimates indicate that the

effective ranges of spatial dependency are 13.113m and 14.898m for vocalization and foraging,

respectively. There is individual-level variation in the spatial dependency parameter (Fig. 2.5)

with maximum and minimum spatial dependency estimates of 45.43m and 4.63m for vocalization

and 69.53m and 5.90m for foraging. The average individual spatial dependency for vocalization

and foraging by sex is 13.877m and 20.180m, respectively, for males and 12.349 and 10.056,

respectively, for females.
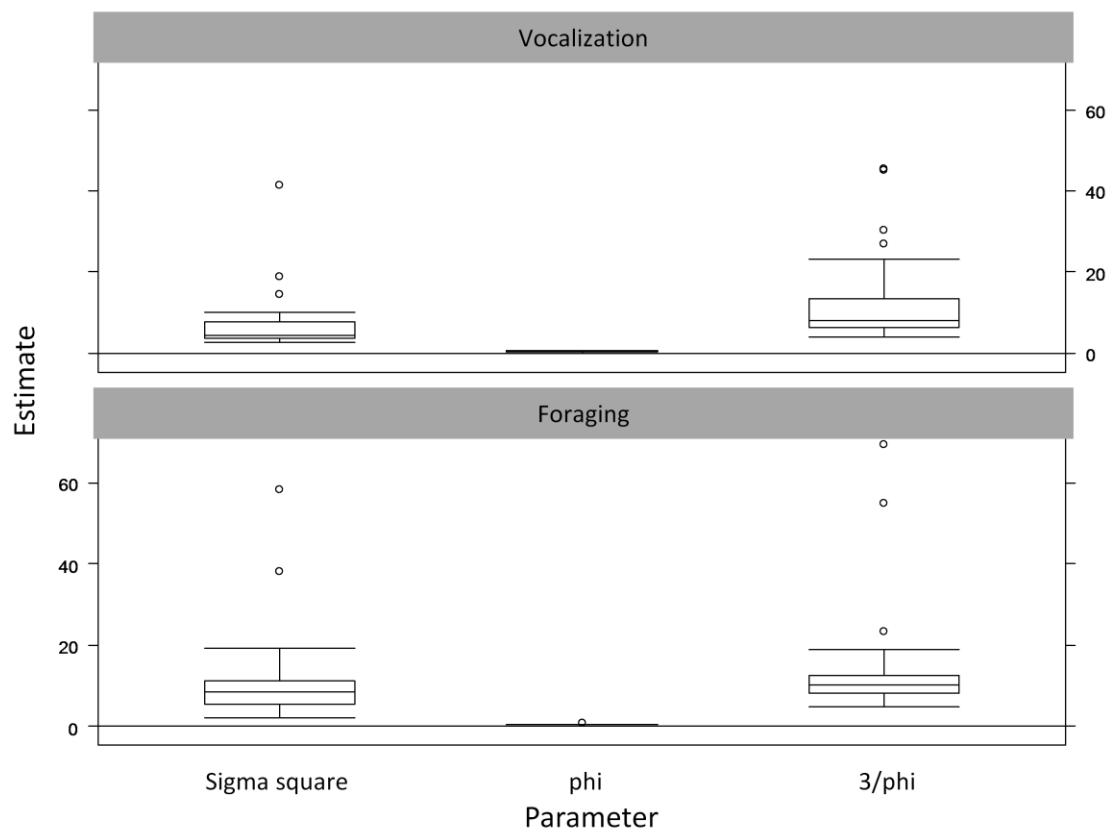
Fig. 2.5. Boxplots of individual parameter estimates for spatial model parameters (σ^2, ϕ, 3/ ϕ) by behavior: vocalization (top panel) and foraging (bottom panel). Boxes indicate first and third quartiles with median shown as a line in the box. Dashed lines extend to ±1.5 times the interquartile range from first and third quartiles. Individual points represent outliers.

3.3 Population-level models

One global population-level model was selected and fit to both the vocalization and foraging data. Riparian habitat and high vegetation perch height position were used as the reference types in the global models; the distance covariate was not included in the population-level models due to a lack of a central location on a population-level (Table 2.5).

The population-selection estimates (β_l^* column 2, Table 2.4) for the covariates in the vocalization model show that alternative habitat types including forest ($\beta_l^* = -1.634$), mountain shrub ($\beta_l^* = -0.677$) and young riparian ($\beta_l^* = -0.531$) habitats are selected less for vocalization by flycatchers relative to riparian habitat, and low ($\beta_l^* = -0.900$) and mid ($\beta_l^* = -0.513$) perch positions are selected less by flycatchers relative to the high perch position. The 95% credible intervals for the forest, mountain shrub, young riparian, low, mid and high covariates do not overlap 0 therefore we can infer that these covariates significantly contributed to the population-level selection model fit.

Table 2.5. Spatial covariate average individual-selection parameter estimates and standard errors.

Spatial Parameter	Average value of individual selection parameter estimate	SE of average individual selection parameter estimates
	Vocalization	
σ^2	7.384	1.681
ϕ	0.371	0.040
$3/\phi$	13.113	2.469
	Foraging	
σ^2	11.755	2.624
ϕ	0.319	0.034
$3/\phi$	14.898	3.289

The population-selection estimates (β_l^* column 2, Table 2.4) for the covariates in the foraging model show that multiple habitat types are selected by flycatchers for foraging and, more specifically, alternative habitat types including forest ($\beta_l^* = 1.415$), mountain shrub ($\beta_l^* = 2.121$) and young riparian ($\beta_l^* = 1.408$) habitats are selected by flycatchers for foraging relative to riparian habitat. Also, low ($\beta_l^* = -0.900$) and mid ($\beta_l^* = -0.542$) perch positions are selected less by flycatchers than the high position for foraging. The 95% credible intervals for the forest, mountain shrub, young riparian, low, mid and high covariates do not overlap 0 therefore we infer that these covariates significantly contributed to the population model's fit.

The population-selection covariate estimates (β_l^* column 2, Table 2.4) and the average individual selection covariate estimates ($\hat{\beta}_{il}$ column 6, Table 2.4) show high accordance overall with some disagreement occurring in coefficient magnitude and sign. More specifically, in the vocalization and foraging model, the population-level coefficient estimate for selection of mid perch position is negative ($\beta_l^* = -0.513$ and -0.542, respectively) while the average individual selection coefficient is positive ($\hat{\beta}_{il} = 3.183$ and 1.826, respectively). Some discrepancy in magnitude and sign between $\hat{\beta}_{il}$ and β_l^* is not surprising given variation in the reference variables used in the individual-level models and differences in model formulations between the individual-level models and the population-level models.

Mean and standard deviation predicted vocalization values vary from 0.16-0.98 and 0.09-0.5 respectively, and mean and standard deviation predicted foraging values vary from 0.02-0.98 and 0.12-0.50 respectively (prediction image examples are presented in the Appendix, Fig. A.2).

4. Discussion

The Bayesian modeling approach presented here is mechanistic based, and provides a powerful approach to analyzing spatially and behaviorally explicit animal resource selection data. In our investigation, we related ecological pattern with process and explored Willow Flycatcher

resource selection to examine not only where vocalization and foraging behavior occurs but why.

In the process, we produced continuous two-dimensional GIS surfaces depicting a flycatcher's

probability of using space for vocalization or foraging throughout its home range. These

selection surfaces can be interpreted as flycatcher behavioral landscapes. In addition, although

Willow Flycatchers are a relatively well studied species, this is the first study to examine spatially

and behaviorally explicit resource selection in the species.

Fig. 2.6. Boxplots of individual parameter vocalization estimates (intercept, mountain shrub, riparian, young riparian, distance, low, mid, high, σ^2, ϕ, $3/\phi$) for male and female Willow Flycatchers. Boxes indicate first and third quartiles with median shown as a line in the box. Dashed lines extend to ±1.5 times the interquartile range from first and third quartiles. Individual points represent outliers.

4.1 Individual and population-level inference

In this study, we observed considerable intraspecific variation in vocalization and

foraging resource selection in Willow Flycatchers, and focused on differences in resource

selection between and among male and female Willow Flycatchers. Intrapopulation differences in habitat selection among male and female Willow Flycatchers were first identified by Sedgwick and Knopf (1992). They found substantial differences between song perch sites used by males and nest sites used by females and speculated that the independent selection of habitats by male and female flycatchers during the breeding season were responsible for these differences. Our study indicates that selection diversity between male and female flycatchers extend to the selection of resources for vocalization and foraging. While both male and female flycatchers appeared to select nesting habitat for vocalizing over non-nesting habitats, male flycatchers experienced greater variation in their selection of habitat types for vocalizing than female flycatchers. Conversely, female flycatchers showed more variation in their selection of habitat position for vocalization.

The images of observed and predicted vocalization behaviors further elucidate differences between male and female flycatchers in their use of space for vocalizing. Male vocalization behavior commonly occurred in tight clusters in the central area of the home range. These spatial vocalization clusters correspond to the male flycatcher's territory or the area of its home range actively defended against conspecifics which likely contains the majority of the individual's song perches. Images of female home range vocalization behavior do not show the same tendencies to vocalize in tight clusters in the center of their home ranges. This pattern finds additional support in the average individual-level distance coefficient which is positive for female flycatchers and negative for male flycatchers. This indicates that, in males, the probability of vocalizing decreases with increasing distance from the center of the home range. The opposite relationship holds true for females in which the probability of vocalizing increases with increasing distance from the nest site.
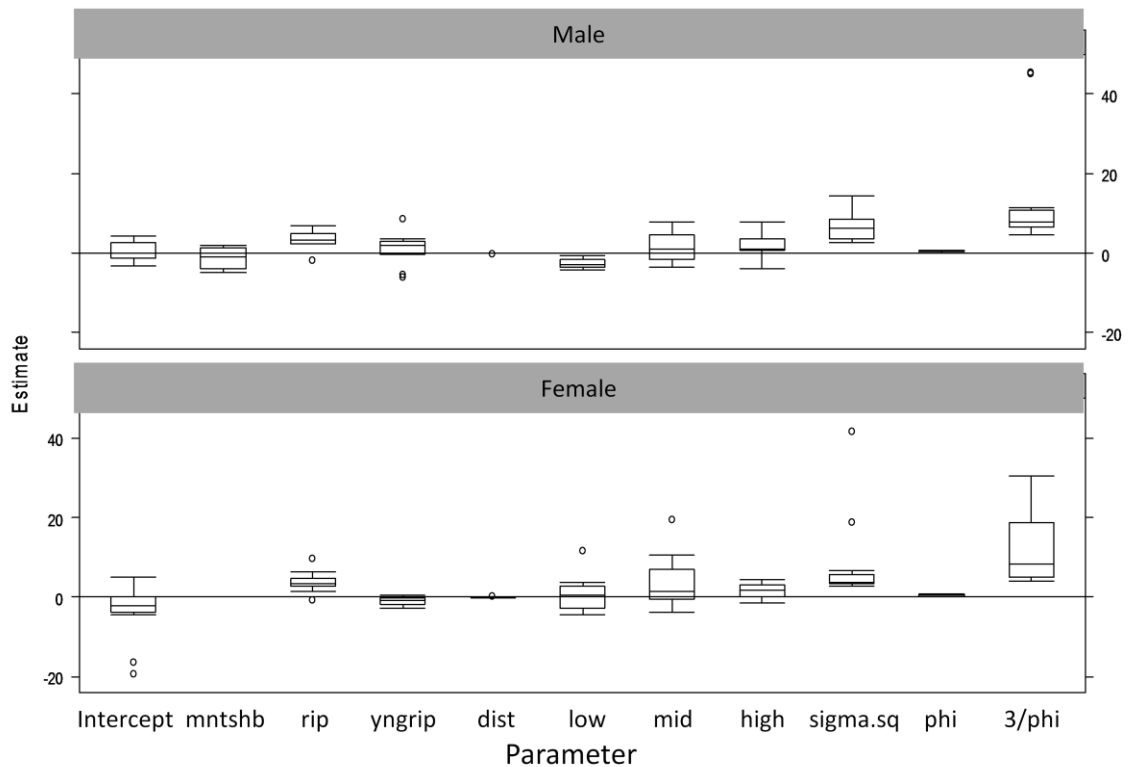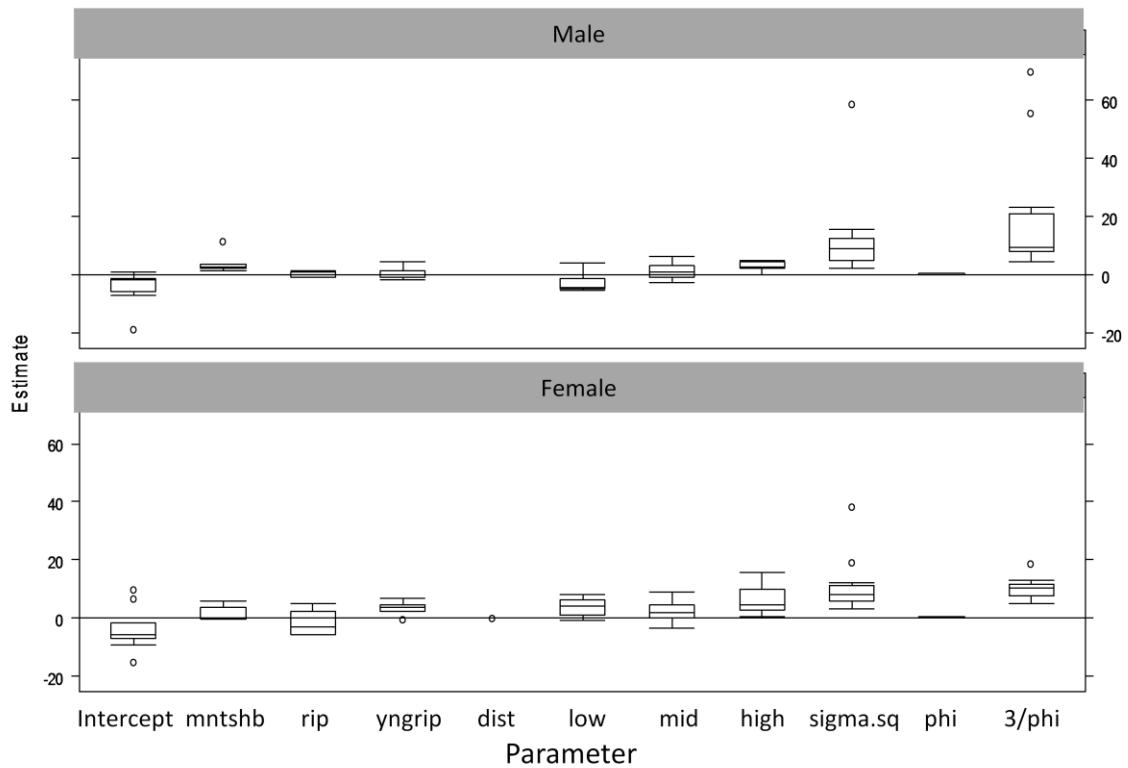
Fig. 2.7. Boxplots of individual parameter foraging estimates (intercept, mountain shrub, riparian, young riparian, distance, low, mid, high, σ^2, ϕ, $3/\phi$) for male and female Willow Flycatchers. Boxes indicate first and third quartiles with median shown as a line in the box. Dashed lines extend to ±1.5 times the interquartile range from first and third quartiles. Individual points represent outliers.

We posit that discrepancies in the role of vocalization in male and female flycatchers can explain the different patterns we observed. Male vocalization commonly occurs in the form of song and is used to establish territory boundaries and attract mates, and male flycatchers typically sing from tall, exposed perches (Sedgwick, 2000). Conversely, female vocalization commonly occurs in the form of a call and is used to maintain social contact with their male mates and as distress signals. To avoid attracting the attention of potential predators during the breeding season, females vocalize from various vegetation positions and are more likely to call at distance away from their nest sites.

We also identified differences between male and females in their foraging behavior. We found evidence that males select higher positions for foraging than females. Akin to our explanation of their vocalization behavior, male's selection of higher habitat positions for foraging may be related to visibility and their requirement to be conspicuous during the breeding season. Alternatively, perch height foraging differences may be the outcome of a resource partitioning or reduced foraging competition mechanism (MacArthur, 1958). Both male and female flycatchers appear to use multiple habitat types for foraging with the models suggesting that they select non-nesting habitats such as mountain shrub and young riparian habitats for foraging. The probability of foraging increased with increasing distance away from either the center of the home range or the nest site in male and female flycatchers, respectively.

The identification and quantification of intraspecific variation in wildlife species such as the Willow Flycatcher is critical for a number of reasons. First, there is growing empirical evidence that males and females of a species interact with and respond to the environment in distinct ways. However, in the majority of bird census and behavioral studies, males are the focal subject as they tend to be more conspicuous. If males and females act independently of one another and have different habitat and resource requirements during the breeding season, then the inference derived from male-centric studies and applied to management and conservation plans that affect the entire species is done so erroneously. We are concerned that singing males have served as the focus of the majority of Willow Flycatcher breeding season habitat and vocalization-based census studies and that the resource needs of female flycatchers have been generally disregarded. In addition, our study suggests that there is considerable variation in the use of habitats for foraging including the use of non-nesting habitats. Since male flycatchers primarily sing in riparian habitat, conservation plans derived from research focused on singing male flycatchers might mistakenly conclude that riparian habitat constitutes the only critical flycatcher habitat. Critical habitats for flycatchers during the breeding season may also include

non-nesting habitats such as mountain shrub and young riparian habitats for foraging in addition to riparian habitat for nesting. Next, the diversity in resource selection measured in this study suggests that researchers need to be careful in selecting appropriate sample sizes for future Willow Flycatcher studies. Understanding the variation in resource selection among individuals is vital given the potential link between intraspecific variation, population-level genetic diversity (Smith et al., 2001) and the potential for animal populations to respond to current and future environmental change.

We infer trends in resource selection at the population-level based on the coefficients derived from the population-level models and the average coefficient values of the individual-level models. In general, inference based on the population-level and average individual-level coefficients are congruent. On a population-level, the flycatchers at Fish Creek showed a tendency to select riparian habitats over other habitat types for vocalization, but they were more diverse in their use of a variety of habitats for foraging. More specifically, the population-level coefficients indicate that flycatchers select mountain shrub habitat relative to riparian and other habitats for foraging. On a population-level, the probability of vocalizing decreased with increasing distance from the center of the home range/nest site and the probability of foraging increased with increasing distance from the center of the home range/nest site.

The use of non-nesting habitats by Willow Flycatchers is evidence that flycatchers may depend upon a more diverse landscape to meet their foraging requirements during the breeding season. Similar patterns suggesting habitat complementation and/or supplementation (Dunning, et al., 1992) have been observed in other species (e.g. Mamo and Bolen, 1999; Tubelis et al., 2004). We posit three reasons why habitat complementation or supplementation may be important to flycatchers at Fish Creek: 1) the availability of food resources may differ in nesting versus non-nesting habitats 2) ease of foraging by flycatchers may vary in nesting versus non-breeding

habitats, and 3) flycatchers may travel distances from their nest sites to forage to avoid attracting predators.

4.2 Home range and core area implications

The images of fitted and predicted vocalization and foraging resource selection provide insight into the spatial aspects of Willow Flycatcher behavior at Fish Creek. Foraging and vocalizing appear as spatially segregated and clustered behavior in many of the images. Fig. A.3 in the Appendix provides an example of an image of fitted vocalization and foraging behavior and the spatial patterns observed in these images confirm the models' results that resource selection is not randomly distributed within the home range. The spatially segregated pattern of space use depicted in the images suggests the existence of two distinct core areas in this individual's home range: one used for foraging and one used for vocalization. The parameters in the spatial process model indicate that foraging behavior has a larger effective spatial range than vocalization behavior which implies that foraging core areas are expected to be larger than vocalization core areas.

We feel that these images can be used to inform our delineation of home range core areas while also providing a more detailed understanding of flycatcher space use behavior. Many studies rely on an arbitrary designation of the core area such as the 50% kernel UD. We argue that the delineation of core areas should not be arbitrary and that a more meaningful core area concept is possible. This could be accomplished by creating images of the fitted probability of a behavior within the home range and identifying the area of the home range with the highest probability of that behavior. Once the core area has been determined, the environmental attributes associated with that region can be identified and compared with the environmental factors comprising the remainder of the home range surrounding the core areas.

4.3 Advantage of the Bayesian framework

The Bayesian approach provides a rigorous framework for modeling animal resource selection. In this study, we formulated resource selection functions as defined by Manly et al. (2002) using hierarchical generalized linear mixed models. The Bayesian approach provides a number of advantages over traditional resource selection modeling approaches. First, the Bayesian framework is flexible and general enough to handle complex problems, and naturally lends itself well to modeling dependent and independent hierarchical relationships among parameters. In animal resource selection, causal relationships are hierarchical, and dependency between the data and the underlying ecological process is intrinsic. Classical generalized linear mixed models can handle hierarchical relationships however model convergence grows increasingly challenging with increasing complexity. Samples of the posterior distribution are derived from conditional probability model statements which is fairly straightforward using random walk MCMC algorithms.

In classical modeling approaches, $\mathbf{X}$ is treated as a constant and $\mathbf{\beta}$ as fixed but unknown. In our Bayesian model, the covariates, parameters and sources of uncertainty are specified using probability statements; we argue that this is a more natural way to think about the factors that influence animal resource selection. For example, in the population-level model, intraspecific uncertainty in vocalization and foraging selection was modeled through the bird-level parameter, $\mathbf{\beta}_{il} \sim \mathrm{N}\left(\mathbf{\beta}_l^*, \sigma_l^2\right)$. Additional sources of uncertainty in our models include the effect of sex or age on resource selection. We did not formulate our models to include sex or age effects however the next generation of flycatcher resource selection population models could feasibly include these additional parameters using prior distributions informed by this and other flycatcher resource studies.

In resource selection studies that compare resource use with availability, the estimate of resource availability is subjective (Erickson et al., 2001; Jones, 2001). In addition, availability is

often assumed to be constant and known although this is rarely the case (Johnson, 1980; Arthur et al., 1996), and researchers often measure availability at temporal and spatial scales congruent with the study and not at scales biologically relevant to the organism (Aebischer et al., 1993; Gates and Evans, 1998). Further, the method used to measure resource availability can have drastic impacts on the study's inference concerning resource selection (Johnson, 1980; Porter and Church, 1987). In nature, resource availability undergoes constant fluctuations that may be better represented as a probabilistic function in a Bayesian framework than a constant and known quantity.

4.4 Alternative modeling approaches

A number of other modeling approaches provide alternative means of analyzing the relationship among behavior, resource selection and space use including discrete choice models (McCracken et al., 1998, Cooper and Millspaugh, 1999, 2001) and resource utilization functions (Marzluff et al., 2001, 2004). Both approaches are easily implemented in a Bayesian framework (e.g. Thomas et al., 2006). Discrete choice models analyze resource selection by measuring the satisfaction acquired by selecting among resources. Their strength lies in their capacity to support fluctuations in resource availability and utility which may better reflect natural situations. Thomas et al. (2006) introduced a Bayesian random effects discrete-choice model for resource selection and applied it to the analysis of caribou resource selection. Also, discrete-choice models can support non-continuous response data structures such as binary or count responses. Resource utilization functions use multiple regression techniques to associate a probabilistic measure of use, as defined by the utilization distribution, with a set of resource variables. In the context of a behavioral analysis, a Bayesian behavioral RUF would require the calculation of behaviorally specific UDs which would then be overlaid on resource maps. The RUF approach uses a continuous measure of probabilistic behavioral use as the response which fits naturally with the Bayesian way of thinking.

4.5 Model limitations and future directions

Only ecologically relevant independent variables were included in the formulation of our Bayesian resource selection functions. However, other ecologically relevant variables exist that may influence flycatcher foraging and vocalizing behavior. Model performance is expected to improve with the inclusion of additional ecologically relevant covariates. Further, the Bayesian framework enables the inclusion of information acquired from other Willow Flycatcher studies and our current models could be updated to include information from previous and future studies. As new models are formulated through the inclusion of new information and additional parameters, model comparison and selection can be conducted using deviance information criterion (DIC), the Bayesian equivalent of Akaike Information Criterion (AIC). The models we have currently formulated do not provide the final word in Willow Flycatcher vocalization and foraging behavior at Fish Creek and should be amended as more information becomes available.

The use of the posterior distribution for producing a posterior predictive distribution has been introduced here. The predictive power of the current set of models outside of Fish Creek is unknown, and due to the small sample sizes of our data, model validation was conducted by through visual inspection. In the future, the models should be validated using subsets of the current Fish Creek flycatcher dataset or using alternative Willow Flycatcher datasets.

References

Aebischer, N.J., Robertson, P.A., Kenward, R.E., 1993. Compositional analysis of habitat use from animal radio tracking data. Ecology 74, 1313-1325.

Arthur, S.M., Manly, B.F.J., McDonald, L.L., Garner, G.W., 1996. Assessing habitat selection when availability changes. Ecology 77, 215-227.

Banerjee, S., Carlin, B.P., Gelfand, A.E., 2004. Hierarchical Modeling and Analysis for Spatial Data. Boca Raton, Chapman and Hall/CRC Press, 472 pp.

Burt, W.H., 1943. Territoriality and home range concepts as applied to mammals. J. Mammal. 24: 346-352.

Cooper, A.B., Millspaugh, J.J., 1999. The application of discrete choice models to wildlife resource selection studies. Ecology 80, 566-575.

Cooper, A.B., Millspaugh, J.J., 2001. Accounting for variation in resource availability and animal behavior in resource selection studies. In: Millspaugh, J.J, Marzluff, J.M. (Eds.), Radio Tracking and Animal Populations. Academic Press, San Diego, USA, pp. 243-273.

Cressie, N. A., 1993. Statistics for Spatial Data., revised ed. Wiley, New York, USA, 928 pp.

Diggle, P. J., Ribeiro, Jr., P.J., 2007. Model-based Geostatistics. Springer, New York, USA, 230 pp.

Dunning, J.B., Danielson, B.J., Pulliam, H.R., 1992. Ecological processes that affect populations in complex landscapes. Oikos 65, 169-175.

Erickson, W. P., McDonald, T. L., Gerow, K. G., Howlin, S., Kern, J. W., 2001. Statistical issues in resource selection studies with radio marked animals. In: Millspaugh, J., Marzluff, J. M. (Eds.), Radio Tracking and Animal Populations. Academic Press, San Diego, USA, pp. 209-242.

Finley, A.O., Banerjee, S., Carlin, B.P., 2009. Package 'spBayes': univariate and multivariate spatial modeling. Accessed from http://blue.for.msu.edu/software on May 10, 2009.

Finley, A.O., Baerjee, S., McRoberts, R.E., 2008. A Bayesian approach to multi-source forest area estimation. Environ Ecol Stat. 15, 241-258.

Gates, J. E., Evans, D.R., 1998. Cowbirds breeding in the central Appalachians: spatial and temporal patterns and habitat selection. Ecol. Appl. 8, 27-40.

Gelman, A., Carlin, J.B., Stern, H.S., Rubin, D.B., 2004. Bayesian Data Analysis. Chapman & Hall, Boca Raton, USA, 696 pp.

Hadfield, J.D., 2009. MCMC methods for multi-response generalised linear mixed models: the MCMCglmm R package. Accessed from http://cran.r-project.org/ on May 8, 2009.

Hayne, D.W., 1949. Calculation of size of home range. J. Mammal. 30, 1-18.

Hooge, P.N., Eichenlaub, B., 1997. Animal movement extension to Arcview: version 1.1. Alaska Biological Science Center, U.S. Geological Survey, Anchorage, AK, USA.

Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61, 65-71.

Jones, J., 2001. Habitat selection studies in avian ecology: a critical review. The Auk 118, 557-562.

Krebs, J. R., 1978. Optimal foraging: decision rules for predators. In: Krebs, R., Davis, N. B. (Eds.), Behavioral Ecology: an Evolutionary Approach. Blackwell Scientific, London, UK, pp. 23-63.

Laver, P. N., Kelly, M. J., 2008. A critical review of home range studies. J. Wildl. Manage. 72, 290-298.

Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., Schabenberger, O., 2006. SAS for Mixed Models, 2nd ed. SAS Publishing, Cary, N.C, USA, 840 pp.

Lima S.L., Zollner, P.A., 1996. Towards a behavioral ecology of ecological landscapes. Trends Ecol. Evol. 11, 131-135.

MacArthur, R.H., 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39, 599-619.

Mamo, L.B., Bolen, E.G., 1999. Effects of area, isolation, and landscape on the avifauna of Carolina bays. J. Field Ornithol. 70, 310-320.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., Erickson, W.P., 2002. Resource selection by animals: statistical design and analysis for field Studies, 2nd ed. Kluwer Academic Publishers, The Netherlands, 240 pp.

Marzluff, J.M., Knick, S.T., Millspaugh, J.J., 2001. High-tech behavioral ecology: modeling the distribution of animal activities to better understand wildlife space use and resource selection. In: Millspaugh, J., Marzluff, J. M. (Eds.), Radio Tracking and Animal Populations. Academic Press, San Diego, USA, pp. 310-326.

Marzluff, J.M., Millspaugh, J.J., Hurvitz, P., Handcock, M.S., 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's Jays. Ecology 85, 1411-1427.

McCabe, R. A., 1991. The Little Green Bird: Ecology of the Willow Flycatcher. Rusty Rock Press, Madison, WI, USA, 171 pp.

McCracken, M.L., Manly, B.F.J., Vander Heyden, M., 1998. The use of discrete-choice models for evaluating resource selection. J. Agr. Biol. Envir. St. 3, 268-279.

Neu, C.W., Byers, C.R., Peek, J.M., 1974. A technique for analysis of utilization availability data. J. Wildl. Manage. 38, 541-545.

Orians, G. H., Pearson, N. E., 1979. On the theory of central-place foraging. In: Horn, D. J., Mitchell, R. D., Stairs, G. R. (Eds.). Analysis of Ecological Systems. Ohio State University Press, Columbus, USA, pp. 155-177.

Paxton E. H., Cardinal, S. N., Koronkiewicz, T. J., 2003. Using radiotelemetry to determine home range size, habitat use, and movement patterns of Willow Flycatchers. Studies in Avian Biology 26, 185-189.

Plummer, M., Best, N., Cowles, K., Vines, K., 2009. coda: output analysis and diagnostics for MCMC. Accessed from http://cran.r-project.org/ on May 10, 2009.

Porter, W.E., Church, K.E., 1987. Effects of environmental pattern on habitat preference analysis. J. Wildl. Manage. 64, 11-23.

Pyle, P., 1997. Identification guide to North American birds-part 1. Slate Creek Press, Bolinas, CA, USA, 732 pp.

Seaman, D.E., Millspaugh, J.J., Kernohan, B.J., Brundige, G.C., Raedeke, K.J., Gitzen, R.A., 1999. Effects of sample size on kernel home range estimates. J. Wildl. Manage. 63, 739-747.

Sedgwick, J.A., 2000. Willow Flycatcher (Empidonax traillii). In: Poole, A. (Eds.), The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, USA. Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/533doi:10.2173/bna.533

Sedgwick, J. A., Knopf, F. L., 1992. Describing Willow Flycatcher habitats: scale perspectives and gender differences. Condor 94, 720–733.

Smith, T. B., Kark, S., Schneider, C. J., Wayne, R. K., Moritz, C., 2001. Biodiversity hotspots and beyond: the need for preserving environmental transitions. Trends Ecol. Evol. 16, 431.

Sogge, M. K., J. C . Owen, E. H. Paxton, S.M. Langridge, T.J. Koronkiewicz., 2001. A targeted mist net capture technique for the Willow Flycatcher. Western Birds 32: 167-172.

Stephens, D. W., Krebs, J. R., 1986. Princeton University Press, Princeton, NJ, USA, 262 pp.

Thomas, D.L., Johnson, D., Griffith, B., 2006. A Bayesian random effects discrete-choice model for resource selection: population-level selection inference. J. Wildl. Manage. 70, 404-412.

Tubelis, D.P., Cowling,A., Donnelly, C., 2004. Landscape supplementation in adjacent savannas and implications for the design of corridors for forest birds in central Cerrado, Brazil. Biol. Conserv. 118, 353-364.

CHAPTER 3

THE CONTRIBUTION OF AQUATIC AND TERRESTRIAL INSECTS TO THE DIET OF

THE WILLOW FLYCATCHER REVEALED BY CARBON AND NITROGEN STABLE

ISOTOPES AND FECAL SAMPLE DISSECTION

ABSTRACT

Willow Flycatchers are an insectivorous, riparian obligated nesting species. Aquatic insects may be an essential component of the Willow Flycatcher diet during the breeding season. We investigated the contribution of aquatic and terrestrial insects to the diet of adult and nestling Willow Flycatchers over the course of two breeding seasons at Fish Creek, Utah using ^{13}C and ^{15}N stable isotopes and fecal sample analysis. Stable isotope analysis detected differences in δ^{13}C but not δ^{15}N signatures between aquatic and terrestrial insects at Fish Creek. The terrestrial insect isotope signature was more enriched in δ^{13}C than the aquatic insect isotope signature. Aquatic insects were found to comprise approximately 1/3 of the diet of adult Willow Flycatchers and 13% of the diet of hatch year birds. Significant differences were found in δ^{13}C between adult and hatch year flycatcher feathers and hatch year flycatcher feathers were more depleted in ^{13}C than adult feathers. Hymenoptera and coleoptera were the most abundant and frequently occurring arthropod orders in the fecal samples. Our study indicates that aquatic insects are an important component of the diet of the Willow Flycatcher at Fish Creek. In addition, adult flycatchers were found to consume a different diet to that which they feed their nestlings at Fish Creek and we discuss potential reasons for this pattern.

Prey subsidies (*sensu* Polis et al. 1997) move from more to less productive habitats, and can provide essential energy for animal consumers inhabiting areas of low productivity (Bustamante et al. 1995, Polis and Hurd 1996). Many such resource exchanges have been

identified in the zone where streams and terrestrial riparian habitats intersect. One such example, the movement of terrestrial insects and leaf fall from the terrestrial to the aquatic environment, has long been recognized as an important source of energy to fish in aquatic environments (Cummins et al. 1973, Vannote et al. 1980, Mason and MacDonald 1982). Less focus has been directed on the opposite flow of energy from the aquatic to the terrestrial environment. Yet, more and more evidence points to the importance of aquatic derived food resources to riparian consumers including spiders (Polis and Hurd, 1995, Sanzone et al. 2003, Kato et al. 2003), lizards (Sabo and Power 2002a,b), birds (Gray 1989, 1993; Nakano and Murakami 2001; Murakami and Nakano 2002), and mammals (Strapp and Polis 2003, Fukui et al. 2006).

The flow of aquatic insect subsidies into adjacent upland habitats may be especially important in arid and semi-arid regions. For example, in Jackson and Fisher's (1986) seminal work, they observed that 97% of the insects originating in a Sonoran desert stream were exported to terrestrial predators within the riparian food web.   In the western United States, riparian habitats often support higher densities and greater diversities of animal consumers than adjacent upland habitats (Stamp 1978, Jackson and Fisher 1986, Sanzone et al. 2003). This trend may be partly due to the emergence of aquatic insects which compliment terrestrial arthropod production thereby expanding the food base available to terrestrial predators.

Although most studies investigating the contribution of food subsidies to the diets of birds have relied on observation of foraging events and identification of individual insect prey items (e.g. Gray 1993, Nakano and Murakami 2001), stable isotopes have been used to measure energy flows from aquatic systems to consumers in riparian habitats such as spiders (Sanzone et al. 2003, Akamatsu et al. 2004, Paetzold et al. 2005), and beetles and ants (Paetzold et al. 2005). The natural abundances of isotope ratios such as carbon (C) and nitrogen (N) have been used to trace the dietary origin of assimilated energy for various passerine bird species residing in tropical rain forests (Herrera et al. 2003), terrestrial deserts (Wolf and del Rio 2003), and marine (Sabat and Martinez

del Rio 2005, Sabat et al. 2006) systems but has yet to be used, to our knowledge, to track energy assimilation in birds in temperate riparian systems.

In this study, we investigate the contribution of aquatic versus terrestrial insects to the diet of the Willow Flycatcher, *Empidonax traillii adastus*, using carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotope values of body feathers from adult and hatch year flycatchers. The Willow Flycatcher is a neotropical migrant that breeds in riparian areas throughout the continental United States, and requires riparian habitats bordering open water for nest site selection. In the intermountain west of the United States, riparian habitats used by Willow Flycatchers are found largely in arid or semi-arid regions. Insects immigrating into the riparian zone from adjacent aquatic habitats may therefore be an essential component of the Willow Flycatcher diet.

Previous work has alluded to the reliance of Willow Flycatchers breeding in non-native, salt cedar dominated habitats on prey subsidies derived from native habitats. Nesting habitat of the Southwestern Willow Flycatcher (*E. t. extimus*), historically dominated by willow (*Salix* spp.) and cottonwood (*Populus* spp.), has largely been replaced by stands of the exotic salt cedar in the Southwestern U.S. Studies have found that although salt cedar (*Tamarix* spp.) dominated riparian habitats are used successfully for nesting, insect prey production in exotic habitats may be insufficient to support breeding flycatchers (DeLoach et al. 2000, DeLay et al. 2002, Wiesenborn and Heydon 2007). Other studies have identified few differences in the Willow Flycatcher diet as a function of native versus non-native habitat and hence concluded that Willow Flycatchers are generalist foragers (Durst et al. 2008). A common pattern across all previous Willow Flycatcher diet studies is that adult Willow Flycatchers consume a distinctive diet from the one they feed to their nestlings. Conversely, some studies have identified differences in diet between male and female adult Willow Flycatchers (Drost et al. 2003) while others have not (Durst et al. 2008). Hence, some debate still remains as to much of a generalist versus specialist forager the Willow

Flycatcher actually is. In addition, it is unknown if diet patterns identified in *E.t. extimus* are common to other subspecies.

In this paper, we investigate energy movement in the form of prey subsidies from the aquatic to the terrestrial environment by measuring Willow Flycatcher's use of aquatic versus terrestrial insects. We use stable isotopes to establish distinct carbon (δ^{13}C) and nitrogen (δ^{15}N) signatures for the aquatic and terrestrial environments. In addition, fecal samples were collected opportunistically from adult and nestling flycatchers. We conduct a fecal sample analysis to corroborate findings from our stable isotope analysis and to compare the diet of the Willow Flycatchers in this study with the diets of Willow Flycatchers from other studies. Our three primary objectives are to: 1) determine the ratio of aquatic versus terrestrial insects utilized by Willow Flycatchers, 2) investigate differences in flycatcher diet as a function of sex and age, and 3) compare and contrast the diet of Willow Flycatchers from Fish Creek with the diet of flycatchers from other locations to ascertain the use of aquatic insects by Willow Flycatchers across studies.

Methods

Field site.-This study was conducted along a three- mile stretch of Fish Creek located east of the inflow to Scofield Reservoir in the Manti-La Sal National Forest in north central, Utah (39°77' N, 111°20' W) during the 2003-2005 breeding season (late May-early August). The Fish Creek drainage is composed of a variety of habitats including mature and young riparian habitat, mountain shrub steppe, upland forest, open water and bare ground. Mature and young riparian habitats are both composed primarily of willow (*Salix* spp.) differing in the ages and heights of the willow canopy. We classified areas composed of willows < 50% canopy cover and <1 meter height as young riparian habitat. At Fish Creek, mature riparian habitat is comprised of willow dominated vegetation with ≥ 50% canopy cover and occurs in discrete patches typically separated by areas of open water, bare ground, or young riparian habitat. Mountain shrub steppe habitat at Fish Creek is

found on south facing aspects and contains a diverse community of native and introduced grasses, forbes including yarrow and larkspur, and shrubs such as big sagebrush (*Artemisia tridentate* sp.), Utah serviceberry (*Amelanchier utahensis*), chokecherry (*Prunus virginiana*), and mountain snowberry (*Symphoricarpos oreophilus*). North facing aspects support mixed-conifer and aspen forests dominated by Englemann's spruce (*Picea engelmanni*), White fir (*Abies concolor*), Douglas fir (*Pseudotsuga menziesii*), and Quaking aspen (*Populus tremuloides*) species.

   Stable isotopes.-Feather samples were collected opportunistically from May 26-August 15 during the banding process over the 2004 and 2005 breeding seasons. While the bird was in hand, we pulled approximately ten lower breast area body feathers. Studies of molting patterns have found that Willow Flycatchers molt their flight feathers on their wintering grounds (Pyle 1997) however there is considerable variation in the timing of their definitive basic body molt which can occur any time from August thru November. At Fish Creek, we observed body molt in territorial adults starting in late July/early August. For this reason, we used adult body feathers for stable isotope analysis rather than tail feathers since the latter reflects flycatcher diet on their wintering grounds. We limited our sampling of feathers in 2004 from Willow Flycatchers known to breed at Fish Creek in 2003. Body feathers were sampled from nestlings starting at ten days of age to minimize the amount of feather sheath on feather samples. Feathers were selected over other body tissues such as blood or claw to minimize the stress of the sampling procedure on the birds, and because there is a wider breath of published material concerning feather than claw stable isotope analyses.

   Insect sampling was conducted in 2004 and 2005 at Fish Creek using Malaise traps. Ten malaise traps were placed along Fish Creek in a variety of habitats to capture the diversity of insect species present. Malaise traps were checked and emptied once per week, and samples were stored in 70% ethanol. Arthropods for stable isotope analysis were randomly selected from malaise trap samples across the breeding season so that the entire breeding season was evenly

sampled. We randomly selected approximately 1000 insects from Malaise samples and identified them to the lowest taxonomic level possible. In addition, insects were categorized as either aquatic or terrestrial based on life cycle. This categorization was not perfect due to variation in the lifecycle of aquatic and semi-aquatic insects. We made every attempt possible to only select those insects that could be considered terrestrial or aquatic obligates to use in stable isotope analysis for determining aquatic and terrestrial insect stable isotope signatures. We obtained fewer obligate aquatic insects from our Malaise traps than obligate terrestrial insects and therefore included all sampled aquatic adult insects in the stable isotope analysis. We randomly selected terrestrial insects to include in our stable isotope analysis from the total number of terrestrial insects identified from our malaise samples.

Feathers and insects were cleaned of dirt and surface oils using repeated washings of a 2:1 chloroform:methanol solution and then air-dried for 24 hours in a fume hood. Previous studies have found that storing arthropod samples in ethanol has little impact on ^{15}N and ^{13}C values (Sarakinos et al. 2002, Syväranta et al. 2008). Nitrogen and carbon isotopes in feather and insect samples were analyzed via continuous-flow isotope ratio mass spectrometry by the Utah State University Isotope laboratory. A 0.1-0.2 mg sample of feather was encapsulated in tin and analyzed with a Europa Scientific SL-2020 system. Analytical precision over all sample runs was better than 0.1‰ for both ^{15}N and ^{13}C. Our stable isotope results are presented in δ notation (δ^{15}N and δ^{13}C) as the deviation from parts per thousand (‰).

Within trophic group differences in δ^{15}N and δ^{13}C signatures (e.g. aquatic versus terrestrial insects, and adult male versus adult female versus nestling flycatchers) were examined using analysis of variance and Welch's *t*-tests assuming unequal variances. All statistical tests were conducted in program R (R Development Core Team 2010). We used a two-source Bayesian mixing model (Parnell and Jackson 2010) to determine the relative contribution of aquatic and terrestrial insects to the flycatcher diet over the 2004 and 2005 breeding seasons. In

contrast to traditional mixing models, Parnell and Jackson's (2010) model allows for variation in isotopic discrimination between prey items and consumer which more accurately reflects changes in stable isotope ratios across trophic levels. The prior distribution of the proportion of aquatic and terrestrial insects contributed to the flycatcher diet was assumed to follow a Dirichlet distribution. Other sources of variation in the Bayesian mixing model include the isotopic value of prey items, the isotopic fractionation value between prey source and consumer and an overall residual error term received normal distributions as priors (see Parnell and Jackson 2010). The model also includes a measure of elemental concentration of carbon in prey sources that was acquired via mass spectrometry.

Laboratory studies of isotopic discrimination between prey source and avian consumers have found that isotopic discrimination values are higher than traditionally assumed (Pearson et al. 2003, Hobson and Bairlein 2003). Negligible $\delta^{13}C$ discrimination factors were historically assumed along the lines of 0‰ to 1‰. In their study of carbon isotope fractionation in Yellow-rumped Warblers, Pearson et al. (2003) observed $\delta^{13}C$ changes of 1.9 to 4.3‰ ± 0.1 depending on tissue when Warblers were fed a diet comprised of 97% mealworms. Hobson and Bairlein (2003) measured $\delta^{13}C$ discrimination factors of +2.7‰ in Garden Warblers fed a diet of mealworms. We used a $\delta^{13}C$ discrimination factor of 2.0 ± 0.1 between insect prey and flycatcher feathers in our Bayesian mixing-models based on these study's findings. This fractionation value is on the lower end of the ranges from the studies of Pearson et al. (2003) and Hobson and Bairlein (2003) because we assume the flycatcher diet is more heterogeneous than the mealworm diet fed to the study animals.

Diet analysis.-Fecal samples were obtained opportunistically from flycatchers during mist-netting and banding throughout the 2003, 2004, and 2005 breeding seasons from approximately May 26-August 15. Willow Flycatchers were randomly selected for capture and radio tracking following territory establishment (n ~ 50). Birds were captured using target

(Sogge et al. 2001) and passive mist-netting techniques. Following capture, birds were sexed and weighed, and banded with a red anodized Federal bird band on one leg and an individualized color aluminum band on the other leg. Flycatchers would often deposit fecal samples either in bird banding bags or on the hand of the bander. Nestling fecal samples were obtained from nestlings aged 7-10 days when nestlings were banded with a red anodized Federal bird band on their right leg.

Fecal sample dissection has been used in Willow Flycatcher studies to reconstruct diet (Wiesenborn and Heydon 2007, Durst et al. 2008). The collection of fecal samples is a less invasive technique for sampling diet than using emetics for regurgitation of stomach contents. Studies have found strong taxonomic correlation between prey items identified through fecal sample dissection and stomach regurgitation. Some bias may be introduced in diet reconstruction with fecal samples due to the under-detection of soft bodied insects (Ralph et al. 1985, Jenni et al. 1990). In addition, stomach regurgitation samples have been found to contain a larger number of prey items on average per sample than fecal samples suggesting that a larger number of fecal samples than regurgitation samples must be acquired for accurate diet reconstruction (Poulin and Lefebvre 1995, Carlisle and Holberton 2006).

Fecal samples were stored individually in 70% ethanol in 10 ml vials. We used a Leica MZ75 with the addition of a Lumina dual light source and a Jenoptik 3.3MP Cooled CCD Firewire Color digital camera with ProgRes Capture Pro 2.5 and Auto-Montage to create 3D photographs of arthropod fragments for analyzing and identifying sample components. References used to assist in identification included Burger et al. (1999) as well as professional entomologist expertise. Insects were identified to as fine of a taxonomic scale as possible but given the variation in the scale of taxonomic identification among arthropod components, statistical and descriptive analysis was conducted at the order-level. Individual insects per sample were identified by using distinct insect characteristics such as antennae, paired fangs, a set of

wings, mandibles, or head capsules. All fecal sample sorting and identification was conducted by a single technician with unlabeled samples.

Fecal samples were separated into two categories: adult and nestlings, but combined across years and across sexes due to small samples sizes. Flycatcher diet was reconstructed by calculating the abundance, frequency and occurrence of the nine major prey types by flycatcher age group. Prey type frequency was quantified as the total number of items of prey type *X* in sample *Y* divided by the total number of prey items in sample *Y*. Occurrence was defined as the proportion of all fecal samples containing prey type *X* (Rosenberg and Cooper 1990, Durst et al. 2008). Frequency measures proportional abundance of prey type *X* while occurrence is a measure of the incidence of prey type *X* across all fecal samples. In combination, frequency and occurrence provides a balanced measure of the diet composition of the sampled population during the sampling period (Durst et al. 2008).

We compared breeding season diet overlap across eight Willow Flycatcher diet studies including: Beal (1912; *n* = 135), Prescott and Middleton (1988, *n* = 7+), DeLay et al. (2002, *n* = 23), Drost et al. (2003, *n* = 50), Wiesenborn and Heydon (2007, *n*= 56), and Durst et al. (2008, *n* = 341). We quantified diet overlap among studies using Pianka's index (Krebs 1994):

$$O_{jk} = \frac{\sum_i^n P_{ij} P_{ik}}{\sqrt{\sum_i^n P_{ij}^2 \sum_i^n P_{ik}^2}}, \tag{1}$$

where P_{ij} is the frequency of prey item i at study site j and P_{ik} is the frequency of prey item i at study site k. Pianka's index measures the percent overlap in diet between sites j and k at the taxonomic level of order. Pianka's index ranges from 0 to 1 with higher values indicating greater degrees of dietary overlap. We used the pgirmess package in program R (available at http://cran.r-project.org/) to estimate Pianka's index.

RESULTS

Stable isotopes.-Over the 2003, 2004, and 2005 breeding seasons at Fish Creek, we

collected feathers from 31 hatch year and 32 adult Willow Flycatchers. Carbon isotopes values

varied more widely among feathers from male than female or hatch year flycatchers (Table 3.1,

Fig. 3.1). δ^{13}C feather values were not found to be influenced by the interaction of year and

flycatcher age ($F_{2,61} = 1.32$, $P = .28$). After applying a Tukey's honest significant differences

test, we identified significant differences in δ^{13}C signatures between adult and hatch year feathers

($P<.0001$). In contrast, δ^{13}C signatures did not differ between male and female flycatchers ($P =$

.60). Hatch year flycatcher feathers, on average, were more ^{13}C depleted than adult flycatcher

feathers.

The feathers from hatch year flycatchers showed less variation in their δ^{15}N signatures

than the feathers from male and female flycatchers, and on average the hatch year feathers were

more depleted in ^{15}N than the adult flycatcher feathers (Table 3.1, Fig. 3.1). No interaction effect

was found between year and age in δ^{15}N signatures. Tukey multiple comparison tests indicated

differences between male and hatch year δ^{15}N signatures ($P < .001$) but no differences in δ^{15}N

values were detected between female and hatch year flycatchers.

δ^{13}C values ranged wider in aquatic insects than in terrestrial insects (Table 3.1, Fig. 3.1).

The opposite was true of δ^{15}N values where greater variation was observed in terrestrial insects

than aquatic insects. An interaction effect between year and prey type was found for δ^{13}C values

($F_{2,135} = 3.91$, $P = .05$) but not for δ^{15}N values. In further exploration, the interaction effect was

due to a decrease in the aquatic insect's mean δ^{13}C value from 2004 to 2005. However, the

difference in mean aquatic insect δ^{13}C value between 2004 and 2005 was not found to be

significant ($t_{47} = -1.53$, $P = .14$). A Tukey multiple comparison test found differences in δ^{13}C but

not δ^{15}N values between aquatic and terrestrial insects ($P = <.001$ and $P = .65$, respectively). The

mean δ¹³C value for aquatic insects was more depleted than the mean δ¹³C value for terrestrial insects.

Mean δ¹³C enrichment, the difference between the average isotope value of potential prey and the isotope values of the individual feathers, from aquatic insects ranged from 3.5 in nestling feathers to 6.7 in feathers from male flycatchers while mean δ¹³C enrichment from terrestrial insects ranged from 1.9 in nestling feathers to 5.1 in feathers from male flycatchers (Table 3.1). Mean change in δ¹⁵N from aquatic insects to feathers ranged from 2.1 in nestling feathers to 4.0 in male flycatchers while mean change in δ¹⁵N from terrestrial feathers ranged from 1.9 in nestling feathers to 3.8 in the feathers of male Willow flycatchers.
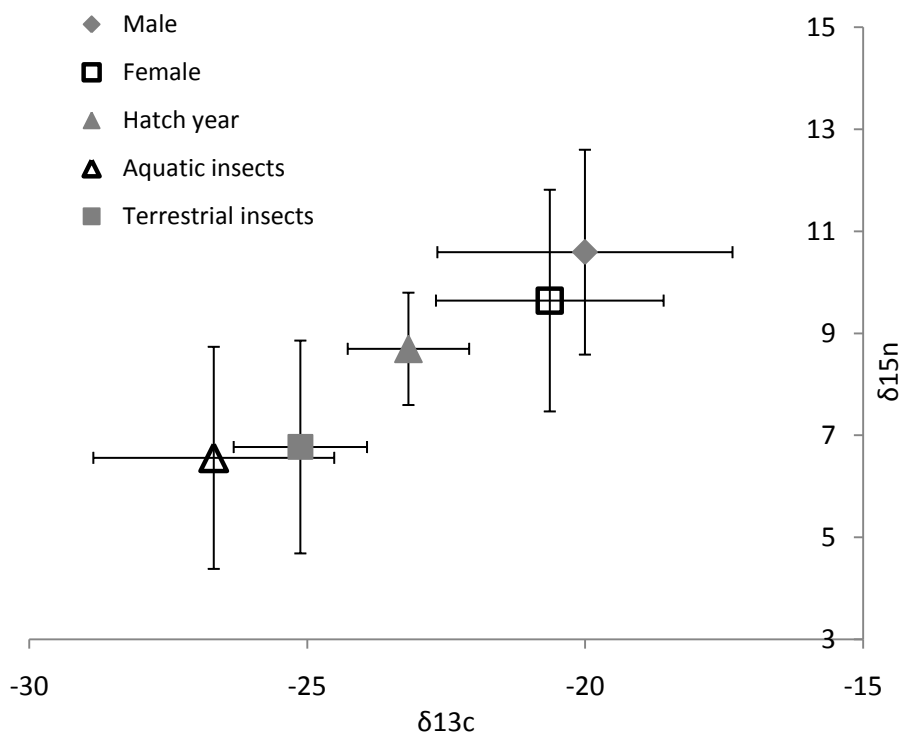
Fig. 3.1. Mean δ13C and δ15N values (±SD) for Willow Flycatcher feathers and potential prey items examined at Fish Creek, Utah, USA.

Table 3.1. Mean δ13C, δ15N values, Δ^{13}C and Δ^{15}N enrichment values (±SD) for Willow Flycatcher and potential prey items.

Sample	n	δ^{13}C (‰) Mean ± SD	δ^{13}C (‰) Range	δ^{15}N (‰) Mean ± SD	δ^{15}N (‰) Range	Δ^{13}C Enrichment (‰) Aquatic Mean ± SD	Δ^{13}C Enrichment (‰) Terrestrial Mean ± SD	Δ^{15}N Enrichment (‰) Aquatic Mean ± SD	Δ^{15}N Enrichment (‰) Terrestrial Mean ± SD
				Willow Flycatchers					
Male	15	-20.0 ± 2.7	-23.5 to -15.2	10.6 ± 2.0	7.5 to 14.4	6.7 ± 0.7	5.1 ± 0.7	4.0 ± 0.6	3.8 ± 0.60
Female	17	-20.6 ± 2.1	-23.7 to -17.1	9.6 ± 2.2	7.7 to 15.2	6.0 ± 0.5	4.5 ± 0.5	3.1 ± 0.6	2.9 ± 0.6
Hatch year	31	-23.2 ± 1.1	-26.1 to -19.4	8.7 ± 1.1	7.4 to 10.9	3.5 ± 0.2	1.9 ± 0.2	2.1 ± 0.2	1.9 ± 0.2
				Potential insect prey					
Aquatic	9	-26.7 ± 2.2	-31.5 to -23.9	6.6 ± 2.2	3.0 to 9.8	--	--	--	--
Terrestrial	8	-25.1 ± 1.2	-28.7 to -22.5	6.8 ± 2.1	0.9 to 12.8	--	--	--	--

Table 3.2. Pianka's index estimates of diet overlap among 7 Willow Flycatcher studies.

	Bakian et al.	Beal	Durst et al.	Drost et al.	Delay et al.	Wiesenborn and Heydon	Prescott and Middleton
Bakian et al.	1	0.945	0.728	0.592	0.927	0.474	0.144
Beal	0.945	1	0.773	0.723	0.955	0.654	0.403
Durst et al.	0.728	0.773	1	0.608	0.781	0.572	0.389
Drost et al.	0.592	0.723	0.608	1	0.776	0.896	0.650
Delay et al.	0.927	0.955	0.781	0.776	1	0.639	0.318
Wiesenborn and Heydon	0.474	0.654	0.572	0.896	0.639	1	0.882
Prescott and Middleton	0.144	0.403	0.389	0.650	0.318	0.882	1

Our Bayesian mixing models detected a greater consumption of terrestrial insects than aquatic insects by male, female and hatch year birds. Aquatic insects comprised 28% ±4.82 SD (posterior high density region = 0 to 67%), 22% ±3.73 SD (posterior high density region = 0 to 56%) and 13% ±1.13 SD (posterior high density region = 0 to 32%) of male, female, and hatch year Willow Flycatchers, respectively. Terrestrial insects comprised 72% ±4.82 SD (posterior high density region = 33% to 100%), 78% ± 3.73 SD (posterior high density region = 44% to 100%), and 87% ±1.13 SD (posterior high density region = 68% to 100%) of male, female, and hatch year Willow Flycatchers, respectively.

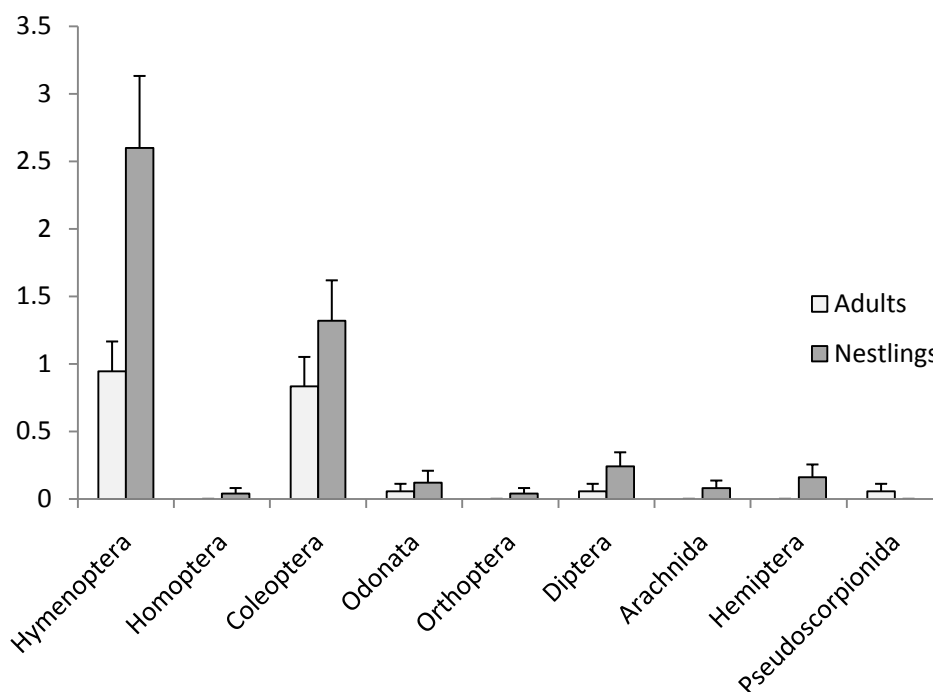Fig. 3.2. Mean abundance (±SD) of nine prey groups for adult ($n = 18$) and nestling ($n = 25$) Willow Flycatchers at Fish Creek, Utah.

Fecal sample analysis.-Fifty-seven fecal samples were collected over the 2003, 2004, and 2005 breeding seasons yielding a total of 150 identifiable prey items (Fig. 3.2). The fecal samples were comprised primarily of hymenoptera and coleoptera but seven other orders of

insects were represented in the samples. We identified approximately 75% of the fragments in the fecal samples. On average, coleoptera and hymenoptera frequency was higher in nestling than adult fecal samples however frequency differences of these prey items were not statistically significant (Fig. 3.3). Hymenoptera and coleoptera occurred in 80% and 60% of nestling fecal samples, respectively, and 61% and 56% of adult fecal samples, respectively (Fig. 3.4). Overall, the nestling fecal samples ($n = 8$ insect orders) were more prey species rich than the adult fecal samples ($n = 5$ insect orders).

Diet overlap among Willow Flycatcher studies ranged from 0.14 (current study and Prescott and Middleton 1988) to 0.95 (Beal 1912 vs. Delay et al. 2002, Table 3.2). The overall diet of Willow Flycatchers sampled in this study most closely resembled the diets sampled by Beal (1912) and DeLay et al. (2002). Diet overlap across all other studies varied from 0.318 in Prescott and Middleton (1988) and DeLay et al. (2002) to 0.955 in DeLay et al. (2002) and Beal (1912).

DISCUSSION

In this study, we investigated the contribution of aquatic insects to the flycatcher diet, examined differences in the diet consumed by adult flycatchers versus the diet adults feed to their nestlings, and compared the diet of Willow Flycatchers at Fish Creek with the diet of Willow Flycatchers reported in previously published studies. We derive three major points from our analysis. First, aquatic insects contribute to the Willow Flycatcher diet at Fish Creek in proportions similar to those found in other bird species. Second, we observed little variation in the diet of male and female adult flycatchers however adult Willow Flycatchers appear to consume a different diet than the one they feed to their nestlings. Third, the diet of Willow Flycatchers at Fish Creek is most similar to the diets described in Beal (1912) and DeLay et al. (2002). We base our conclusions on evidence from both stable isotope and fecal sample analyses.
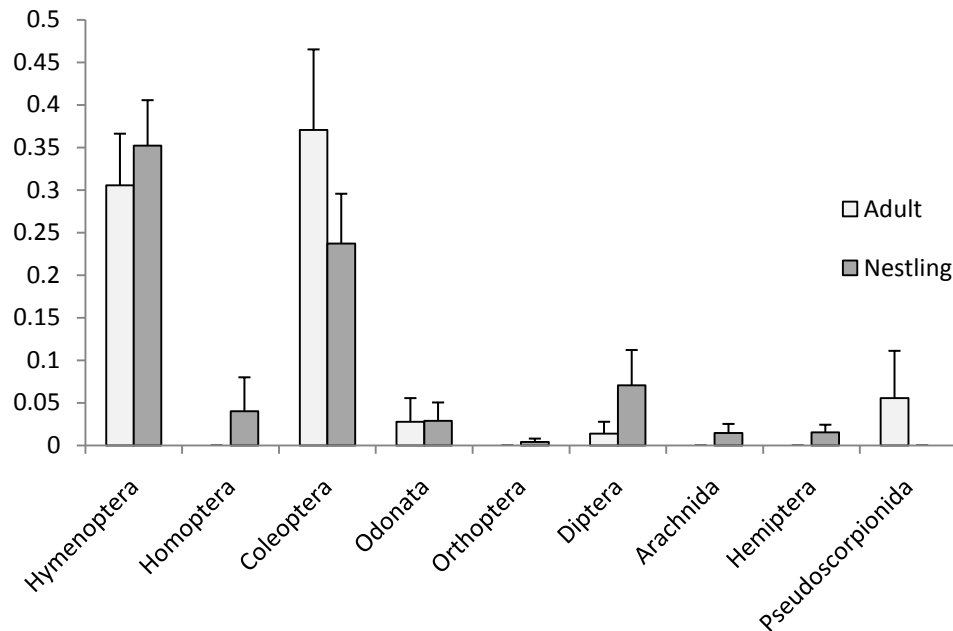
Fig. 3.3. Mean diet frequency/sample (±SD) of nine prey groups for adult (*n* = 18) and nestling (*n* = 25) Willow Flycatchers at Fish Creek, Utah.

*Contribution of Aquatic insects.-*Although terrestrial insects comprised large proportions of the diet of adult and hatch year Willow Flycatchers at Fish Creek during the 2004 and 2005 breeding seasons, aquatic arthropod subsidies comprised almost 1/3 of the diet of adult Willow Flycatchers and 13% of the diet of hatch year birds. These findings are consistent with results from previous studies investigating consumption of aquatic insects in a range of bird species (Nakano and Murakami 2001, Murakami and Nakano 2002). Nakano and Murakami (2001) showed that aquatic insects comprised 15.5% and 31.8% of the diets of two summer resident flycatcher species, the Brown Flycatcher and the Narcissus Flycatcher, at Horonai stream in Hokkaido, Japan.
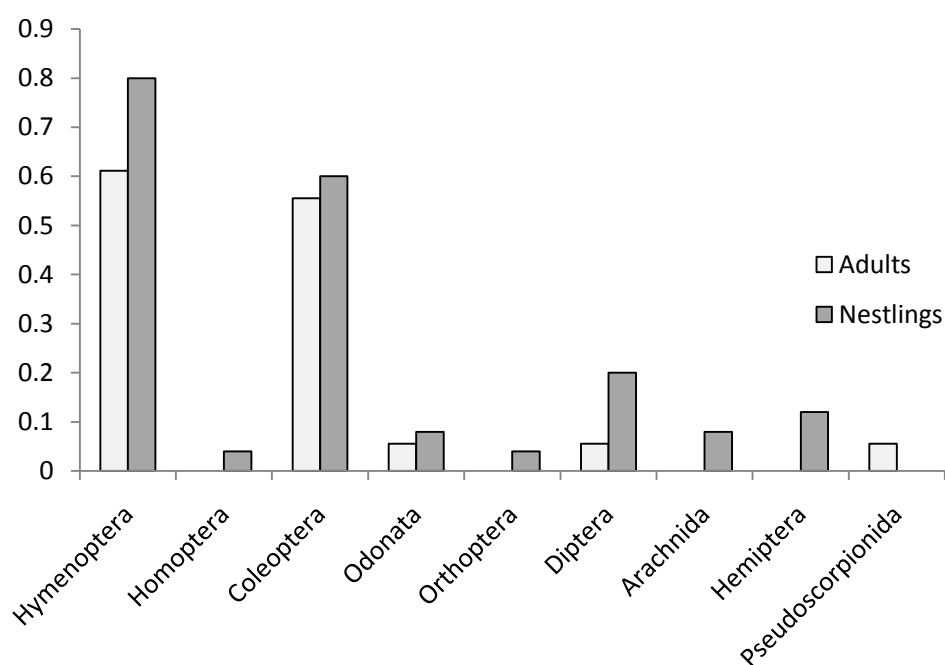
Fig. 3.4. Occurrence of nine prey groups for adult (*n* = 18) and nestling (*n* = 25) Willow Flycatchers at Fish Creek, Utah.

Evidence from this study, as well as previous Willow Flycatcher diet studies, suggests that the use of aquatic insects by Willow Flycatchers may be influenced by the insect productivity in the riparian breeding habitats as well as the habitats adjacent to nesting habitat. Wiesenborn and Heydon (2007) found that flycatchers nesting in Tamarisk dominated habitats in Arizona relied heavily on Odonata derived from aquatic habitats and concluded that in *Tamarisk* dominated habitats with low in situ arthropod production, insect subsidies from adjacent habitats may be essential to the Willow Flycatcher during the breeding season. In contrast, DeLay et al. (2002) investigated variation in Willow Flycatcher diet in birds breeding in native riparian habitat in the Gila Valley, New Mexico, and found only evidence of low use of aquatic insects by flycatchers. This variation in the use of aquatic insect subsidies appears to reflect relative productivity of habitats surrounding the riparian zone. The potential arthropod productivity of flycatcher nesting habitat should be considered by land managers when identifying areas to

protect for flycatchers during the breeding season. Depending on the breeding location, habitats

adjacent to riparian land cover may be an essential source of food resources to Willow

Flycatchers during the breeding season.

Willow Flycatcher's dependence on aquatic insects is likely to vary temporally across the

breeding season. Peak benthic productivity in temperate creeks typically occurs during spring

(Sumner and Fisher 1979), and correspondingly, aquatic insect availability may also peak during

spring. Specific timing of aquatic insect emergence varies across species (Corbet 1964) and is

influenced by local variation in nutrition and climate (Needham et al. 1935, Sweeney and

Vannote 1982).   Aquatic insect hatches can provide abundant but temporally limited and

stoichastic sources of food. This was observed at Roosevelt Lake where one breeding male

Willow Flycatcher was radio-tracked moving approximately 2 kilometers from his home range to

feed on a mayfly hatch on the Salt River (Cardinal and Paxton 2004).

Our mixing models measured Willow Flycatcher's average use of aquatic and terrestrial

at Fish Creek during body feather molt which typically occurs late in the breeding season. We did

not capture Willow Flycatcher's use of aquatic insects towards the beginning of the breeding

season but suspect that it could be higher than the levels observed in this study due to the timing

of peak aquatic arthropod emergence, variation in the insect productivity of terrestrial habitats,

and the observation of high foraging of aquatic insects in the spring by other bird species in

temperate systems (Smith et al. 1998, Nakano and Murakami 2001, Gende and Willson 2001).

Diet differences in adult and nestling flycatchers.-Male and female Willow Flycatchers

did not differ statistically in their $\delta^{13}C$ or $\delta^{15}N$ values and although the mixing models found that

the diet of male flycatchers was comprised of a higher proportion of aquatic insects than the diet

of female flycatchers, these differences were not statistically significant. These results

corroborate findings from other Willow Flycatcher diet studies that have identified only subtle

degrees of diet differences between male and female flycatchers (DeLay et al. 2002, Drost et al.

2003, Wiesenborn and Heydon 2007, Durst et al. 2008). We did observe considerable individual variation in stable isotope values among adult Willow Flycatchers likely reflecting individual differences in their foraging behavior. Stream geomorphology, riparian habitat heterogeneity and variation in benthic productivity are known to affect the flux of emerging aquatic insects (Iwata et al. 2003, Baxter et al. 2005). Individual variation in carbon and nitrogen stable isotope values among adult flycatchers may also reflect spatial variation in the availability of aquatic insects across home ranges.

Previous studies have consistently observed variation in the type and proportions of prey types consumed by adult Willow Flycatchers versus that fed to nestling flycatchers (Prescott and Middleton 1988, Drost et al. 2003, Wiesenborn and Heydon 2007, Durst et al. 2008). Our study indicates that diet differences between adults and nestlings are also present in their use of aquatic insects. A number of factors may explain the discrepancy between adult and nestling flycatchers in their consumption of aquatic insects. First, adult Willow Flycatchers may be selectively feeding nestlings different prey items than they select for themselves due to differences in dietary requirements for adults and nestling birds (Newton 1967). Adult flycatchers may be selecting prey items with higher nutrient content and, more specifically, predaceous insects which have been found to contain greater nitrogen content than herbaceous insects (Fagen et al. 2002). Herbaceous and predaceous insects from aquatic (e.g. aquatic Diptera versus Odonata) and terrestrial (e.g. pollen-feeding bees versus *Camponotus* sp.) habitats were identified in fecal samples of nestling flycatchers. However, we encountered a greater number of predaceous terrestrial insects than predaceous aquatic insects in the nestling's fecal samples.

To examine if differences in nitrogen content exist between aquatic and terrestrial insects, we looked post-hoc at the mass spectrometry results which provide measurements of nitrogen concentration in the insect samples used in the stable isotope analysis. In our sample, a pattern began to emerge where terrestrial insects (mean = 0.12, SD = 0.002) contained higher

concentrations of nitrogen than aquatic insects (mean = 0.11, SD. = 0.003, P = .06, t_{46} = -1.94).

We suspect that at Fish Creek a greater number of predaceous insects are produced in mountain

shrub steppe and upland forest habitats than in aquatic habitats. Adult flycatchers may be

intentionally selecting predaceous terrestrial insects to feed to their young. If this is the case, then

this is the second piece of evidence we have identified that indicates that alternative habitats

bordering riparian habitat including mountain shrub steppe and upland forest are important for

providing food resources to Willow Flycatchers during the breeding season. Further study

involving experimentation is required however to determine if adult flycatchers are preferentially

selecting predaceous terrestrial arthropods to feed to their young at Fish Creek.

Alternatively, diet differences between nestling and adult Willow Flycatchers may be the

result of temporal differences in feather sampling. Nestling feather development occurs largely in

July at Fish Creek while adult body feather molt begins in August. Nestling and adult feather

isotope signatures therefore reflect two distinct time periods at Fish Creek with potentially

different arthropod availability.

We expected δ^{15}N enrichment to follow a step-wise progression from prey source to

consumer tissue within the range of 3-5‰ (Peterson and Fry 1987, Mizutani et al. 1992, Hobson

and Bairlein 2003). This expectation was satisfied in the nitrogen enrichment of adult flycatcher

feathers from terrestrial and aquatic arthropod prey however mean nitrogen enrichment levels

were lower than we expected in nestling feathers. Hatch year feathers were found to be more

depleted in ^{15}N than male but not female feathers. Since δ^{15}N values indicate the trophic-level at

which a consumer is foraging, we suggest four possible scenarios responsible for differences in

^{15}N between male and hatch year feathers. One, we may have missed sampling an insect food

source consumed primarily by males that is more ^{15}N enriched on average than the insects we

sampled. Conversely, we may have missed a food source commonly fed to nestlings that is more

^{15}N depleted than the food items we sampled. Differences in the feather structure itself between

hatch year and adult feathers may be responsible for differences in nitrogen enrichment between adult and nestling flycatcher feathers. Finally, as Willow Flycatcher's body molt may occur any time from late July thru November, we may have unknowingly sampled body feathers grown during fall migration. Carbon and nitrogen isotope signatures would thus reflect the diet consumed by Willow Flycatchers while on migration rather than the Fish Creek diet.

*Using stable isotopes in bird diet analysis.-*The precision of our aquatic and terrestrial insect estimates depends on the accuracy of the $\delta^{13}C$ discrimination factor used in our mixing models. The change in $\delta^{13}C$ from prey source to feather has been found to vary considerably across bird species and prey items (Mizutani et al.1992, Hobson and Bairlein 2003). We used a $\delta^{13}C$ trophic discrimination factor of 2.0 ± 0.1 and based this choice on laboratory studies that were conducted with bird species and diets most similar to the Willow Flycatcher (Hobson and Bairlein 2003, Pearson et al. 2003). A more accurate determination of the $\delta^{13}C$ discrimination factor to use in our mixing models would require laboratory experiments of isotope fractionation in Willow Flycatchers fed a homogeneous insect diet. The benefit of using a Bayesian mixing model over traditional mixing models (e.g. Phillips and Gregg 2001, 2003) is its ability to incorporate some of the uncertainty in trophic enrichment factor into model parameter estimation. However, there remains a considerable need for additional laboratory experiments to provide precise diet-tissue discrimination factors for use in isotope mixing-models for ascertaining wild bird population diets (Gannes et al. 1997, Martinez del Rio et al. 2009).

To further address the problem of $\delta^{13}C$ isotopic discrimination uncertainty, we conducted a post-hoc exploration of the influence of varying $\delta^{13}C$ discrimination factor on flycatcher diet composition by incrementally increasing the $\delta^{13}C$ discrimination factor by 0.5‰ starting at 1.0‰ and ending at 4.5‰. We found that the diet output from male and female mixing-models to behave robustly across the range of $\delta^{13}C$ isotopic discrimination values. For example, in the male flycatcher mixing-models, the mean proportion of their diet comprised of aquatic insects ranged

from 28% to 30% across the entire range of $\delta^{13}C$ trophic enrichment values. Greater variation was observed in the proportion of aquatic and terrestrial insects comprising the hatch year flycatchers under varying $\delta^{13}C$ trophic enrichment values. The mean contribution of aquatic insects to the hatch year diet was observed to increase with increasing $\delta^{13}C$ trophic enrichment value so that their diet appeared to be dominated by aquatic insects when using trophic enrichment values at the extreme end of the range (4.5‰). Given these post-hoc findings, we feel confident in our choice of a 2.0‰ isotopic discrimination factor.

Diet comparisons with other studies.-We examined diet overlap in Willow Flycatchers across seven flycatcher studies including six previously published diets as well as the diet reported in this study. In combination, the six previously published diet studies examined Willow Flycatcher diet in varying depths across much of their North American breeding range including parts of Canada. Four out of the six studies specifically investigated diet of the federally listed endangered Southwestern Willow Flycatcher during the breeding season at various sites in California, Arizona and New Mexico using fecal sample analyses (Delay et al. 2002, Drost et al. 2003, Wiesenborn and Heydon 2007, Durst et al. 2008). Beal (1912) collected stomach contents from 135 Willow Flycatchers in 17 states and three Canadian provinces from May to September. Given his sampling time frame, it is likely that some of his samples came from birds in migration and the diet samples from migrating birds do not reflect their diet during the breeding season adding a source of error to our investigation of diet overlap during the breeding season. Prescott and Middleton (1988) collected gut samples from seven adult Willow Flycatchers, and insect prey samples from an unspecified number of nestlings with neck ligatures in Guelph, Ontario. In contrast to other flycatcher diet studies, Prescott and Middleton (1988) treated individual diet prey items as the individual sample rather than the stomach or fecal sample.

There is considerable variation in diet overlap across Willow Flycatcher populations, and the pattern in dietary overlap cannot be entirely explained by geographic proximity. The diet of

the Fish Creek Willow Flycatchers most closely resembles the diet sampled by Beal (1912) and

Delay et al. (2002). In Beal (1912), Willow Flycatcher diet was sampled from across their North

American breeding range while DeLay et al. (2002) examined diet in a population of

Southwestern Willow Flycatchers breeding in the Gila Valley, New Mexico. Willow

Flycatcher's high consumption of Hymenoptera and Coleoptera was the common trend across

these three studies. Fish Creek Willow Flycatcher diet was most dissimilar from the diet of

nestling Willow Flycatchers in southeastern Ontario. The diet of the Ontario population of

nestling Willow Flycatchers was dominated by Diptera species, and although the authors did not

quantify the diet of adult flycatchers in their study, they did observe differences in the diet of

adult and nestling flycatchers. Part of the discrepancy between the Fish Creek and Ontario

flycatcher diets may be due to differences in diets sampled; nestling flycatchers were the focus in

the Ontario study while we examined diet in both adult and nestling flycatchers. Diptera species

comprised a larger proportion of the diet of nestling flycatchers at Fish Creek than adult

flycatchers although not at levels anywhere close to those observed in the Ontario population.

The Ontario nestling population's diet may be unique among the diets of the flycatcher

populations studied while the flycatcher diet described by Beal (1912) was most congruent with

other flycatcher diets. Beal's (1912) Willow Flycatcher sample included a wide geographic range

while the other flycatcher studies examined flycatcher diet in distinct populations. Beal (1912)

appears to have captured the general diet of Willow Flycatchers across broad geographic scales

while other studies have demonstrated the variability in Willow Flycatcher diets on finer

geographic scales. Also, if Willow Flycatchers are generalist foragers (Durst et al. 2008), we

may expect flycatcher diets to differ among sites due to differences in the distribution of

arthropod populations, local and regional composition and structure of habitats, climate patterns,

and random forces.

*Conclusions and management implications.-*Willow Flycatcher diet at Fish Creek is largely comprised of terrestrial insects however aquatic insects make up 20%-30% of the diet of adult flycatchers. Similar to other studies, we found considerable differences in the diets consumed by adults compared to the diet they feed their nestlings. Further, many of the insects identified in fecal samples were likely produced in non-riparian habitats, either aquatic or upland terrestrial habitats. The use of insect subsidies derived from neighboring habitats by Willow Flycatchers suggests that the availability of adjacent habitat types may be important for producing food resources to complement in situ riparian arthropod production. As conservation and management plans are focused on preserving or restoring habitat for the Willow Flycatcher, in addition to preserving riparian habitat for breeding, wildlife managers need to consider the movement of insect prey across habitat boundaries. If low insect productivity in riparian habitat is suspected, adjacent habitats should be preserved to provide the food resources required by Willow Flycatchers during the breeding season.

LITERATURE CITED

Akamatsu, F., H. Toda, and T. Okino. 2004. Food source of riparian spiders analyzed by using stable isotope ratios. Ecological Research 19: 655-662.

Baxter, C.V., K.D. Fausch, and W. C. Saunders. 2005. Tangled webs: Reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology 50: 201-220.

Beal, F.E.L. 1912. Food of our more important flycatchers. US Bureau of Biological Survey, Bulletin 4.

Burger, J.C., M.A. Patten, J.T. Rotenberry, and R.A. Redak. 1999. Foraging ecology of the California gnatcatcher deduced from fecal samples. Oecologia 120:304-310.

Bustamante, R.H., G.M. Branch, and S. Eekhout. 1995. Maintenance of an exceptional intertidal grazer biomass in South Africa: Subsidy by subtidal kelp. Ecology 76: 2314-2329.

Cardinal, S.N., and E.H. Paxton. 2004. Home range, movement, and habitat use of the Southwestern Willow Flycatcher, Roosevelt Lake- 2003. U.S. Geological Survey Report to the U.S. Bureau of Reclamation, Phoenix, AZ. 25 pp.

Carlisle, J. D., and R.L. Holberton. 2006. Relative efficiency of fecal versus regurgitated samples for assessing diet and the deleterious effects of a tarter emetic on migratory birds. 2006. Journal of Field Ornithology 77: 126-135.

Corbet, P.S. 1964. Temporal patterns of emergence in aquatic insects. Canadian Entomologist 96: 264-279.

Cummins, K.W., R.C. Petersen, F.O. Howard, J.C. Wuycheck, and V.I. Hold. 1973. The utilization of leaf litter by stream detritivores. Ecology 54: 336-345.

DeLay, L.S., S.H. Stoleson, and M. Farnsworth. 2002. A quantitative analysis of the diet of Southwestern Willow Flycatchers in the Gila Valley, New Mexico. Available from http://sbsc.wr.usgs.gov/cprs/research/projects/swwf/Reports/NM_SWWF_Diet_Report_2 002.pdf. Accessed May 13, 2010.

DeLoach, C. J., R. I Carruthers, J. E. Lovich, T. L. Dudley, and S. D. Smith. 2000. Ecological interactions in the biological control of saltcedar (*Tamarix* spp.) in the United States: Toward a new understanding. Pages 819-873 *in* Proceedings of the X International Symposium on Biological Control of Weeds 4-14 July (N.R. Spencer, Ed.), Montana State University, Bozeman.

Drost, C.A., E.H. Paxton, M.K. Sogge, and M.J. Whitfield. 2003. Food habitats of the Southwestern Willow Flycatcher during the nesting season. Studies in Avian Biology 26:96-103.

Durst, S.L., T.C. Theimer, E.H. Paxton, and M.K. Sogge. 2008. Age, habitat, and yearly variation in the diet of a generalist insectivore, the Southwestern Willow Flycatcher. The Condor 110: 514-525.

Fagan, W.F., E. Siemann, C. Mitter, R.F. Denno, A.F. Huberty, H.A. Woods, and J.J. Elser. 2002. Nitrogen in insects: Implications for tropic complexity and species diversification. American Naturalist 160: 784-802.

Fukui, D., M. Murakami, S. Nakano, and T. Aoi. 2006. Effect of emergent aquatic insects on bat foraging in a riparian forest. Journal of Animal Ecology 75: 1252-1258.

Gannes, L. Z., D. M. O'Brien, and C. Martinez del Rio. 1997. Stable isotopes in animal ecology: Assumptions, caveats, and a call for more laboratory experiments. Ecology 78: 1271-1276.

Gende, S.M., and M.F. Willson. 2001. Passerine densities in riparian forests of southeast Alaska: Potential effects of anadromous spawning salmon. The Condor 103: 624-629.

Gray, L.J. 1989. Emergence production and export of aquatic insects from a tallgrass prairie stream. Southwestern Naturalist 34: 313-318.

Gray, L.J. 1993. Response of insectivorous birds to emerging aquatic insects in riparian habitats of a tallgrass prairie stream. American Midland Naturalist 129: 288-300.

Herrera, L.G., K.A. Hobson, M. Rodriguez, and P. Hernandez. 2003. Trophic partitioning in tropical rain forest birds: Insights from stable isotope analysis. Oecologia 136: 439-444.

Hobson, K.A., and F. Bairlein. 2003. Isotopic fractionation and turnover in captive Garden Warblers (*Sylvia borin*): Implications for delineating dietary and migratory associations in wild passerines. Canadian Journal of Zoology 81: 1630-1635.

Iwata, T., S. Nakano, and M. Murakami. 2003. Stream meanders increase insectivorous bird abundances in riparian deciduous forests. Ecography 26: 325-327.

Jackson, J.K., and S.G. Fisher. 1986. Secondary production, emergence and export of aquatic insects of a Sonoran desert stream. Ecology 67: 629-638

Jenni, L., Reutimann, P., and S. Jenni-Eiermann. 1990. Recognizability of different food types in alimentary flushes of *Sylvia* Warblers. Ibis 132: 445-453.

Kato, C., T. Iwata, S. Nakano, and D. Kishi. 2003. Dynamics of aquatic insect flux affects distribution of riparian web-building spiders. Oikos 103: 113-120.

Krebs C.J. 1994. Ecological Methodology, 2nd ed. Benjamin Cummings Press, Menlo Park, California.

Martinez del Rio, C., N. Wolf, S.C. Carleton, and L.Z. Gannes. 2009. Isotopic ecology ten years after a call for more laboratory experiments. Biological Reviews 84: 91-111.

Mason, C.F., and S.M. MacDonald. 1982. The input of terrestrial invertebrates from tree canopies to a stream. Freshwater Biology 12: 305-311.

Mizutani, H., M. Fukuda, and Y. Kabaya. 1992. ^{13}C and ^{15}N enrichment factors of feathers of 11 species of adult birds. Ecology 73: 1391-1395.

Murakami, M., and S. Nakano. 2002. Indirect effect of aquatic insect emergence on a terrestrial insect population through bird predation. Ecology Letters 5: 333-337.

Nakano, S., and M. Murakami. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. Proceedings of the National Academy of Sciences of the United States of America 98: 166-170.

Needham, J.G., J.R. Traver, and Y. Hsu. 1935. The Biology of Mayflies. Comstock Publishing Company, Ithaca, New York.

Newton, I. 1967. The adaptive radiation and feeding ecology of some British finches. Ibis 109: 33-98.

Paetzold, A., C.J. Schubert, and K. Tockner. 2005. Aquatic terrestrial linkages along a braided-river: Riparian arthropods feeding on aquatic insects. Ecosystems 8: 748-759.

Parnell, A., and A. Jackson. 2010. Stable Isotope Analysis in R. [Online.] Available at http://cran.r-project.org/web/packages/siar/index.html. Accessed on May 31, 2010.

Pearson, S.F., D.J. Levey, C.H. Greenberg, and C. Martinez del Rio. 2003. Effects of elemental composition on the incorporation of dietary nitrogen and carbon isotopic signatures in an omnivorous songbird. Oecologia 135: 516-523.

Peterson, B.J., and B. Fry. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics 18: 293-320.

Phillips D.L., and J.W. Gregg. 2001. Uncertainty in source partitioning using stable isotopes. Oecologia 127: 171–179.

Phillips D.L., and J. W. Gregg. 2003. Source partitioning using stable isotopes: Coping with too many sources. Oecologia 136: 261–269.

Polis, G.A., and S.D. Hurd. 1995. Extraordinarily high spider densities on islands: Flow of energy from the marine to terrestrial food webs and the absence of predation. Proceedings of the National Academy of Sciences 92: 4382-4386.

Polis, G.A., and S.D. Hurd. 1996. Linking marine and terrestrial food webs: Allochtonous input from the ocean supports high secondary productivity on small islands and coastal land communities. American Naturalist 147: 396-423.

Polis, G.A., W.B. Anderson, and R.D. Holt. 1997. Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics 28: 289-316.

Poulin, B., and G. Lefebvre. 1995. Additional information on the use of tartar emetic in determining diet of tropical birds. The Condor 97: 897-902.

Prescott, D.R.C., and A.L.A. Middleton. 1988. Feeding-time minimization and the territorial behavior of the Willow Flycatcher (*Empidonax traillii*). Auk 105: 17-28.

Pyle, P. 1997. Identification Guide to North American Birds. Slate Creek Press, Bolinas, California.

R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0 [Online] Available at http://www.R-project.org.

Ralph, C.P., S.E. Nagata, and C.J. Ralph. 1985. Analysis of droppings to describe diets of small birds. Journal of Field Ornithology 56: 165-174.

Rosenberg, K.V., and R.J. Cooper. 1990. Approaches to avian diet analysis. Studies in Avian Biology 13: 80-90.

Sabat, P. and C. Martinez del Rio. 2005. Seasonal changes in the use of marine food resources by *Cinclodes nigrofumosus* (furnariidae, aves): Carbon isotopes and osmoregulatory physiology. Revista Chilena De Historia Natural 78: 253-260.

Sabat, P., K. Maldonado, J.M. Farina, and C.M. del Rio. 2006. Osmoregulatory capacity and the ability to use marine food sources in two coastal songbirds (*Cinclodes: Furnariidae*) along a latitudinal gradient. Oecologia 148: 250-257.

Sabo, J.L., and M.E. Power. 2002a. River-watershed exchange: Effects of riverine subsidies on riparian lizards and their terrestrial prey. Ecology 83: 1860-1869.

Sabo, J.L., and M.E. Power. 2002b. Numerical response of lizards to aquatic insects and short-term consequences for terrestrial prey. Ecology 83: 3023-3036.

Sanzone, D.M., J.L. Meyer, E. Marti, E.P. Gardiner, J.L. Tank, and N.B. Grimm. 2003. Carbon and nitrogen transfer from a desert stream to riparian predators. Oecologia 134: 238-250.

Sarakinos, H.C., M.L. Johnson, and M.J. Vander Zanden. 2002. A synthesis of tissue-preservation effects on carbon and nitrogen stable isotope signatures. Canadian Journal of Zoology 80: 381-387.

Smith, R., M. Hamas, M. Dallman, and D. Ewert. 1998. Spatial variation in foraging of the Black-throated Green Warbler along the shoreline of Northern Lake Huron. The Condor 100: 474-484.

Sogge, M. K., J. C. Owen, E. H. Paxton, S.M. Langridge, and T.J. Koronkiewicz. 2001. A targeted mist net capture technique for the Willow Flycatcher. Western Birds 32: 167-172.

Stamp, N.E. 1978. Breeding birds of a riparian woodland in south-central Arizona. Condor 80: 64-71.

Strapp, P., and G. A. Polis. 2003. Marine resources subsidize insular rodent populations in the Gulf of California, Mexico. Oecologia 134: 496-504.

Sumner, W.T., and S.G. Fisher. 1979. Periphyton production in Fort River, Massachusetts. Freshwater Biology 9: 205-212.

Sweeney, B.W., and R.L. Vannote. 1982. Population synchrony in mayflies: A predator satiation hypothesis. Evolution 36: 810-821.

Syväranta J, S. Vesala, M. Rask, J. Ruuhijärvi, and R.I. Jones. 2008. Evaluating the utility of stable isotope analyses of archived freshwater sample materials. Hydrobiologia 600: 121-130.

Wiesenborn, W.D., and S.L. Heydon. 2007. Diet of Southwestern Willow Flycatcher compared among breeding populations in different habitats. Wilson Journal of Ornithology 119: 547-557.

Wolf, B.O., and C. Martinez del Rio. 2003. How important are columnar cacti as sources of water and nutrients for desert consumers? A review. Isotopes in Environmental and Health Studies 39: 53-67.

Vannote, R.L., G.W. Hinshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Science 37: 130-137.

CHAPTER 4

SPACE USE COMPARISONS IN TWO POPULATIONS OF WILLOW FLYCATCHER,

EMPIDONAX TRAILLII[1]

Abstract. The Willow Flycatcher, *Empidonax traillii*, has experienced population declines throughout its range in the western United States with one subspecies *Empidonax traillii extimus* listed as an endangered species. Consequently, most of the research on Willow Flycatchers has been focused on the federally endangered Southwestern Willow Flycatcher, *E.t. extimus*. In this study, we compare and contrast space use characteristics in two populations of Willow Flycatchers, one belonging to the *E.t. extimus* subspecies and the other belonging to the *E.t. adastus* subspecies as a function of breeding site, breeding status, and sex. Willow Flycatchers were radio-tagged and tracked over the course of two breeding seasons at Fish Creek (2003, 2004, *E.t. adastus*) and three breeding seasons at Roosevelt Lake (2003-2005, *E.t. extimus*). Differences in home range size, core area size, proportion of core area comprised of riparian habitat, home range habitat richness and home range heterogeneity were found among breeding-flycatchers as a function of breeding site and sex. Variation in space use characteristics as a function of breeding site, breeding status, and sex indicates that a number of different mechanisms may be driving space use in Willow Flycatchers over the breeding season.

INTRODUCTION

Knowledge of an animal's use of space is vital for effective conservation and management planning. Currently, avian population managers in need of demographic and habitat requirement information for the active management of Willow Flycatcher populations rely on research studies conducted on the endangered *E. t. extimus* subspecies.   In this study, we compare home range and core area space use in two populations of Willow Flycatchers, an *E.t.*

---

[1] Coauthored by Bakian, A.V., K.A. Sullivan, and E.H. Paxton

extimus population breeding at Roosevelt Lake, Arizona and a population of *E.t. adastus* breeding

at Fish Creek, Utah to examine the generality of the studies of space use in one population for

managing other populations.

The Willow Flycatcher (*Empidonax traillii*) is a small, neo-tropical migrant that depends

upon riparian habitat for survival and reproduction throughout the continental United States (Fig.

1.1). The Southwestern Willow Flycatcher (*Empidonax traillii extimus*; SWFL) is a federally

endangered subspecies with a breeding distribution spanning six states including Arizona, New

Mexico, southern Colorado, southern Utah, Nevada and Southern California (U.S. Fish and

Wildlife Service 2002). Population declines in the Southwestern Willow Flycatcher are primarily

the result of wide-spread habitat loss, degradation or modification (U.S. Fish and Wildlife Service

1993, Marshall and Stoleson 2000). Since receiving federal endangered species protection in

1995 (U.S. Fish and Wildlife Service 1995), SWFLs have been the subject of detailed population

surveys, monitoring and demographic study (e.g. Paxton et al. 1997, English et al. 1999,

Kenwood and Paxton 2001, Newell et al. 2003, Causey et al. 2005, Paxton et al. 2007).

The *Empidonax trailli adastus* (WIFL) subspecies of Willow Flycatcher breeds

throughout the intermountain west and Great Basin region of the U.S including Utah, Colorado,

Wyoming, Idaho, Nevada, eastern California, eastern Oregon and eastern Washington. Similar to

the SWFL, this sub-species of flycatcher restricts its breeding to riparian woodlands that typically

occur in isolated patches. Populations of *E.t. adastus* are also in decline (Schlorff 1990, Sauer et

al. 1997, Stefani et al. 2001) yet it has received considerably less research attention.

We used ratio-telemetry to track female and male flycatchers at Fish Creek and male

flycatchers at Roosevelt Lake during the breeding season. Previous estimates of Willow

Flycatcher space use (e.g. home range, territory, or core area) have relied primarily on mapping

the movement of individual's within the landscape based on visual and auditory identification

(Walkinshaw 1966, Eckhardt 1979, Stafford and Valentine 1985, Flett and Sanders 1987, Prescott

and Middleton 1988). Territorial mapping techniques have been found to underestimate the true space requirements in some passerines (Hanski and Haila 1988, Anich et al. 2009). In addition, as singing is uncommon in female Willow Flycatchers (Sedgwick 2000), radio-telemetry may more accurately capture space use than territory mapping in females as well as males.

The mechanisms responsible for intraspecific variation in home range size are poorly understood (Kjellander et al. 2004, Saïd and Servanty 2005). Potential variables that may influence home range size variation within a species include sex and age (Cederlund and Sand 1994), reproductive status (Bertrand et al. 1996), population density (Kjellander et al. 2004) and landscape heterogeneity (Kie et al. 2002). Landscape structure and composition can influence home range and core area size by impacting the distribution of food resources (Smith and Shugart 1987), the availability of shelter (Fisher 2000) and the presence of predators (reviewed in Whittingham and Evans 2004). The patch and landscape level vegetation structure of Willow Flycatcher habitats differ between Roosevelt Lake and Fish Creek. At Roosevelt Lake, temporal fluctuations in reservoir water levels due to the operation of Roosevelt Dam have produced a mosaic of riparian woodland stands with varying vegetation age and canopy heights (Paxton et al. 2007). Riparian woodland stands are embedded in a xeric landscape comprised of open areas and Sonoran desert scrub habitat. In contrast, Fish Creek has patches of fairly uniform riparian willow stands situated in a broad canyon bordered by upland forest and mountain shrub habitats (Bakian unpublished data). We predict that differences in flycatcher home range and core area size are influenced by variation in the habitat vegetation structure and pattern at Fish Creek and Roosevelt Lake. In addition, we expect space use metrics to vary as a function of flycatcher sex due to behavioral differences between male and female flycatchers. Our study's primary objective is to compare and contrast space use in Willow Flycatchers including home range and core area size, home range and core area habitat heterogeneity and habitat composition as a function of breeding site, and breeding status and flycatcher sex.
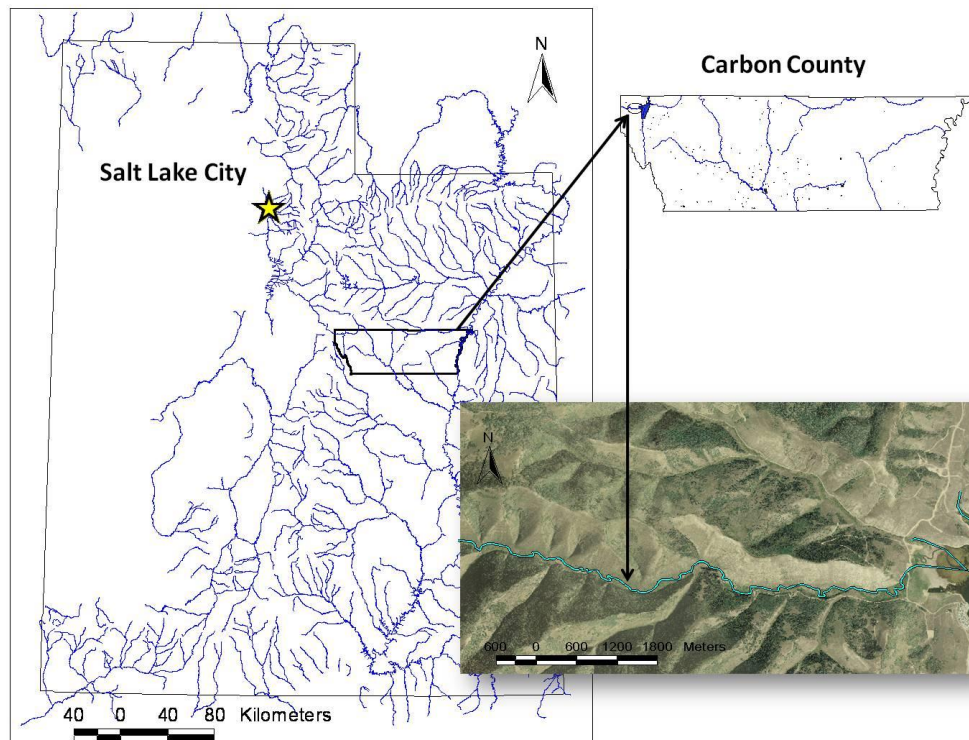
FIGURE 4. 1. Location of Fish Creek, in Manti-La Sal National Forest, Carbon County, Utah.

METHODS

STUDY AREA

Two geographically disparate populations of Willow Flycatchers were examined in this study. The first is a population of *Empidonax traillii adastus* breeding at Fish Creek, a perennial, high elevation stream in Manti-La Sal National Forest, Utah (Fig. 4.1). The second group is a population of the federally endangered Southwestern Willow Flycatcher, *Empidonax traillii extimus*, breeding along the Salt River and Tonto Creek inflows of Roosevelt Lake, Gila County, Arizona (Fig. 4.2).
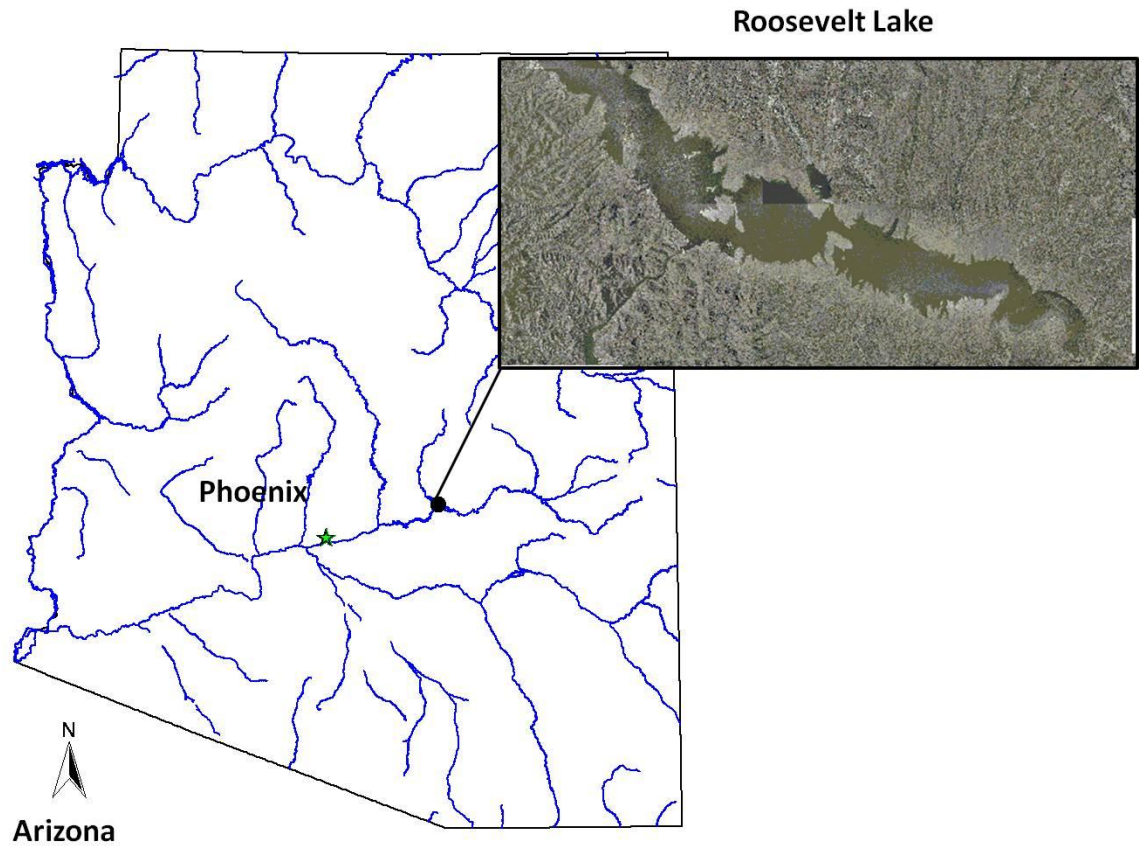
FIGURE 4.2. Location of Roosevelt Lake, Arizona.

Breeding habitat differed by both vegetation composition and riparian patch size between the two study sites. The Fish Creek drainage is composed of linear patches of thick, willow dominated (*Salix* spp.) riparian habitat with a maximum canopy height of 5 meters. These distinct riparian patches range from 0.29 ha to 2.5 ha and are bordered by mountain shrub steppe habitat on southern slopes characterized by big sagebrush (*Artemisia tridentate* sp.), Utah serviceberry (*Amelanchier utahensis*), chokecherry (*Prunus virginiana*), mountain snowberry (*Symphoricarpos oreophilus*) and various shrubsteppe grasses. Riparian habitat is bordered by upland mixed-forest habitat with Englemann's spruce (*Picea engelmanni),* White fir (*Abies concolor*) Douglas fir (*Pseudotsuga menziesii*) forest, and Quaking aspen (*Populus tremuloides*)

species on north-facing canyon slopes. Riparian patches are separated by open water. Each

distinct patch of riparian habitat typically contained a single pair of breeding flycatchers during

the study period (Bakian personal observation).

The Roosevelt Lake study site is a low elevation (~690 m) desert riparian zone comprised

of patches of riparian habitat ranging from 0.2 ha to 43 ha which are separated by bare ground,

scrub habitat, emergent riparian habitat or open water. Mature riparian habitat patches are

composed of Gooding's willow (*Salix gooddingii*), exotic saltcedar (*Tamarix ramosissima*) or a

combination of the two. Sonoran desert uplands surround flycatcher breeding habitat and consist

of palo verde (*Cercidium microphyllum*), creosote (*Larrea tridentate*), saguaro cacti (*Carnegiea

gigantea*), and screwbean mesquite (*Prosopis pubescens*) (see Paxton et al. 2007, Cardinal 2005

for more detail). In contrast to Fish Creek, riparian habitat patches at Roosevelt Lake often

support more than one pair of nesting Willow Flycatchers.

CAPTURE AND TRANSMITTER ATTACHMENT

Data was collected over the 2003 and 2004 breeding seasons at Fish Creek and over the

2003, 2004 and 2005 breeding seasons at Roosevelt Lake. Willow Flycatchers typically arrive at

Fish Creek in late May and at Roosevelt Lake in early May. Following arrival and territory

establishment, Willow Flycatchers were selected for capture and radio transmitter attachment by

assigning a number to each territory and drawing a number at random. Both male and female

flycatchers were studied at Fish Creek while only male flycatchers were sampled at Roosevelt

Lake due to the endangered status of the subspecies. Sex was determined based on behavior, the

presence of a brood patch and lack of a cloacal protuberance in females, and the presence of a

cloacal protuberance and lack of a brood patch in males. Occasionally wing chord and tail length

was used to aid in determining sex (Table 3 in Pyle 1997, USGS unpublished data). At Roosevelt

Lake, the sex of some flycatchers had been previously identified using sex-specific genetic

markers (Cardinal 2005).

Willow Flycatchers were captured using both passive and target mist-netting techniques (Sogge et al. 2001). Following capture, birds were individually banded with an individually numbered, color-anodized Federal bird band on one leg, and a colored metal band on the other leg (Koronkiewicz et al. 2005). We used the Holohil (Carp, Ontario) LB-2N (Utah and Arizona) or BD-2N (Arizona only) radio transmitters (21 day expected battery life; weight range 0.40-0.48 g). A lightweight grid-cloth was glued to the back of the transmitter to create a more textured surface area prior to attachment. Following capture, an area of feathers was removed on the lower back of the bird approximately 1.5cm above the uropygial gland. Transmitters were attached using a glue-on method (Johnson et al. 1992, Paxton et al. 2003) with Skin-bond® medical adhesive (Smith and Nephew®). The final weight of the transmitters including medical adhesive and grid-cloth was 0.46-0.50 g (approximately 3.8%-4.2% of the flycatcher's weight). Flycatchers were released following 5 minutes of adhesive drying time, and the entire banding and transmitter application process took less than 20 minutes.

RADIO-TRACKING

Radio-tracking was started the day following transmitter attachment to provide time for the birds to acclimate to the presence of the transmitter (Suedkamp Wells et al. 2003). Each flycatcher was radio-tracked at least four times a day within at least 2 out of 4 pre-established time periods: AM early (0600-0915), AM late (0916-1230), PM early (1231-1545) and PM late (1546-1900). Individual tracking sessions were separated by at least 30 minutes to guarantee biological independence (White and Garrot 1990) of sequential tracking locations with the goal of collecting at least 30 locations per bird. Tracking equipment used included R-1000 Telemetry receivers (Communications Specialists, Inc.), and standard hand-held 3-element yagi antennas (Biotrack Equipment).

Flycatchers were located using the homing-in method (Paxton et al. 2003), and exact location was pin-pointed through visual confirmation or estimated through triangulation. The

bird's geographical point location and position error was recorded in Universal Transverse Mercator coordinates via a handheld Global Positioning System (Garmin Etrex Legend) after the flycatcher moved from its pin-pointed location. Information recorded at point location included the bird's behavior, habitat type, vegetation substrate, height position of the flycatcher in the vegetation, observation of foraging event, and vocalization type if heard.   Radio-tracking was conducted for the lifetime of the transmitter battery or until the flycatcher became undetectable for other reasons.

Willow Flycatchers were categorized as "breeding" if they maintained and defended a territory, exhibited pair-mating behavior, and attempted/succeeded in nesting. Flycatchers were categorized as non-breeding if they were territorial and mate-paired but radio-tracked pre or post-breeding season, if they were territorial but not mate-paired, or if they exhibited "floater" behavior in which flycatchers were present but did not actively defend a territory (Sherry and Holmes 1989, Newton 1992).

DATA ANALYSIS

Home range and core area estimation. Home range is defined as an area that an organism normally uses to forage, breed and care for young (Burt 1943). We used the 95% fixed-kernel utilization distribution (UD) with least squares cross validation for estimating individual flycatcher home ranges. The 95% fixed-kernel UD corresponds to the area of landscape encompassing the 95% probability distribution for individual flycatchers. Kernel UD approaches are considered among the more rigorous home range quantification approaches (Kernohan et al. 2001). Fixed-kernel methods have been found to produce unbiased estimates of home range size when at least 30 telemetry locations are available for estimation (Seaman et al. 1999). We restricted our home range analysis to flycatchers with at least 28 radio locations. Home ranges were estimated in ArcView 3.3 using the ANIMAL MOVEMENT extension (Hooge and Eichenlaub 1997).

Core areas are areas within the home range that receive intensive use (Kernohan et al. 2001). Often, the 50% fixed kernel UD is used to represent home range core areas (Laver and Kelly 2008). The application of the 50% fixed kernel UD to identify core areas is arbitrary and lacking in biological support for many species. We used a core area estimation method described by Seaman et al. (1998) that determines core area probability isopleth size based on identifying the maximum isopleth containing a greater than expected density rule.

Habitat composition. We identified the habitat composition of home ranges and core areas from high resolution, rectified, aerial photographs of Fish Creek and Roosevelt Lake. The habitat types present at Fish Creek included mature riparian habitat (riparian vegetation > 1 meter height), young riparian habitat (riparian vegetation <1 meter height), mountain shrub steppe, upland forest, or other (bare ground and open water). Roosevelt lake habitat types included mature riparian habitat (riparian vegetation > 5 years old), young/emergent riparian habitat (riparian habitat < 5 years old), upland habitat (Sonoran desert upland vegetation), scrub (tamarisk dominated patchy vegetation), and other (bare ground and open water). At both Roosevelt Lake and Fish Creek, Willow Flycatchers select mature riparian habitat for nest site placement (Paxton et al. 2007, Bakian personal observation). Vegetation classification as determined by aerial photograph was validated through field checks.

We measured a number of home range and core area metrics for each Willow Flycatcher including home range size (in hectares), core area size (in hectares), the proportion of the home range comprised of mature riparian habitat, the proportion of the core area comprised of mature riparian habitat, home range habitat heterogeneity, core area habitat heterogeneity, home range habitat richness, and core area habitat richness. Habitat richness was measured as the number of habitat types present in each individual flycatcher's home range and core areas. Shannon's diversity index was used to estimate home range and core area heterogeneity (*H*),

$$H = \frac{-\sum_{i=1}^{S} p_i \ln p_i}{\ln S} \tag{1}$$

where S = habitat richness, and p_i = proportion of home range or core area comprised of habitat type i.

Statistical analysis. One-way Analysis of Variance (ANOVA) was used to test for differences among Fish Creek female flycatchers, Fish Creek male flycatchers, and Roosevelt Lake male flycatchers in core UD isopleth size, home range size, core area size, home range and core area habitat composition (proportion comprised of riparian habitat), home range and core area habitat richness, and core area and home range habitat heterogeneity. The Student-Newman-Keuls (SNK) test and two-tailed t-tests assuming unequal variances were used for multiple-comparison testing following statistically significant overall ANOVA tests. Two-tailed t-tests assuming unequal variances was also used to test for differences in space use characteristics among breeding and non-breeding SWFLs at Roosevelt Lake. Separate ANOVAs were used to test differences among all Willow Flycatchers, breeding Willow Flycatchers and non-breeding Willow Flycatchers. To meet the assumption of normality, home range and core area size was natural log transformed prior to statistical analysis.

Separate linear regression models were fit to predict home range and core area sizes (natural log transformed) based on home range and core area metrics. Maximal home range and core area models included the following variables (with model variable name and type in parentheses): flycatcher sex (SEX, dummy variable), breeding status (BREED, dummy variable), population site (SITE, dummy variable), proportion of home range (HRRIP, continuous variable) or core area (CORIP, continuous variable) comprised of mature riparian habitat, and home range (HRHETERO, continuous variable) or core area heterogeneity (COHETERO, continuous variable). Models were evaluated with Akaike's information criteria for small sample sizes (AIC$_c$; Burnham and Anderson 2002). AIC$_c$ weights were computed by standardizing AIC$_c$

values across models to sum to 1.0 which provides a measure of each individual model's

likelihood among all models in the model set (Burnham and Anderson 2002). Statistical analysis

and modeling were conducted using SAS software, version 9.2 (SAS Institute 2008), and an

alpha=0.05 was assumed for all statistical tests.

RESULTS

RADIO-TELEMETRY

In 2003, 2004, and 2005, a total of 93 Willow Flycatchers were radio tagged and tracked

at Fish Creek and Roosevelt Lake. At Fish Creek, 13 females, 14 males and 8 flycatchers of

unknown sex were tracked and 1371 total radio locations were collected. The number of radio

locations ranged from 5-95/flycatcher with an average of 39.5 locations/bird.   At least 28 radio

locations were collected in 24 Willow Flycatchers (female $n = 12$, male $n = 12$) at Fish Creek. Of

the Willow Flycatchers with sufficient radio telemetry locations to estimate home range, 18 were

categorized as breeding and 6 were categorized as non-breeding (Table 4.1). Fifty-eight male

Willow Flycatchers were radio-tracked at Roosevelt Lake from 2003-2005 and 1827 total radio

locations were collected. The number of radio locations among the Roosevelt Lake flycatchers

ranged from 3-71 points with an average of 33 locations/bird. Sufficient radio locations for

conducting analysis were collected on 31 male flycatchers out of which 18 were categorized as

breeding and 13 were categorized as non-breeding.

SPACE USE

Differences between flycatcher populations in space use were found primarily among

breeding Willow Flycatchers (Table 4.1). Male breeding flycatcher's mean core area size at Fish

Creek was significantly larger than the mean size of female Fish Creek flycatcher's core areas

($t_{15.245} = -4.12$, $P = <.001$) and Roosevelt Lake male flycatcher's core areas ($t_{14.262} = 3.58$, $P =$

.003; Table 4.1). Similarly, mean home range size was significantly larger for male flycatchers at

Fish Creek than for female flycatchers at Fish Creek ($t_{12.374} = -3.32$, $P = .006$) and male flycatchers at Roosevelt Lake ($t_{17.311} = 4.67$, $P = <.001$, Table 4.1). Among breeding birds, female flycatchers at Fish Creek had a greater proportion of riparian habitat in their core areas than male flycatchers at Fish Creek ($t_{9.75} = -2.17$, $P = .01$) or Roosevelt Lake ($t_{17.27} = 3.92$, $P < .01$). Differences in the proportion of riparian habitat in their core areas did not differ between Fish Creek males and Roosevelt Lake males ($t_{22.52} = 1.63$, $P=.12$). The mean home range heterogeneity in the home ranges of male flycatchers at Fish Creek was significantly greater than the mean home range heterogeneity in the home ranges of Fish Creek female ($t_{15.037} = -2.48$, $P = .03$) and Roosevelt lake male ($t_{12.677} = 2.38$, $P = .03$) flycatchers.   Finally, among breeding flycatchers, Fish Creek male flycatcher home ranges had higher mean habitat richness than the home ranges of Roosevelt Lake male flycatchers ($t_{15.181} = 2.49$, $P = .03$). No differences were found in core area isopleth size, proportion of riparian habitat comprising the home range, core area habitat richness, or core area habitat heterogeneity among breeding flycatchers as a function of site or sex.

In the comparisons across all Willow Flycatchers regardless of breeding status, only mean home range habitat heterogeneity differed significantly by population. Fish Creek male flycatcher home ranges were significantly more heterogeneous than the home ranges of male Roosevelt Lake flycatchers ($t_{20.983} = 2.63$, $P = .02$; Table 4.1). Among the non-breeding flycatchers, core isopleth size, core area size, home range size, proportion of riparian habitat in core areas, proportion of riparian habitat in home ranges, core area habitat richness, home range habitat richness, core area heterogeneity and home range heterogeneity were not found to differ significantly as a function of flycatcher site or sex (Table 4.1).

The Seamen et al. (1998) rule was used to identify core areas in each home range. The kernel UD isopleth selected to represent core area did not vary statistically as a function of breeding site. Figure 4.3 displays the total number of times that each probability isopleth was

selected to represent the core area boundary. The average kernel UD size selected was 35% in

the Fish Creek female flycatcher population, 40% in the Fish Creek male flycatcher population

and 38.71% in the Roosevelt Lake male flycatcher population (Table 4.1).
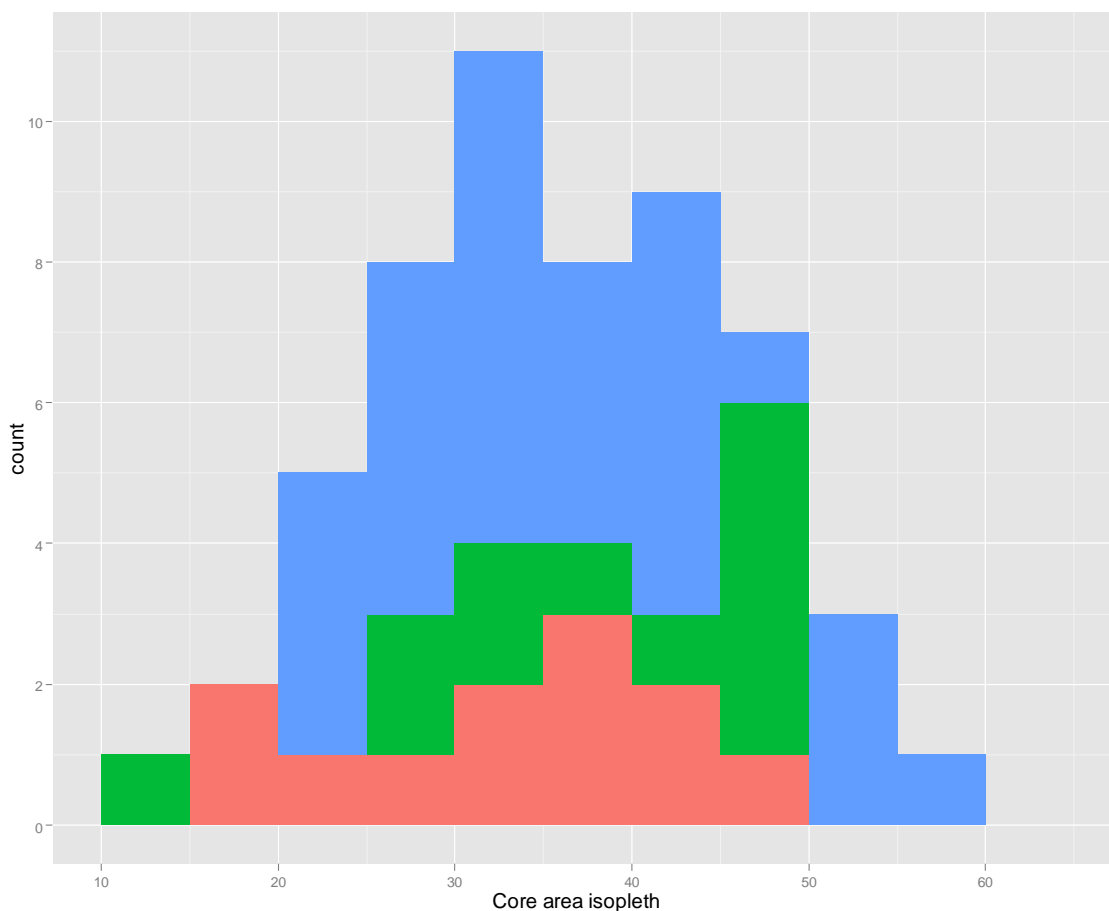
FIGURE 4.3. Counts of the kernel UD isopleth selected to represent the core area boundary using the Seaman et al. 1998 rule for each Willow Flycatcher by breeding site and sex: Fish Creek females (pink), Fish Creek males (green), and Roosevelt Lake males (blue).

When differences in space use were examined as a function of breeding status at

Roosevelt Lake, some space use metrics were found to differ between breeding and non-breeding

flycatchers (Table 4.2). Small sample sizes of non-breeding flycatchers as a function of sex at

Fish Creek precluded us from conducting an analysis of breeding versus non-breeding Fish Creek

flycatchers (*n* non-breeding male flycatchers = 3 , *n* non-breeding female flycatchers = 3, Table

4.1). Average core area isopleth size was larger in breeding than non-breeding flycatchers (t $_{28.86}$ = -2.19, P = .04). Non-breeding flycatchers maintained larger mean core areas (t$_{14.32}$ = 2.88, P = .01) and mean home range sizes (t$_{13.88}$ = 2.88, P = .01) than breeding flycatchers. Other space use characters were not found to differ between breeding and non-breeding flycatchers at Roosevelt Lake (Table 4.2).

PREDICTING HOME RANGE AND CORE AREA SIZE

Eighteen models (nine home range and nine core area specific models) were fit to explore the relationship between home range and core area size and home range metrics and population attributes (Table 4.3). The home range model with the highest AIC$_c$ weight (0.35) included breeding status and home range heterogeneity to predict home range size. The second most likely model (w_i= 0.17) included the effect of sex in addition to breeding status and home range heterogeneity to predict home range size. Breeding status was negatively associated with home range size while increasing home range heterogeneity was positively associated with home range size (Table 4.4). Figure 4.4 illustrates the strong linear relationship between home range habitat heterogeneity and home range size and that this pattern appears independent of population.

The core area model with the highest AICc weight (0.35) included sex, breeding status, and core area heterogeneity. The second most likely model (w_i = 0.23) included the effect of site in addition to sex, breeding status and core area heterogeneity on predicting core area size (Table 4.4). Both the breeding categorization and female sex were found to have a negative effect on core area size while core area heterogeneity and core area size were positively associated (Table 4.4). Figure 4.5 illustrates the strong linear relationship between core area habitat heterogeneity and core area size as a function of breeding site.

TABLE 4.1. Sample size (N), mean, and standard error (SE) of home range and core area metrics for Fish Creek female Willow Flycatchers, Fish Creek male Willow Flycatchers, and Roosevelt Lake male Willow Flycatchers further stratified by breeding status with F-statistic and P-value from one-way ANOVA analysis.

Metric	n	Fish Creek Females Mean	SE	n	Fish Creek Males Mean	SE	n	Roosevelt Lake Males Mean	SE	F	df	P
					All Willow Flycatchers							
Core isopleth	12	35	2.85	12	40	3.26	31	38.71	38.71	0.68	2,52	.51
Core area size[a] (ha)	12	0.23	0.13	12	0.60	0.28	31	1.87	1.87	2.28	2,52	.11
Home range size[a] (ha)	12	2.03	0.82	12	4.10	1.72	31	23.69	23.69	1.53	2,52	.23
Proportion core area riparian[b]	12	0.84	0.07	12	0.72	0.08	28	0.54	0.54	3.15	2,49	.05
Proportion home range riparian[c]	12	0.58	0.08	12	0.35	0.06	28	0.42	0.42	2.08	2,49	.14
Core area habitat richness	12	2	0.39	12	2.5	0.36	28	2.07	2.07	0.72	2,49	.49
Home range habitat richness	12	3.42	0.36	12	4.17	0.27	27	3.30	3.30	2.68	2,48	.08
Core area habitat heterogeneity	12	0.23	0.09	12	0.41	0.10	28	0.25	0.25	1.54	2,49	.23
Home range habitat heterogeneity	12	0.51	0.07	12	0.70	0.06	27	0.49	0.49	3.43	2,48	.04
					Breeding Willow Flycatchers							
Core isopleth	9	32.78	3.24	9	40	4.08	18	41.67	2.39	2.16	2,33	.13
Core area size[a] (ha)	9	0.04	0.02	9	0.35	0.12	18	0.08	0.04	11.14	2,33	<.01
Home range size[a] (ha)	9	0.87	0.50	9	2.64	0.75	18	0.61	0.26	9.01	2,33	.<01
Proportion core area riparian[b]	9	0.96	0.03	9	0.75	0.09	16	0.51	0.11	5.13	2,31	.01
Proportion home range riparian[c]	9	0.31	0.07	9	0.59	0.07	16	0.44	0.09	2.68	2,31	.08
Core area habitat richness	9	1.44	0.34	9	2.22	0.40	16	1.94	0.11	1.92	2,31	.16
Home range habitat richness	9	3	0.37	9	4	0.33	16	3.00	0.22	3.42	2,31	.05
Core area habitat heterogeneity	9	0.09	0.07	9	0.35	0.12	16	0.25	0.04	2.72	2,31	.08
Home range habitat heterogeneity	9	0.40	0.06	9	0.66	0.08	16	0.44	0.04	4.64	2,31	.02
					Non-breeding Willow Flycatchers							
Core isopleth	3	43.33	3.33	3	40	5.77	13	34.62	2.15	1.78	2,16	.20
Core area size[a] (ha)	3	0.78	0.41	3	1.35	1.06	13	4.34	2.14	0.03	2,16	.97
Home range size[a] (ha)	3	5.49	1.97	3	8.49	6.74	13	55.65	29.93	0.01	2,16	.99
Proportion core area riparian[b]	3	0.47	0.12	3	0.65	0.17	12	0.58	0.12	0.16	2,15	.85

Metric	n			Mean			SE			F	df	P
Proportion home range riparian[c]	3	0.74	0.10	3	0.84	0.05	11	0.39	0.08	1.24	2,14	.32
Core area habitat richness	3	3.67	0.33	3	3.33	0.67	12	2.25	0.43	1.74	2,15	.21
Home range habitat richness	3	4.67	0.33	3	4.67	0.33	11	3.73	0.38	1.37	2,14	.29
Core area habitat heterogeneity	3	0.65	0.12	3	0.60	0.21	12	0.26	0.10	2.58	2,15	.11
Home range habitat heterogeneity	3	0.81	0.09	3	0.79	0.01	11	0.58	0.08	2.01	2,14	.17

TABLE 4.2. Sample size (N), mean and standard error (SE) of home range and core area metrics for breeding (breed) and non-breeding (non-breeding) Willow Flycatchers at Roosevelt Lake with t statistic, degrees of freedom (df), and *P*-value from two-tailed t-tests assuming unequal variances.

Metric	n		Mean		SE		t	df	P
	Breed	Non-breed	Breed	Non-breed	Breed	Non-breed			
Core isopleth	18	13	41.67	34.62	2.39	2.15	-2.19	28.86	.04
Core area size[a] (ha)	18	13	0.081	4.34	0.04	2.14	2.88	14.32	.01
Home range size[a] (ha)	18	13	0.61	55.65	0.26	29.92	2.88	13.88	.01
Proportion core area riparian[b]	16	12	0.51	0.58	0.11	0.12	0.42	24.52	.68
Proportion home range riparian[c]	16	11	0.56	0.61	0.09	0.08	0.38	24.71	.70
Core area habitat richness	16	12	1.94	2.25	0.11	0.43	0.71	12.47	.49
Home range habitat richness	16	11	3	3.73	0.22	0.38	1.64	16.67	.12
Core area habitat heterogeneity	16	12	0.25	0.26	0.04	0.10	0.10	14.59	.92
Home range habitat heterogeneity	16	11	0.44	0.58	0.05	0.08	1.54	16.66	.14

[a]Natural log transformed for analysis, non-tranformed values reported for mean and S.E.
[b]Proportion of core area comprised of riparian habitat.
[c]Proportion of home range comprised of riparian habitat.

TABLE 4.3. Candidate models predicting core area and home range size. Models with the lowest AICc and highest weights w_i are best supported.

Model	K^a	AICc	ΔAICc	w_i	R^2
Home range					
BREED + HRHETERO	3	36.59	0	0.35	0.42
SEX + BREED + HRHETERO	4	38.05	1.46	0.17	0.42
SITE + BREED + HRHETERO	4	38.31	1.72	0.15	0.42
SEX + BREED + SITE + HRHETERO	5	38.37	1.78	0.14	0.44
HRHETERO	2	38.77	2.18	0.12	0.37
SEX + BREED + SITE + HRHETERO + HRRIP	6	39.57	2.98	0.08	0.45
HRRIP	2	52.49	15.90	<0.001	0.17
BREED	2	67.55	30.96	<0.001	0.24
Intercept	1	80.30	43.71	<0.001	0
Core area					
SEX + BREED + COHETERO	4	28.67	0	0.36	0.63
SEX + BREED + SITE + COHETERO	5	29.51	0.84	0.23	0.64
BREED + COHETERO	3	29.61	0.94	0.22	0.61
SEX + BREED + SITE + COHETERO + CORIP	6	31.24	2.57	0.10	0.64
SITE + BREED + COHETERO	4	31.57	2.90	0.08	0.61
COHETERO	2	38.35	9.68	<0.001	0.52
BREED	2	69.82	41.15	<0.001	0.25
CORIP	2	70.71	42.04	<0.001	0.11
Intercept	1	83.44	54.77	<0.001	0

^{a}Number of model parameters.

TABLE 4.4. Coefficient estimates (β) and standard errors (S.E.) for best fit home range size and core area size regression models.

Variable	β	S.E.	p
Home range			
BREED	-0.89	0.44	.05
HRHETERO	3.91	0.87	<.001
Core area			
SEX	-0.70	0.42	.10
BREED	-1.24	0.38	.002
COHETERO	4.39	0.62	<.001

DISCUSSION

In this study, we compared space use metrics in two populations of Willow Flycatchers as a function of breeding status and sex. We expected breeding site to have the strongest influence on space use due to differences in habitat structure at Fish Creek and Roosevelt Lake however we found that variation in space use across Willow Flycatchers appears to be influenced by breeding status and flycatcher sex as well as by breeding site.

In the nine space use metrics we examined, only core area habitat heterogeneity did not vary statistically by breeding status, flycatcher sex or breeding site. The lack of variation in core area heterogeneity as a function of flycatcher sex, breeding status or site appears to illustrate Willow Flycatcher's need to breed in mature riparian habitat. This seems to be especially true for the core areas of females which are almost completely comprised of mature riparian habitat. Heterogeneity shows little variation among flycatchers because the majority of the core area is composed of a single patch of mature riparian habitat. This finding is consistent with previous work that identified little variation in the presence and density of willows at the microplot scale within the territories of Willow Flycatchers (Sedgwick and Knopf 1992).

CORE AREA SIZE

The kernel UD isopleth selected to represent individual flycatcher's core areas within the home range ranged from 15% to 60% across all Willow Flycatchers we studied with an average kernel UD isopleth size of 35% for female flycatchers and 40% for male flycatchers. Many bird space use studies use a 50% kernel UD isopleth to represent core area (e.g. Elchuk and Wiebe 2003, Vega Rivera et al. 2003). Our use of a rule-based approach to identify core areas suggests that the application of the 50% kernel UD isopleth does not accurately reflect the core area of most Willow Flycatchers. The 50% kernel UD overestimates the size of core area in the home ranges of most the Willow Flycatchers tracked in this study. The accurate delineation of home range core areas is important because behavior has been found to vary in core areas relative to

other parts of the home range (Indermaur et al. 2009; Bakian in preparation). The regular use of

the 50% kernel UD is likely done for convenience and to facilitate cross-study comparisons. We

found the application of a rule-based core area procedure to be straight-forward and easy to

implement in a GIS framework. The use of data distribution-driven approaches to delineate core

area boundaries has been suggested elsewhere (Hodder et al. 1998; Barg et al. 2005, Wilson

2010) and we also encourage researchers to use non-arbitrary methods of delineating core areas

whenever possible.

BREEDING FLYCATCHERS

As we expected, we found that breeding male flycatchers at Roosevelt Lake maintained

smaller home ranges than male breeding flycatchers at Fish Creek. We hypothesized a priori that

any observed differences in home range size were due to variation in the distribution and

structure of breeding habitat at Fish Creek and Roosevelt Lake. Home ranges of breeding males

at Fish Creek were more heterogeneous. Home range size has been found to be inversely related

to home range quality as home ranges will expand to the point that they encompass resources

sufficient to optimize fitness (Harestad and Bunnell 1979). If habitat quality differences are

driving home range size in Willow Flycatchers then our findings suggest that breeding habitat at

Fish Creek is of lower quality than at Roosevelt Lake. Our findings and more specifically our

linear models provide support for the resource-dispersion hypothesis (Macdonald 1983) which

predicts that home range size will increase with increasing resource patchiness or heterogeneity.

Riparian habitat patch sizes at Fish Creek are relatively small averaging 1.40 hectares and

ranging from 0.29 hectares to 2.5 hectares. In comparison, patch sizes at Roosevelt Lake range

from 0.2 ha to 43 ha (Paxton et al. 2007). Previous research with Southwestern Willow

Flycatchers has found that they will not nest in mature riparian patches less than 10 meters wide

(Sogge and Marshall 2000). In addition, SWFLs have been found to cluster their home ranges

into small sections of large mature riparian patches while leaving large stretches of riparian

habitat unused (Whitfield and Enos 1996, Paxton et al. 1997, Sferra et al. 1997). Previous studies

have reported minimum patch sizes of 0.6 ha required for selection by Southwestern Willow

Flycatchers (Sogge and Marshall 2000). If Willow Flycatchers require buffer zones within habitat

patches, then the size of mature riparian patches at Fish Creek may be on the smaller end of the

range of patch sizes that Willow Flycatchers will select for breeding. Willow Flycatchers may

limit the density within individual patches at Fish Creek to provide adequate buffer zones within
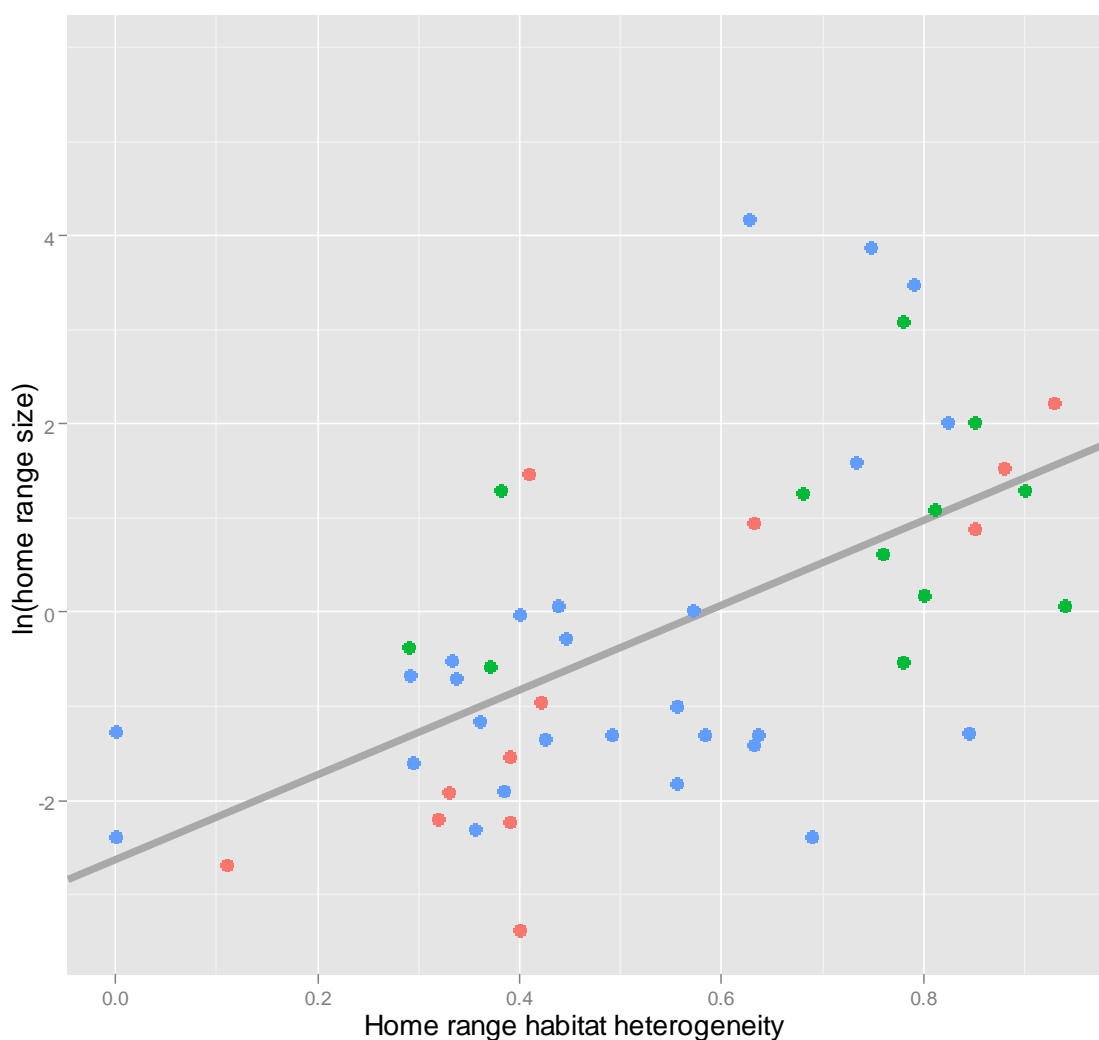
patches.

FIGURE 4.4. Relationship between home range habitat heterogeneity and the natural log of home range size (ha) as a function of sex and breeding site: Fish Creek females (pink), Fish Creek males (green) and Roosevelt Lake males (blue). Adjusted R^2 = .35.

Conversely, Fish Creek male flycatchers may maintain larger home ranges because habitat is not a limiting factor at Fish Creek. Population density and home range size are inversely related (Kjellander et al. 2004, Wang and Grimm 2007) and flycatcher density appears to be higher at Roosevelt Lake than Fish Creek. However, it has been reported elsewhere that flycatchers reach their highest densities in mesic sites (Sedgwick and Knopf 1992) such as Fish Creek. Fish Creek flycatcher home ranges may be larger and more heterogeneous because the microclimate transitions at habitat boundaries are less abrupt than at Roosevelt Lake where riparian habitat is bordered by xeric uplands and open areas.

The home ranges and core areas of female breeding Willow Flycatchers were smaller than the home ranges of male breeding Willow Flycatchers at Fish Creek. We suspect that females at Fish Creek maintained smaller home ranges than males at Fish Creek due to behavioral differences during the breeding season. Female flycatchers are required to center their activity around the nest site as they are primarily responsible for nest construction and egg incubation (McCabe 1991). Conversely, a study by Stafford and Valentine (1985) investigating territory sizes in a Willow Flycatcher population in central Sierra Nevada reported larger territory sizes for female than male flycatchers. Although female SWFLs were not sampled at Roosevelt Lake, we predict based on our findings that the core area and home ranges of female SWFLs at Roosevelt Lake are smaller than the core area and home ranges of female and male flycatchers at Fish Creek and male SWFLs at Roosevelt Lake.

NON-BREEDING FLYCATCHERS

In our categorization of breeding versus non-breeding flycatchers, we did not distinguish between territorial flycatchers radio-tracked during pre and post-breeding periods, territorial unpaired flycatchers and floaters due to small sample sizes in the latter two groups. Space use metrics in radio-tracked non-breeding flycatchers did not appear to be influenced by flycatcher sex or population site. This suggests that when flycatchers are free from the energetic costs of

breeding, Willow Flycatchers will expand their home range size. Alternatively, the opposite relationship may exist in which resource availability is more sparse pre and post-breeding and flycatchers are increasing their space use during these periods to meet their resource needs. Estimates of home range size in Willow Flycatchers during the pre and post-breeding stages may also include long-range movements that were conducted to prospect for future territory site establishment (Bayne and Hobson 2001).
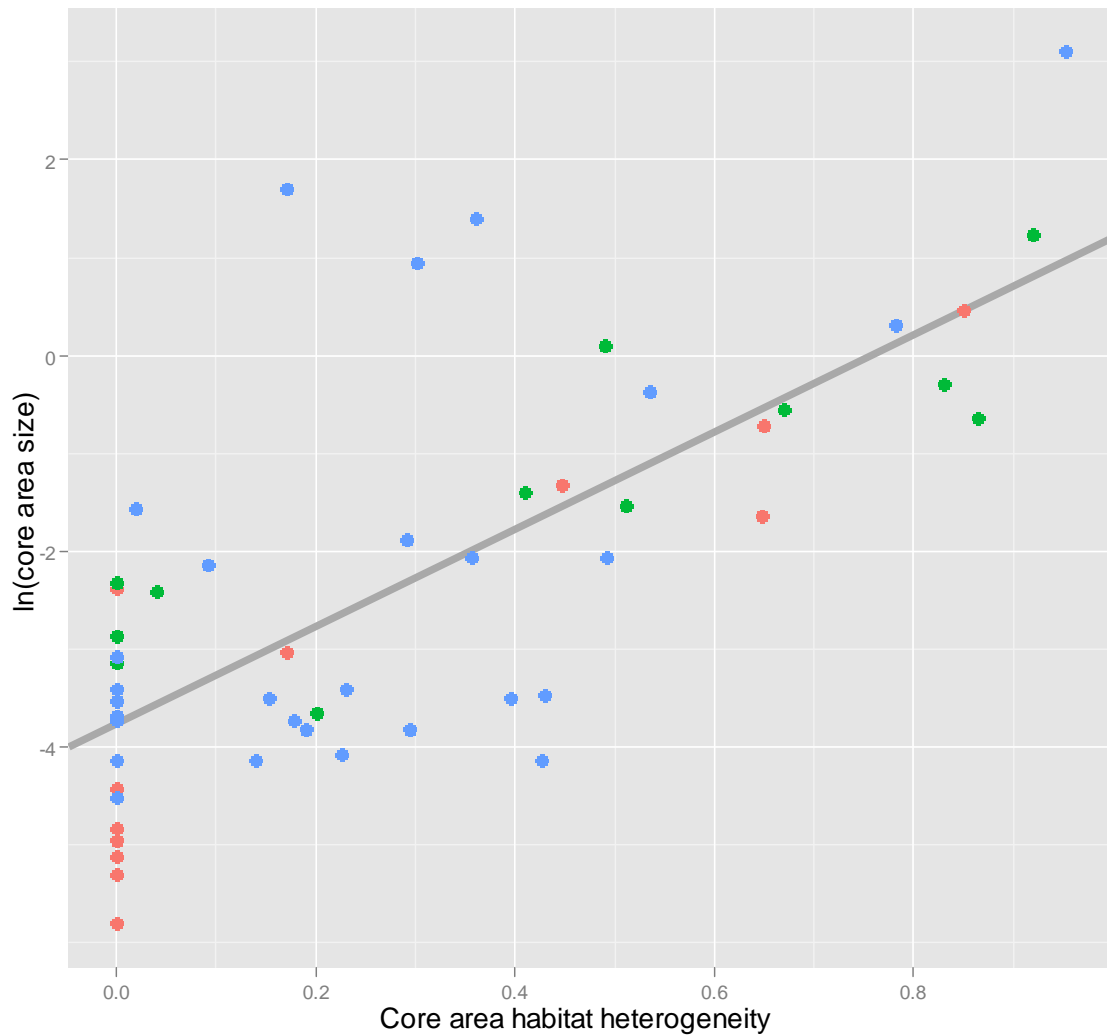

FIGURE 4.5. Relationship between core area habitat heterogeneity and the natural log of core area size (ha) as a function of sex and breeding site: Fish Creek females (pink), Fish Creek males (green) and Roosevelt Lake males (blue). R^2 = .51.

Home range expansion during pre and post-nesting periods has not been observed in many bird species. Some studies have found home range size to be consistent across pre-breeding, breeding, and post-breeding stages in other neo-tropical migrants (Vega Rivera et al. 2003, Garza et al. 2005) as well as other populations of the Willow Flycatcher (Stafford and Valentine 1985). Given the small sample size of floater and territorial, non-mated paired flycatchers in our Roosevelt Lake study sample, the trends we identified here do not appear to be driven by unmated flycatchers.

We did not test for differences in space use metrics between breeding and non-breeding flycatchers at Fish Creek. As space use metrics were not found to differ among non-breeding flycatchers as a function of breeding site, we feel that the differences observed in space use in breeding versus non-breeding flycatchers at Roosevelt Lake may also be common to Fish Creek flycatchers.

MANAGEMENT IMPLICATIONS

Previous estimates of flycatcher home range and territory size using territory mapping techniques range from 0.3 ha in the Sierra Nevada Mountains of California (Flett and Sanders 1987) to 1.72 ha in the Colorado Rockies (Eckhardt 1979). Problems associated with these studies include their reliance upon territorial mapping using re-sight or recapture techniques and their focus primarily on male flycatchers. Territory mapping techniques may underestimate home range size (Anich et al. 2009) and our findings suggest that this may be the case with Willow Flycatchers. The average home range size for breeding males at Fish Creek is larger than any previously reported estimate of Willow Flycatcher home range or territory size. Willow Flycatchers do not vocalize throughout their home range and are difficult to detect when not vocalizing (Bakian, in preparation). The area defined by male song is more likely to represent the boundary of an individual's defended territory rather than the home range.   Resource use patterns collected within the territory may not represent the resources acquired from the entire home

range. The home range size of female flycatchers, who do not sing conspicuously throughout the

breeding season, is even more challenging to accurately estimate in the absence of radio-tracking.

In this study, we found that home range size varies as a function of breeding site, breeding status

and sex. This suggests that multiple characteristics of the population need to be considered when

protecting landscape space for Willow Flycatchers during the breeding season as space use shows

considerable fluctuation. To accurately determine which mechanisms are responsible for

variation in space use, home range characteristics should be considered relative to habitat quality

and fitness measures.

Our findings indicate that patterns in space-use among non-breeding Southwestern

Willow Flycatchers may be relevant to other populations of non-breeding Willow Flycatchers.

This appears to be the case for both male and female non-breeding flycatchers. Patterns in space

use in breeding Southwestern Willow Flycatchers do not seem to be generalizable to non-SWFL

populations whether male or female. Local factors appear to influence inter-population

differences in home range size. Of interest would be to determine if common patterns in space

use are observed among breeding Willow Flycatchers inhabiting mesic versus xeric areas. If so,

this would suggest that habitat quality for Willow Flycatchers vary as a function of larger scale

climatic factors.

LITERATURE CITED

Anich, N.M., T.J. Benson, and J.C. Bednarz. 2009. Estimating territory and home-range sizes: do singing locations alone provide an accurate estimate of space use? Auk 123:626-634.

Barg, J.J., J. Jones, and R.J. Robertson. 2005. Describing breeding territories of migratory passerines:
suggestions for sampling, choice of estimator, and delineation of core areas. Journal of Animal Ecology 74: 139-149.

Bayne, E. M., and K. A. Hobson. 2001. Movement patterns of adult male Ovenbirds during the post-fledging period in fragmented and forested boreal landscapes. Condor 10: 343-351.

Bertrand M.R., A.J. DeNicol, S.R. Beissinger, and R.K. Swihart 1996. Effects of parturition on home ranges and social affiliations of female white-tailed deer. Journal of Wildlife Management 60: 899–909.

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

Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. J. Mammal. 24: 346-352.

Cardinal, S.N. 2005. Conservation of Southwestern Willow Flycatchers: home range and habitat use by an endangered passerine. M.S. thesis, Northern Arizona University, Flagstaff, AZ.

Causey, C.F., M.G. Pollock, S.L. Durst, P.J. Newell, E.H. Paxton, and M.K. Sogge. 2005. Survivorship and movements of Southwestern Willow Flycatchers at Roosevelt Lake, Arizona—2005. U.S. Geological Survey report to the Bureau of Reclamation, Phoenix, AZ.

Cederlund, G., and H. Sand. 1994. Home range size in relation to age and sex in moose. Journal of Mammalogy 75: 1005-1012.

Eckhardt, R.C. 1979. The adaptive syndromes of two guilds of insectivorous birds in the Colorado Rocky Mountains. Ecological Monographs 49: 129-149.

Elchuk, C.L. and K.L. Wiebe. 2003. Home-range size of Northern Flickers (*Colaptes auratus*) in relation to habitat and parental attributes. Canadian Journal of Zoology 81: 954-961.

English, H.C., E.H. Paxton, and M.K. Sogge. 1999. Survivorship and movements of Southwestern Willow Flycatchers in Arizona—1999. U.S. Geological Survey report to the Bureau of Reclamation, Phoenix, AZ.

Fisher, D.O. 2000. Effects of vegetation structure, food and shelter on the home range and habitat use of an endangered wallaby. Journal of Applied Ecology 37: 660-671.

Flett, M.A., and S.D. Sanders. 1987. Ecology of a Sierra Nevada population of Willow Flycatchers. Western Birds 18: 37-42.

Garza, V., F. Suarez, J. Herranz, J. Traba, E.L. Garcia De La Morena, M.B. Morales, R. Gonzalez, and M. Castaneda. 2005. Home range, territoriality, and habitat selection by the Dupont's Lark *Chersophilus Duponti* during the breeding and post-breeding seasons. Ardeola 52: 133-146.

Hanski, I. K., and Y. Haila. 1988. Singing territories and home ranges of breeding Chaffinches: visual observation vs. radio-tracking. Ornis Fennica 65:97-103.

Harestad, A.S., and Bunnell F.L. 1979. Home range and body weight – a reevaluation. Ecology 60: 389–402.

Hodder, K.H., R.E. Kenward, S.S. Wallis, and R.T. Clarke. 1998. Estimating core areas: a comparison of techniques using the common buzzard (Buteo buteo). Journal of Raptor Research 32: 82-89.

Hooge, P.N. and B. Eichenlaub. 1997. Animal movement extension to Arcview. ver. 1.1. Alaska Biological Science Center, U.S. Geological Survey, Anchorage, AK.

Indermaur,L., M. Gehring, W. Wehrle, K. Tockner, and B.Naef-Daenzer. 2009. Behavior-based scale definitions for determining individual space use: requirements of two amphibians. The American Naturalist 173: 60-71.

Johnson, G. D., J. L. Pebworth, and H. O. Krueger. 1992. Retention of transmitters attached to passerines using a glue-on technique. Journal of Field Ornithology 62:486-491.

Kenwood, K.E., and E.H. Paxton. 2001. Survivorship and movements of Southwestern Willow Flycatchers in Arizona—2001. U.S. Geological Survey report to the Bureau of Reclamation, Phoenix, AZ.

Kernohan, B.J., R.A. Gitzen, and J.J. Millspaugh. 2001. Analysis of animal space use and movements, p.125-166. *In* J.J. Millspaugh and J.M. Marzluff [Eds.], Radio tracking and animal populations. Academic Press, San Diego, CA.

Kjellander, P., A.J.M. Hewison, O. Liberg, J.M. Angibault, E. Bideau, and B. Cargnelutti. 2004. Experimental evidence for density dependence of home range size in roe deer (*Capreolus capreolus* L.): A comparison of two long-term studies. Oecologia 139: 478-485.

Kie, J.G., R. T. Bowyer, M.C. Nicholson, B.B. Boroski, and E.R. Loft. 2002. Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. Ecology 83: 530-544.

Koronkiewicz, T. J. , E. H. Paxton, and M. K. Sogge. 2005. A technique to produce aluminum color-bands for avian research. Journal of Field Ornithology 76: 94-97.

Laver, P. N., and Kelly, M. J. 2008. A critical review of home range studies. Journal of Wildlife Management 72, 290-298.

Macdonald, D.W. 1983. The ecology of carnivore social behaviour. Nature 301: 379-384.

Marshall, R.M. and S.H. Stoleson. 2000. Threats, p.13-24. *In* D.M. Finch and S.H. Stoleson [Eds.], Status, ecology, and conservation of the Southwestern Willow Flycatcher. U.S. Forest Service General Technical Report RMRS-GTR-60.

McCabe, R. A. 1991. The little green bird. Ecology of the Willow Flycatcher. Rusty Rock Press, Madison, WI.

Newell, P.J., E.H. Paxton, and M.K. Sogge. 2003. Survivorship and movements of Southwestern Flycatchers at Roosevelt Lake, Arizona-2003. U.S. Geological Survey report to the Bureau of Reclamation, Phoenix.

Newton, I. 1992. Experiments on the limitation of bird numbers by territorial behavior. Biological Reviews of the Cambridge Philosophical Society 67:129-173.

Paxton, E. H., S. N. Cardinal, and T. J. Koronkiewicz. 2003. Using radiotelemetry to determine home range size, habitat use, and movement patterns of Willow Flycatchers. Studies in Avian Biology 26:185-189.

Paxton, E.H., S. Langridge, and M.K. Sogge. 1997. Banding and population genetics of Southwestern Willow Flycatchers in Arizona—1997 Summary Report. U.S. Geological Survey / Northern Arizona University report.

Paxton, E.H., M.K. Sogge, S.L. Durst, T.C. Theimer, and J.R. Hatten. 2007. The ecology of the southwestern willow flycatcher in central Arizona—a 10-year synthesis report: U.S. Geological Survey Open-File Report 2007-1381.

Prescott, D.R.C., and A.L.A. Middleton. 1988. Feeding-time minimization and the territorial behavior of the Willow Flycatcher (*Empidonax traillii*). Auk 105: 17-28.

Pyle, P. 1997. Identification guide to North American birds. Slate Creek Press, Bolinas, CA.

SAS Institute. 2008. SAS version 9.2. SAS Institute, Cary North Carolina, USA

Saïd, S., and S. Servanty. 2005. The influence of landscape structure on female Roe Deer home-range size. Landscape Ecology 20: 1003-1012.

Sauer, J.R., J.E. Hines, G. Gough, I. Thomas, and P.G. Peterjohn. [Online]. 1997. The North American breeding bird survey results and analysis. Version 96.4 <http://www.mbr.nbs.gov/bbs/bbs.html>. Patuxent Wildlife Research Center, Laurel, Maryland (15 October 2010).

Schlorff, R.W. 1990. Report to the Fish and Game Commission: status review of the Willow Flycatcher (*Empidonax traillii*) in California. California Department of Game and Fish: Sacramento, California. Department Candidate Special Status Report 90-1.

Seaman, D.E., B. Griffith, and R.A. Powell. 1998. KERNELHR: A program for estimating animal home ranges. Wildlife Society Bulletin 26: 95-100.

Seaman, D.E., J.J. Millspaugh, B.J. Kernohan, G.C. Brundige, K.J. Raedeke, and R.A. Gitzen. 1999. Effects of sample size on kernel home range estimates. The Journal of Wildlife Management 63: 739-747.

Sedgwick, James A. [Online]. 2000. Willow Flycatcher (*Empidonax traillii*) *In* A. Poole [Ed.], The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, NY. <http://bna.birds.cornell.edu/bna/species/533doi:10.2173/bna.533> (December 2010).

Sedgwick, J.A., and F.L. Knopf. 1992. Describing Willow Flycatcher habitats: scale perspectives and gender differences. The Condor 94: 720-733.

Sferra, S.J., T.E. Corman, C.E. Paradzick, J.W. Rourke, J.A. Spencer, and M.W. Sumner. 1997. Arizona Partners in Flight Southwestern Willow Flycatcher survey: 1993-1996 summary report. Arizona Game and Fish Department, Phoenix. Nongame Technical Report 113.

Sherry, T. W., and R. T. Holmes. 1989. Age-specific social dominance affects habitat use by breeding American Redstarts (*Setophaga ruticilla*): A removal experiment. Behavioral Ecology and Sociobiology 25:327-333.

Smith, T.M., and H.H. Shugart. 1987. Territory size variation in the Ovenbird: the role of habitat structure. Ecology 68: 695-704.

Sogge, M.K., and R.M. Marshall. 2000. A survey of current breeding habitats. *In* D.M. Finch and S.H. Stoleson [Eds.], Status, ecology and conservation of the Southwestern Willow Flycatcher. Gen. Tech. Rep. RMRS-GTR-60. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Sogge, M. K., J. C. Owen, E. H. Paxton, S. M. Langridge, and T. J. Koronkiewicz. 2001. A targeted mist net capture technique for the Willow Flycatcher. Western Birds 32:167-173.

Stafford, M.D., and B.E. Valentine. 1985. A preliminary report on the biology of the Willow Flycatcher in central Sierra Nevada. California and Nevada Wildlife Society Transactions 21: 66-77.

Stefani, R. A., H. L. Bombay, and T. M. Benson. 2001. Willow Flycatcher, in Sierra Nevada forest plan amendment final environmental impact statement, U. S. Forest Service, Pacific Southwest and Intermountain Regions 3: 143–195.

Suedkamp Wells, K. M., J. J. Millspaugh , M. R. Ryan, and M. W. Hubbard. 2003. Effects of radio-transmitters on fecal glucocorticoid levels in captive Dickcissels. Condor 105:805-810.

U.S. Fish and Wildlife Service. 1993. Proposal to list the Southwestern Willow Flycatcher as an endangered species and to designate critical habitat. Federal Register 58:39495–39522.

U.S. Fish and Wildlife Service. 1995. Final rule determining endangered status for the Southwestern Wil-low Flycatcher. U.S. Federal Register 60: 10694-10715.

U.S. Fish and Wildlife Service. 2002. Southwestern Willow Flycatcher (*Empidonax traillii extimus*) final recovery plan. U.S. Fish and Wildlife Service, Albuquerque, New Mexico.

Vega Rivera, J.H., W.J. McShea, and J.H. Rappole. 2003. Comparison of breeding and postbreeding movements and habitat requirements for the Scarlet Tanager (*Piranga olivacea*) in Virginia. Auk 120: 632-644.

Walkinshaw, L. H. 1966. Summer biology of Traill's Flycatcher. Wilson Bulletin 78:31-46.

Wang, M., and V. Grimm. 2007. Home range dynamics and population regulation: an individual-based model of the common shrew *Sorex araneus*. Ecological Modelling 205: 397-409.

White, G. C., and R. A. Garrot. 1990. Analysis of wildlife radio-tracking data. Academic Press, New York.

Whitfield, M.J., and K.M. Enos. 1996. A Brown-headed Cowbird control program and monitoring for the Southwestern Willow Flycatcher, South Fork Kern River, California. California Department of Fish and Game, Sacramento, Final report for contract #FG4100WM-1.

Whittingham, M.J., and K.L. Evans. 2004. The effects of habitat structure on predation risk of birds in agricultural landscapes. Ibis 2004: 210-220.

Wilson, R.R. [Online]. 2010. Identifying and understanding the spatial distribution of bobcat and coyote behavior. All Graduate Theses and Dissertations, Paper 657. <http://digitalcommons.usu.edu/etd/657> (November 2010).

CHAPTER 5

CONCLUSIONS

Spatial heterogeneity drives ecological processes and impacts population-level dynamics (Kareiva 1990). Given the wide-spread alteration of natural landscapes currently underway, understanding how wild populations respond to environmental heterogeneity is more important now than ever. The Willow Flycatcher, a neo-tropical migrant, is a species facing population declines throughout much of its range in the western United States (Sedgwick 2000). Environmental heterogeneity may impact Willow Flycatcher population dynamics in a variety of ways including their dispersal and migration, reproductive fitness, resource selection patterns and space use. My research specifically examines the selection of resources for vocalization and foraging by Willow Flycatchers at individual and population-level scales, Willow Flycatcher's use of aquatic and terrestrial prey subsidies, and variation in space use characteristics in two geographical disparate populations of Willow Flycatchers. In combination, the findings I report illustrate some ways that Willow Flycatchers respond to spatial heterogeneity. In addition, the patterns in resource selection and space use in Willow Flycatchers identified in this study have important species-level conservation and management implications.

In chapter 2, I formulated spatial Bayesian resource selection functions to investigate behavioral resource selection in Willow Flycatchers at individual and population-scales. Results from the individual-level models illustrate the high degree of intraspecific variation in vocalization and foraging resource selection exhibited by Willow Flycatchers. Resource selection functions are often formulated on a population-level ignoring intraspecific variation in selection (e.g. Sawyer et al. 2006, Belant et al. 2010). In addition, wildlife managers typically base their conservation plans on inference derived from population-level studies. However, for species that live in a meta-population like the Willow Flycatcher, species management that is done without

considering intra-specific variation may lead to deleterious effects over the long-term (Pulliam 1988).

Ecologists increasingly use more and more sophisticated analytical tools to model wildlife-environment relationships. They are improving the realism of their models through the use of hierarchical frameworks and the addition of random effects. In chapter 2, I introduced a novel approach to modeling flycatcher behavior using spatial Bayesian resource selection functions. Output from these models was used to produce predictive images of behavior which may be interpreted as "behavioral landscapes." These behavioral landscapes create the link between space use and behavior; a link that has been largely missing from resource selection and space use research (Lima and Zollner 1996, Marzluff et al. 2001).

Sedgwick and Knopf (1992) investigated differences in habitat selection between male and female flycatchers. They observed variation in habitat selection as a function of sex at the nest and song perch scale. My research further elucidates differences in the ecology of male and female flycatchers. I compared and contrasted resource selection, and space use among male and female flycatchers. Only subtle differences in diet were observed as a function of sex while considerable differences were found in vocalization resource selection and space use characteristics. In general, breeding females require less space during the breeding season than breeding males as indicated by home range and core area size comparisons. Interestingly, this pattern seems to dissolve during the pre and post-breeding periods. Further, males are more likely than females to vocalize from high vegetation perches. Discrepancies in space use among males and females are likely the result of sex-specific differences in behavior during the breeding season (Gowaty 1996, Sedgwick 2000). Sex-based behavioral differences may go largely ignored when managing wild passerines populations yet the accumulation of sex-specific inference improves the feasibility of managing landscapes for both sexes.

I observed that vocalization and foraging often occur in spatially disparate areas of the home range. This suggests that multiple core areas exist within the home ranges of Willow Flycatchers. This finding along with the estimates of core area size I made in chapter 4 using the Seaman et al. (1998) rule shows that researchers need to reconsider their arbitrary use of the 50% kernel UD to represent core area. This is certainly the case for Willow Flycatchers in which core areas appear to be better represented by the 35% to 40% kernel UD than the 50% kernel UD. In addition, the clustered distribution of vocalization behavior indicates that both male and female flycatchers do not vocalize throughout their home ranges. Bird researchers need to be aware of this when conducting census studies based on sight or sound.

Willow Flycatcher's selection of alternative habitats for foraging at Fish Creek was an unexpected finding. The presence of high-levels of heterogeneity in the flycatcher home ranges at Fish Creek suggests that the availability of multiple habitat types may be important to this flycatcher population. The use of non-riparian habitats by Willow Flycatchers has not been previously documented. This may be the result of Southwestern Willow Flycatcher based studies dominating the literature as SWFLs have not been observed to use alternative habitats for foraging during the breeding season (Cardinal 2005). The use of alternative habitats may be a characteristic of Willow Flycatchers inhabiting mesic zones. Further study is required to determine if this is a common pattern among Willow Flycatcher populations breeding in mesic areas.

My research provides evidence that landscape configuration may be important to Willow Flycatchers breeding at Fish Creek. The diet component of my study demonstrates that Willow Flycatchers consume both aquatic and terrestrial insects. I found evidence suggesting that adult flycatchers are differentially feeding their nestlings predaceous insects. Other Willow Flycatcher studies have observed similar patterns (Prescott and Middleton 1988, Drost et al. 2003, Wiesenborn and Heydon 2007, Durst et al. 2008). At Fish Creek, adjacent habitats such as

mountain shrub, upland forest and open water may produce greater numbers of predaceous insects than the riparian zone. Insect prey derived in alternative habitats bordering riparian habitat may move into the riparian zone to compliment in situ insect production.

This study was conducted in part to determine the relevance of SWFL based studies to non-SWFL populations. My research uncovered considerable differences in space use characteristics between flycatchers as a function of breeding site and breeding status. Breeding status was found to influence home range characteristics as non-breeding flycatchers used larger areas of the landscape than breeding flycatchers. Similar patterns in space use characteristics were observed in non-breeding flycatchers regardless of breeding site. This suggests that Willow Flycatchers use the largest portion of the landscape towards the beginning and end of the Willow Flycatcher breeding season. Conversely, space use patterns have been found to be largely consistent across the entire breeding season in other neo-tropical migrants (Vega Rivera et al. 2003, Garza et al. 2005). Differences in space use among breeding flycatchers as a function of breeding site indicates that it is inappropriate to apply information gleaned from SWFL-based studies to manage non-SWFL populations.

In conclusion, in this study, I tested Willow Flycatcher's response to environmental heterogeneity, developed a novel modeling approach to analyze behavioral resource selection, and increased our understanding Willow Flycatcher ecology. This was the first study that I am aware of that compared and contrasted space use in different populations of Willow Flycatcher. Finally, future research projects and improved Willow Flycatcher management plans may develop out of this study's major findings.

LITERATURE CITED

Belant, J.L., B. Griffith, Y. Zhang, E.H. Follmann, and L.G. Adams. 2010. Population-level resource selection by sympatric brown and American black bears in Alaska. Polar Biology 33: 31-40.

Cardinal, S.N. 2005. Conservation of the Southwestern Willow Flycatchers: home range and habitat use by an endangered passerine. M.S. thesis, Northern Arizona University, Flagstaff, AZ.

Drost, C.A., E.H. Paxton, M.K. Sogge, and M.J. Whitfield. 2003. Food habitats of the Southwestern Willow Flycatcher during the nesting season. Studies in Avian Biology 26:96-103.

Durst, S.L., T.C. Theimer, E.H. Paxton, and M.K. Sogge. 2008. Age, habitat, and yearly variation in the diet of a generalist insectivore, the Southwestern Willow Flycatcher. The Condor 110(3): 514-525.

Garza, V., F. Suarez, J. Herranz, J. Traba, E.L. Garcia De La Morena, M.B. Morales, R. Gonzalez, and M. Castaneda. 2005. Home range, territoriality, and habitat selection by the Dupont's Lark Chersophilus Duponti during the breeding and post-breeding seasons. Ardeola 52: 133-146.

Gowaty, P.A. 1996. Field studies of parental care in birds: new data focus questions on variation among females. Advances in the Study of Behavior 26: 477-531.

Kareiva, P. 1990. Population dynamics in spatially complex environments: theory and data. Philosophical Trans. of the Royal Society of London 330: 175-190.

Lima S.L., and P.A. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. Trends in Ecology and Evolution 11, 131-135.

Marzluff, J.M., S.T. Knick, J.J. Millspaugh. 2001. High-tech behavioral ecology: modeling the distribution of animal activities to better understand wildlife space use and resource selection, p. 310-326. *In* Millspaugh, J.J., and J.M. Marzluff [Eds.], Radio tracking and animal Populations. Academic Press, San Diego, CA.

Prescott, D.R.C., and A.L.A. Middleton. 1988. Feeding-time minimization and the territorial behavior of the Willow Flycatcher (*Empidonax traillii*). Auk 105: 17-28.

Pulliam, R.H. 1988. Sources, sinks, and population regulation. American Naturalist 132: 652-661.

Sawyer, H., R.M. Nielson, F. Lindzey, and L.L. McDonald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. Journal of Wildlife Management 70: 396-403.

Seaman, D.E., B. Griffith, and R.A. Powell. 1998. KERNELHR: A program for estimating animal home ranges. Wildlife Society Bulletin 26: 95-100.

Sedgwick, J.A. 2000. Willow Flycatcher (*Empidonax traillii*), *In* A. Poole [Ed.], The Birds of North America Online Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/533

Sedgwick, J. A., and F.L. Knopf. 1992. Describing Willow Flycatcher habitats: scale perspectives and gender differences. Condor 94: 720–733.

Wiesenborn, W.D., and S.L. Heydon. 2007. Diet of Southwestern Willow Flycatcher compared among breeding populations in different habitats. Wilson Journal of Ornithology 119: 547-557.

Vega Rivera, J.H., W.J. McShea, and J.H. Rappole. 2003. Comparison of breeding and postbreeding movements and habitat requirements for the Scarlet Tanager (*Piranga olivacea*) in Virginia. Auk 120: 632-644.
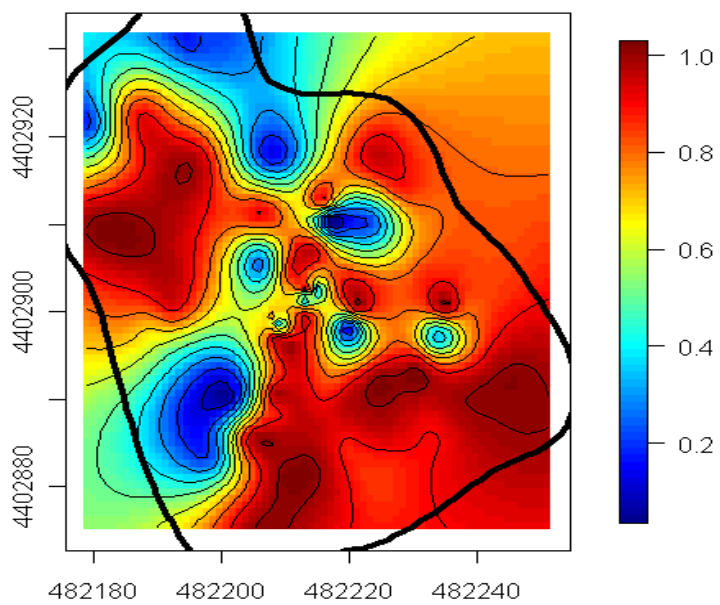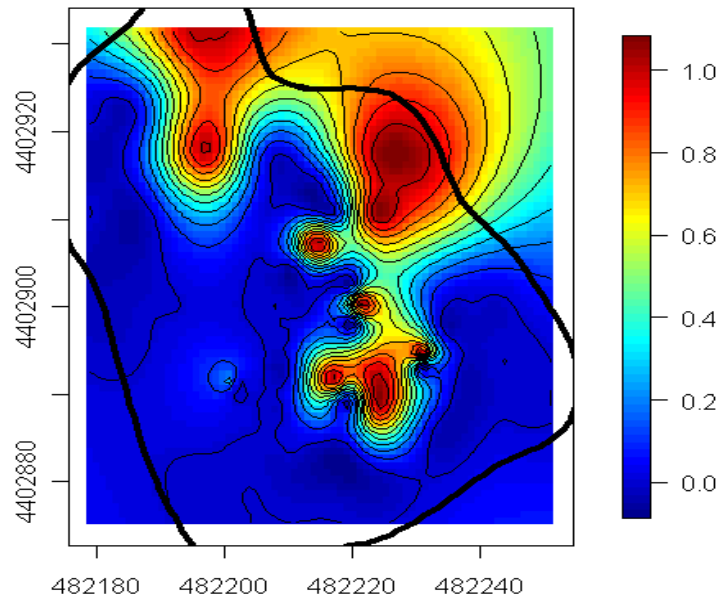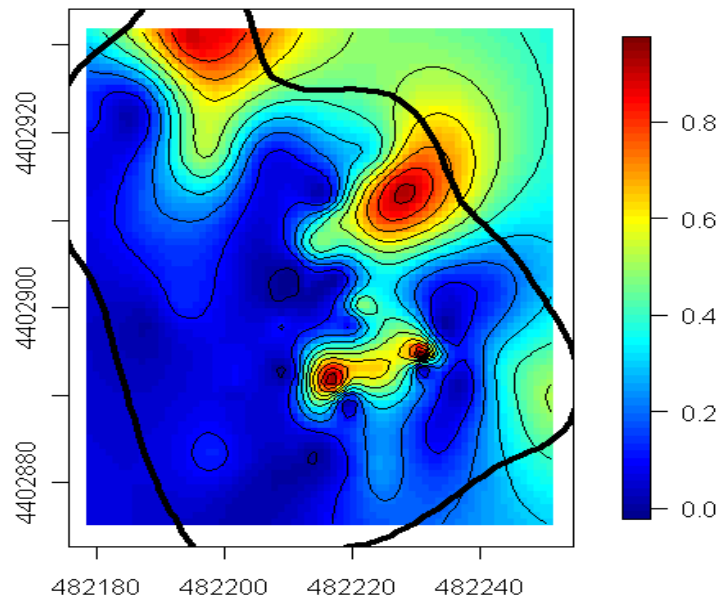
APPENDICES
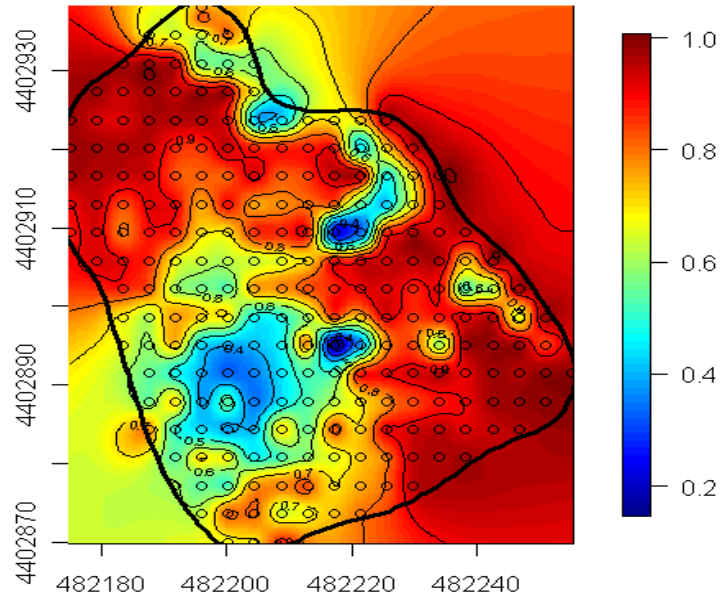
APPENDIX A

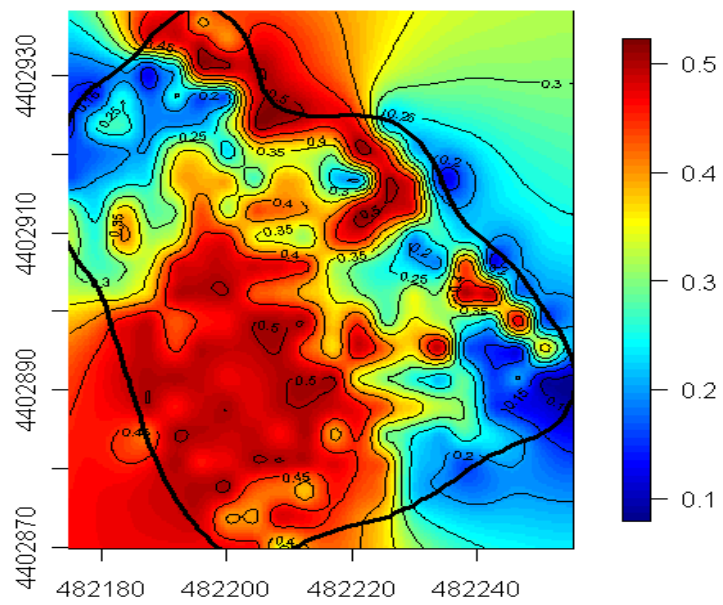
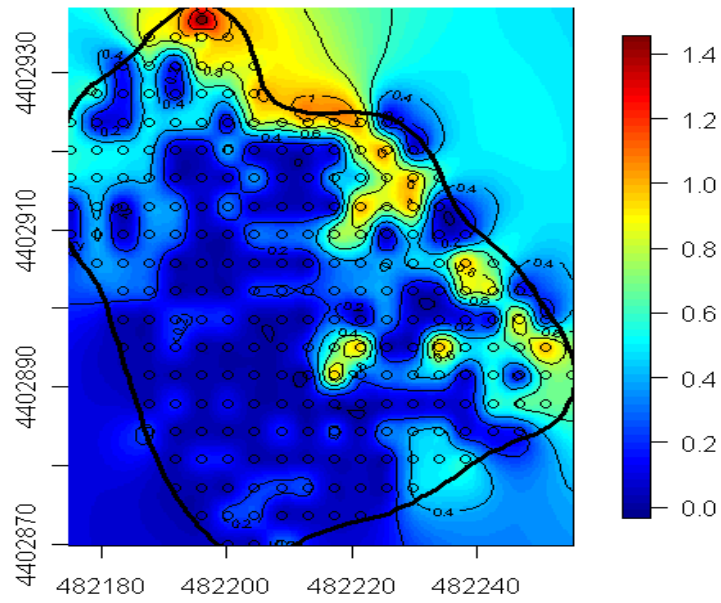Chapter 2 supplemental material
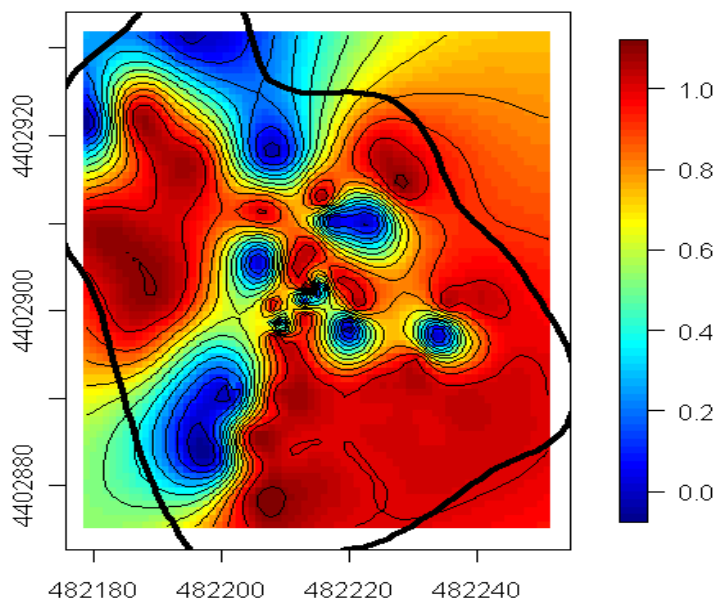
(a)

(b)

(c)

(d)

Fig. A.1. WIFL #1 observed (a) vs. fitted (b) vocalization behavior, and observed (c) vs. fitted (d) foraging behavior.
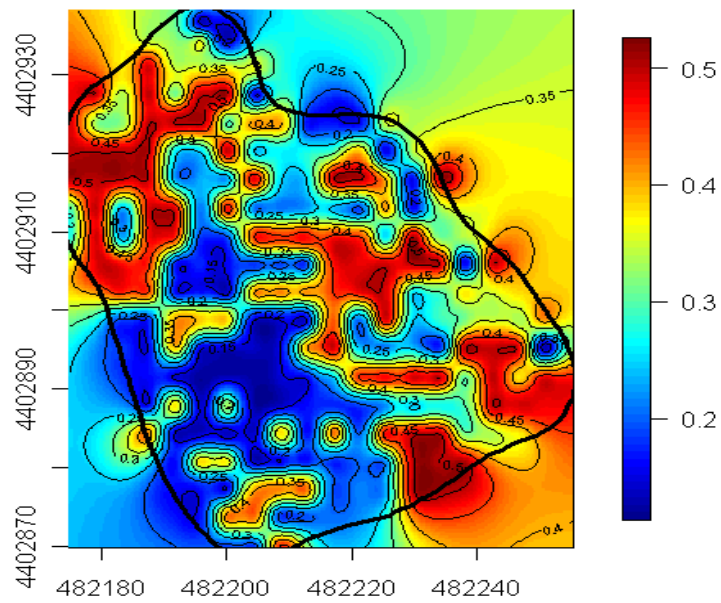
(a)

(b)

(c)

(d)

Fig.A.2. WIFL #1 mean predicted vocalization behavior with prediction grid locations (a), standard deviation predicted vocalization (b), mean predicted foraging with prediction grid locations (c), and standard deviation predicted foraging (d).
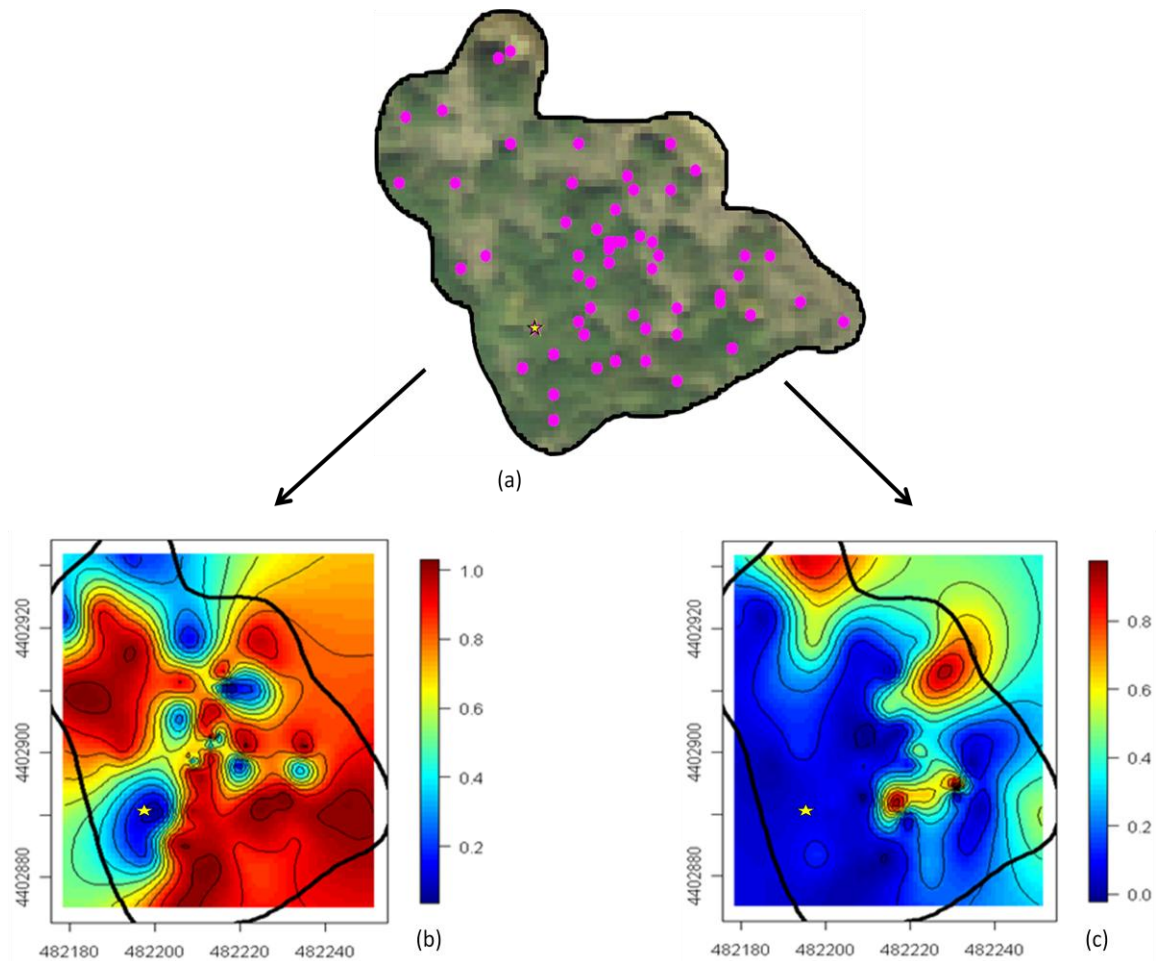
Fig. A. 3. Comparison of approaches to visualizing home range space use: 95% utilization distribution (UD, black outline) using a fixed-kernel estimator (a), probability of vocalization behavior within 95% utilization distribution from fitted Bayesian generalized linear spatial model, scale ranges from 0.0 (dark blue) to 1.0 (red) (b), and probability of foraging behavior withing 95% utilization distribution from fitted Bayesian generalized linear spatial model, scale ranges from 0.0 (dark blue) to 1.0 (red). Nest site location represented by gold star.

APPENDIX B

Co-authorship permission letter

February 14, 2011

Amanda Bakian
Department of Biology
Utah State University
5305 Old Main Hill
Logan, Utah 84322-5305
avbakian@gmail.com

Dear Dr. Paxton,

I am in the process of preparing my dissertation in the Department of Biology at Utah State University, and will be completing my degree in March of 2011. Utah State University's School of Graduate Studies requires all co-authors of dissertation chapters from dissertations written in a multiple-paper format to grant permission to use co-authored materials in dissertations. I am requesting your permission to include the dissertation chapters co-authored by you as shown below. The chapters listed below, as you know, are not currently published in peer-refereed journals. I will use my dissertation to cite the material unless the chapters are published in a peer-refereed journal prior to the completion of my dissertation.

Please indicate your approval of this request by signing in the space provided below.

If you have any questions, please contact me.
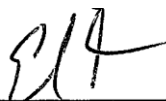
Thank you for your consideration,

Amanda V. Bakian

_____

I hereby grant permission to Amanda V. Bakian to use the following material in her dissertation:

Bakian, A.V., Sullivan, K.A. and E.H. Paxton. 2011. Identifying spatial patterns of behavior in Willow Flycatchers, *Empidonax traillii*, using Bayesian resource selection functions. Chapter 2 *In* Behavioral Responses of Willow Flycatchers, *Empidonax traillii*, to a Heterogeneous Environment. Doctoral Dissertation, Utah State University.

Bakian, A.V., Sullivan, K.A. and E.H. Paxton. 2011. Spatial behavior in Willow Flycatchers: a comparison of two populations. Chapter 4 *In* Behavioral Responses of Willow Flycatchers, *Empidonax traillii*, to a Heterogeneous Environment. Doctoral Dissertation, Utah State University.

Signed: _____

Dated: ___2/15/11_____

CURRICULUM VITAE

AMANDA V. BAKIAN
319 South 800 East, Apt. #5 ◊ Salt Lake City, Utah 84102 ◊ 801.599.3049 ◊
avbakian@gmail.com

SUMMARY OF PROFESSIONAL QUALIFICATIONS

- o Strong data analysis and problem solving skills
- o Project management and leadership experience
- o Effective communicator
- o Demonstrated team player

Research Experience
- o Design and analysis of biological and social science experiments in academic and industry settings.
  - o Formulated hierarchical generalized linear mixed models to analyze a spatially explicit animal resource selection database.
  - o Conducted a survival analysis of student member cohorts in scientific ornithological societies.
  - o Designed a large scale avian and vegetation line transect survey study.

Collaborative Activities and Team Work
- o Contributed scientific expertise to research teams in the U.S. and Japan.
  - o Conducted numerous research projects in collaboration with National Science Foundation ADVANCE grant principal investigators.
  - o Investigated statistical network properties of ecological communities with research team at the University of Kyoto, Japan.
  - o Developed a faculty database tracking recruitment, retention, and promotion of USU science and engineering faculty, and assisted USU administrators with database acquisition.

Leadership and Project Management
- o Supervised field research crew, undergraduate research assistants, and coordinated research projects.
  - o Managed field crew, acquired funding and organized research budget for multi-year animal resource selection study.
  - o Supervised undergraduate research assistants in field and laboratory techniques, data entry, independent research projects, and assisted with poster presentation preparation.

EDUCATION
- o PhD in Biology/Ecology, Utah State University, Logan, Utah, GPA 3.90 (Expected spring 2011)
- o MS in Statistics, Utah State University, Logan, Utah, GPA 3.84 (April 2009)
- o BA in Biology, Colby College, Waterville, Maine (May 1998)

Employment History

Epidemiologist, Utah Registry of Autism and Developmental Disabilities, Department of Psychiatry, University of Utah, Salt Lake City, Utah (January 2010-Present)
Autism and developmental disabilities surveillance, risk factor and trend analyses, and database management.

- o Analysis of the sociodemographic and obstetric risk factors associated with autism and intellectual disabilities.
- o Spatial analysis of autism cases.
- o Manage ACCESS database for six member autism abstraction team.

Graduate Research Assistant, National Science Foundation ADVANCE Grant: SBE 0244922, Utah State University, Logan, Utah (February 2005-December 2009)
Conducted multiple studies to investigate career disparities between women and men science and engineering faculty.

- o Analyzed teaching load, job satisfaction, and work productivity differences between men and women faculty using generalized linear, sample comparison, and multivariate statistical models.
- o Formulated deterministic and stochastic matrix models to project changes in women's representation among science and engineering faculty.
    - ▪ Developed a website to host models as an interactive, on-line tool.
- o Crafted a survey to examine differences in career and family expectations between male and female biology/ecology graduate students.
    - ▪ Supervised a 5 member survey team at the 2007 Ecological Society of America meeting.
- o Developed and managed a faculty database to track the recruitment, retention and promotion of USU faculty.
- o Conducted a survival analysis of male and female graduate student members of two North American Ornithological Societies to project changes in membership composition.
- o Mentored and evaluated undergraduate student researchers in data collection, analysis, and preparation of research posters.

Graduate Research Assistant, US Geological Survey, Utah State University, Logan, Utah (2002-January 2011)
Designed observational study to investigate Willow Flycatcher habitat and resource selection.

- o Supervised three field technicians, managed project budget, and acquired project funding.
- ▪ Formulated Bayesian spatial generalized linear mixed models to describe and predict bird behavior.
- o Investigated Willow Flycatcher diet through carbon and nitrogen stable isotope analysis.

National Science Foundation EAPSI Fellow, Kyoto University, Kyoto, Japan (June-September 2008)

- o Research with Dr. Takayuki Ohgushi investigating the statistical network properties of plant-herbivore ecological communities.
- o Selected to serve as alumni representative to the 2009 NSF EAPSI program.

Biometric Consultant, Salt Lake City, Utah (February 2006 – Present)

Experimental design and analysis, statistical consulting, and database development for clients.
- Developed an avian and vegetation transect survey study, and formulated avian species distribution models that served as the basis for restoration plans in Teton Valley, Idaho for Intermountain Aquatics, Driggs, Idaho.
  - Built project-specific ACCESS database.
- Developed R tutorials for the Mountain Studies Institute, Silverton, CO.
- Statistical consulting for Utah State University doctoral students.

Graduate Teaching Assistant, Department of Biology, Utah State University, Logan, Utah (August 2002- May 2005) Instructed 30-120 students/semester in the following courses:
- Introduction to Biology lab, Human Physiology lab and Ornithology.

Wildlife Biologist, various US federal agencies (Spring 1998-August 2002)
- Conducted a population demography study of the federally endangered Southwestern Willow Flycatcher for the US Geological Survey, Flagstaff, AZ.
- Participated in a study of fire effects on cavity nesting birds for the USDA Forest Service, Rocky Mountain Research Station, Boise, ID.
- Worked on a population demography study of the federally endangered Mariana Crow with the US Fish and Wildlife Survey, Rota Island, Northern Mariana Islands.

COMPUTER SKILLS
- SAS, R/S+, SPSS, ArcGIS, EXCEL, ACCESS, Program Distance.

AWARDS and GRANTS
- NSF EAPSI (East Asian and Pacific Summer Institutes for Graduate Students) Fellowship, 2008
- Datus M. Hammond Memorial Scholarship, Department of Biology, Utah State University, 2007-2008
- Claude E. ZoBell Scholarship, College of Science, Utah State University, 2006-2007
- Graduate Student Symposium Best Paper Presentation, Utah State University, 2004 and 2007
- USU Ecology Center Graduate Student Research Grant, Utah State University, 2003-04, 2005-06, and 2006-07
- Women and Gender Research Institute Grant, Utah State University, 2003
- Frank M. Chapman Grant, American Museum of Natural History, 2003

PUBLICATIONS
- Lorenz, T., **A.V. Bakian**, K.A. Sullivan, and C. Aubry. 2011. Clark's Nutcracker cache site selection and seed dispersal effectiveness. The Auk *In press*.
- Zimmerman-Pinborough, J., and **A.V. Bakian**. 2010. Utah autism rates climb. The Utah Special Educator 33: 10-11.
- **Bakian, A.V.** and K.A. Sullivan. 2010. The effectiveness of institutional intervention on minimizing demographic inertia and improving the representation of women faculty in higher education. International Journal of Gender, Science and Technology 2: 206-234.

o Zimmerman-Pinborough, J., D. Bilder, **A.V. Bakian**, R. Satterfield, P.S. Carbone, B.E. Nangle, H. Randall, and W.M. McMahon. 2011. Sociodemographic risk factors associated with autism spectrum disorders and intellectual disabilities. Autism Research *In review*.

o Zimmerman-Pinborough, J., **A.V. Bakian**, E. Fombonne, D. Bilder, J. Taylor, and W. McMahon. 2011. Changes in the administrative prevalence of autism spectrum disorders: Contribution of special education and health from 2002-2008. Journal of Autism and Developmental Disabilities *In review*.

o Bilder, D., Zimmerman-Pinborough, J., **A.V. Bakian** , Miller, J., Dorius, J., Nangle, B., and W. McMahon. 2011. Prenatal, perinatal, and neonatal factors associated with intellectual disability. Pediatrics *In review*.

o **Bakian, A. V**., and E. H. Paxton. 2004. Home range, movement, and habitat use of Willow Flycatchers, Fish Creek, Utah – 2003. U.S. Geological Survey report to the U.S. Bureau of Reclamation, Salt Lake City. 24 pp.

SELECTED PRESENTATIONS

o **Bakian, A.V.**, and K.A. Sullivan. 2011. The use of aquatic and terrestrial insects by Willow Flycatchers. Joint meeting of the AFO/COS/WOS. Kearney, Nebraska.

o **Bakian, A.V.** , J. Pinborough-Zimmerman, and W. McMahon. 2011. Utah Autism and Developmental Disabilities Monitoring: Site specific evaluation plan. Annual Meeting of the CDC's Autism and Developmental Disabilities Network. Atlanta, Georgia.

o Lorenz, T .J., K. A. Sullivan, and **A. V. Bakian**. 2010. Cache site selection in Clark's nutcracker. Joint meeting of the Cooper Ornithological Society, American Ornithologists' Union, and Society of Canadian Ornithologists. San Diego, CA.

o Pinborough-Zimmerman, J., and **A.V. Bakian**. 2010. Utah Autism and Developmental Disabilities Network: Progress Report. Annual Meeting of the CDC's Autism and Developmental Disabilities Network. Atlanta, Georgia.

o Sullivan, K.A. and **A.V.Bakian**. 2009. Who is getting the jobs in ornithology? And why? Joint meeting of the American Ornithologists' Union and Cooper Ornithological Society, Portland, OR.

o Sullivan, K.A. and **A.V.Bakian**. 2009. Mate choice and reproductive success among early career scientists. The Animal Behavior Society's Annual Meeting, Snowbird, Utah.

o Sullivan, K.A. and **A.V.Bakian**. 2008. Work-family decisions during the transition from graduate school to professional scientist. The New Norm of Faculty Flexibility Conference, Iowa State University, Ames, Iowa.

o Sullivan, K.A. and **A.V.Bakian**. 2008. Transitioning from student to professional scientist: Who gets the jobs and why. The Animal Behavior Society's Annual Meeting, Snowbird, Utah.

o Sullivan, K.A. and **A.V. Bakian**. 2008. Who gets the jobs in ornithology? And why? Joint annual meeting of the American Ornithologists' Union, the Cooper Ornithological Society, and the Society of Canadian Ornithologists, Portland, Oregon.

o **Bakian, A.V.** and K.A. Sullivan. 2008. Advancing women faculty at Utah State University: USU goals, outcomes, and research. International Women in Science Symposium, Hokkaido University, Sapporo, Japan.

o **Bakian, A.V.**, K.A. Sullivan, E.H. Paxton, and R. Wilson. 2007. Finding biological relevance in the home range concept: The application of a Bayesian kriging approach to analyzing and predicting animal space use. 77th Annual meeting of the Cooper Ornithological Society, Moscow, Idaho & 2007 meeting of the Ecological Society of America, San Jose, California.

- Christensen, B.T., **A.V. Bakian**, and K.A. Sullivan. 2007. Investigating the diets of Willow Flycatchers using carbon stable isotopes. Annual Undergraduate Posters on the Hill, Salt Lake City, Utah.
- **Bakian, A.V.**, K.A. Sullivan, and E.H. Paxton. 2006. Finding biological relevance in the 'core area' concept: A study using Willow Flycatcher radio-telemetry data. IV North American Ornithological Conference, Veracruz, Mexico.
- K.A. Sullivan, **A.V. Bakian**, and S. Ellis. 2006. Leaving the flock: The effects of gender on society participation. Animal Behavior Society's Annual Meeting, Snowbird, Utah.
- **Bakian, A.V.** and K.A. Sullivan. 2006. Gender impacts core area habitat use and selection behavior: A study using Willow Flycatchers. The Animal Behavior Society's Annual Meeting, Snowbird, Utah.
- **Bakian, A.V.** 2005. Willow Flycatcher breeding success at Fish Creek: 2003-2005. Utah Ornithological Society's Annual Conference, Logan, Utah.
- K.A. Sullivan, **A.V. Bakian**, and S. Ellis. 2005. Members of the flock: The participation of women in ornithological societies. American Ornithologists' Union's Annual Meeting, Santa Barbara, California.
- **Bakian, A.V.** 2005. An analysis of teaching load differences based on gender and rank on 3 levels of organization at Utah State University. ADVANCE: Annual Institutional Transformation Conference, Arlington, Virginia.
- **Bakian, A.V.**, K.A. Sullivan, and E.H. Paxton. 2004. Looking beyond the corridor: The use of non-riparian habitat types by Willow Flycatchers at Fish Creek. Cooper Ornithological Society's Annual Meeting, LaCrosse, Wisconsin.
- **Bakian, A.V.** 2003. Using radio telemetry to track Willow Flycatchers: Strategies, successes, and surprises Utah Ornithological Society's Annual Conference, Salt Lake City, Utah.
- **Bakian, A.V.**, and K.A. Sullivan. 2003. Researchers flock to bird behavior: A discussion of why avian studies have historically dominated the behavioral ecology literature. Cooper Ornithological Society's Annual Meeting, Flagstaff, Arizona.

INVITED TALKS

- **Bakian, A.V.** 2009. Networking in Nippon: Analyzing ecological and building social networks in the Land of the Rising Sun. National Science Foundation EAPSI pre-departure orientation, Arlington, VA.
- **Bakian, A.V.** and R. Wilson. 2008. Finding biological relevance in the home range concept: The application of a Bayesian kriging approach to analyzing animal space use. Utah State University.
- **Bakian, A.V.** 2006. Gender impacts core area habitat use and selection behavior: A study using Willow Flycatchers. Western Birding Conference/Utah Ornithological Society's Annual Meeting, Brigham City, Utah.