

Bird and butterfly community structure and songbird nest success
in montane meadows of the Greater Yellowstone Ecosystem

by

Ron Edward VanNimwegen

A thesis submitted to the graduate faculty
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Major: Ecology and Evolutionary Biology

Program of Study Committee:
Diane M. Debinski, Major Professor
Rolf Koford
Kirk Moloney

Iowa State University

Ames, Iowa

2004

Graduate College
Iowa State University

This is to certify that the master's thesis of

Ron Edward VanNimwegen

has met the thesis requirements of Iowa State University

Signatures have been redacted for privacy

TABLE OF CONTENTS

CHAPTER ONE. GENERAL INTRODUCTION	1
Thesis Organization	1
CHAPTER TWO. WATERWAY DENSITY AS A LOCAL PREDICTOR OF SONGBIRD NEST SUCCESS IN WILLOW HABITATS	5
Abstract	5
Introduction	6
Methods	9
Results	14
Discussion	15
Acknowledgements	18
Literature Cited	18
Figures and Tables	23
CHAPTER THREE. RELATIONSHIPS BETWEEN SHIFTS IN BIRD AND BUTTERFLY COMMUNITY STRUCTURE AND ENVIRONMENTAL CHANGE	35
Abstract	35
Introduction	36
Methods	41
Results	48
Discussion	51
Acknowledgements	54
Literature Cited	54
Figures and Tables	62
CHAPTER FOUR. GENERAL CONCLUSIONS	74
Figure	79
ACKNOWLEDGEMENTS	80

CHAPTER ONE: GENERAL INTRODUCTION

Thesis Organization

This thesis consists of four chapters resulting from research conducted in the Greater Yellowstone Ecosystem (GYE) of Wyoming and Montana, U.S.A., between the years of 1997 and 2004. Chapter One (this chapter) describes the overall research goals and objectives of the two subsequent chapters, each of which will be submitted for publication in separate ecological journals. This chapter also details the contributions of the collaborators involved in the following two chapters.

Chapter Two, "*Waterway density as a local predictor of songbird nest success in willow habitats,*" addresses potential causes of nest predation on Yellow Warblers (*Dendroica petechia*) in the southern region of our study area, Grand Teton National Park (GTNP). It is a single-species study conducted at a local scale; that is, the factors hypothesized to affect nest predation were measured within the space of each nest territory. The study essentially hypothesized that predation was the chief cause of nest failures in willow habitats of GTNP, and assumed that snakes were the predator primarily responsible for these failures. Although we did not directly measure snake density in our study sites, we used a surrogate measure of surface water density, based on studies that found strong associations between garter snakes and aquatic habitats.

We assessed the effect of waterway density on nest success using a statistical procedure known as *logistic-exposure*. This is a recently published technique that represents another step along the decades of evolving methods of analyzing nest success. Using this method, we quantified the importance of waterway density relative to two other commonly used metrics: nest concealment and distance to a nearby road. These variables provided a

collection of candidate statistical models from which we selected the highest ranked model based on Akaike Information Criterion (AIC) weights. We repeated the model comparison technique with progressively simpler models, and the one that emerged from this iterative process was used in our interpretation of how surface waterway density affects nest success of Yellow Warblers in GTNP.

The third chapter, “*Exploring relationships between bird and butterfly community shifts and environmental change*,” addresses research conducted in the same region (GYE), but on a community-level, including songbirds and butterflies. While the second chapter deals with the productivity of one species, Chapter Three turns our attention to the relative abundance of several species in their respective communities; that is, species composition. Additionally, while chapter two studied relationships within a single habitat type, we now consider the bird and butterfly communities among several habitat classes.

We begin this chapter by describing how Landsat images were used to initially classify a hydrological gradient of montane meadows into distinct habitat types, and then how those same images were used to assess the vegetative condition (Normalized Difference Vegetation Index, or NDVI) of the meadow vegetation over several years. The GYE was divided into a northern region (Gallatins) in northwest Wyoming and southwest Montana, and a southern region (Tetons) in Grand Teton National Park and Bridger-Teton National Forest. Sampling sites were chosen to represent the different meadow types (M-types) and became the basis of several years of bird and butterfly abundance surveys.

To characterize and quantify the changes in these communities, we used non-metric multidimensional scaling (NMDS) to ordinate each site-year in a plot of “similarity” space. When the species composition of several sites changed in a similar manner over time, we

attempted to relate these changes to NDVI changes over the same period. This technique required a contemporary methodology that combined the unconstrained ordination of NMDS with a regression function of site-specific NDVI values.

Depending on the region (Gallatins vs. Tetons) and the taxon (birds or butterflies), communities varied in direction and length of their concurrent shifts in ordination space over time. Some communities varied greatly, but over time showed no consistent shift in any one direction. Others showed very little change over time, indicating stable community structures. Finally, one taxon-region combination (Gallatin butterflies) showed a somewhat consistent change (in direction and length) in community composition over a period of time when NDVI also showed *its* most dramatic change.

Several broad scale correlations have been shown between NDVI and climate, especially in terms of precipitation. We propose that the short term associations that we observed in this study can serve as long term indicators of continuing change in climate, vegetative condition, and community composition.

My graduate committee at Iowa State University was composed of Dr. Diane M. Debinski (my major professor), Dr. Kirk A. Moloney, and Dr. Rolf R. Koford. Dr. Debinski and Dr. Moloney are associate professors from the department of Ecology, Evolution, and Organismal Biology (EEOB). Dr. Koford is a cooperative professor in the department of Natural Resource Ecology and Management (NREM).

Chapter Two resulted from fieldwork conducted by myself and a field assistant, Amanda Hetrick in 2002 and Julie Perrett in 2004. Dr. Debinski also lent field assistance, but her major contribution as the secondary author and investigator stemmed from her help in writing, editing, study design, and finding a diverse assortment of funding sources for this

project. I selected the final study sites, coordinated data collection, chose the method of analysis, and produced the final manuscript.

In Chapter Three, I was primarily responsible for organizing the growing collection of field data from surveys that Dr. Debinski had been coordinating for several years. As primary investigator and author, she formulated the hypotheses and guided me to the resources from which I acquired the analytical techniques that allowed us to test those hypotheses. She provided the majority of the writing, while we shared in editing and interpretation of results. I also assisted in the field surveys, along with many previous graduate students since the project's conception. Dr. Mark Jakubauskas, the third author, is an Assistant Research Professor and Assistant Scientist with the Kansas Applied Remote Sensing (KARS) Program, part of the Kansas Biological Survey at the University of Kansas. He also serves as a Courtesy Assistant Professor with the Department of Geography at the University of Kansas. Dr. Jakubauskas was instrumental in deriving the original habitat classification scheme and the resulting maps that were used to select our actual sampling sites. He also personally trained me in the utilization of contemporary remote sensing analytical software, allowing me to generate the site-specific NDVI values needed for our investigation.

On both projects, Dr. Koford and Dr. Moloney provided valuable input on study designs, data analysis and interpretation, provided direction to the resources I required, and answers to the questions I could not answer on my own. My entire committee helped refine this thesis with editing suggestions and corrections, and was therefore integral to the quality of the final product.

CHAPTER TWO: WATERWAY DENSITY AS A LOCAL PREDICTOR OF SONGBIRD NEST SUCCESS IN WILLOW HABITATS

A paper to be submitted to *The Condor*

Ron E. VanNimwegen and Diane M. Debinski

Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, IA 50011

Abstract

Yellow Warblers (*Dendroica petechia*) are abundant songbirds in willow habitats, with nest failures primarily attributable to predation. We hypothesized that snakes (especially the wandering garter snake, *Thamnophis elegans vagrans*) were important nest predators of Yellow Warbler nests and that areas that attracted snakes would suffer higher predation rates. We estimated nest success at two willow sites at Grand Teton National Park and related daily nest survival probability (s) to a suite of explanatory variables. These variables included measures of waterways (assumed to attract snakes), measures of nest characteristics, and proximity to nearby roads. We used information-theoretic techniques to compare global and reduced models based on Akaike Information Criterion (AIC) weights. AIC weights favored the reduced model using a single variable: the length of waterways (waterway density) within a 20-meter radius of each nest. This variable was significant in the Pacific Creek study site; the logistic-exposure model parameter estimate was -0.048 with a 95% confidence interval = [-0.086, -0.012]. We modeled daily nest survival as a function of waterway length. While parameter precision and other nest failure causes must naturally be taken into account, we concluded that waterway density, an indirect measure of snake

density and thus snake predation, did have a significantly negative correlation with nest success.

Introduction

While relative abundance surveys are convenient and efficient measures of population trends in songbirds, perhaps an even more important assessment of such trends is nest success (Mayfield 1975, Klett and Johnson 1982, Stephens et al. 2003). Ornithologists have attempted to determine which factors are likely to affect nest success and to what degree (Heske et al. 2001, Chalfoun et al. 2002). The nesting period is a critical stage in the life history of altricial songbirds, during which the nest is vulnerable to predation, brood parasitism, and environmental stresses (Winter et al. 2000). An optimal nesting strategy would involve several “decisions” on nest construction and location that minimize these costs, while maximizing fitness benefits such as local food and mate abundance.

Willow dominated habitats of Grand Teton National Park (GTNP) are typically characterized by a mixture of tall (*Salix boothii*) and short (*Salix wolfii*) willow shrubs in extremely hydric soils with high water tables (Debinski et al. 2000). The dense stem arrangement of these shrubs provides a complex three-dimensional structure (foliage height diversity), which in turn provides a variety of possible nesting strategies. Because of this variety of nesting options there is a high diversity of songbird species in these willow habitats and the Yellow Warbler (*Dendroica petechia*) consistently ranks among the highest in abundance (Saveraid et al. 2001).

While it seems obvious that nest concealment, height, and substrate would aid in predator avoidance, the density of predators in the surrounding area should play an equally if not more important role. Given the growing popularity of landscape ecology, nesting studies

have shifted their focus to factors occurring beyond the immediate vicinity of the nest, rather than predator defense features of the nest itself (Winter 1999, Herkert et al. 2003, Phillips et al. 2003). Surely the best way of measuring potential predation pressure in a given area is to directly survey the various predator populations in the area of interest. However, with the convenience of geographical information systems (GISs) and global positioning system (GPS) units, it might be more feasible to survey landscape features suspected to attract predators as an indirect measure of predation pressure. Although indirect, if landscape features are accurate measures of nest success, this will arm managers with more efficient tools to measure songbird productivity, especially in large landscapes where predator surveys would become too costly and time consuming.

In assessing nest success, apparent nest success has traditionally been defined as the percentage of nests that produce fledglings (Johnson 1979). At least one nestling must fledge for that nest to be considered successful, and a sample of nests is required to calculate such an estimate. Mayfield (1975) expanded this measure to correct a bias in apparent nest success resulting from nests that fail before being discovered, and the new parameter generated was (s), the daily probability or rate of nest survival. This estimate was based on the number of days a nest was actually under observation (termed “exposure days”) and not how long the nest was presumed to have survived. The Mayfield estimator still required multiple nests to generate a single measure of success, making local landscape factors that vary among nests impossible to study. Several researchers (Maxson and Riggs 1996, Aebischer 1999, Burhans and Thompson 1999, Garrettson and Rohwer 2001) remedied this problem by using logistic regression to measure survival probabilities of individual nests. Finally, Schaffer (2004) proposed a variation on logistic regression, termed logistic-

exposure, which incorporates the observation interval (exposure days) and the ability to consider a suite of categorical and continuous explanatory factors. He further enhanced this analysis with an information-theoretic method of model comparison enabling researchers to weight different variables and levels of model complexity (Anderson et al. 2000, Anderson and Burnham 2002).

This study focused on the nest success of Yellow Warblers in willow habitats of GTNP as a function of local habitat features. Here, we define “local” at its extreme: the area of an individual nesting pair’s territory (approximately a 20-meter radius based on our sample). We treated predation as the primary cause of nest failure, and snakes as a likely nest predator, although mammalian and avian predators could not be ruled out, and are discussed later. Preliminary data on twenty-nine nests in 2002 indicated that all nest failures were attributed to predation, rather than parasitism or abandonment. All failed nests remained intact but empty and we only found evidence of one attempted case of brood parasitism. In two cases of nest failure, we directly observed snakes in the act of predation. Recent video camera studies have shown snakes to be a major, yet previously underestimated, predator of songbirds and their nests (Lystrup 1952, Stake and Cimprich 2003, Weatherhead and Blouin-Demers 2004), and the stem structure of willows would facilitate the climbing ability of any small animal, including snakes.

Many snakes prefer aquatic habitats; for example, the wandering garter snake (*Thamnophis elegans vagrans*) was most often found near streams, rivers, and lakes in the region of our study (Koch and Peterson 1995). These snakes feed mostly on mollusks (snails and slugs), amphibians (frogs and salamanders), and possibly small fish. Bird nests are probably depredated opportunistically when parental activity is observed by the snake

(Cooper et al. 1999). While nest contents may not be a primary food source for snakes, snakes could be a primary predator on bird nests. On this basis, we chose to use waterways as our “landscape-predation index” in analyzing nest success of Yellow Warblers in willow habitats.

We hypothesized that higher densities of waterways would lead to higher densities of snakes, and therefore a higher probability of opportunistic predation events resulting in lower daily survival probabilities of Yellow Warbler nests. Using the logistic-exposure method, we estimated the magnitude of effect that waterway density had on daily nest survival. We modeled daily nest survival as a function of waterway density. On this basis, we predict that fine scale landscape measures such as waterway density within a single nesting pair’s territory can be reliable estimators of nest success. The ability to assess productivity with readily available tools, time-tested nest monitoring techniques, and existing landscape data sets represents a new and efficient method of analyzing nest success.

Methods

Site selection

We chose two sites in which to sample Yellow Warbler nests. Both were dominated by willows (mostly *S. boothii*) and were adjacent to a paved secondary road. The first site, named Pacific Creek (PC), covered 215 total contiguous hectares while the second site, named Willow Flats (WF), covered 1400 hectares. The areas we sampled within each site were a fraction of these total areas; we found 14 nests in the PC site, spanning an area of 11.1 hectares, and 14 nests in the WF site, spanning an area of 19.8 hectares.

Nest searching and nest variables

Within our sampling areas, we tried to find as many nests as possible, most of which were found by observing parental behavior (Martin and Geupel 1993). Once a nest was found, we recorded its contents by viewing them with a mirror-pole, thereby minimizing our disturbance of the willow branches. We also marked its location with a GPS unit, recorded its height from the ground, and the height of the willow in which it was built. We then monitored each nest every one to five days and recorded whether or not it was still active. The resulting nest data included the length of each visitation interval in days (t), and whether or not the nest had survived each interval ($1 = \text{yes}$, $0 = \text{no}$). On the last interval, we recorded the nest as successful (survived) if we observed or heard Yellow Warbler fledglings within the willow shrub containing the nest, or any shrub directly adjacent to it. We also defined a nest as successful if it had only “partially” fledged; that is, a portion of the nestlings had fledged, were observed alive nearby, and the remaining nestlings were still alive. If the nest was empty and we could find no evidence of fledglings on the last visit (in those cases, parents were absent and/or silent) we defined the nest a failure (survival = 0).

Landscape metrics

We created GIS maps of nest and waterway locations overlaid on aerial photos of 1-meter per pixel resolution, and then quantified the waterway features in the landscape with respect to each nest location in two ways. For each nest, using ESRI® ArcMap 8.3 (ESRI 2002), we determined the distance in meters from the nest to the waterway, and second, we determined the density (length in meters) of that waterway that occurred within a given radius of the nest. The accuracy of nest locations were confirmed by a) marking their location when the GPS “averaging error” fell below four meters, and b) by corroborating their plotted location

on the photo overlays (1-m resolution photos allowed us to distinguish individual willow plants in most cases).

Distance measures are popular, easy to measure, and appropriate when the features of interest are linear edges, such as those resulting from agricultural land parcels that abut nesting habitats (Fletcher and Koford 2003). However, the willow habitats in our study contained several small, circuitous flowing waterways, as well as many large irregularly shaped edges of standing water (we considered both to be important snake habitats and will hereafter use the term waterway to refer to both forms). Since the circuitous nature of these internal “edge-like” features could confound the simplicity of the distance measure (Fig. 1), we chose to include waterway distance and waterway density to reflect potential influences the waterways could have on a nest. To estimate waterway density, we used a 20-meter radius around the nest reflecting the approximate territory size of the Yellow Warbler, based on the geographical data from our nest sample.

We used three features characterizing the nest to reflect potential point-level effects on nest survival. Nest height (NH) and vegetation height (VH) were directly estimated in meters, while a third variable, nest position (NP), was a function of NH and VH as follows:

$$NP = 1 - \left| 0.5 - \frac{NH}{VH} \right| \quad (1)$$

NP reached its maximum when the nest was at the vertical center of the vegetation, theoretically posing the greatest possible physical obstacle to predators or concealment from predators, assuming nests are vulnerable to predation from both vertical directions.

Since the nearby road in each site was virtually linear, we used the distance to the road as a landscape variable (rather than a road density measure similar to our waterway

variable above). Klett and Johnson (1982) found that blue-winged teal nests suffered lower predation when located farther from roads. Finally, we used the study site itself (PC or WF) as a categorical variable to test for site-level differences in nest survival and for possible interactions with the previously defined variables.

Calculating nest success

The logistic-exposure method of analyzing nest success was recently proposed by Schaffer (2004) as an alternative to the popular logistic regression methods. In essence, it models daily nest survival (s) as a logistic function of some explanatory variable (x):

$$s(x) = \frac{e^{\beta_0 + \beta_1 x}}{1 + e^{\beta_0 + \beta_1 x}} \quad (2)$$

As with logistic regression, we can express the log odds ratio as a linear function of x , also known as a logit function:

$$\log_e \left[\frac{s(x)}{1 - s(x)} \right] = \beta_0 + \beta_1 x \quad (3)$$

This linear function is defined by the intercept and slope parameters β_0 and β_1 , respectively, and estimates of these parameters were generated by the logistic-exposure analysis. Equation 2 can be evaluated once parameter estimates are generated from the analysis, and daily survival estimates can be calculated for arbitrary values of the explanatory variable x . The novel modification of the logistic-exposure model is found in the modified logit function, where the observation interval (exposure days) t is included. If we let θ equal the probability of a nest surviving a visitation interval of t days (s^t), we have the following link function for a generalized linear model where $g(\theta)$ is the modified link:

$$g(\theta) = \log_e \left[\frac{\theta^{\frac{1}{\theta}}}{1 - \theta^{\frac{1}{\theta}}} \right] \quad (4)$$

Model selection and variable comparison

We used PROC GENMOD in SAS® 8.2 (SAS Institute 1999) to evaluate daily nest survival in terms of our various explanatory variables. Each visitation interval was treated as an observation and the model assumed that daily survival (s) was equal for nest-days having equal values of explanatory variables. We defined our two water variables, three nest variables, and two “other” variables (Table 1) and began with six “global” models as candidates (Table 2). We did not use more than one water variable or nest variable in any single model since all were highly correlated with one another (all $|r| > 0.66$ except for VH x NP, where $r = -0.24$).

With several candidate models to compare, we used the information-theoretic method of model selection (Anderson and Burnham 2000), which employs Akaike Information Criterion (AIC) values to assign relative weights to each model. We compared the first six models to choose the best candidate and used the variables in that model in subsequent comparisons, thus reducing our number of water and nest variables to one each. We also made a preliminary inspection of those variables’ significance within the chosen model (Table 3).

Having chosen a global model in the previous comparison, we then compared it with four “reduced” models, using its water, nest, and road variables each with the site variable and their interaction (Table 4). The best fitting model of this comparison was again chosen by AIC weight, and indicated whether a reduced model was adequate, or if the global model

should be retained. We again inspected the best-fitting model for the significance of its individual variables (Table 5), based on the X^2 values resulting from the maximum likelihood functions of the logistic-exposure's generalized linear model. This model also produced standard errors and their associated Wald's 95% confidence intervals. Any significant interaction between the site variable and a water, nest, or road variable would then be cause to evaluate the significant variable within each site, analyzing each site as a separate dataset.

After these model comparisons and eliminations, we used the resulting significant variable(s) to generate predictive models of nest success using Equation 1. The model thus plotted daily survival probability s as a function of x . We included the raw data of successful versus unsuccessful nests (ultimate fate) as a function of waterway density (Fig. 5), and an aerial view of our nest locations with respect to the waterway variation in the PC site (Fig. 6).

Results

When comparing our first six models, we found Model #1a to be the top candidate, with an AIC weight of 0.396 (Table 2). That model included WATER_DENSITY, NP, ROAD, and SITE as explanatory variables. Therefore, we eliminated the WATER_DISTANCE, NH, and VH variables from further analyses.

In our next round of comparisons, the model with WATER_DENSITY and SITE (and their interaction) was the best-fitting model with an AIC weight of 0.749 (Table 4). Of these effects, SITE and the WATER_DENSITY * SITE interaction were significant, indicating that WATER_DENSITY may have had a strong effect in one site while not in the other. Our final model comparison tested this possibility; by analyzing the WATER_DENSITY effect alone in each site separately, we found it to be significant in Pacific Creek while not in the Willow Flats (Table 5).

Of the original variables constructed for our models, WATER_DENSITY was shown to have a significant effect when it was in the full model (#1a), in its interaction with SITE in the reduced model (#1b), and when it was the sole variable in the PC site. To evaluate the predictive ability of the parameter estimate for WATER_DENSITY, we solved for daily survival probability in Equation 1 using parameters from our last model (-0.0483 as the slope β_1 , 5.8966 as the intercept β_0 , and values of WATER_DENSITY ranging from 0 to 80 meters as the explanatory variable x). We also calculated the probability of surviving the entire nesting period, assuming a 26-day for the full nesting period (based on average laying, incubation, hatching, and brooding times of our sample), and plotted both survival measures as a function of waterway quantity (Fig. 2). The standard errors of our estimate and intercept were 0.0192 and 1.0974, respectively. Using the Wald confidence limits, we plotted a 95% interval around the daily survival and fledging survival functions (figs. 3 and 4, respectively).

Discussion

We hypothesized that waterways would affect nest success of Yellow Warblers in willow habitats and we found evidence supporting this prediction in the PC study site. The failure of the WF nests to follow this model could have been due to avian predation. We observed a family of Common Ravens (*Corvus corax*) that concentrated its activities in the middle of the area where our nests were located. Coincidentally, we observed the ravens' greatest activity during our study period centered among a small group of aspens (*Populus tremuloides*) near several of our low-water density nests. Most of these nests failed, contrary to what our hypothesis would have predicted. Ravens were usually perched high in the aspens when we were in the WF area, but occasionally we witnessed them maneuvering within individual willow shrubs. Also, though large-billed birds, we have observed ravens grooming each

other in extremely precise manners, suggesting more coordination than one might expect from their bulky appearance. Therefore, despite their size, our observations suggest that ravens probably possess the physical articulation (through perching and bill dexterity) to remove eggs from a warbler nest without disturbing the structure of the nest itself. It would not be unreasonable to attribute at least some of the large number of nest failures to the local raven breeding pair and offspring. We generally discounted mammalian predators from our list of “usual suspects” due to the lack of shell fragments in any of the failed nests, along with the nearly perfectly preserved structure of the failed nests.

Although our waterway parameter had a “significant effect” on daily nest survival in terms of statistical modeling, we must acknowledge that waterway density was merely a proxy for the true hypothesized effect: predation. In addition, we must consider the limitations in the predictability of the model due to the precision in our estimate. We modeled daily nest survival as a function of waterway density by using our observed range of waterway values (using Equation 2 and solving for s , see METHODS). A seemingly small standard error is magnified when daily survival probabilities are scaled to the probabilities of entire nesting periods (s^d), where d is the number of days in the nesting period (Fig. 3). The lack of precision in our parameter estimate (large standard errors) is most likely due to small sample size. The lower nest success of the WF site effectively halved the sample size for estimating the waterway density effect. Although large standard errors can result from a poorly fitted statistical model, our global model performed well in a Hosmer-Lemeshow goodness of fit test ($X^2 = 3.52$, $df = 7$, $P = 0.833$), as did the reduced models. Log transforming our waterway variable and splitting it into categorical classes did not improve the precision; on the contrary, such models typically had poor AIC weights.

Combining the logistic-exposure method of analyzing nest success with the model selection criterion based on AIC weights provides several advantages to previous methods. First, nest-specific factors can now be modeled. Early Mayfield methods recommended sample sizes of several nests to generate a reliable estimate of daily survival, and that one estimate would have to apply to the entire region that provided such a sample. Second, the logistic nature of the statistical model constrains daily survival estimates to values between zero and one, where previous methods did not (e.g., Klett and Johnson 1982).

Finally, information theoretic techniques of model selection, model averaging, and parameter estimation are providing a new paradigm for revealing true ecological processes that are sometimes vulnerable with the traditional numerically sensitive significance testing (Anderson and Burnham 2000). They can provide a legitimate argument to choose a simple model over a complex one, or vice versa. They lend support to a model of intermediate complexity and aid in variable selection by doing so. Should several models prove nearly equal in passing the AIC criteria, those models can be properly weighted to provide more accurate parameter estimates, and ultimately more accurate predictions of nest success and songbird productivity.

As for Yellow Warblers in willow habitats in GTNP, we have always witnessed high densities of this species, based on general observations and data from related research projects (Debinski et al. 2000, Saveraid et al. 2001). This investigation suggests that small areas within willow habitats may be vulnerable to failures, yet productive areas apparently remain in sufficient quantities to maintain a healthy population.

High water tables are necessary for the persistence of willows, and surface water tends to be found where willows are at their thickest and densest in terms of foliage and

shrub densities. Knopf and Sedgwick (1992) found that Yellow Warbler nest site selection was most correlated with large consolidated assemblages of willows as opposed to isolated shrubs, and less dependent on a great number of individual shrub characteristics. We tended to find contiguous patches of tall willows near waterways, so this implies a trade-off between preferred nesting habitat and predator density, with both being a function of surface water. A winning strategy in such a scenario would be to nest in a recently dried up waterway, where the willows are still dense, but the lack of surface water has removed the garter snakes' primary prey source. Since Yellow Warblers tend to feed mostly on foliage insects (Salt 1957) that do not require standing water, the foraging needs would not be compromised by this nesting strategy either.

Acknowledgements

We wish to thank the University of Wyoming – National Park Service Research Station and the Denver Zoological Foundation for supporting this research. We thank the other researchers who use these facilities for the collaborative atmosphere their presence brings to the station. Grand Teton National Park's department of science and resources has been consistently cooperative with our efforts as well. Thanks also to the research technicians Amanda Hetrick and Julie Perrett for their expertise and good natured work ethic in the field.

Literature Cited

- AEBISCHER, N.J. 1999. Multi-way comparisons and generalized linear models of nest success: Extensions of the Mayfield method. *Bird Study* 46:22-31.
- ANDERSON, D.R., AND K.P. BURNHAM. 2000. Model selection and multimodel inference : a practical information-theoretic approach. Springer, New York.

- ANDERSON, D.R., AND K.P. BURNHAM. 2002. Avoiding pitfalls when using information-theoretic methods. *Journal of Wildlife Management* 66:912-918.
- ANDERSON, D.R., K.P. BURNHAM, AND W.L. THOMPSON. 2000. Null hypothesis testing: Problems, prevalence, and an alternative. *Journal of Wildlife Management* 64:912-923.
- BURHANS, D.E., AND F.R. THOMPSON III. 1999. Habitat patch size and nesting success of Yellow-breasted Chats. *Wilson Bulletin* 111:210-215.
- CHALFOUN, A.D., M.J. RATNASWAMY, AND F.R. THOMPSON, III. 2002. Songbird nest predators in forest-pasture edge and forest interior in a fragmented landscape. *Ecological Applications* 12:858-867.
- COOPER, R.J., R.R. WILSON, G.D. ZENITSKY, S.J. MULLIN, J.A. DECECCO, M.R. MARSHALL, D.J. WOLF, AND L.Y. POMARA. 1999. Does nonrandom nest placement imply nonrandom nest predation? – a reply. *Condor* 101:920-923.
- DEBINSKI, D.M., M.E. JAKUBAUSKAS, AND K.KINDSCHER. 2000. Montane meadows as indicators of environmental change. *Environmental Monitoring and Assessment* 64:213-225.
- ESRI, 2002. ArcMap. Environmental Systems Research Institute. Redlands, California.
- FLETCHER, R.J., AND R.R. KOFORD. 2003. Spatial responses of Bobolinks (*Dolichonyx oryzivorus*) near different types of edges in northern Iowa. *Auk* 120:799-810.
- GARRETTSON, P.R., AND F.C. ROHWER. 2001. Effects of mammalian predator removal on production of upland-nesting ducks in North Dakota. *Journal of Wildlife Management* 65:398-405.

- HERKERT J.R., D.L. REINKING, D.A. WIEDENFELD, M. WINTER, J.L. ZIMMERMAN, W.E.
JENSEN, E.J. FINCK, R.R. KOFORD, D.H. WOLFE, S.K. SHERROD, M.A. JENKINS, J.
FAABORG, S.K. ROBINSON. 2003. Effects of prairie fragmentation on the nest success
of breeding birds in the midcontinental United States. *Conservation Biology* 17:587-
594.
- HESKE, E.J., S.K. ROBINSON, AND J.D. BRAWN. 2001. Nest predation and neotropical
migrant songbirds: piecing together the fragments. *Wildlife Society Bulletin* 29:52-
61.
- JOHNSON, D.H. 1979. Estimating nest success: the Mayfield method and an alternative.
Auk 96:651-661.
- KLETT, A.T., AND D.H. JOHNSON. 1982. Variability in nest survival rates and implications to
nesting studies. *Auk* 99:77-87.
- KNOFF, F.L., AND J.A. SEDGWICK. 1992. An experimental study of nest-site selection by
Yellow Warblers. *Condor* 94:734-742.
- KOCH, E., AND C.R. PETERSON. 1995. *Amphibians and Reptiles of Yellowstone and the
Grand Teton National Parks*. University of Utah Press, Utah.
- LYSTRUP, H.T. 1952. A garter snake captures a young bird. *Yellowstone Nature Notes*
26:10-11.
- MARTIN, T.E., AND G.R. GEUPEL. 1993. Nest-monitoring plots – methods for locating nests
and monitoring success. *Journal of Field Ornithology* 64:507-519.
- MAXSON, S.J., AND M.R. RIGGS. 1996. Habitat use and nest success of overwater nesting
ducks in westcentral Minnesota. *Journal of Wildlife Management* 60:108-119.

- MAYFIELD, H.F. 1975. Suggestions for calculating nest success. *Wilson Bulletin* 87:456-466.
- PHILLIPS, M.L., W.R. CLARK, M.A. SOVADA, D.J. HORN, R.R. KOFORD, AND R.J. GREENWOOD. 2003. Predator selection of prairie landscape features and its relation to duck nest success. *Journal of Wildlife Management* 67:104-114.
- RODEWALD, A.D. 2004. Nest-searching cues and studies of nest-site selection and nesting success. *Journal of Field Ornithology* 75: 31-39.
- SALT, G.W. 1957. An analysis of avifaunas in the teton mountains and Jackson Hole, Wyoming. *Condor* 59:373-393.
- SAS Institute. 1999. SAS/STAT Users Guide, version 8.2. SAS Institute, Cary, North Carolina.
- SAVERAID, E.H., D.M. DEBINSKI, K. KINDSCHER, AND M.E. JAKUBAUSKAS. 2001. A comparison of satellite data and landscape variables in predicting bird species occurrences in the Greater Yellowstone Ecosystem, USA. *Landscape Ecology* 16:71-83.
- SHAFFER, T.L. 2004. A unified approach to analyzing nest success. *Auk* 121:526-540.
- STAKE, M.M. AND D.A. CIMPRICH. 2003. Using video to monitor predation at black-capped vireo nests. *Condor* 105:348-357.
- STEPHENS S.E., D.N. KOONS, J.J. ROTELLA, AND D.W. WILLEY. 2003. Effects of habitat fragmentation on avian nesting success: a review of the evidence at multiple spatial scales. *Biological Conservation* 115:101-110.
- WEATHERHEAD, P.J. AND G. BLOUIN-DEMERS. 2004. Understanding avian nest predation: why ornithologists should study snakes. *Journal of Avian Biology* 35:185-190.

WINTER, M. 1999. Nesting biology of Dickcissels and Henslow's Sparrows in southwestern

MISSOURI PRAIRIE FRAGMENTS. WILSON BULLETIN 111:515-526.

WINTER, M., D.H. JOHNSON, AND J. FAABORG. 2000. Evidence for edge effects on multiple

levels in tallgrass prairie. Condor 102:256-266.

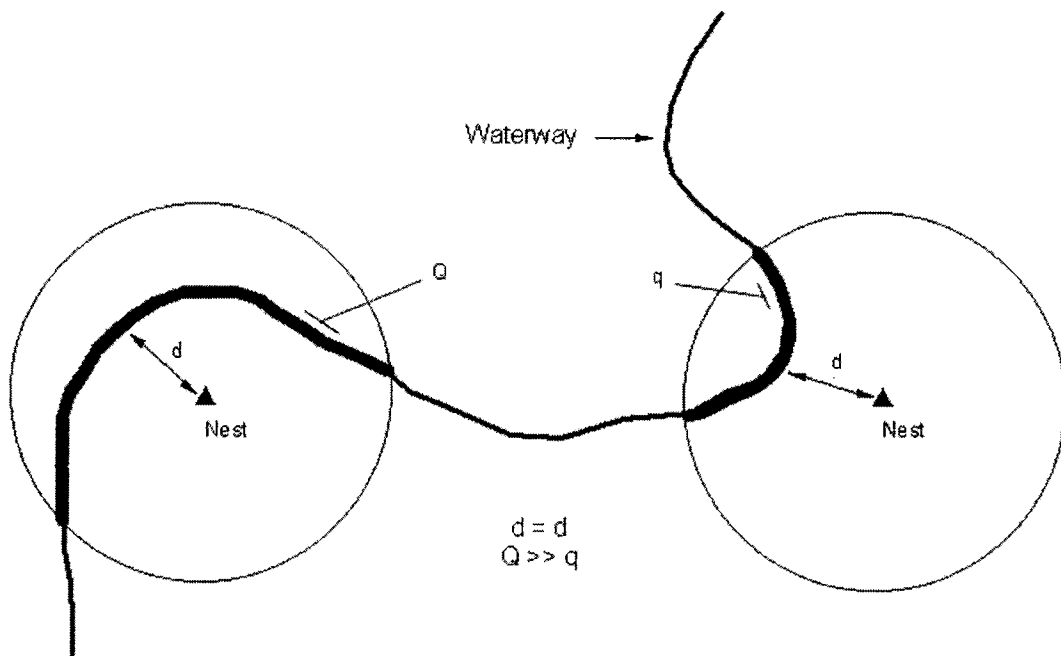


Figure 1. Potential discrepancy between distance and density measures of linear landscape features when they are circuitously shaped rather than linear. The distance measures (d) are equal for the two nests (black triangles within circular territories) while the quantity measures are not nowhere near equal (length of the Q segment is more than twice that of the q segment).

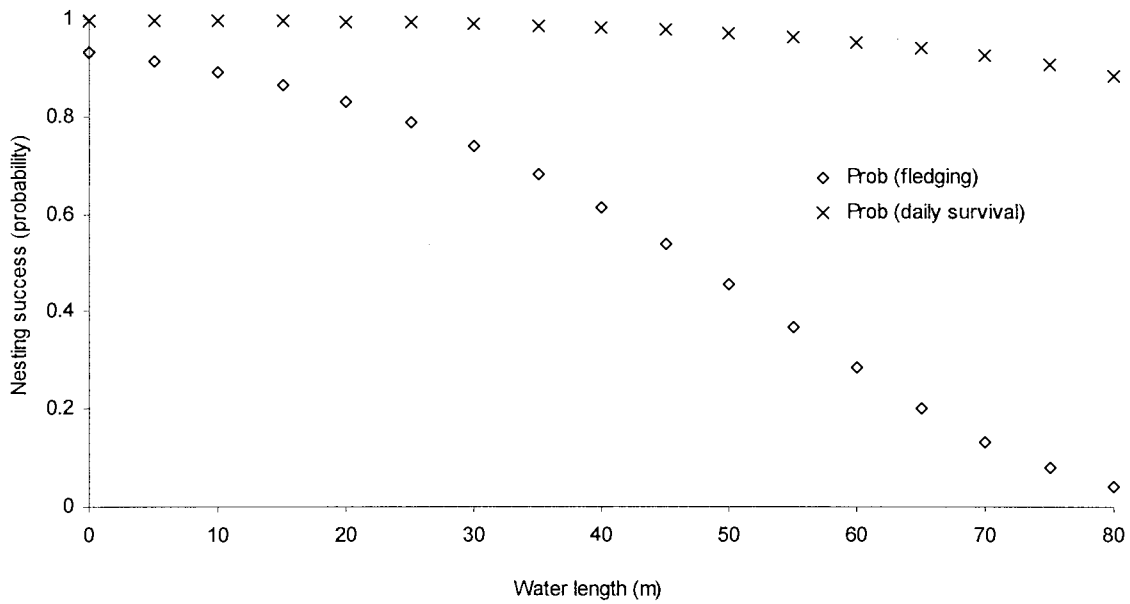


Figure 2. Projected probabilities of daily nest survival and of surviving the entire nest period (fledging) for waterway lengths of 0 to 80 meters based on the parameter estimate of the WATER_DENSITY variable from a logistic-exposure model (WATER_DENSITY = length of waterway within a 20-meter radius of each nest). Fledging probability was based on daily survival raised to the power of 26 days (on average) in a Yellow Warbler nesting period. Parameter estimate and confidence interval was used from the Pacific Creek site.

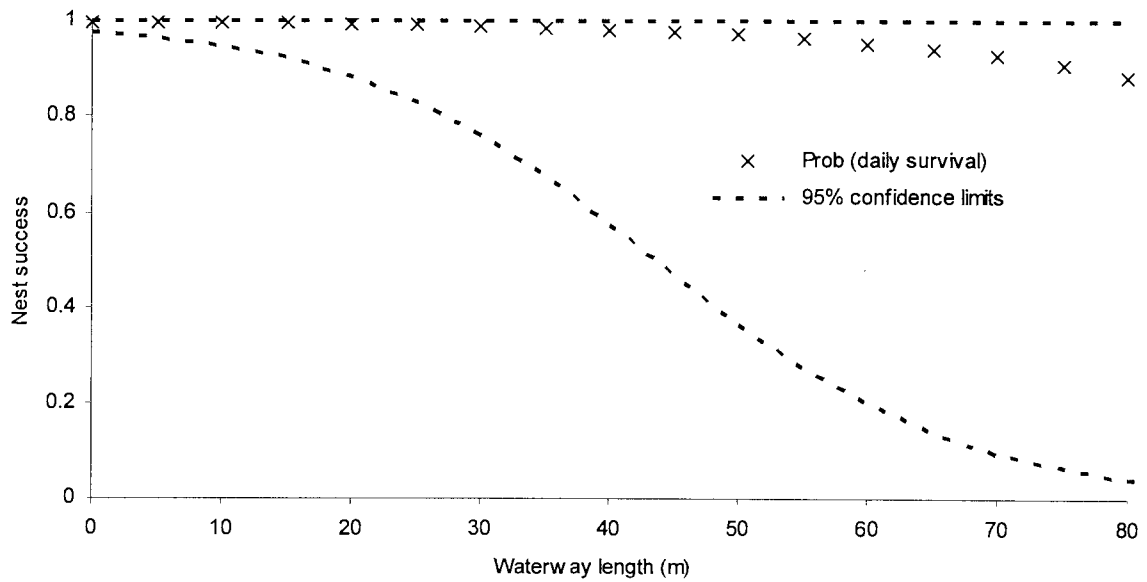


Figure 3. Projected probability of daily nest survival with 95% confidence limits based on the WATER_DENSITY parameter estimate and its Wald confidence limits from a logistic-exposure model (WATER_DENSITY = length of waterway within a 20-meter radius of each nest). Parameter estimate and confidence interval was used from the Pacific Creek site.

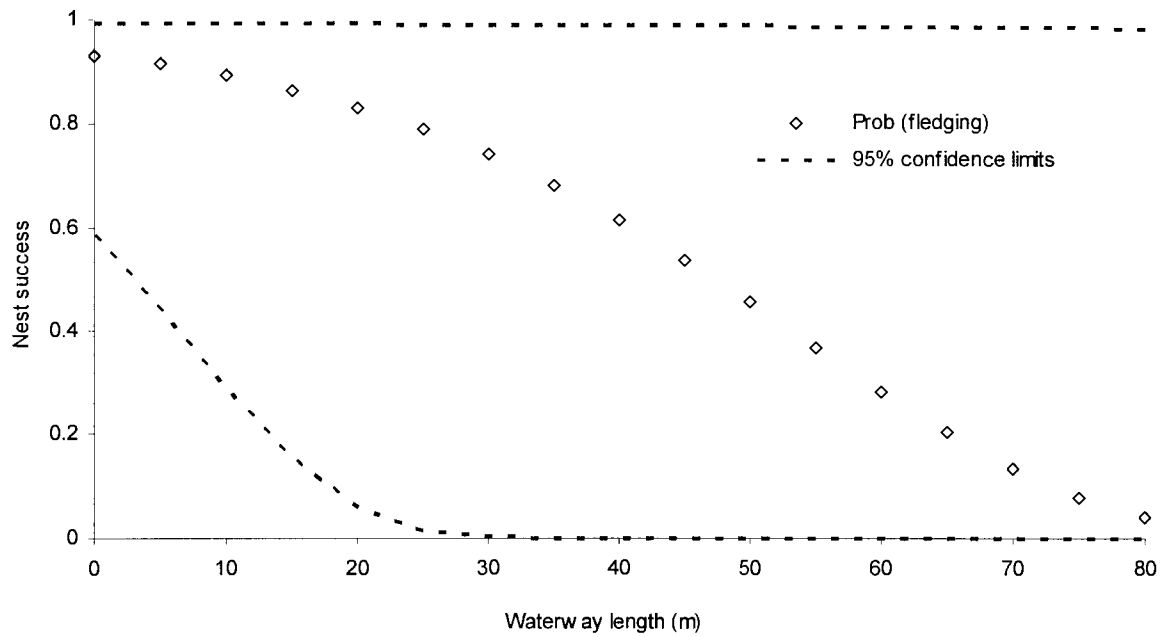


Figure 4. Projected probability of surviving the entire nest period (fledging) based on a 26-day nesting period, the WATER_DENSITY parameter estimate, and its Wald confidence limits from a logistic-exposure model (WATER_DENSITY = length of waterway within a 20-meter radius of each nest). Fledging probability was based on daily survival raised to the power of 26 days (on average) in a Yellow Warbler nesting period. Parameter estimate and confidence interval was used from the Pacific Creek site.

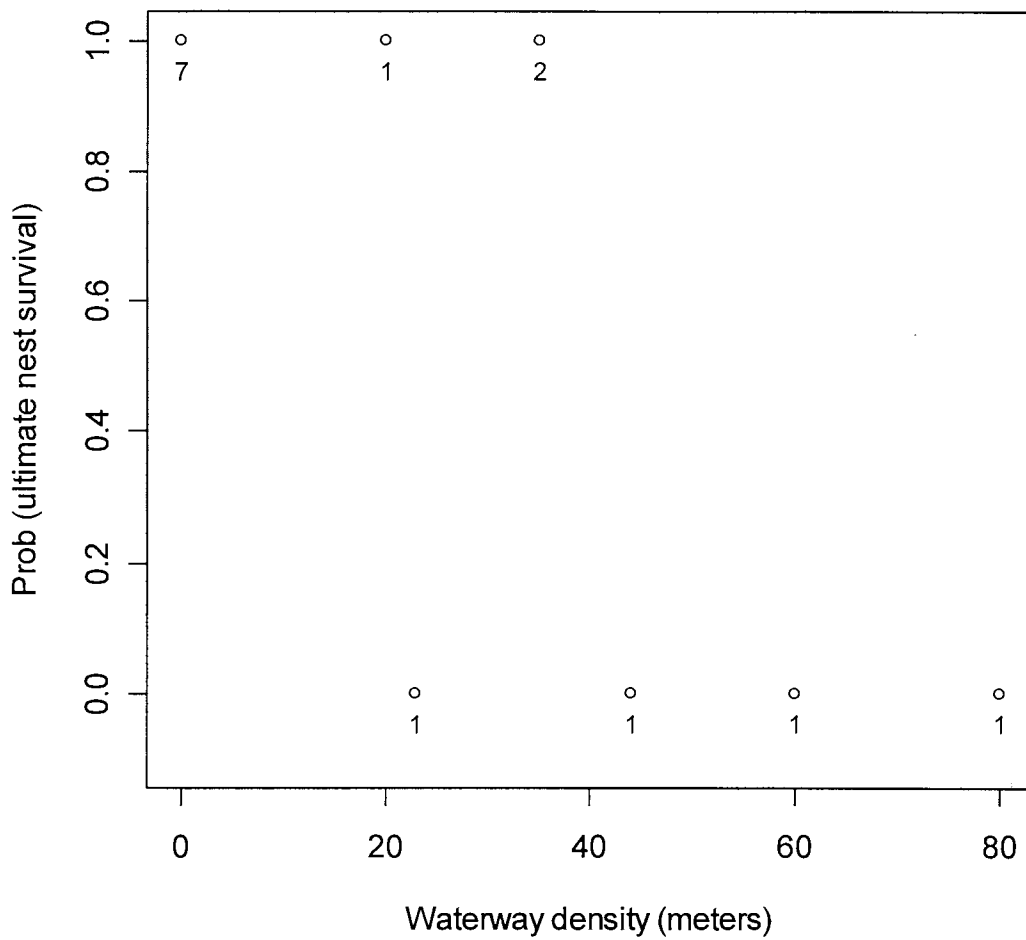


Figure 5. Raw data from the Pacific Creek site plotting observed probabilities of surviving the entire nest cycle. Probabilities of successes = 1 and failures = 0, while the subscript numeral under each point indicates the sample size (number of nests: total N = 14).

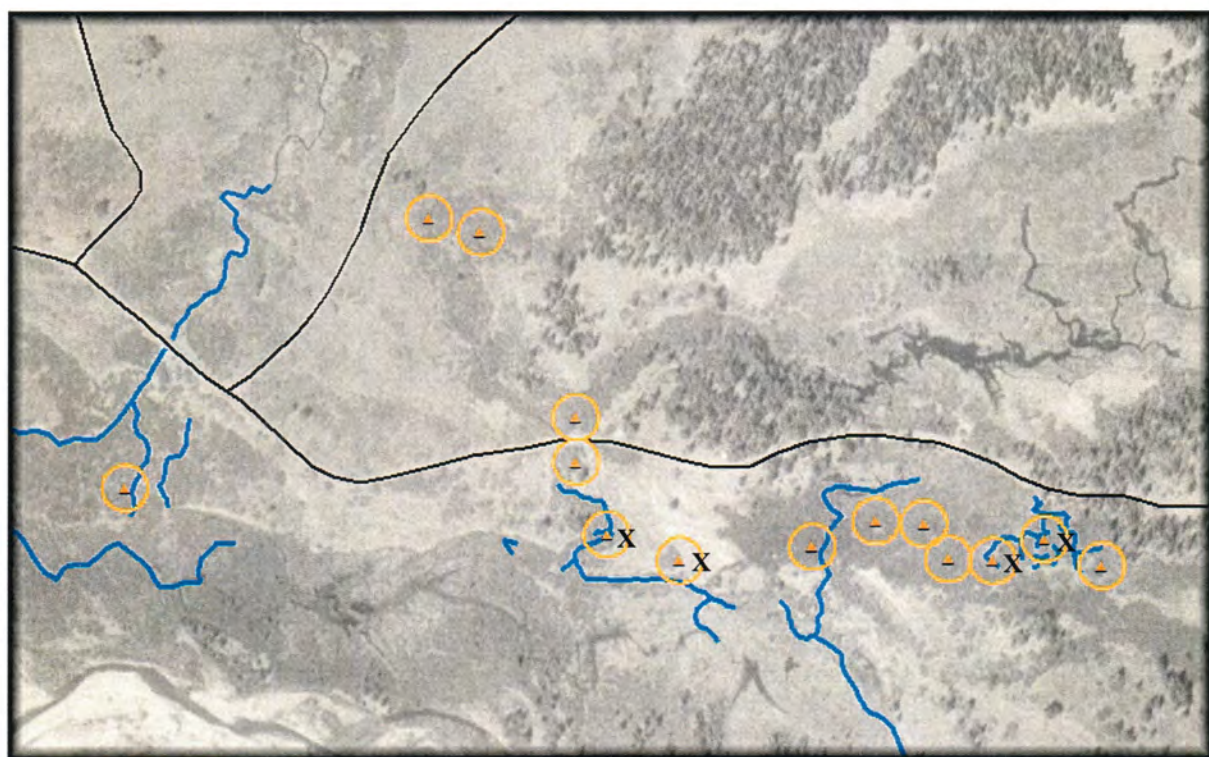


Figure 6. Nest locations (gold triangles), 20-meter radius territories (circles), and waterway density (blue lines) in the Pacific Creek site. Xs denote nests that eventually failed (did not fledge young). Black lines represent paved and gravel roads.

Table 1. Variable definitions for three categories of variables (Water, Nest, and Other). These variables were used in logistic-exposure models of varying complexity and compared using AIC weights (Tables 2 and 4).

Model variable category

Water variables

WATER_DENSITY = length of waterway within a 20 meter radius buffer of each nest

WATER_DISTANCE = the minimum distance from each nest to the nearest waterway

Nest variables

VH = Vegetation height, maximum height of willow shrub containing the nest

NH = Nest height, height of nest from ground at base of willow shrub

NP = Nest position, see equation in text (pg. 11)

Other variables

ROAD = minimum distance from each nest to the nearest road (paved or gravel)

SITE = categorical levels WF or PC (Willow Flats or Pacific Creek, respectively)

Table 2. Comparison of six possible combinations of explanatory variables included in logistic-exposure models of daily nest survival probability. None of the models used more than one variable from a predefined category; refer to Table 1 for variable categories and definitions. AIC weights were used to select model #1a.

Logistic-exposure models	AIC weights
1a. <i>WATER_DENSITY</i> + <i>NP</i> + <i>ROAD</i> + <i>SITE</i>	0.396
2a. <i>WATER_DENSITY</i> + <i>NH</i> + <i>ROAD</i> + <i>SITE</i>	0.135
3a. <i>WATER_DENSITY</i> + <i>VH</i> + <i>ROAD</i> + <i>SITE</i>	0.132
4a. <i>WATER_DISTANCE</i> + <i>NP</i> + <i>ROAD</i> + <i>SITE</i>	0.151
5a. <i>WATER_DISTANCE</i> + <i>VH</i> + <i>ROAD</i> + <i>SITE</i>	0.098
6a. <i>WATER_DISTANCE</i> + <i>NH</i> + <i>ROAD</i> + <i>SITE</i>	0.088

Table 3. Effect details based on the highest weighted model (#1a from Table 2). Sample size was 28 nests with one degree of freedom for each effect.

Effect	Estimate	Std Err	Wald 95% Confidence Limits		Chi-sq	P>Chi-sq
Intercept	-0.628	2.526	-5.579	4.323	0.06	0.804
<i>WATER_DENSITY</i>	-0.043	0.019	-0.079	-0.007	5.38	0.020
<i>NP</i>	7.924	4.669	-1.227	17.074	2.88	0.090
<i>ROAD</i>	0.004	0.003	-0.003	0.011	1.37	0.242
<i>SITE</i>	4.044	1.393	1.313	6.775	8.42	0.004

Table 4. Comparison of seven logistic-exposure models including the full model from Table 2 (listed here as model #2b.) and six reduced models. Refer to Table 1 for variable categories and definitions. AIC weights were used to select model #1b.

Logistic-exposure models	AIC weights
1b. <i>WATER_DENSITY + SITE + WATER_DENSITY*SITE</i>	0.749
2b. <i>WATER_DENSITY + NP + ROAD + SITE</i>	0.182
3b. <i>NP + SITE + NP*SITE</i>	0.034
4b. <i>ROAD + SITE + ROAD*SITE</i>	0.027
5b. <i>ROAD</i>	0.007
6b. <i>WATER_DENSITY</i>	0.000
7b. <i>NP</i>	0.000

Table 5. Effect details based on the highest weighted model (1b from Table 3). Sample size was 28 nests with one degree of freedom for each effect. Refer to Table 1 for variable categories and definitions.

Effect	Estimate	Std Err	Wald 95% Confidence Limits		Chi-sq	P>Chi-sq
Intercept	2.189	0.387	1.429	2.948	31.92	< 0.001
<i>WATER_DENSITY</i>	0.004	0.018	-0.031	0.039	0.05	0.827
<i>SITE</i>	3.714	1.158	1.445	5.983	10.29	0.001
<i>WATER_DENSITY*SITE</i>	-0.053	0.026	-0.104	-0.001	4.02	0.045

Table 6. Effect details of the WATER_DENSITY variable in analyses performed separately in each site. Sample sizes were 14 nests for each site and one degree of freedom for each effect. Refer to Table 1 for variable categories and definitions.

Site	Effect	Estimate	Std Err	Wald 95% Confidence Limits		Chi-sq	P>Chi-sq
PC	Intercept	5.897	1.097	3.746	8.047	28.87	< 0.001
	<i>WATER_DENSITY</i>	-0.048	0.019	-0.086	-0.012	6.34	0.012
WF	Intercept	2.189	0.387	1.430	2.948	31.93	< 0.001
	<i>WATER_DENSITY</i>	0.003	0.018	-0.032	0.039	0.030	0.861

CHAPTER THREE: EXPLORING RELATIONSHIPS BETWEEN BIRD AND BUTTERFLY COMMUNITY SHIFTS AND ENVIRONMENTAL CHANGE

A paper to be submitted to *Ecological Applications*

Diane M. Debinski¹, Ron E. VanNimwegen¹, and Mark E. Jakubauskas²

¹ *Department of Ecology, Evolution, and Organismal Evolution, Iowa State University, Ames, Iowa 50011 USA*

² *Kansas Applied Remote Sensing (KARS) Program, University of Kansas, Lawrence, Kansas 66045 USA*

Abstract

We compared interannual variability in both remotely sensed data and ecological communities in montane meadows during a time of decreasing precipitation to examine how ecological habitats and communities may be responding to climate change in the Greater Yellowstone Ecosystem. We used Landsat satellite imagery to classify these meadows into six meadow types along a hydrological gradient. The northern portion of the ecosystem, or Gallatin region, has smaller average patch sizes separated by ridges of mountains, whereas the southern portion of the ecosystem, or Teton region has much larger patches within the Jackson Hole valley. Both support a similar suite of butterfly and bird species, which were surveyed annually from 1997-2001. The Gallatin region showed more overall among-year variation in the Normalized Difference Vegetation Index (NDVI) when meadow types were pooled within regions, perhaps because the patch sizes are smaller on average. Bird and butterfly abundances showed significant relationships relative to meadow type and NDVI. We identified several key species that are tightly associated with specific meadow types along the hydrological gradient. Comparing taxonomic groups, fewer birds showed specific habitat affinities than butterflies in both Gallatin and Teton regions. We believe that birds

are responding to differences in habitat structure among meadow types, and that they are using the landscape at a coarser scale than the butterflies. Comparing regions, the Teton region showed higher predictability of community assemblages as compared to the Gallatin region. However, the Gallatin region exhibited more significant temporal trends with respect to butterflies. These results may imply that the larger Teton meadows will show more predictable (i.e., static) species-habitat associations, but that the smaller Gallatin meadows may be an area that will exhibit the effects of global climate change faster.

Introduction

As scientists explore the implications of global climate change, much of the focus has been on abiotic factors such as carbon fluxes and atmospheric composition. Studies are emerging that reflect shifts in community composition and phenology, as well as poleward distributional shifts (Brown et al. 1997, Parmesan et al. 1999, Fitter and Fitter 2002, Parmesan and Yohe 2003, Root et al. 2003). Changes in ecological (biotic) communities are excellent indicators of possible consequences of environmental change, providing models to predict changes over time (e.g., Thomas et al. 2004). The methodology for predicting potential ecological effects of climate change, however, is not well developed because the number of high quality, long-term ecological data sets is still somewhat limited.

Climate change models predict warmer temperatures, lower snowfall, and drier conditions for montane ecosystems in the Rocky Mountain region (Romme and Turner 1991). Montane meadows, defined here as persistently non-forested habitats in mountain ecosystems, encompass a broad hydrological gradient, from hydric (e.g., sedge and willow) to xeric (e.g., sagebrush) sites. The seasonal and interannual variation in these meadows is detectable using satellite remotely sensed imagery (Debinski et al. 2000). Ecologically,

montane meadows are inhabited by short-lived plants and highly mobile animal species that can exhibit quick responses to changes in the environment. They are also some of the most pristine and biologically diverse areas in the U.S. The extent and range of habitat-related variation presently occurring in these habitats is not known. Without data on this variation, it will be impossible to determine whether climate change is affecting ecological communities until large-scale changes, including loss of species, occur.

Our goal was to quantify interannual landscape-level and ecological variability in montane meadow communities during a time when local annual precipitation was declining (1997-2001, Fig. 1). The central hypothesis for the research was that landscape-level variables (e.g., habitat type as characterized using remotely sensed data) and ecological response variables (e.g., species' distribution patterns) are particularly sensitive to climate variations and thus can serve as early indicators of regional climate change.

We have been studying montane meadow biodiversity of plants, birds, and butterflies annually in the Greater Yellowstone Ecosystem (GYE) since 1992 (Debinski et al. 1999, 2000). We have used satellite imagery to classify meadow types along a moisture gradient. The midpoint of the moisture gradient, mesic meadows, have the highest magnitude of seasonal and interannual variation in spectral reflectance (a surrogate for aboveground photosynthetically active biomass) (Debinski et al. 2000). These mesic meadows also support the highest species diversity of plants and butterflies (Debinski et al. 2000). Bird diversity is highest in the hydric meadows.

Our first objective was to document interannual variability in montane meadow patch conditions using remotely sensed data. We used remotely sensed data as a landscape-scale surrogate for processes occurring within the ecosystem. A "patch" was defined here as a

homogenous area of one meadow type, as classified by satellite data. Meadow types were classified using remotely sensed data, and vegetation condition was assessed annually using Normalized Difference Vegetation Index ($NDVI = \frac{\text{near-infrared reflectance} - \text{red reflectance}}{\text{near-infrared reflectance} + \text{red reflectance}}$ Jensen 2000). We hypothesized that smaller meadows, especially in the hydric to mesic range, would exhibit greater interannual variability in spectral response. Because smaller meadows have a larger edge to area ratio, they have a smaller "mass" from which to maintain internal conditions. We expected that this higher variability might imply that smaller patches are more vulnerable to shifting to a new point along the hydrological gradient under climate change. Since our NDVI calculations were site- and year-specific, we could statistically relate those values directly to the community data we collected at those sites. The National Climate Data Center (NCDC) climate data was only regional. Therefore, we used changes in NDVI as a method to quantify the effects of changing climatic conditions within each meadow type. Large-scale studies have shown strong correlations between NDVI and seasonal weather patterns, especially precipitation (Schultz and Halpert 1993, Yang et al. 1997, Yang et al. 1998).

Our second objective was to link species distributions from a single-species and a community perspective to these meadow types. Although previous community studies, for example with butterflies, have predicted species occurrence patterns in relation to environmental variables such as elevational gradients (e.g., Fleishman et al. 2001, Fleishman et al. 2003), we did not know whether ecological communities would also reflect differences based upon meadow types separated by remotely sensed data. We chose species from two distinct and commonly studied taxonomic groups that were both high in species diversity (birds and butterflies). We hoped to identify species showing strong habitat affinities with

particular meadow types along the hydrological gradient or that show distinctive trends of maximum abundance at particular points along the hydrological gradient. Finally, we wanted to document temporal changes in species abundance patterns relative to changes in habitat condition. We expected butterflies to respond quickly to climate change because they respond to the condition of the vegetation, whereas birds were expected to change more slowly because they respond more to the structure of the vegetation. We hypothesized that species would show interannual shifts in abundance that were correlated with habitat changes. For example, we expected that as mesic sites became more xeric during hotter, drier years, mesic butterfly communities would shift to sites that had previously been considered more hydric sites.

Multispectral satellite remote sensing provides a powerful means for detecting and characterizing environmental changes at multiple spatial and temporal scales. Analysis of changing spectral patterns can provide precursor measurements of terrestrial ecosystem dynamics (Lancaster et al. 1996, Ustin et al. 1993). Time series analysis of multispectral imagery has allowed scientists to examine phenological phenomena such as green-up, duration of green period, onset of senescence, and change in seasonally-dependent biophysical variables such as leaf area index, biomass, and net primary productivity (Roller and Colwell 1986, Becker and Choudhury 1988, Gallo and Eidenshink 1988, Achard and Brisco 1990, Teng 1990). Similarly, there are a plethora of papers examining remote sensing applications to predicting presence of one species or a number of species individually (Cardillo et al. 1999, Kerr et al. 2001, Hepinstall et al. 2002). Environmental assessment programs are increasingly linking remotely sensed imagery, digital elevation models, and field information to integrate descriptions of small-scale processes up to regional and global

scales (O'Neill et al. 1997). By calibrating remotely sensed multispectral data with ground measurements of biotic properties, habitat condition measured at sample points can be extrapolated across a large geographic region (Graet 1990). Here we extend this process of calibration and extrapolation by developing a remote sensing-based measure of habitat variation and relating this measure to species distribution patterns.

The tightly constrained ecosystem of the montane meadows provides an excellent model for examining interannual variability in ecological communities. The vegetation of montane meadows is an essential component of the data collection and analysis. Vegetation is a component part of the ecological community, but it is also a component of the habitat for the bird and butterfly communities. Individual plant species have a range of hydrological conditions and soils under which they can persist, and we expected those adapted to hydric conditions to exhibit ranges reflecting local hydrology. Birds and butterflies are representatives of the primary and secondary consumer levels. Both taxa show a high diversity of species and can respond quickly to changes in environmental conditions. Butterflies respond to microhabitat, plant structure and plant chemical composition. Over one hundred species of butterflies occur in the Yellowstone ecosystem (Debinski and Pritchard 2002) and many are closely correlated with specific meadow habitats (Debinski et al. 2001). Further, a strong connection between climate and butterflies has been recognized by many authors (e.g., Pollard and Yates 1995). The implications of changes in climate for butterflies are potentially serious (Dennis 1993), and particular concern has been expressed about montane butterfly communities where habitats are predicted to contract (Pullin 1995). Bird communities reflect the condition of many aspects of the ecosystem and often respond to spatial and temporal variation in a species-specific fashion (Steele et al. 1984, Taper et al.

1995). Moreover, they are conspicuous, ubiquitous, intensively studied, and often appear to be more sensitive to environmental changes than other vertebrates (Morrison 1986). We have found strong relationships between the songbird community and each of the specific meadow types in the ecosystem (Saveraid et al. 2001).

Many previous attempts to define evidence of environmental change have failed because of their narrow focus, utilizing one or a few species (Cairns 1986, Landres et al. 1988, Kremen 1992) or only addressing one ecological level of response. From the perspective of climate change assessment many papers document or predict abiotic environmental changes as a consequence of climate change. For example, Lighthill et al. (1994) predicts increased cyclone activity, Pavlidis and Shcherbakov (2002) have modeled future coastline changes, and a host of mechanisms were proposed that link precipitation changes to differing patterns of soil erosion (Nearing 2001, Nearing et al. 2004). Our approach is novel in that we assess landscape changes (abiotic) and link them to changes across multiple taxonomic groups (biotic) at the level of the ecological community during a time when environmental conditions are undergoing change.

Methods

Image selection

A seasonal series of Landsat Thematic Mapper (TM) multispectral satellite imagery during the snow-free period was used to assess interannual variability in meadow condition from 1996-2002. One scene of Landsat TM data was selected for each year during the height of the growing season (mid-July). We chose the following scene dates, each of which represented minimal cloud cover and a midpoint in the annual growing season: 15-July-1997, 18-July-1998, 23-July-2000, and 2-July-2001. Each scene had a resolution of 30 meters per

pixel and consisted of seven bands of the electromagnetic spectrum (blue, green, red, near-infrared, two middle-infrared, and one thermal band that spanned the wavelengths of bands 2 through 4 at twice the spatial resolution, or 15 meters per pixel).

Sampling sites

We have built an extensive database of plant, butterfly, and bird community data, and remotely sensed data from 1996-2002 (e.g., Jakubauskas et al. 1998, Kindscher et al. 1998; Debinski et al. 1999, Debinski et al. 2002) in two regions of the ecosystem: the northern "Gallatins" region that includes the Gallatin National Forest and northwestern portion of Yellowstone National Park; and the southern "Tetons" region that includes Grand Teton National Park and the Bridger-Teton National Forest. The two regions have very distinct landscapes, and differ significantly in patch size (Fig. 2), but support similar meadow types and plant, bird, and butterfly diversity.

Sampling sites were identified using remotely sensed classification of the montane meadow habitats to identify a moisture gradient in montane meadows (Jakubauskas and Debinski 1995). These sites comprised a hydrologic gradient and were classified into six meadow types (hereafter termed M-types), ranging from extremely hydric (M1) to extremely xeric (M6) meadows. Field investigations confirmed the moisture gradient predicted for the meadows (Jakubauskas et al. 1998, Kindscher et al. 1998, Debinski et al. 2000). M1 and M2 meadows are willow (*Salix* spp.) thickets and sedge (*Carex* spp.) marshes respectively with some standing water. M3 meadows are mesic meadows characterized by diverse forb and grass coverage. M4 meadows are of medium moisture with cinquefoil (*Potentilla* spp.) and mixed herbaceous vegetation, while M5 meadows have a mixture of sagebrush (*Artemisia tridentata*) and herbaceous vegetation. M6 meadows are characteristically xeric, rocky, and

dominated by sagebrush. Field sampling was used to collect data on the distribution of plant, bird, and butterfly species. Five sites of each M-type were established in each region, but no M4s were found in the Tetons. Therefore, we sampled thirty sites in the Gallatins and twenty-five sites in the Tetons.

Pixel value calibration between satellite images and NDVI calculations

Each 30m resolution image was geographically referenced using control points, and radiometrically adjusted to a common range using invariant targets. All scenes were Landsat 5 Thematic Mapper (TM) images, except the 2001 scene, which was a Landsat 7 Enhanced Thematic Mapper Plus (ETM+) image. Differences in sensor calibration between these satellites required that we inspect the 2001 scene for the possible need of pixel value adjustments. We only inspected Bands 3 (red) and 4 (near infrared), because these were the bands used to calculate the normalized vegetation difference index (NDVI).

The pixel adjustment process involved three steps. First, we chose several invariant points ($n = 14$); that is, locations where the pixel values should not have changed among years. These locations consisted of three general land cover types: water, gravel/rock, and shaded forest. Next, we compared pixel values of these invariant points. Band 4 did not differ significantly between Landsat sensors, but Band 3 differed for all invariant cover types (water, gravel, and shaded forest; $P < 0.0001$). Finally, we plotted Band 3 pixel values of the Landsat 7 against the averaged Landsat 5 values for all invariant points and found a linear relationship ($R^2 > 0.99$, $P < 0.0001$). We used that function to adjust Band 3 in the 2001 scene and used the adjusted image in our subsequent NDVI calculations and analyses.

For each scene, we calculated the NDVI of a 90x90-meter ground area (3x3 pixels) centered in each of our 55 sites. To streamline the process, we used Erdas Imagine® V8.2 to

apply a 3x3 low-pass convolution filter to each image. This filter averaged each pixel value with its eight surrounding pixels, and used the resultant values to create a new image. From that image, we extracted the site-specific pixel values for bands 3 and 4 to perform the NDVI calculations for each site ($\text{NDVI for Landsat TM} = [\text{Band 4} - \text{Band 3}] / [\text{Band 4} + \text{Band 3}]$). We used site-specific NDVI values in our subsequent bird and butterfly community analyses. We also averaged the NDVI values across sites for each meadow type and plotted the interannual changes over the seven-year period (Figs. 3-4). We also examined the effects of M-type, region, and year (as a categorical value) using ANOVA and Tukey's HSD differences.

Climate Data

We obtained daily climate data for the GYE area from the NCDC. We chose three weather stations (Stations 240775: Big Sky, 485345: Lake Yellowstone, and 486440: Moran 5WNW) to represent the extent of the GYE and acquired the daily precipitation data for each station for 1985 to 2003. We averaged the daily values across stations, thus eliminating the gaps in climate data that can result from an occasional malfunctioning weather station. This data set provided a long term context within which we could assess the relative precipitation changes that occurred during our study period (Fig. 1).

Identifying indicator species

We conducted plant, bird and butterfly surveys each summer from 1997 to 2001 (excluding 1999, when our sampling efforts were diverted to a related study). Two taxa and two regions provided four taxon-region datasets for individual analyses. Since there were no M4s found in the Tetons based on our classification scheme, we only used Gallatin datasets

after removing M4s. With 25 sites in each region and four years of surveys, each taxon-region dataset consisted of 100 “site-years.”

We have focused our analysis here on the birds and butterflies because the plant community is summarized indirectly by changes in NDVI. For each region, we removed all rare species; that is, those whose total relative abundance for the entire study period was less than ten. For a given site and year, relative abundance was calculated as the total number of a species divided by the number of surveys performed. We also removed species not identified to the species level. For birds only, we removed colonial bird species such as swallows that were probably not using the area for nesting, but rather foraging there on a temporary basis. Similarly, we removed “flyover” species that were seen but never stopped in the site as we were sampling. Our resultant data set consisted of 17 total bird species (10 in the Gallatins and 16 in the Tetons) and 30 butterfly species (23 in each region).

For *individual* species, we used Student’s t tests to determine which species of birds and butterflies were significantly more abundant in certain hydrological groups, pooled over M-types. These groups were termed hydric (M1s and M2s pooled), mesic (M3s and M4s), and xeric (M5s and M6s).

Predictability of ecological communities

To estimate *community*-level predictability, we used bird and butterfly species compositions to perform discriminant analyses (DAs), which classified site-years into M-types based on relative species abundances. The more species we used as discriminating variables, the more site-years were classified as the correct M-type. Discriminating performance can be quantified and tested among DA models with a jackknife validation technique. Also known as cross validation, this technique removes a single sampling entity

from the data, derives classification functions from the remaining dataset, and then applies those functions to the removed entity to predict its category (in our case, M-type). By plotting the percentage of site-years correctly classified ($100 - \text{misclassification \%}$) by the number of discriminating variables (species) included in the analysis, we generated “performance curves.” Each curve reached an asymptote (at or below 100%) at the point where additional species do not improve the discriminating performance of the DA (Fig. 5). These curves were then qualitatively compared among taxa and regions to determine how consistent each community’s component species remained in their respective habitat types. The first ten species chosen in a stepwise manner with PROC STEPDISC in SAS® 8.2 (SAS Institute, 1999) were also noted to compare with species identified as indicators in the previous section. Choosing ten species was based on a subjective observation of the performance curves; at ten species, a high degree of M-type discrimination was accomplished relative to the asymptote, especially in the Teton region. To assess how well species composition corresponded with our remotely sensed habitat classification scheme of M-types, we used nonmetric multidimensional scaling (NMDS; Kruskal 1964), an unconstrained ordination technique. NMDS is unconstrained in the sense that the configuration of site-years (points) observed in the ordination plot is derived entirely from the species abundance data, and is not dependent on any hypothesized underlying gradient data. Site-years closer to each other on the ordination plot have more similar species compositions than those farther apart. Function “isoMDS” from the MASS library in the R-project (R Development Core Team 2004) statistical package was used for the NMDS. Since this is a distance-based ordination (rather than eigenanalysis-based), we chose the Bray-Curtis dissimilarity index (Faith et al. 1987) as our measure of ecological distance.

We then overlaid hypothesized gradient, or environmental variables onto the NMDS plots without disrupting the configuration of the original ordinations using function “envfit” from the VEGAN library (Dixon 2003). First, we added M-type as a categorical variable, which overlaid labeled centroids for each M-type on the plot. Additionally, since each point in the ordination represented a site-year combination, the four survey years were also overlaid as categorical variables to look for temporal changes in species composition. Finally, we overlaid NDVI as a continuous variable to determine if it was correlated with any temporal shifts in species compositions across years. We evaluated temporal and NDVI effects on species composition both among and between M-types for all four taxon-region data set combinations.

Combining the function “envfit” with NMDS (or any other ordination) provides a unique compromise between the classical “subjective” evaluations of unconstrained ordination (Økland 1996) and the hypothesis-driven constrained methods such as the now popular canonical correspondence analysis (CCA: Ter Braak 1986). Overlaying environmental (gradient) variables on an ordination using “envfit” also generates an R^2 measure of fit and a “significance” value based on the probability that random permutations of the environmental variables would yield a higher degree of fit than the true environmental variables.

It is important to note, however, that environmental variables overlaid with “envfit” are *independently* modeled effects, and not part of a globally modeled combination of effects such as that used by CCA. Therefore, one effect cannot be evaluated in the context of, or after having “partialled” out the variation of others. It is also important to note that NMDS plots are simply maps reflecting ecological dissimilarity; their axes are arbitrary and do not

extract orthogonal variation from a data set the way an eigenanalysis-based ordination does. A common difficulty in the latter form of ordination is deciding from which axis to interpret your site scores. With NMDS and function “envfit” all dimensions are considered simultaneously and the original ordination’s configuration is left intact.

Results

Between region landscape differences

The major landscape differences between our two study regions were mean patch size and edge-to-area ratio of patches (Fig. 2). The Gallatins (total area = 4035 ha, total patches (N) = 2181, mean = 1.85 ha) have significantly smaller patches ($t = 5.929$, $df = 1595$, $P < 0.001$) and higher edge ratios ($t = 7.589$, $df = 2443$, $P < 0.001$) than the Tetons (total area = 3683 ha, total patches (N) = 1148, mean = 3.21 ha).

NDVI and climate trends

The Gallatins showed more among year variability in NDVI than the Tetons, as evidenced by their F-ratios (Gallatins: $F = 1.87$, $df = (3,96)$, $P = 0.140$; Tetons: $F = 1.02$, $df = (3,96)$, $P = 0.386$). In an ANOVA relating NDVI to region, year, and M-type effects, NDVI did not differ between regions (Gallatins and Tetons: $F = 1.16$, $df = (1,199)$, $P = 0.282$). NDVI did not differ between M1s, M2s, and M3s, but those three as a group were higher than M5s, which in turn were higher than M6s, using separately run contrasts between these groups in the ANOVA (Figs. 3 and 4: $F = 240.70$, $df = (4,199)$, $F = <0.001$). NDVI differed among years ($F = 16.05$, $df = (3,199)$, $P < 0.001$). The greatest difference in years was between 1997 and 2000 (Tukey’s HSD with $\alpha = 0.05$). Climate trends over the long term (1985-2003) were stochastic, but within a limited range for most years, except for a noticeable drying trend from 1996-2001 (Fig. 1).

Identifying indicator species and community predictability

We identified species that were significantly more abundant in wet, mesic, or dry meadows (Table 1), and characterized them as having a hydrological affinity to these pooled classifications. The top ten species selected by the stepwise DA analysis (Table 2) were considered to be those whose abundance had the greatest effect on separating M-types.

We used DA to analyze how tightly sites clustered by species composition. This worked especially well for butterflies in the Tetons. We also plotted DA performance curves to examine how many species were required to correctly classify site-years by M-type. DA performance curves were qualitatively higher for butterflies than for birds in both the Gallatins and the Tetons. While the butterfly species composition could be used to obtain 90-100% accuracy in classifying M-types, birds barely reached 70% in the Gallatins, and over 90% in the Tetons. DA performance curves were higher in the Tetons than in the Gallatins for both taxa, but more so for the butterflies (Fig. 5), where Gallatin sites reached maximal %site-years correctly classified at much lower levels (~80%) than the Tetons (100%).

By combining the DA performance curves with the NMDS ordinations overlaid with M-type centroids (and their associated R^2 values: Table 3), we can rank the M-type affinities by taxon-region. That is, both methods of comparison indicate butterflies to be more predictable in separating M-type than birds (in both the Gallatins and Tetons). Furthermore, the Tetons birds and butterflies are more predictable in separating M-types than the Gallatin birds and butterflies, respectively.

NMDS provided a finer resolution of temporal changes in site-specific species composition. In an example ordination plot of Teton butterflies (Fig.6), each site is color-

coded by M-type. Similar M-types are closely grouped, indicating similar species compositions in those sites. The adjacency and slight overlap in some M-types reflect the ordinal nature of our M-type classification scheme. The overlay of M-types as categorical variables are indicated by labels that represent the centroid or mean of that group's ordination scores (coordinates). The categorical *Year* values are represented by “+” symbols since they are so close together that their labels would overlap and be indistinguishable. The continuous variable NDVI is represented by an arrow pointing in the direction of increasing values (see also figures 3 and 4, where “low” M-types have high NDVI values).

NMDS plots for birds in both the Gallatins and Tetons were similar to that just described by Teton butterflies; namely, in their lack of temporal effects. However, the Gallatin butterfly data set warranted further investigation (Fig. 7), because the Year centroids showed a greater separation than the other taxon-region plots ($R^2 = 0.06$, $P = 0.052$; the low R^2 value is the result of the overriding fit of the data to M-type, which spreads the Year values of each site-year across the first dimension of the plot: NMDS1). We therefore used the Gallatin butterfly NMDS ordination and connected only the 1997-2000 site-years with arrows (Fig. 8). By visual inspection, nearly all arrows are directed upward, showing a similar shift in species composition simultaneously in fifty site-years. We regressed the NDVI values over this ordination (Fig. 8) using “envfit,” but the oblique angle to the community shifts did not suggest a relationship between NDVI and the composition changes. The fact that all M-types were included in the plot meant we were showing an NDVI trend that was effectively mimicking the M-type gradient. A connection between NDVI and species composition needed to be analyzed within M-types to find any relationships that might exist.

Figure 9 shows the results of such within M-type analyses; here we can see that for each M-type, the Year and NDVI arrows point at a variety of angles to one another. The Year arrow indicates the temporal change in species composition (the average change in position of the five site-years in each M-type from 1997 to 2000). These shifts coincide with the drop in NDVI during that period, hence we would expect opposite pointing arrows (indicating negative correlations). Of all the M-types, the mesic meadows (M3s) showed the strongest such relationship, based on a qualitative observation of the angles and lengths between the regressed Year and NDVI vectors.

Discussion

Interannual variability in montane meadow patch condition

Our first objective was to examine interannual changes in patch quality, as determined by site-specific NDVI values. Given that the Gallatins showed more overall among-year NDVI variation than the Tetons, we have evidence at a regional scale that our hypothesis of higher variability of NDVI in smaller patches is supported. We also found that in both regions, the greatest decline in NDVI was between 1997 and 2000 (nearly equal to the drop from 1998 to 2000). This period generally coincides with the drying trend we observed in our long term precipitation data set.

Species-habitat associations

Our second objective was to identify species-habitat associations. We have identified several key species that have strong habitat associations along the hydrological gradient. When we pooled M-types into three classes (wet, mesic, and dry), several bird and butterfly species showed a significant affinity to those groups as evidenced by their relative abundances (Table 1). The Gallatin and Teton regions had similar numbers of such species

for mesic and xeric meadows, but the Teton region had several more bird and butterfly species showing an affinity for hydric meadows. This could be due to the landscape differences between the two regions (patch sizes of hydric meadows are much larger in the Tetons). Our stepwise method of DA also revealed those species most responsible for discriminating among habitat types.

Predictability of ecological communities

The CDA performance curves and NMDS ordination techniques allowed us to compare regions at the entire community level without necessarily detailing every species' abundance trends. With long term datasets, observers vary from year to year, and differences among observers' surveying ability should be taken into account. Multivariate techniques such as DA and NMDS rely on species composition rather than individually modeled species abundance trends. We are assuming that if differences in surveyor ability varied among years, the counts of birds and butterflies maintained consistent species compositions.

Our results allowed us to compare DA performance curves among years, regions, and taxa. We interpreted higher curves as systems with larger average patch size that show less spillover and stronger habitat affinities as seen in our previous work (Debinski et al. 2000). These associations could potentially imply higher production, assuming less time is wasted by individuals in the "wrong" habitats, or at edges of their ranges where population would be less dense. The Gallatins showed less specific habitat affinities than the Tetons in both bird and butterfly communities. Furthermore, fewer birds showed specific habitat affinities than butterflies in both Gallatin and Teton regions. We expected this for the Gallatins based on known landscape differences (mean patch sizes), and the higher mobility and migratory habits of birds may explain their lower degree of habitat affinity. Birds also respond strongly

to the height and structure of shrubby vegetation (Knopf and Sedgwick 1992), and NDVI does not provide enough information to factor these variables into the analysis.

With respect to year effects, Gallatin butterflies showed strong trends. Figure 8 highlights the consistency of the downward trend in NDMS ordination scores between 1997 and 2000. It is primarily the mesic meadow butterfly communities showing the strongest negative correlation for NDVI vs. Year trend when looking within each M-type (Figure 9). Thus, species such as *Phyciodes campestris*, *Lycaena helloides*, and *Coenonympha haydenii* may be especially important to monitor over time.

We have shown some striking patterns of association between species abundance, NDVI and precipitation patterns and taken a new approach to the analysis of ecological community data from a temporal perspective. Previous authors have used bird or butterfly communities to identify indicators (Morrison 1986, Kremmen 1992) and even conducted this research in the context of environmental gradients at a fine geographic scale (e.g., Fleishman et al. 1998, 2000) and/or climate change at a coarse geographic scale (Parmesan et al. 1999, Root et al. 2003). Here we have linked community changes with climate change at a fine geographic scale. It was fortuitous that the period that we chose to examine was a time during which the ecosystem was experiencing a drying trend. Meadows across the spectrum of hydrology – not just the hydric sites – showed significant NDVI changes over time. If certain meadow types decrease in size over the long term, the current Gallatin landscape could potentially serve as a future representation of the Teton landscape, but only in the mesic to hydric range. We believe that this area is a key area to continue monitoring from the perspective of global climate change. Understanding how interannual climate variability

affects this pristine ecosystem will aid us in projecting the implications of climate variability and change at a more regional scale.

Acknowledgements

Sincere thanks go out to the University of Wyoming – National Park Service Research Center (AMK Ranch: Dr. Henry Harlow, director) for funding and accommodating our research team over the years. We also thank Bill Miller of the Denver Zoological Foundation for funding, collaboration, and general camaraderie. Additional funding was provided by the Iowa Space Grant Consortium and the Grand Teton Natural History Association. Data collection during 1997-2000 was funded by a grant from the Environmental Protection Agency (EPA) through their Ecological Assessment and Restoration program. Although funded by the EPA (through grant 96-NCERQA-1A to Debinski et al.), it has not been subjected to the Agency's peer review and therefore does not necessarily reflect the views of the Agency and no official endorsement should be inferred. Statistical consulting was provided by Kirk Moloney and Philip Dixon of Iowa State University. Finally, thanks to the many field technicians who have helped over the years, especially Amanda Hetrick and Julie Perret.

Literature Cited

- Dennis, R. L. 1993. Butterflies and climate change. Manchester University Press, New York, New York, USA.
- Achard, F. and F. Blasco. 1990. Analysis of vegetation seasonal evolution and mapping of forest cover in West Africa with the use of NOAA AVHRR HRPT data. Photogrammetric Engineering and Remote Sensing **56**:1359-1365.

- Angermeier, P. L., and J. R. Karr. 1986. Applying an index of biotic integrity based on stream-fish communities: Considerations in sampling and interpretation. *North American Journal of Fisheries Management* **6**:418-429.
- Becker, F., and B. J. Choudhury. 1988. Relative sensitivity of Normalized Difference Vegetation Index (NDVI) and Microwave Polarization Difference Index (MPDI) for vegetation and desertification monitoring. *Remote Sensing of Environment* **24**:297-311.
- Brown, J. H., T. H. Valone, and C. G. Curtin. 1997. Reorganization of an arid ecosystem in response to recent climate change. *Proceedings of the National Academy of Science of the United States of America* **94**:9729-9733.
- Cairns, J., Jr. 1986. The myth of the most sensitive species. *BioScience* **36**:670-672.
- Cardillo, M., D. W. Macdonald, and S. P. Rushton. 1999. Predicting mammal species richness and distributions: testing the effectiveness of satellite-derived land cover data. *Landscape Ecology* **14**:423-435.
- Cody, M. L., 1993. Bird diversity components within and between habitats in Australia. Pages 147-158 *in* R. E. Ricklefs and D. Schluter, editors. *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago, Illinois, USA.
- Debinski, D. M., C. Ray, and E. H. Saveraid. 2001. Species diversity and the scale of the landscape mosaic: do scales of movement and patch size affect diversity? *Biological Conservation* **98**:179-190.

- Debinski, D. M., M. E. Jakubauskas, and K. Kindscher. 2000. Montane meadows as indicators of environmental change. *Environmental Monitoring and Assessment* **64**:213-225.
- Debinski, D. M., M. E. Jakubauskas, and K. Kindscher. 1999. A remote sensing and GIS-based model of habitats and biodiversity in the Greater Yellowstone Ecosystem. *International Journal of Remote Sensing* **20**:3281-3292.
- Debinski, D. M., M. E. Jakubauskas, K. Kindscher, E. H. Saveraid, and M. Borgognone. 2002. Predicting meadow communities and species occurrences in the Greater Yellowstone Ecosystem. Pages 499-506 *in* J. M. Scott, P. J. Heglund, M. Morrison, M. Raphael, J. Haufler, and B. Wall, editors. *Predicting species occurrences: Issues of scale and accuracy*. Island Press, Covello, California, USA.
- Dixon, P. 2003. VEGAN, a package of R functions for community ecology. *Journal of Vegetation Science* **14**:927-930.
- Faith, D. P., P. R. Minchin, and L. Belbin. 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* **69**:57-68.
- Fitter, A. H., and R. S. R. Fitter. 2002. Rapid changes in flowering time in British plants. *Science* **296**:1689-1691.
- Fleishman, E., G. T. Austin, and A. D. Weiss. 1998. An empirical test of Rappaport's rule: elevational gradients in montane butterfly communities. *Ecology* **79**:2482-2493.
- Fleishman, E., J. P. Fay, and D. D. Murphy. 2000. Upsides and downsides: contrasting topographic gradients in species richness and associated scenarios for climate change. *Journal of Biogeography* **27**:1209-1219.

- Fleishman, E., R. Mac Nally, J. P. Fay, and D. D. Murphy. 2001. Modeling and predicting species occurrence using broad-scale environmental variables: an example with butterflies of the Great Basin. *Conservation Biology* **15**:1674-1685.
- Fleishman, E., R. Mac Nally, and J. P. Fay. 2003. Validation tests of predictive models of butterfly occurrence based on environmental variables. *Conservation Biology* **17**:806-817.
- Gallo, K. P., and J. Eidenshink. 1988. Differences in visible and near-IR responses and derived vegetation indices for the NOAA-9 and NOAA-10 AVHRRs: A case study. *Photogrammetric Engineering and Remote Sensing* **54**:485-490.
- Hepinstall, J. A., W. B. Krohn, and S. A. Sader. 2002. Predicting meadow communities and species occurrences in the Greater Yellowstone Ecosystem. Pages 499-506 *in* J. M. Scott, P. J. Heglund, M. Morrison, M. Raphael, J. Haufler, B. Wall, editors. *Predicting Species Occurrences: Issues of Scale and Accuracy*. Island Press, Covello, California, USA.
- Jakubauskas, M. E., K. Kindscher, and D. M. Debinski. 1998. Multitemporal characterization and mapping of montane sagebrush communities using Indian IRS LISS-II imagery. *Geocarto International* **13**:65-74.
- Jakubauskas, M. E., and D. M. Debinski. 1995. An integrated spectral and ecological approach to mapping forest and meadow communities of the Greater Yellowstone Ecosystem. Association of American Geographers Annual Meeting, Chicago, Illinois, USA.
- Jensen, J. R. 2000. *Remote Sensing of the Environment: An Earth Resource Perspective*. Prentice Hall, Upper Saddle River, New Jersey, USA.

- Kindscher, K. A. Frasier, M. E. Jakubauskas, and D. M. Debinski. 1998. Identifying wetland meadows in Grand Teton National Park using remote sensing and average wetland values. *Wetlands Ecology and Management* **5**:265-273.
- Kerr, J. T., T. R. E. Southwood, and J. Cihlar. 2001. Remotely sensed habitat diversity predicts butterfly species richness and community similarity in Canada. *Proceedings of the National Academy of Science* **98**:11365-11370.
- Knopf, F.L., and J.A. Sedgwick. 1992. An experimental study of nest-site selection by Yellow Warblers. *Condor* **94**:734-742.
- Kremen, C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications* **2**:203-217.
- Kruskal, J. B. 1964. Nonmetric multidimensional scaling: a numerical method. *Psychometrika* **29**: 115-129.
- Lancaster, J., D. Mouat, R. Kuehl, W. Whitford, and D. Rapport. 1996. Time series satellite data to identify vegetation response to ecosystem stress as an indicator of ecosystem health. *Proceedings, Shrubland Ecosystem dynamics in a Changing Environment*. General Technical Report **INT-GTR-338**. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, Utah.
- Landres, P. B., J. Verner, and J. W. Thomas. 1988. Ecological uses of vertebrate indicator species: A critique. *Conservation Biology* **2**:316-329.
- Lighthill, J., G. Holland, W. Gray, C. Landsea, G. Craig, J. Evans, Y. Kurihara, and C. Guard. 1994. Global climate-change and tropical cyclones. *Bulletin of the American Meteorological Society* **75**:2147-2157.

- Morrison, M. L. 1986. Bird populations as indicators of environmental change. *Current Ornithology* **3**:429-451.
- Nearing, M.A., F.F. Pruski, and M.R. O'Neal. 2004. Expected climate change impacts on soil erosion rates: a review. *Journal of Soil and Water Conservation* **59**:43-48.
- Nearing, M.A. 2001. Potential changes of rainfall erosivity in the U.S. with climate change during the 21st century. *Journal of Soil and Water Conservation* **56**:229-232.
- Økland, R. H. 1996. Are ordination and constrained ordination alternative or complementary strategies in general ecological studies? *Journal of Vegetation Science* **7**:289-292.
- O'Neill, R. V., C. T. Hunsaker, K. B. Jones, K. H. Riitters, J. D. Wickham, P. M. Schwartz, I. A. Goodman, B. Jackson, and W. S. Baillargeon. 1997. Monitoring environmental quality at the landscape scale: Using landscape indicators to assess biotic diversity, watershed integrity, and landscape stability. *BioScience* **47**:513-519.
- Parnesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**:37-42.
- Parnesan, C., N. Ryrholm, C. Stefanescu, J. K. Hill, C. D. Thomas, H. Descimon, B. Huntley, L. Kaila, J. Kullberg, T. Tammaru, J. Tennent, J. A. Thomas, and M. Warren. 1999. Poleward shift of butterfly species' ranges associated with regional warming. *Nature* **399**:579-583.
- Pavlidis, Y.A., and F.A. Shcherbakov. 2002. Possible ways of the development of coasts and shelves in the Russian inland seas under the condition of climate warming and sea level rise. *Oceanology* **42**:868-876.

- Pollard, E., and T. J. Yates. 1995. Monitoring butterflies for ecology and conservation. Chapman and Hall, London, United Kingdom.
- Pullin, A. S. 1995. Ecology and conservation of butterflies. Chapman and Hall, London, United Kingdom.
- R Development Core Team. 2004. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Roller, N. E., and J. E. Colwell. 1986. Coarse-resolution satellite data for ecological surveys. *BioScience* **36**:468-475.
- Romme, W. H. and M. G. Turner. 1991. Implications of global climate change for biogeographic patterns in the Greater Yellowstone Ecosystem. *Conservation Biology* **5**:373-386.
- Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. *Nature* **421**:57-60.
- Saveraid, E. H., D. M. Debinski, K. Kindscher, and M. E. Jakubauskas. 2001. A comparison of satellite data and landscape variables in predicting bird species occurrences in the Greater Yellowstone Ecosystem. *Landscape Ecology* **16**:71-83.
- Schultz, P. A. and M. S. Halpert. 1993. Global correlation of temperature, NDVI and precipitation. *Advances in Space Research* **13**:277-280.
- Steele, B. B., R. L. Bayn, Jr., and C. V. Grant. 1984. Environmental monitoring using populations of birds and small mammals: Analysis of sampling effort. *Biological Conservation* **30**:157-172.
- Taper, M. L., K. B. Gaese, and J. H. Brown. 1995. Individualistic responses of bird species to environmental change. *Oecologia* **101**:478-486.

- Teng, W. L. 1990. AVHRR monitoring of U.S. crops during the 1988 drought. *Photogrammetric Engineering and Remote Sensing* **56**:1143-1146.
- Ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* **67**:1167-1179.
- Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B. F. N. Erasmus, M. F. De Siquiera, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A. S. Van Jaarsveld, G. F. Midgley, L. Miles, M. A. Ortega- Huerta, A. T. Peterson, O. Phillips, and S. E. Williams. 2004. Extinction risk from climate change. *Nature* **427**:145-148.
- Ustin, S. L., M. O. Smith, and J. Adams. 1993. Remote sensing of ecological processes: A strategy for developing and testing ecological models using spectral mixture analysis. Pages 339-357 in J. R. Ehleringer and C. B. Field, editors. *Scaling Ecological Processes: Leaf to Globe*. Academic Press, San Diego, California, USA.
- Yang, W., L. Yang, and J. W. Merchant. 1997. An assessment of AVHRR/NDVI-ecoclimatological relations in Nebraska, U.S.A. *International Journal of Remote Sensing* **18**:2161-2180.
- Yang, L., B. K. Wylie, L. L. Tieszen, and B. C. Reed. 1998. An analysis of relationships among climate forcing and time-integrated NDVI of grasslands over the U.S. Northern and Central Great Plains. *Remote Sensing of the Environment* **65**:25-37.

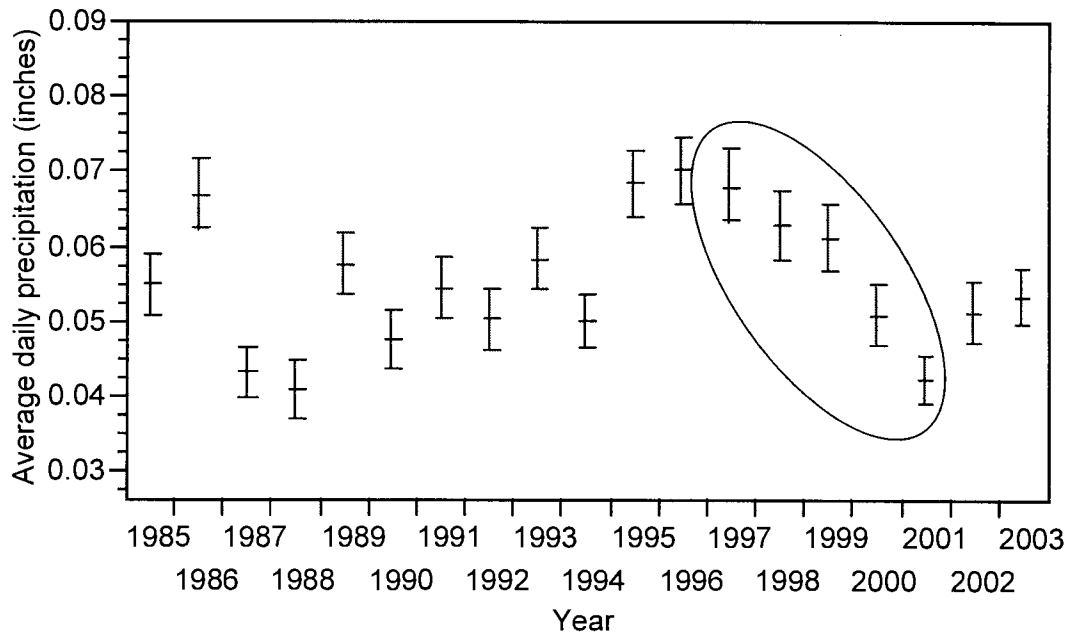


Figure 1. Average daily precipitation in study area from 1985-2003. Note the general drying trend from 1996-2001 ($R^2 = 0.64$, $P < 0.001$). We used three weather stations (Stations 240775:Big Sky, 485345: Lake Yellowstone, and 486440: Moran 5WNW) to represent the extent of the GYE study region.

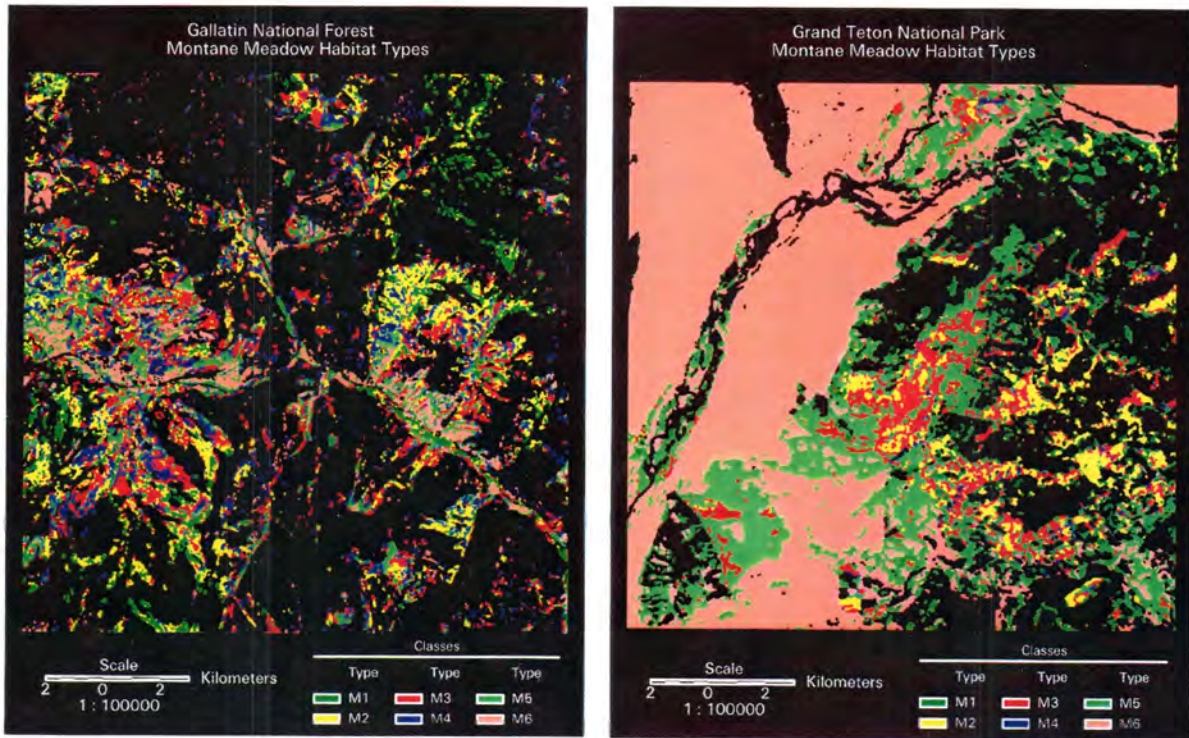


Figure 2. A comparison of landscape mosaics found in the Gallatin study area (left) and Teton study area (right). These images show the diversity of meadow types (M1-M6) as classified by SPOT imagery. M1 meadows (green) are the most hydric and M6 (pink) meadows are the most xeric. Non-meadow habitats (forests, aquatic, anthropogenic, bare ground, etc.) are masked out and shown as black. Note the striking difference in meadow size between the landscapes, especially in M5 and M6 meadows. M4 meadows were not present in the Teton study area, based on our classification scheme and were dropped from statistical analyses in this study.

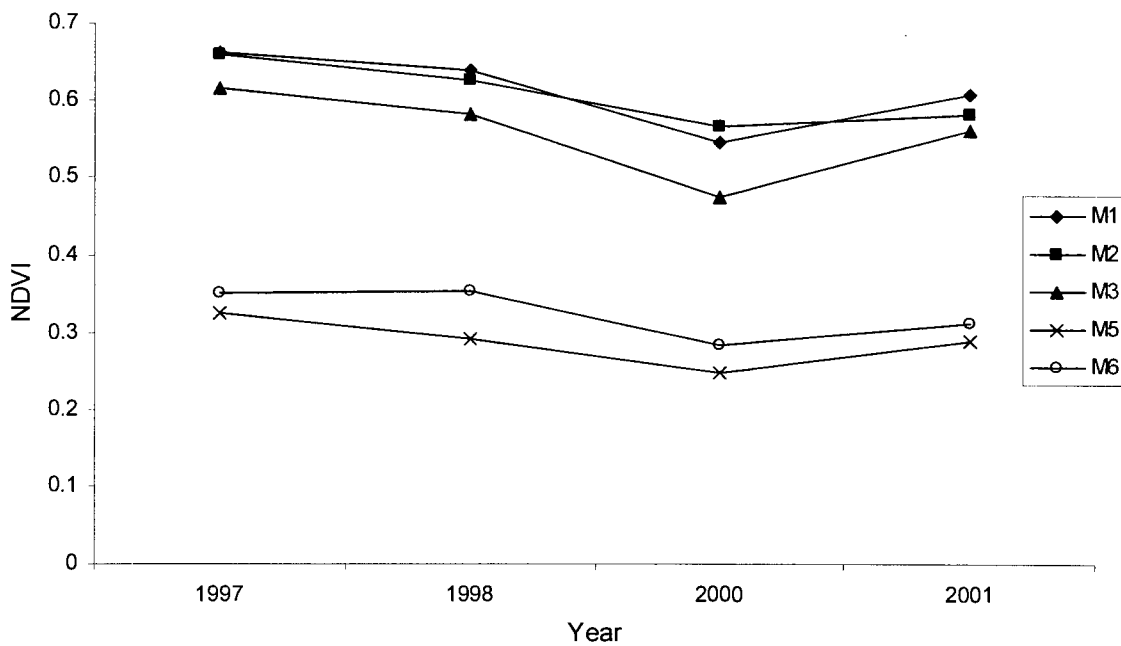


Figure 3. Inter-annual mean NDVI change in twenty-five Gallatin sites from 1997-2001 (without 1999), based on Landsat imagery. In general, wet meadows (M1-M2) show higher mean NDVI values than dry meadows (M5-M6).

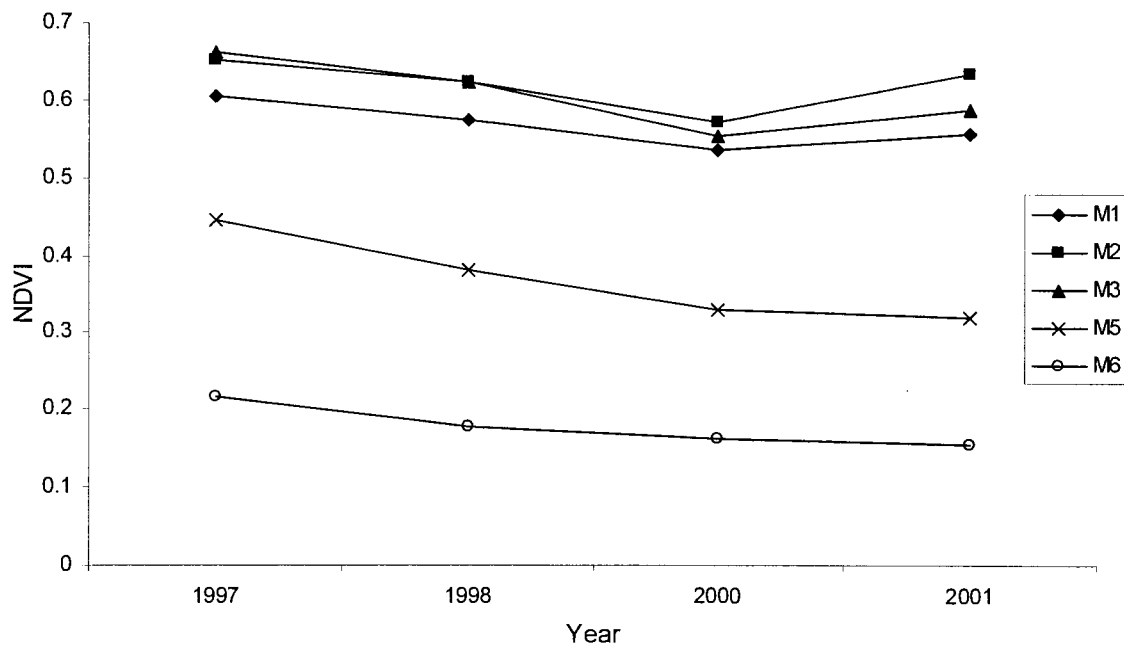


Figure 4. Inter-annual mean NDVI change in twenty-five Teton sites from 1997-2001 (without 1999), based on Landsat imagery. In general, wet and mesic meadows (M1-M3) show higher NDVI values than dry meadows (M5-M6).

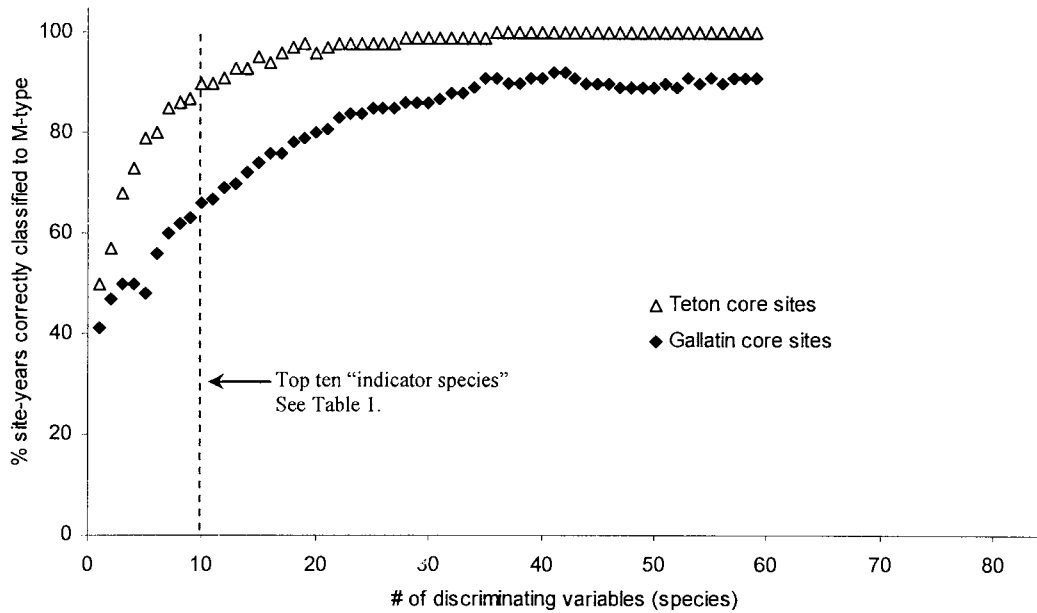


Figure 5. DA performance curves comparing the Gallatins and Tetons using species compositions of butterflies to discriminate among meadow types (M-types). As more discriminating variables (butterfly species) were added to the model (in stepwise fashion), the more site-years were correctly classified to known M-type.

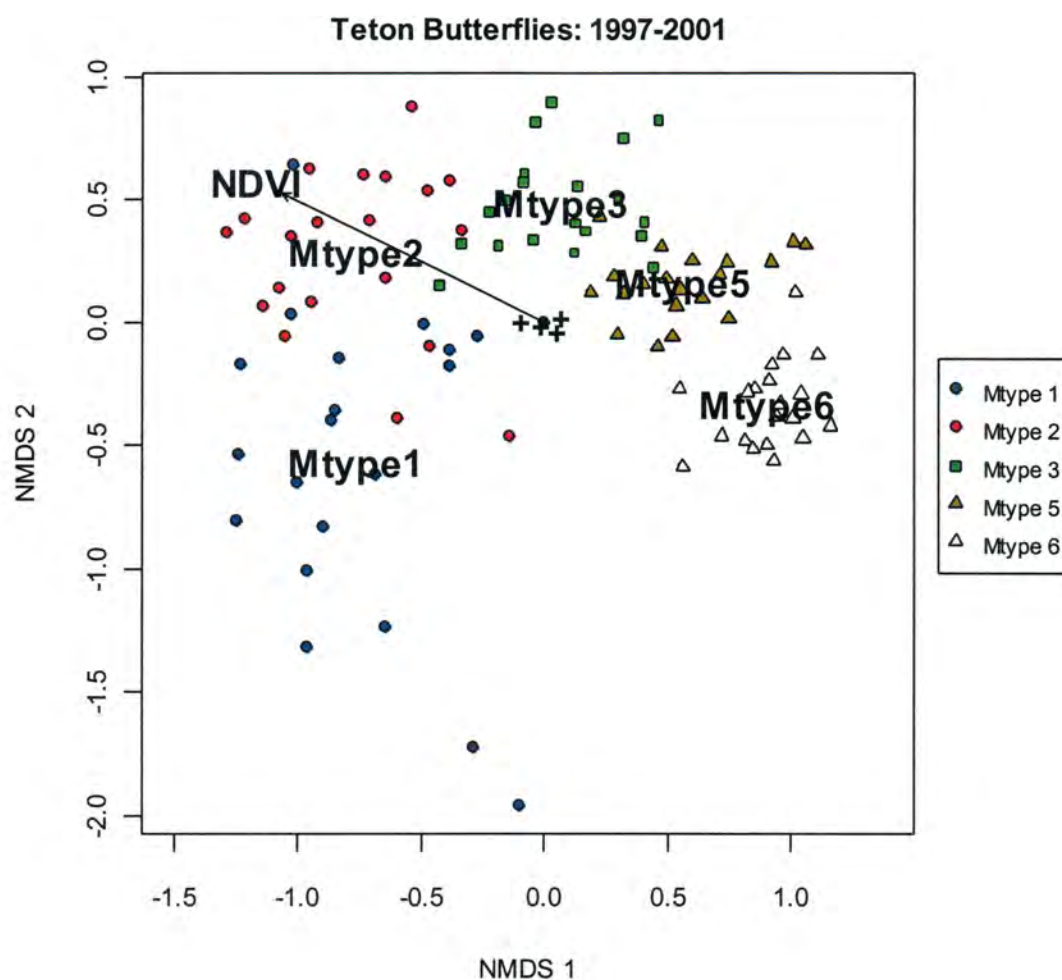


Figure 6. For Teton butterflies, 100 site-years were plotted using nonmetric multidimensional scaling (NMDS). The site-years were color coded by meadow type (M-type), whose mean scores are labeled centroids (categorical variable) by the function "envfit" in the VEGAN library used in the R-project statistical package. A second categorical overlay of Year is represented by the "+" symbols rather than labels which would be indistinguishable do their lack of separation. The third overlay is the continuous NDVI variable pointing in the direction of increasing NDVI values at each site-year.

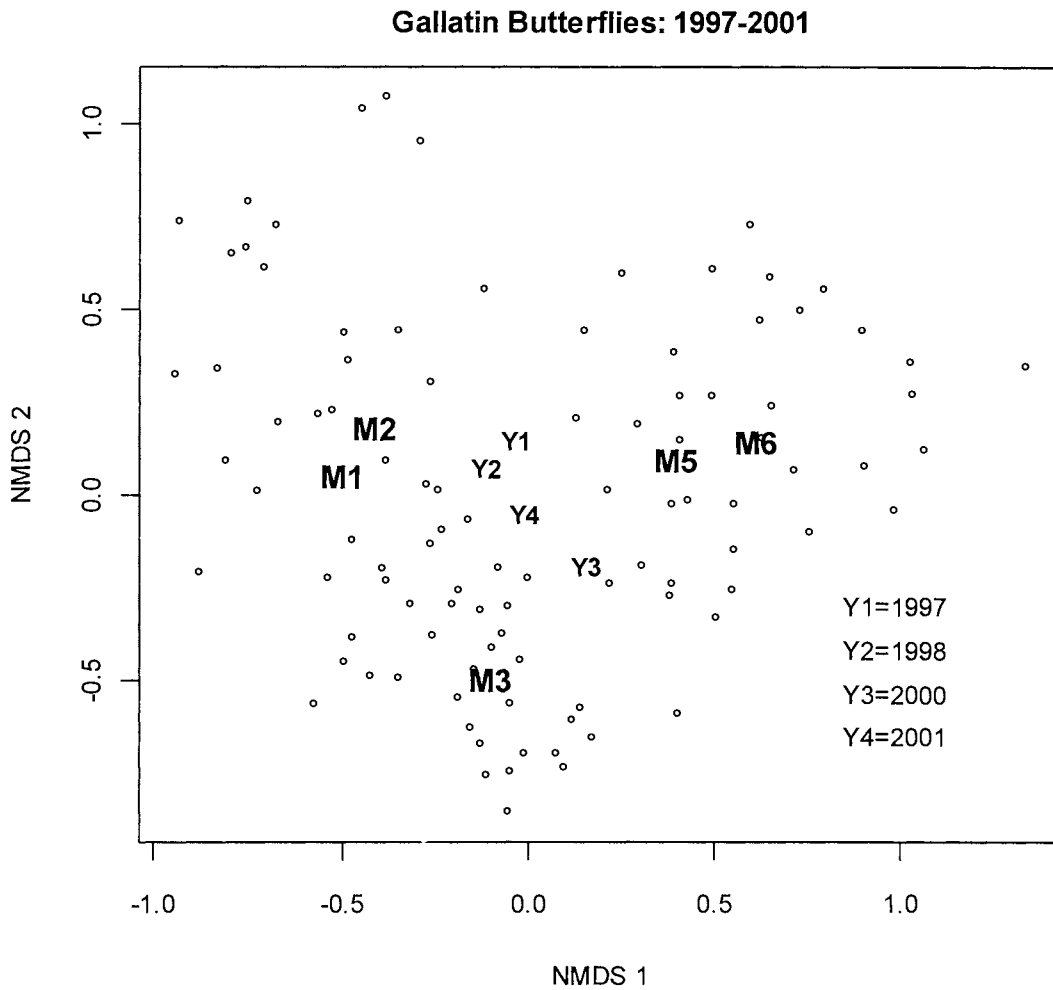


Figure 7. NMDS ordination of Gallatin butterflies with site-years de-emphasized to show differences in centroids of survey years. The largest separation ($R^2 = 0.06$, $P = 0.064$) is between 1997 and 2000, which became the pairwise comparison for the rest of our analyses relating temporal community change to NDVI.

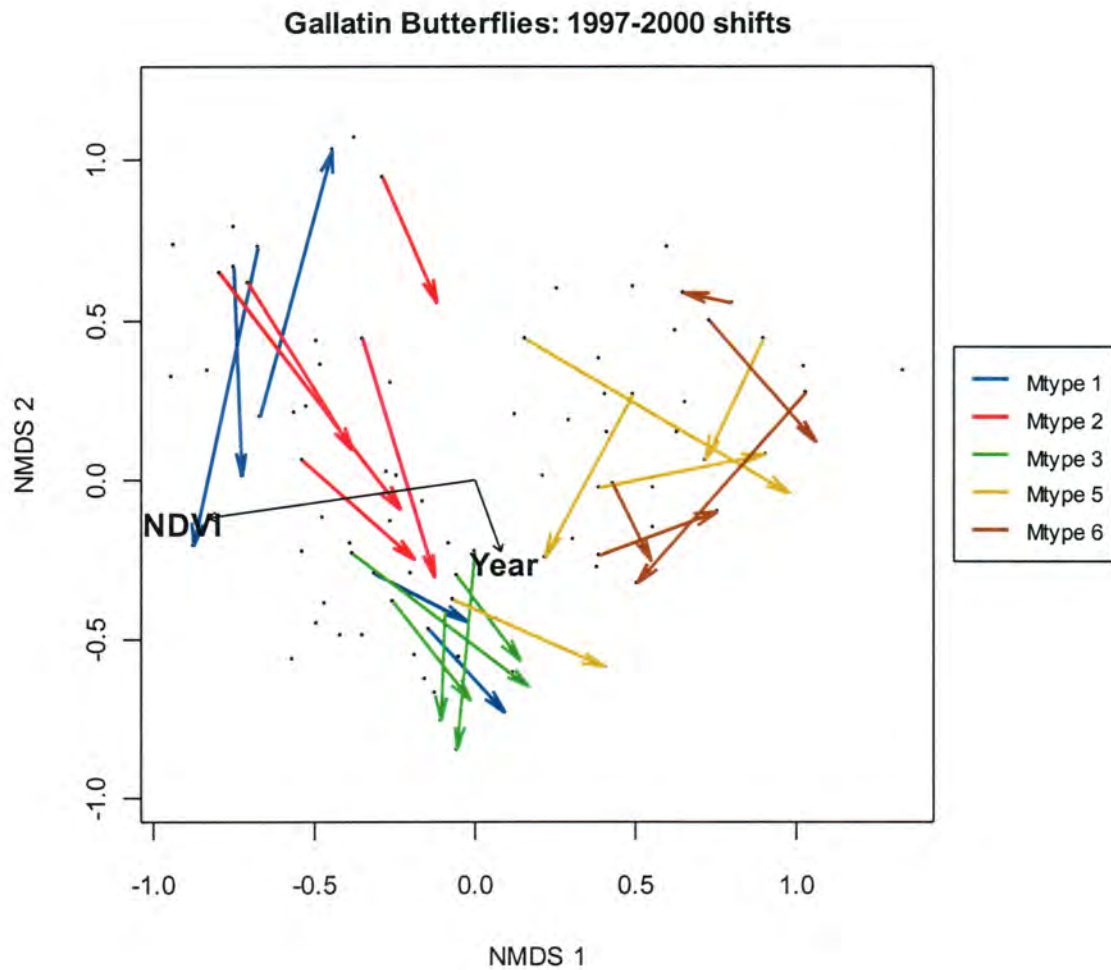
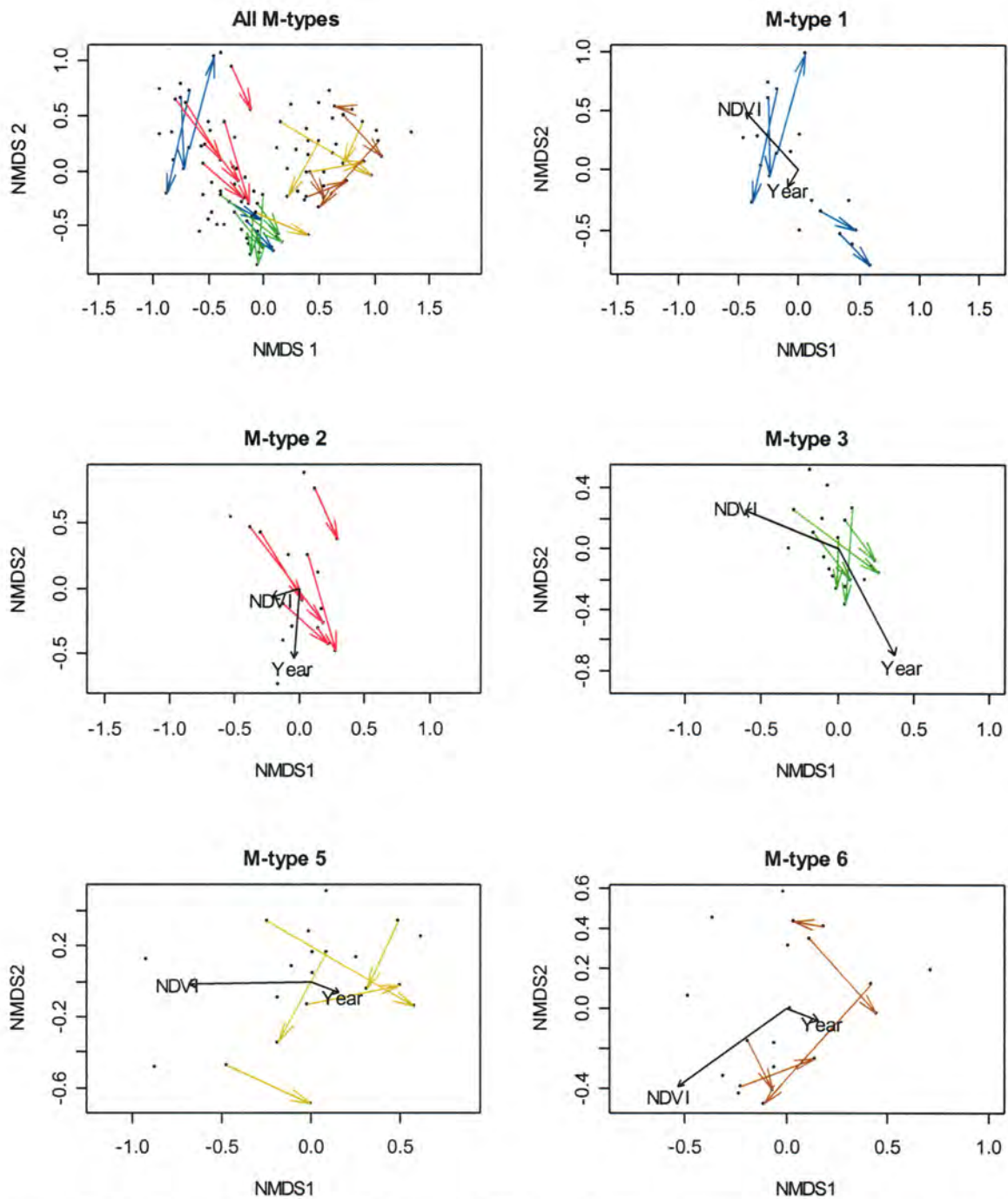


Figure 8. Gallatin butterfly site-years in an NMDS ordination showing arrows of individual sites shifting from 1997 to 2000. Since NDVI is overlaid on all M-types in this plot, it is effectively reflecting the change in the broad context of habitat diversity, or meadow type (M-type), due to NDVI being higher at lower M-types.



Colors: M1 = blue, M2 = red, M3 = green, M5 = gold, M6 = brown, with all arrows pointing from 1997 to 2000.

Figure 9. For Gallatin Butterflies, the correlations between NDVI and Year were plotted for individual meadow types (M-types), using the original configuration of site-year coordinates from the complete ordination plot that included all M-types (upper left, from Fig. 8). NDVI and Year appear negatively correlated in M5s and M3s, but the shifts were strongest in *both* Year and NDVI in M3s.

Table 1. Bird and butterfly hydrological affinities for Gallatins and Tetons based on relative abundance in different meadow types from 1997-2001. Meadow types M1 and M2 were pooled as *Hydric*, M3 and M4 as *Mesic*, M5 and M6 as *Xeric*. Species were listed when their abundance in one hydrologic type was significantly higher than both other hydrologic types (Student's *t*, $\alpha = 0.05$).

Birds		Butterflies	
Gallatins (14 species)	Tetons (17 species)	Gallatins (24 species)	Tetons (24 species)
Hydric			
Common Yellowthroat	Brewer's Blackbird	<i>Boloria selene</i>	<i>Boloria frigga</i>
Lincoln's Sparrow	Common Snipe	<i>Erebia epipsodea</i>	<i>Boloria selene</i>
Savannah Sparrow	Common Yellowthroat	<i>Pieris napi marginalis</i>	<i>Erebia epipsodea</i>
	Fox Sparrow	<i>Plebejus saepiolus</i>	<i>Lycaena hyllus</i>
	Lincoln's Sparrow		<i>Phyciodes selenis</i>
	Savannah Sparrow		<i>Plebejus saepiolus</i>
	Song Sparrow		<i>Speyeria cybele</i>
	Willow Flycatcher		
	Yellow Warbler		
Mesic			
(None)	White-crowned Sparrow	<i>Coenonympha haydenii</i>	<i>Glaucopsyche lygdamus</i>
		<i>Lycaena helloides</i>	<i>Lycaeides idas</i>
		<i>Phyciodes campestris</i>	<i>Lycaena helloides</i>
			<i>Speyeria mormonia</i>
Xeric			
Chipping Sparrow	Brewer's Sparrow	<i>Cercyonis oetus</i>	<i>Cercyonis oetus</i>
Vesper Sparrow	Vesper Sparrow	<i>Coenonympha tullia</i>	<i>Coenonympha tullia</i>
		<i>inornata</i>	<i>inornata</i>
		<i>Lycaena heteronea</i>	<i>Lycaena heteronea</i>
		<i>Oeneis chryxus chryxus</i>	<i>Plebejus icarioides</i>
		<i>Parnassius phoebus</i>	
		<i>smintheus</i>	

Table 2. Top ten discriminating bird and butterfly species in the Gallatins and Tetons. These were chosen using the stepwise variable selection option of discriminant analysis (DA) and are listed in the order they were entered into the DA model. DAs were used to discriminate among meadow types (M-types) using species abundances from 1997-2001.

Gallatin Birds	Teton Birds	Gallatin Butterflies	Teton Butterflies
Lincoln's Sparrow	Yellow Warbler	<i>Cercyonis oetus</i>	<i>Lycaena heteronea</i>
Chipping Sparrow	Brewer's Sparrow	<i>Lycaena heteronea</i>	<i>Cercyonis oetus</i>
Vesper Sparrow	Common Yellowthroat	<i>Phyciodes campestris</i>	<i>Coenonympha tullia inornata</i>
Savannah Sparrow	Vesper Sparrow	<i>Plebeju icarioides</i>	<i>Erebia epipsodea</i>
Brewer's Blackbird	Savannah Sparrow	<i>Erebia epipsodea</i>	<i>Speyeria mormonia</i>
Dark-eyed Junco	Lincoln's Sparrow	<i>Parnassius phoebus smintheus</i>	<i>Plebejus icarioides</i>
White-crowned Sparrow	Fox Sparrow	<i>Oeneis chryxus chryxus</i>	<i>Boloria frigga</i>
Common Yellowthroat	Brewer's Sparrow	<i>Coenonympha haydenii</i>	<i>Plebejus saepiolus</i>
Brewer's Sparrow	White-crowned Sparrow	<i>Boloria selene</i>	<i>Lycaena idas</i>
American Robin	Willow Flycatcher	<i>Pieris napi marginalis</i>	<i>Glaucopsyche lygdamus</i>

Table 3. Ranking of taxon-regions by meadow type (M-type) separation based on goodness-of-fit (R^2) from function “envfit” in the VEGAN library for the R-project statistical package. M-type was used as a categorical variable and fit to an NMDS ordination of site-years with $k = 4$ dimensions. Ordinations were based on bird and butterfly Bray-Curtis community similarity. For regions, the Tetons (birds and butterflies) formed “tighter” groups than in the Gallatins, and within each region the butterflies formed tighter M-type groups than the birds.

Region-taxon	M-type R^2	P ($>R$)
Teton Butterflies	0.81	< 0.001
Teton Birds	0.65	< 0.001
Gallatin Butterflies	0.58	< 0.001
Gallatin Birds	0.46	< 0.001

CHAPTER FOUR: GENERAL CONCLUSIONS

Our work in the Greater Yellowstone Ecosystem (GYE) has provided us with research opportunities that investigate different taxa and habitats at a variety of scales. Every day it is growing more difficult to call an area “natural” or “pristine” so whenever those characters can be approximated, we cannot waste the opportunity to study them.

We centered our investigations on one very large system, and approached it at two very different scales. In Chapter Two, we started at the fine scale of a single species’ nest site selection behavior and how a simple choice of nest location might influence an individual’s reproductive fitness. Our most popular way to date of measuring this fitness is by estimating nest success, using new and hopefully improved methods that themselves continue to evolve in the practice of field ecology. It could be considered risky for a graduate student to base his thesis on employing a newly published field method, rather than utilize more traditional approaches with a longer legacy of publication.

Nevertheless, we chose the logistic-exposure method to measure the nest success of Yellow Warblers in willow habitats in Grand Teton National Park (GTNP). Although, we considered a small suite of explanatory factors that could affect nest success, we were primarily concerned with one in particular: waterway density within each nesting territory of our Yellow Warblers.

Our hypothesis was that even though lush willows could provide some of the highest degrees of concealment for a warbler nest, some predators would be in a position to find that nest if the parents were observed in the area. Furthermore, if that area contains a small scale landscape feature that attracted such predators, we could entertain a “bad neighborhood” hypothesis that made nest success dependent not only on concealment, but on location.

Our suspected predators were snakes; the depredated nests were nearly always in perfect condition except for the fact they were empty and parentless. We have not ruled out avian predators, or even mammals small enough to climb up through the dense maze of willow branches that fill the space between the nest and the ground. Avian predators have the maneuverability to get to a nest and literally “tweeze” out the small warbler eggs, and we did witness a great deal of raven activity at one of our sites.

For the site that was not confounded by raven presence, however, and despite a small sample size even for ecologists, we did indeed find statistical significance in the effect of our waterway density on Yellow Warbler nest success. The logistic-exposure method, along with the application of information-theoretic techniques of model selection allowed us to estimate daily nest survival with a 95% confidence range that did not include zero. Our precision could undoubtedly have benefited from a larger sample size, and it would be naïve to think that one predation mechanism could dominate the fate of all nests in all sites. It is possible, though, that one landscape metric such as waterway density, could set the stage for several alternative mechanisms, any of which could also lower nest success.

Consider, for example, a hypothetical short-term versus a long-term drying trend in an otherwise stable willow habitat. High water tables and surface water would promote thick contiguous tall willow stands, and increase the quantity of nesting habitat in the area. However, if this same surface water attracted potential nest predators in sufficient densities, each individual nest would suffer lower probabilities of success, resulting in a trade off between habitat density and predation pressure (Fig. 1).

If this system underwent a short term drying trend that removed the surface water while most of the willows root systems still had access to a high water table, the nesting

habitat would remain, while the suspected predator's primary prey base (amphibians, aquatic insects, and small fish) would disappear. This would create temporary opportunities for high nest success rates in recently desiccated waterways.

However, should such a drying trend to continue over the long term, the condition of the willows would eventually decline, becoming similar to the thinner, shorter, and more "spindly" willows we often observed at the edge of the willow habitats. These areas were typically where soil was dryer and plants other than willows became dominant. A long term drying trend would therefore lower overall nesting productivity of Yellow Warblers after an apparent short term increase.

Regardless of the mechanism and the local rates of nest success in GTNP, Yellow Warblers have remained quite abundant in tall willows for several years, and they are not the only songbirds that currently thrive in that type of habitat. This brings us to the third chapter of this thesis which looks beyond the single species and the single habitat.

Our community level study included not only willow habitats, but a full continuum of meadow types occurring along a hydrological gradient. Gradients are of great interest to community ecologists and our first goal was to determine if bird and butterfly communities, in terms of their composition, would characterize that hydrological gradient.

The typical underlying gradient is usually measured on the ground at sites where the communities are sampled, but in our case, we classified our gradient into discrete meadow habitat types from multispectral satellite imagery. A satellite image can be thought of as a stack of photos, each capturing a specific bandwidth of the electromagnetic spectrum. By combining several layers of frequencies beyond the capacity of our own vision, we can

characterize and classify a hydrological gradient from a type of “pixel clustering” computing process.

After deciding on these meadow types, we sampled the bird and butterfly communities for several years, resulting in an extensive data set of relative abundances, or species compositions. We used the NMDS ordination technique to arrange our study sites in a plot of “similarity space” based solely on species composition data, without any meadow type (M-type) information whatsoever. Based on the species compositions alone, the ordination method partitioned our study sites into well defined M-types, just as we had partitioned the satellite images before ever conducting a single animal survey.

Our next goal was to see if we could relate a temporal shift in those communities to some other gradient that might be shifting the hydrological gradient we had originally defined. Climate change would have the ability to do just that, since temperature and precipitation comprise such a great deal of hydrology. Admittedly, topography, geology, soils, and a host of other factors could also shift a hydrological gradient, but most of these effects are not suspected to be changing at any rates near that of some currently proposed climate change models.

An ideal design to link climate to community change would be to have fully and continually operational weather units at each study site where plant and animal community data are collected, but this was not within the resources of our study. Instead, we chose to use another site-specific metric to act as a surrogate for climate change. That metric is NDVI and it too can be calculated from satellite imagery. In large scale ecological studies, there are unforeseen sources of variability that make causal links like this one a difficult prospect. The

behavior of the animals we studied combined with the patch size and configuration of their landscape could have confounded our efforts in ways we have yet to determine.

However, we did find that in the Gallatins, the butterfly communities do indeed change in a predictable fashion related to NDVI as long as that relationship is observed within a given M-type, and we further know that the mesic meadows are most likely to reveal this relationship. Armed with this preliminary information, we can look for similar regions with similar taxa and landscape configurations and apply similar methods in an attempt to discover similar processes. We have to keep in mind that we have a hypothesized causal chain upon which we are extrapolating future conditions. To strengthen that chain we have background research relating climate to NDVI. Our own statistical tests have shown a correlation between NDVI and our M-type classification scheme. And finally, we have found instances where several communities have simultaneously shifted during the same time period that precipitation and NDVI have done the same.

There are challenges to using satellite imagery as a data source due to atmospheric conditions and equipment calibrations, but these techniques continue to improve over time and satellite image's utility in ecological research is sure to grow. If one utility is to reveal ecological and biotic processes at the reduced expenses of ground truthing, it will be well worth the effort.

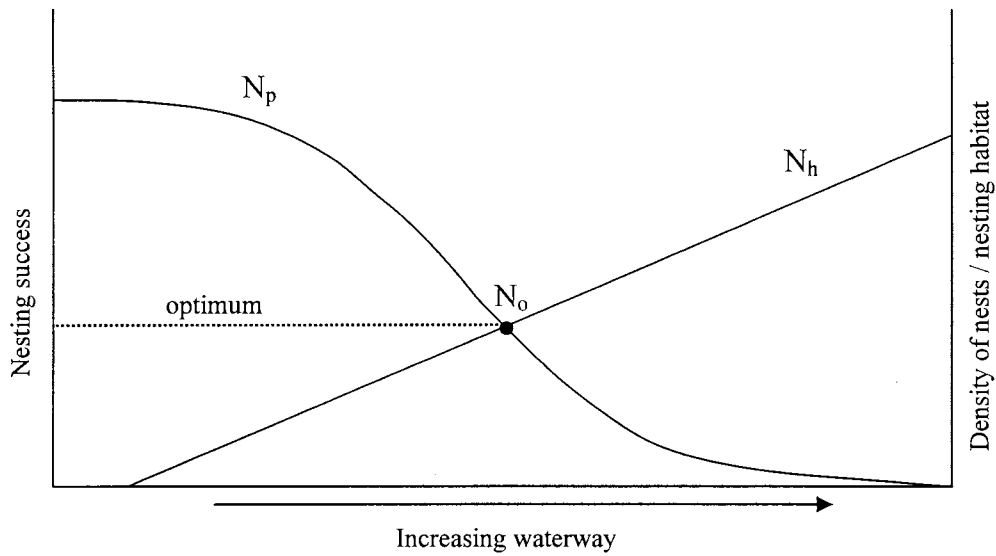


Figure 1. A theoretical model of the conflicting effects of waterways on overall nesting productivity. The line N_p represents declining nest survival due to predation (Chapter Two), while N_h shows the increasing density of nesting habitat near waterways (personal observation). The optimum productivity in this static situation is at point N_o . A drying trend that removes surface water (and the primary prey base of snakes) while nesting habitat persists will shift N_h to the left allowing the optimum productivity N_o to increase, while a long-term drying trend would lower the N_h line, eventually decreasing N_o .

ACKNOWLEDGEMENTS

It will be impossible for me to list all the people and organizations that have made it possible for me to attain this goal, but perhaps a mental walk through the past few years will help jog my memory. I am going to list people in the order that I met or encountered them, so as not to imply any relative “importance” of any one individual; everyone named on this page played an essential role in my education. So, starting in 1999 when I reentered ISU to finish my B.S. after over a decade of absence, here are the people to whom I owe a great debt of gratitude:

Lyn VanDePol, John Burnett, Bonnie Bowen, Kevin deLaplante, Sidner Larson, Devery Fairbanks, Bill Clark, Jim Dinsmore, Louis Best, Diane Debinski and family (James, Zoe, and Hayden), Neal Smith National Wildlife Refuge, Pauline Drobney, Rolf Koford, Stephanie Shepherd, Tammy Stafford, Bill Crumpton, Jonathan Wendel, Katy Reeder, Philip Dixon, Tricia Knoot, Andy Wiewel, Jen Vogel, Amanda Hetrick, Hank Harlow and family (Mary Ann and Tyler), National Park Service, University of Wyoming, Brian Miller (Denver Zoological Foundation, CO), Monica Turner, Kirk Moloney, Brent Danielson, Brian Wilsey, Rob Wallace, Tracy Walker, Mark Jakubauskas, Jessica Skibbe and family (Adam), Martin Cody, Julie Perrett, the EEB Field Trippers and finally, all the faculty, staff, and students I’m forgetting in AECL, EEB, ELVIS, NREM, and EEOB, including the students whom I’ve taught over the past five years.

Most of all, I owe a special thanks to my entire family, and the gang at McCormick.