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Author
Clapp, Mary Katherine

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Interactions at the permeable boundary between water and land in California's high Sierra

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Approved:

Gail L. Patricelli, Chair

Thomas P. Hahn

Sharon P. Lawler

Committee in Charge

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I believe that conservation is inextricably linked with actively supporting and honoring the sovereignty of Indigenous people and their stewardship practices on the land. I acknowledge roles that both academic institutions and public lands formation have played in perpetuating injustices toward Indigenous peoples. As an ecologist and as a modern inhabitant of this landscape, I step into the opportunity to take part in its decolonization by including both Indigenous histories and futures in my work, and by actively supporting efforts toward Indigenous sovereignty and leadership in land stewardship, for the benefit of the places we all cherish and all the beings therein.

ABSTRACT

In this dissertation, I investigate the roles that aquatically derived resources play in the community structure and foraging behavior of wild birds in high-elevation regions of the Sierra Nevada mountains of California.

Wilderness designations protect ecologically important areas from intense human development, which is critical to conserving them but also poses a challenge in accessibility to studying them. To address the need for data-rich methodology in wilderness, I piloted the use of passive acoustic monitoring (PAM) to collect data on the community composition and activity of birds breeding in alpine areas in 6 headwater basins throughout Sequoia and Kings Canyon National Parks (SEKI). In my first chapter, I investigated the potential for acoustic indices—mathematical measurements of variation in acoustic activity—to be used as proxies for avian diversity within three large acoustic datasets from U.S. National Parks that differ in spatial breadth and gamma diversity. Using a Random Forest with several widely used acoustic indices to predict observed species richness in 5,670 minutes of audio recording, I found that acoustic indices predict coarse but not fine differences in species richness. I discuss opportunities and limits in the application of acoustic indices as reliable measures of avian diversity in research and management contexts.

Trout introductions to historically fishless high-elevation lakes cause trophic cascades within the aquatic system, resulting in simplified, species-poor food webs and major reductions in aquatic insect emergences. In the Sierra Nevada, over half of all historically fishless lakes now contain self-sustaining populations of trout, but the effects of this landscape-level disturbance on the surrounding terrestrial food web are largely unknown. In my second chapter, I investigated whether introduced trout impact the adjacent avian community via a reduction in aquatic insect emergences, a potentially valuable food source for birds. While avian alpha diversity (species richness) did not differ between lake types, I documented significant turnover in community composition, with fish-containing and fishless lakes diverging in the relative abundances of several alpine bird species common in the regional species pool. Differences in overall avian abundance between lake types approached statistical significance but were subtle: estimated avian abundance at fishless lakes was higher by roughly 1 individual per 300m sampling radius. Preliminary analysis of a Before-After, Control-Impact experiment involving fish removal at a study lake revealed a significant twofold increase in overall bird abundance following trout removal. The magnitude of this increase in bird abundance may be indicative of a response to a short-term increase in aquatic primary production but may also suggest that currently fish-containing lakes would be capable of hosting a greater abundance of birds in the absence of trout.

The third chapter investigates how seasonality shapes the role of aquatic resources in the diets of breeding mountain white-crowned sparrows (MWCS). I used stable isotope analysis of carbon and nitrogen to quantify both trophic position and origin (aquatic or terrestrial) of the diets of nestling MWCS. Both trophic position and the proportion of food of aquatic origin of nestling diet changed directionally over the course of the season, with late-hatching nestlings being provisioned a diet both lower in trophic position and in aquatically derived prey than early-season nestlings. I discuss the nutritional benefits of aquatic prey items to consumers and how both seasonality and resource availability may impact both adult provisioning behavior and nestling quality.

As global climate change accelerates warming and drying, especially in the alpine and at high latitudes, I argue that understanding the dynamic connections between the aquatic and terrestrial food webs is necessary to identifying, managing, and conserving climate refugia in these areas. Through observational and experimental field study at both the landscape and individual scales, I elucidate previously undocumented links between aquatic and terrestrial systems, demonstrate how the introduction of fishes to high-elevation waterways disrupts those linkages, and provide information about methodologies that can aid in efficient, data-rich, and minimally invasive research in critically important and imperiled wilderness areas.

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CHAPTER 1: Investigating the power and limitations of acoustic indices as proxies for avian biodiversity

ABSTRACT

Remote sensing technologies, such as acoustic monitoring, are transforming the field of ecology. The resulting Big Data contain biological information and have the potential to elucidate patterns and processes at greater pace and scale, but widening the bottleneck between data collection and analysis remains a major challenge. The use of passive acoustic monitoring (PAM) to sample and monitor vocal animal populations has grown in popularity over the past decade and is an exemplar of both the promises and challenges of ecological Big Data. Here, we employ acoustic indices—mathematical expressions of the diversity of sounds present in audio recordings from 42 sites in three western U.S. National Parks—to evaluate under what conditions they perform well at providing reliable, biologically relevant information. We use a Random Forest approach and found that multiple indices do predict coarse differences in species richness. Our models performed less well at distinguishing small differences in richness (fewer than 5 species) and tended to overpredict richness in low-diversity recordings and underpredict in high-diversity recordings. We discuss both the benefits and limitations of acoustic indices for studies of avian biodiversity and offer potential applications where acoustic indices are likely to reliably reflect changes in diversity and meet research objectives.

INTRODUCTION

Both our basic understanding of ecology and our ability to conserve ecosystems depend on our ability to describe patterns and track changes in biodiversity. Choosing the correct analytical tool is no trivial process, and depends on the resources, spatial extent, organisms involved, and aims of the study. Advancements in remote sensing technology such as camera traps, acoustic recorders, and drones, have great potential to expand the pace and extent of biodiversity monitoring. Their utility ultimately rests on the extraction of meaningful biological information from the terabytes of data they generate.

Passive acoustic monitoring (PAM) is an example of such a methodological advance: recorders can be deployed for weeks at a time and return terabytes of information about the biological, geological, and human activity of a place, creating a permanent and unbiased record of its “soundscape” or sonic thumbprint (Pijanowski et al. 2011b, Merchant et al. 2015). As recording and data storage technology has become more affordable, both commercially available and custom-made PAM devices have been deployed worldwide to address conservation and management issues including monitoring anthropogenic activity including illegal resource extraction operations, geological and hydrological activity such as sediment movement, and biological activity. Thus, acoustic recorders have rapidly increased in popularity among researchers, conservation organizations, and land management agencies in service to their goals of empirical study, conservation, and management.

The major benefits of using acoustic data include increased sampling breadth across time and space, the removal of observer effects, the ability to collect fine-scale data in areas that are difficult to access, and the collection of an enduring record of the soundscape for re-analysis. With respect to avian studies, to date, several dozen studies have compared the utility of PAM with the traditional standard of point count data. The majority found that, given enough sampling time, recorders either match or outperform human observers in capturing the species richness (the number of species present) in the vocal community (Darras et al. 2019). Additionally, using acoustic data can yield more accurate estimates of occupancy when the probability of false positive detections can be modeled—something that cannot be done using data collected by traditional means such as point counts (Rempel et al. 2019). There is also evidence that the presence of a human observer influences vocal activity in an area, suggesting that the traditional "gold standard" of point count surveys may also chronically underestimate abundance and bias against species with lower detection probability (Jorge et al. 2018). Thus, acoustic monitoring in general has the potential to improve the survey of vocal animals and inferences about their populations and communities.

However, the utility of acoustic data is contingent upon efficient analysis, which remains problematic. In the case of avian data, extracting community-level estimates of occupancy currently requires an observer experienced in auditory bird identification to spend hundreds of hours annotating acoustic data (Alquezar and Machado 2015, Thompson et al. 2017). Some semi-automated species identification tools are available (e.g. KaleidoscopePro, RavenPro's band-limited energy detector) and have been applied successfully to projects focused on single species (Borker et al. 2015, Wood et al. 2019) but others have not, citing the problem of unacceptably high false positive rates (Knight et al. 2017, Wilhite et al. 2020).

Beyond the individual species and toward the community, even for with relatively low numbers of vocalizing species, the time required to train and optimize recognizers for every species in the community toward the goal of generating community diversity measures can be unfeasible to prohibitive (Towsey et al. 2014, Gasc et al. 2017). Unsupervised machine learning approaches to species-level detection in audio recordings have great promise to unlock large acoustic datasets, but require expertise in computer science and remain largely inaccessible to most practicing ecologists (Briggs et al. 2012, Priyadarshani et al. 2017). Rapid growth exists in the arena of automated species recognition using machine learning, but its current state of development is still years away from widespread and user-friendly implementation because it still requires advanced technical knowledge in programming to build and evaluate models. Furthermore, the application of unsupervised machine-learning approaches is limited to datasets for which there are ample training data—tens to hundreds of labeled vocalizations per species are needed to train algorithms, and even more are needed for model validation. This may not be possible for areas of extremely high biodiversity or endemism, such as forested equatorial regions. Therefore, a rapid and repeatable method to assess biodiversity in audio recordings is still in high demand for researchers and land managers who lack the time, niche expertise, and/or resources to develop custom species recognizers.

Soundscape ecology is the science of describing and predicting ecological patterns based on acoustic patterns over space and time (Pijanowski et al. 2011b). The soundscape itself is the dynamic but unique sonic thumbprint of a landscape; the sum total of biophony (sounds originating from living things), geophony (sounds originating from geophysical features such as running water or rockfall), and anthrophony (sounds originating from human-made objects) (Pijanowski et al. 2011b). Acoustic indices are mathematical expressions of variation in acoustic space that summarize variation in sound pressure level (or amplitude) across time, over frequency, or both. Several indices have been developed specifically to describe differences in biophonic (as opposed to anthrophonic or geophonic) activity (Towsey et al. 2014). In contrast to approaches that rely on the identification of species, multiple acoustic indices can be calculated simultaneously on enormous datasets (multiple terabytes or petabytes) in a matter of hours or days of passive computing time. User-friendly and freely available packages in R (*seewave* and *soundecology*), as well as open-source scripts from previous studies, are customizable based on one's recording equipment, schedules, and settings (Sueur et al. 2008a, Merchant et al. 2015, Buxton et al. 2018b, Villanueva-Rivera and Pijanowski 2018). This vast reduction in post-processing time makes acoustic indices an attractive option for the analysis of acoustic data.

Applying acoustic indices to studies of ecology necessitates that index values reflect ecological patterns. Researchers have found that acoustic complexity indices correlate with differences in ecological patterns and processes such as songbird migration phenology (Buxton et al. 2016, Oliver et al. 2018), land cover (Pekin et al. 2012), seabird colony size (Borker et al. 2014), and in some cases, biodiversity (Buxton et al. 2018b). While some studies have found strong positive relationships between indices and biodiversity, others find weak to no relationships between indices and common metrics of diversity such as species richness (Mammides et al. 2017, Eldridge et al. 2018, Jorge et al. 2018) and community dissimilarity (Lellouch et al. 2014). One explanation for this mixed evidence is that the field is new, and methods of employment and analysis still vary widely. Using multiple indices in combination as opposed to just one has resulted in better predictions of richness and vocal activity (Buxton et al. 2018b, Bradfer-Lawrence et al. 2019), but results are still inconsistent across gradients of diversity and ecoregion. For example, suites of indices performed well in predicting richness in temperate but not tropical environments (Eldridge et al. 2018), and in two (temperate) montane areas but not for underwater sound (Buxton et al. 2018b). For acoustic indices to be used in rapid assessment of biodiversity, work that investigates why acoustic indices are indicative of biodiversity in some contexts and less so in others is needed.

Here, we use acoustic indices as a means to assess avian vocal biodiversity in montane habitats in three National Parks in western North America, all of which employed PAM for different ecological study aims. We tested the assumption that acoustic indices reflect ecological patterns in biodiversity by creating a "ground-truthed" dataset: a subset of recordings from each Park for which the sounds present were manually identified to species by an expert, yielding per-recording estimates of species richness. On that same subset of recordings, we calculated a suite of widely used acoustic indices, and, using a Random Forest approach, asked whether the indices were effective predictors of our manually collected measures of diversity. We grew Random Forest models for all three Parks together as well as each Park alone, predicting that because of the wider range of acoustic activity represented between Parks, acoustic indices would more accurately predict vocal species richness values when all data were included. To explore how the vocal properties of individual species affect the variation in indices' ability to predict species richness, we examined differences in the bandwidth, center frequency, and duration of species' calls in a further subset of the data. We use these results to provide recommendations for contexts in which acoustic indices may be useful for characterizing diversity in the acoustic environment and discuss caveats to this approach.

METHODS

Field Data Collection

Acoustic data were collected at a total of 42 recording sites within three different western U.S. National Parks (Figure 1.1): alpine (>3,000 meters in elevation) lakesides in Kings Canyon and Sequoia National Parks (10 sites, hereafter the "Lakes" dataset), Giant Sequoia (*Sequoiadendron giganteum*) forest in Kings Canyon National Park (9 sites, hereafter the "Sequoia" dataset), and across an 168 to 3327 meter elevational gradient in Denali National Park

(23 sites, hereafter the "Denali" dataset, Table 1.1). The original purposes for collecting each of these datasets vary, as well as the equipment and the recording schedules used (Table 1.S1, Supplemental Material).

Acoustic Data Processing

In order to efficiently process the many terabytes of audio data collected, and to standardize sampling rate between each dataset, we converted each audio file into 1-second, 1/3-octave resolution, using an open-source end-to-end calibration method that yields absolute sound pressure level in dB L_{eq}, which are comparable between different recorder types (Merchant et al. 2015). One-third octave bands are logarithmically grouped bins of frequencies and are widely employed in characterizations of ambient environmental noise (Merchant et al. 2015).

Calculation of Acoustic Indices

We calculated a suite of 28 acoustic indices that have been used in previous studies with similar aims (Buxton et al. 2018a, 2018b). Indices represent changes in acoustic content across bands of time, frequency, or both, and are summarized in Appendix S4 of Buxton et al. (2018*b*).

Manual Annotations of Acoustic Data

To assess the relationship between acoustic indices and observed vocal diversity, we created a ground-truthed subset of audio data comprised of 10-minute segments for which all vocalizing species present were identified by experts. The methods differ slightly by study location, as described below.

Alpha diversity, or local diversity, can be summarized by a strict count of species (species richness) or an abundance-weighted measure of richness (e.g., Shannon entropy, Simpson Index). Abundance-weighted measures are more informative but are often more costly or time-consuming to collect in the field (Broms et al. 2015). The same is true for collecting these data from acoustic recordings; thus, for each 10-minute audio segment, we collected one of two types of data that differed in the amount of detail annotated: the comprehensive “Richness-Activity” dataset and the less detailed “Richness-Only” dataset. For the Richness-Activity Dataset, every audible signal was identified to yield both a count of the number of species (species richness, see below) and a rate of vocalizations per species/taxon (vocal activity, see below). This process took between 20-45 minutes per 10-minute file. For the Richness-Only dataset, one vocalization per species/taxon per file was identified to yield a species richness value per 10-minute file; this took roughly 15-20 minutes per 10-minute file.

i. Lakes Dataset

Both Richness-Activity and Richness-Only data were collected on the Lakes Dataset by MKC. For Richness-Activity, we randomly selected 124 10-minute segments of audio between 9 and 12 July, 2015 from morning hours (0510-0910) from all 10 sites. This date window was the only period during bird breeding in which all recorders were successfully recording. Using RavenPro, we placed a selection box around each sound and annotated it to species whenever possible (Bioacoustics Research Program 2014). We marked every sound we could not confidently identify and reviewed these with 1-2 experts in bird identification by sound. When consensus on ID could not be reached, we marked the sound as “unknown.” To minimize observer bias, we hid all identifying information about the location, date and time of the recordings by temporarily renaming the files. We used high-quality sound-cancelling headphones (Bose QuietComfort 25) to minimize variation in the ambient environment that would interfere with hearing. We observed that it was difficult to reliably identify sounds with an absolute maximum amplitude of greater than ~40 dB; therefore, we only annotated sounds that exceeded this amplitude.

For the Richness-Only dataset, we annotated at least one vocalization per species present in an additional 74 10-minute samples from the Lakes recordings. Thus, we had 198 samples for which Vocal Species Richness could be calculated (124 from the Richness-Activity Dataset and 74 from the Richness-Only dataset), and 124 samples for which Shannon Vocal Diversity and Total Number of Vocalizations could be reported in addition to richness.

ii. Sequoia Dataset

Another expert in bird identification annotated a subset of 8-10 10-minute recordings from each of the 9 sites in the Sequoia dataset following a similar protocol to that of the "Richness-Activity" Lakes dataset. In addition, the annotations were made using a single cursor mark rather than a selection box, so frequency and time information of individual calls was not retained.

iii. Denali Dataset

This set of 15-minute files was annotated using a semi-automated method developed by D.H.B., which employed the Band-Limited Energy Detector in RavenPro to automatically detect and label putative vocalizations. The output—an array of unlabeled vocalizations for each file—was annotated for audible species by trained observers. Observers also annotated false detections. Identification was independently validated by another observer to minimize categorization error. Because the rate of false negatives (vocalizations present in the recording, but which went undetected by the automated detector) was not verified for this method, these data are used for species richness only (Richness-Only dataset). The 15-minute files and associated annotations were truncated to 10 minutes each for consistency with the Sequoia and Lakes datasets in this analysis.

Measures of Alpha Diversity in Annotated Recordings

For all 688 10-minute samples across all three study locations, we calculated avian vocal species richness (the number of bird species vocally present). For the 124 recordings in the Richness-Activity dataset, we also calculated a measure of diversity weighted by call abundance—Shannon Vocal Diversity— using diversity() in the R package *vegan* (Oksanen et al. 2019). It is important to note that Shannon diversity indices are calculated using vocal activity rather than true numbers of individuals. Although increased vocal diversity may positively relate to abundance, this relationship is only beginning to be examined and has not been well-established (Pérez-Granados et al. 2019). Thus, we interpret the Shannon values here not as abundance-weighted diversity in the strict sense, but as a measure of diversity weighted by vocal activity.

For all datasets, calls tagged “unknown” or “uncertain” were removed from subsequent analysis because they were most often either faint vocalizations or one-syllable calls. By removing them, species richness may have been underestimated and/or very rare species undercounted. The alternative, treating each unknown vocalization type as a new species, would likely result in overestimation of species richness in the acoustic recordings.

The sounds of mammals, insects, and humans were also present in recordings. They were labeled to species when possible (e.g., “PIKA” for American Pika (*Ochotona princeps*)) and otherwise labeled to the lowest accurate taxonomic classification possible (e.g. “insect”, “human”). Activity-weighted measures of diversity that include all vocal animals are likely to be predicted better by acoustic indices naïve to species identity as compared to those that include only birds. However, for these datasets, the inclusion of non-avian animal sounds in diversity measurements introduce a problem in the calculation of diversity metrics: non-avian animals that vocalize represent a much smaller fraction of their respective taxonomic groups compared to birds, the majority of which vocalize daily (for example, dozens of small mammal species can be found around alpine lakes, but only pika and marmot vocalize regularly). Non-avian vocalizations therefore cannot be not used reliably to represent the diversity of that taxonomic group.

Furthermore, we wanted to evaluate the performance of acoustic indices on estimating avian diversity, which is one of the most common use-cases of PAM and since many rapid appraisals of biodiversity focus on avifauna as indicators of habitat quality (Gasc et al. 2017). We therefore report on models whose response variables include bird sounds only. This may not be true for other ecosystems in which non-avian animals contribute heavily to the soundscape (e.g., anurans and insects in tropical forests).

Predicting biodiversity with acoustic indices using Random Forests

Using multiple acoustic indices as predictor variables in a flexible modeling framework, as opposed to using a single index, has been successful in other attempts to find relationships between indices and biological processes of interest, including species diversity (Buxton et al. 2018b, Bradfer-Lawrence et al. 2019). The Random Forest is conglomeration of classification and regression trees (CARTs), a type of machine learning procedure (Breiman 2001). They are often used for highly multivariate data such as acoustic indices because they do not make assumptions about the distributions of predictor variables and are more robust to multicollinearity compared to other methods (Murphy et al. 2010). Random Forests perform better than linear models in previous studies of acoustic indices (Buxton et al. 2018b).

We used a Random Forest procedure to predict observed avian species richness (hereafter 'Richness') using 28 acoustic indices as predictor variables. Using the package *randomForest* in R, we fit a global model for Richness for each dataset alone, as well as for all datasets combined. The datasets differed in mean species richness per site (Figure 1.3), so the purpose of combining the three datasets was to build more generalizable predictive model by increasing the variation sampled with respect to species richness. Before running the model, we assessed multicollinearity among indices using qr-matrix decomposition with a threshold of p = 0.1 (function 'multi.collinear' in R package "rfUtilities") (Evans and Murphy 2019), and removed indices that were highly colinear (above the threshold of p = 0.1) from the global model.

We used a model selection procedure to find the most parsimonious model with the highest predictive power and the fewest predictor variables (Murphy et al. 2010), and then used this top model to generate predicted values of richness for the 688 10-minute samples for which observed richness was known. Finally, in order to investigate the relative importance of each index on the predictive power of the model, we report the mean percentage increase in MSE (mean squared error) of the model when values for that variable is randomized. The indices with the most predictive power will have the largest mean percent increase in MSE.

For the Lakes and Sequoia Richness-Activity datasets (122 and 77 files, respectively), we grew an additional set of Random Forests for the response variable of Shannon Vocal Diversity, because we had collected information about the calling rate of each species within those recordings.

Individual- and Species-Level Variation in Call Structure

Acoustic indices measure differences in sound pressure level across regularly spaced bands of time and frequency; however, birds and other vocal animals differ in the spectral and temporal characteristics of their vocalizations and in their vocal behavior (e.g. song rate, time of day, perch height), and may unevenly weight indices. These differences and their potential impact on acoustic indices have received very little attention in the growing literature on soundscapes. We used data on the spectral properties of vocalizations from the Lakes Richness-Activity dataset (124 10-minute files) to examine this variation among species and its potential effect on acoustic index values. During annotation of the Lakes Richness-Activity dataset, we manually created a selection box around each vocalization in the spectrogram, so that the front and back of the selection box measured the start and end time of the vocalization. In the event of a repeated call bout in which the space between syllables exceeded the duration of the call itself (for example, the male flight call of American Pipit, *Anthus rubescens*), the entire bout was boxed as a single vocalization (Figure 1.2). The top and bottom edges of the selection box were drawn to fully contain the frequency range of the vocalization. On each selection, we collected RavenPro measures for Duration in seconds (difference between end and start time), Bandwidth (difference between the 95% and 5% frequencies, calculated as the frequency value that divides the selection into two intervals above and below 95% and 5% respectively), and Center Frequency in Hz (the frequency that divides the selection into two intervals of equal energy).

RESULTS

Measures of Alpha Diversity in Annotated Recordings

Species richness per recording differed between sites and was on average highest in the Sequoia dataset (mean = 6.12 species/recording; variance = 11.9), followed by Denali (mean = 4.29; variance = 10.1, Fig. 1.3). The Lakes dataset had the lowest mean richness (3.66 species/recording) and lowest variance (2.86) between recordings (Table 1.1). Lower variance between samples indicates that sites in the Lakes dataset are more similar to one another in richness than are sites in either the Sequoia or the Denali datasets.

In the Lakes Richness-Activity dataset (122 files), we detected 22 bird species and 3 mammal species in total, comprising 86% and 9% of all annotations respectively (n=13,532). Less than 0.2% were comprised of insect and anthrophonic noise, and the remaining 4.8% of annotations were marked as uncertain or unknown. Mountain white-crowned Sparrows (*Zonotrichia leucophrys oriantha*; WCSP) were the single most vocally abundant species: their vocalizations comprised 45.2% of all vocalizations.

Performance of Acoustic Indices

Table 1.2 summarizes each of the Richness models we ran. Acoustic indices were roughly predictive of observed avian species richness in the top Random Forest model using all three datasets combined ($R^2 = 0.600$; MSE = 3.51, Figure 1.4). Modeling each dataset individually generally resulted in poorer relationships, with the exception of the Denali dataset. The Lakes dataset showed the weakest relationship between index values and observed richness ($R^2 = 0.165$; MSE = 2.38). Indices were weakly predictive of species richness in the Sequoia dataset ($R^2 = 0.534$; MSE = 5.44) and moderately predictive in the Denali dataset ($R^2 = 0.670$; MSE = 3.38).

In addition to differing in their predictive power, study-specific and combined models differed in the relative importance of individual indices as predictor variables, and the categorical covariate for each of the three datasets ('Dataset') emerged as an important covariate in the combined model, resulting in a 14.48% increase in MSE if randomized in the model (Figure 1.5a). For the combined model, the most important variables that emerged were AA (a measure of the amount of time that noises exceed background level within the sample), and Hm (a measure of acoustic entropy) each resulting in an increase of MSE of >20% if randomized (Figure 1.6a,b). Variable importance among the three site-specific models also varied (Figure 1.5b-d). Hm and AA were the only indices common to all site-specific top Random Forests.

The top RF model for all three datasets underpredicts richness in locations with high diversity and overpredicts in recordings with low diversity (Figure 1.8a-c). Overall, site-level richness values in the Sequoia dataset are predicted with the highest accuracy. In some cases, especially in the Lakes dataset, using indices as proxies for richness would lead a researcher to rank sites differently or fail to detect differences in richness than they would if using the ground-truthed data.

In the Lakes dataset, Shannon Vocal Diversity was also poorly predicted by indices (R^2 = 0.122, MSE=0.164). In the Sequoia dataset, Shannon Vocal Diversity was weakly predicted by indices (R^2 = 0.504, MSE=0.205). These model fits are similar to the Richness models for the same datasets.

Variation in the acoustic space of bird vocalizations

In the Lakes dataset, we found that birds varied widely in both the bandwidth and duration of their calls (Figure 1.9). Interspecies variation along either of these axes could influence acoustic indices, which are calculated over bins of time, frequency or both.

Along the frequency axis, some birds exhibit a large range of center frequencies in their vocal repertoires, and others' vocalizations fall within a narrower frequency range, reflected in both bandwidth (Figure 1.9) and center frequency (Figure 1.10) properties. This could be due to the presence of both songs and calls in their repertoire (as is the case with American Robin, *Turdus migratorius*), or to frequency modulations within songs or a large song repertoire (Rock Wren, *Salpinctes obsoletus*). Rarer species may not have their entire repertoires represented. In any case, when this acoustic information is reduced to SPL in 1-second 1/3 octave band resolution, this means that certain bird repertoires span more bins than others, thus unevenly "weighing" the several indices that incorporate differences in SPL between frequency bins (Figure 1.10).

Birds also vary in the temporal component of their vocalizations, with mean duration of vocalizations ranging from 0.34 seconds (Cassin's Finch, *Haemorhous cassinii*) seconds to 2.19 seconds (Spotted Sandpiper, *Actitis macularius*) (Figure 1.9). Any vocalization longer than 1 second in duration, and especially those which modulate in frequency across that time, will increase the values of any acoustic index that measures differences in SPL over time. This includes variation in whether a species tends to sing multiple song types in fairly rapid succession within a bout, such as the Rock Wren, or in temporally more sparse bouts, such as the Hermit Thrush.

DISCUSSION

Acoustic Indices and Avian Diversity

Overall, we found that acoustic indices can predict coarse but not fine-scale differences in species richness, one of the most common measures of biodiversity, as suggested by the moderately good fits of the model built with all three datasets. The R^2 value of 0.60 of this model is similar to those of other published Random Forests predicting diversity using acoustic indices (Buxton et al. 2018a). However, we found that model performance varied widely by dataset, which provides evidence that the performance of acoustic indices in predicting avian species richness may not be reliable for all projects.

Of the three models built from their datasets alone, the Denali model performed the best, predicting observed richness in those sites with less variability than the global model. This is likely because the Denali dataset encompassed more variation at the site level with respect to gamma richness (the global species pool), elevation, and habitat than did the Sequoia and Lakes datasets, as well as at the recording level, with temporal sampling occurring from 0300 to 1000 across all sites (Figure 1.3, Table 1.S1, Table 1.S2c). The top Sequoia model predicted observed richness with some accuracy, but the Combined model did a better job of predicting Richness in Sequoia recordings than did the site-specific model. The poor fit for the Lakes dataset alone could be due to the relative prevalence of geophony (mostly wind and rain) in the alpine soundscape compared with the soundscapes of other ecosystems. Previous studies report obvious peaks in acoustic index values in the morning and evening hours when bird song and other vocal animals tend to be more active, including in the Sequoia dataset used in this study (Pijanowski et al. 2011b, Merchant et al. 2015). However, this is not the case with the Lakes dataset: instead, several acoustic indices peak mid-afternoon, possibly due to the presence of gusty afternoon wind at these locations (Figure 1.11). Many other studies have reported on the influence of background noise on index performance (Sueur et al. 2014). If geophony (or other non-target signals) is common and/or particularly loud, and biophony is also relatively low throughout the dataset, especially the indices that are calculated using SPL relative to maxima or background SPL within that recording (such as AA, ADI, or AR; see Appendix S4 in Buxton et al. 2018*b*), index values may not track subtler differences in biophony as reliably as they would in recordings where acoustic energy in the "bio" band dominates the soundscape.

A non-mutually exclusive explanation could be that there is not sufficient variation in species richness among the recording locations within the Lakes study for the indices to distinguish. The result that predictive power of the model improved significantly after tripling the range of richness values by including multiple datasets supports this explanation. This intuitive result—that patterns are more likely to emerge when the variation measured is maximized—has important implications for implementation of acoustic indices in studies of biodiversity. It suggests that the utility of acoustic indices as a proxy for biodiversity depends heavily on the aims of the researcher and the study system in question. For studies where richness or vocal activity is expected to vary substantially across space, time, or treatments, acoustic indices may prove useful in detecting those differences. In contrast, indices may not uncover differences in situations where treatment effect size or total variation in species richness is expected to be low or is unknown, due to the fact that the residual variation in the system is sufficiently large to make nuanced changes undetectable. This may limit the utility of these metrics for some studies comparing biodiversity before and after disturbance, or between disturbed and undisturbed sites within a habitat type, if those changes are more driven by community assembly (turnover) as opposed to alpha diversity (species loss).

The collection of call-level data in the Lakes Richness-Activity dataset allowed us to explore the relationship of acoustic indices and properties of biodiversity at a more nuanced level than species richness. Using vocal rate (the number of calls per recording per species) to generate a Shannon Vocal Diversity index, we found that Random Forests of acoustic indices performed similarly in predicting variation in a measure of alpha diversity scaled by activity rate as they did variation in Richness (Table 1.2). However, great care needs to be taken in using such a measure, as currently, very few studies have assessed the relationship between vocal activity as captured by a single microphone scales reliably and relative abundance of individuals (but see Peréz-Granados et al. 2019 and Bradfer-Lawrence et al. 2020). Arrays of microphones can be powerful tools for estimating abundance (Blumstein et al. 2011, Mennill et al. 2012), but the vast majority of passive acoustic monitoring projects use a single microphone per site out of the need to prioritize spatial coverage and minimize post-processing time of recordings (Sugai et al. 2019). Until further study directly linking vocal activity to abundance at the community level, Shannon Vocal Diversity needs to be interpreted as a measure of activity rather than abundance. As such, measures of vocal activity, although they are better predicted by indices, may not provide researchers or land managers with information of conservation value, if true relative abundance is the variable of interest. Methods that compare counts of individuals from traditionally collected point count observations with acoustic activity annotated in recordings would shed light on this currently missing link. There is compelling evidence that observer presence can alter bird vocal activity and thus individual counts/estimates of abundance in traditional point count surveys, a source of bias that could be resolved by passive acoustic monitoring (Jorge et al. 2018). Additionally, most of the work comparing acoustic indices to measures of diversity use species richness, likely because of how much extra effort is required to collect data on vocal activity (from recordings) and abundance (from field surveys). If strong links can be made between vocal activity rate and individual counts, Shannon Vocal Activity (and consequently, acoustic indices that reflect this soundscape property abstractly), could be one of the more useful applications of this tool.

Variation in frequency and duration of bird vocalizations

For an acoustic index to scale reliably with richness, it should be robust to differences between species in the length, bandwidth, and amplitude of vocalizations such that each species' vocal signature weights it equally. However, birds (and vocal animals at large) display remarkable diversity in their vocalizations, driven largely by natural and sexual selection for inter- and intra-species communication (Andersson 1994, Bradbury and Vehrencamp 2011). It has recently been hypothesized that vocal diversity may also be driven by competition for "acoustic space" within a landscape similar to the way finite space engenders competition for niches in ecological communities (Pijanowski et al. 2011a, Robert et al. 2019). This diversity leads to number of factors related to the biology of vocal animals that could theoretically impact index calculations that can be grouped roughly into two groups: 1) the physical characteristics of their vocalizations and 2) their behavior.

Multiple characteristics of vocalizations may affect index values. For example, species with larger than average repertoires, lengthy vocalizations, and/or wide frequency ranges may artificially inflate indices, whereas species with shorter, quieter, or less verbose vocalizations may contribute comparatively less weight to indices. With regard to behavior, vocal species differ in their vocal activity over days, seasons, by sex, and by association with different habitat types within which sound travels differently. The distance between the bird and the microphone will impact the amplitude of that vocalization in the recording, and thus lead to differences in a subset of the acoustic indices which employ amplitude in their calculations. Vocal activity in birds is also related to breeding status and territoriality; therefore, birds with territories within the sampling radius of the microphone will result in louder, more frequent vocalizations than those from birds with territories further away. This may result in acoustic sampling that is biased against less common birds. For acoustic indices to be useful indicators of diversity, they must be robust to this variation, yet very few studies have investigated how these sources of variation impact index values.

One study assessed the impact of variation in call characteristics on the performance of acoustic indices by simulating artificial bird assemblages of equal richness that varied in species identity, signal amplitude, and number of sounds, and testing whether 7 commonly used acoustic indices were robust to that variation (Gasc et al. 2015). They found that no index they tested (including Hf, Ht, Mamp, ACI, and AR, which were employed in our study) was invulnerable to changes in community-level call characteristics. Another recent study directly assessed the effect of sound complexity on index values by simulating 10-minute files comprised of varying levels of background noise, calling rate. They found that the five different indices varied inconsistently with respect to the signal-to-noise ratio, complexity, temporal frequency, and richness of sound units (Zhao et al. 2019). In this study, we did not explicitly test the impact of call characteristics on index values through direct manipulation, but we did measure and describe spectral characteristics of the bird assemblage in the Lakes dataset in order to determine how variable species are in their "acoustic space." We found substantial inter-species variation in their vocal frequency ranges, with some species' vocal repertoires spanning 6-7 frequency bands while others' span only 1 or 2 (Figure 1.10). If the vocal bandwidth of a rarer species overlaps with that of a more common species, the contributions of the rarer species to the soundscape may go "undetected" in calculations of acoustic indices. For example, losses in Dusky Flycatcher (DUFL) or Cassin's Finch (CAFI) in real communities may go completely undetected in index calculations due to the fact that they vocalize less often and at the same frequency as common species such as White-crowned Sparrow (WCSP).

Because many acoustic indices measure change over bins of time, variation in call duration may also disproportionately impact indices. Birds with vocalizations that are simpler, quieter, shorter, or more stereotyped, (e.g. calls of suboscines such as flycatchers), may contribute less to acoustic complexity measurements than birds with complex repertoires or multiple vocalization types. In contrast, birds that typically vocalize for longer bouts (e.g. American Pipit, Figure 1.2) may inflate indices. Furthermore, some species may vocalize more frequently or for longer periods throughout the day compared to others. Further work could investigate the effect of diel vocal behavior on indices—collecting large sets of continuous acoustic data make these types of inquiries possible because they can be mined for fine-scale patterns such as diel calling rate (Thompson et al. 2017).

The consequence of underestimating the presence of (or failing to detect the loss of) rare species can have harmful effects in the context of conservation and management projects. In many scenarios of species loss, rare, endemic, and specialist species are often the most vulnerable to local extinction (Henle et al. 2004, Urban 2015). Rarities and specialists can also hold disproportionately large roles in ecosystem function and stability, meaning their loss could disproportionately impact ecosystem function more than the loss of an equivalent number or biomass of a common species (Mouillot et al. 2013, Leitão et al. 2016), but see (Hillebrand et al. 2008). Declines or losses of rare species may go undetected if analysts are relying solely on acoustic indices to estimate diversity, assess ecosystem health, or evaluate effective restorations—all contexts for which the use of acoustic indices has been recommended. Similarly, indices may fail to detect differences in systems where the primary effect of disturbance is not a difference in richness but turnover in bird community, for example through the replacement of native species by invasive ones. We therefore currently advocate caution in applying the use of acoustic indices without sufficient knowledge of the natural history of one's system, personnel trained in aural species identification for ground-truthing purposes, or resources to adequately sample across relevant space or time gradients.

Previous studies have described inconsistency in the predictive power of indices among habitats and levels of species richness (Buxton et al. 2018a). Our results expand on what we know about in which habitats and levels of diversity acoustic indices perform reliably: we find good performance in mid-elevation montane habitat, consistent with previous work (Eldridge et al. 2018) but poor performance at both low (<4 species) and high levels (>10 species) of richness. The fact that the models begin to underpredict species richness at the upper bounds of its variability suggests that acoustic indices may "saturate" at a certain level of acoustic activity and fail to detect additions of new species. Evidence of acoustic indices "saturating" in this way is also documented in other studies (Sueur et al. 2008b, Zhao et al. 2019). These issues could be resolved by machine-learning (ML) approaches that automatically detect and identify vocalizations, rather than using indices. Given adequate training data, automated ML recognizers are robust to the drawbacks of indices we outline here— they can detect rare or infrequently vocalizing species, provide more interpretable estimates of biodiversity based on species—while retaining the major benefits of passive acoustic monitoring in general (unbiased record, greater spatial and temporal coverage, avoidance of observer bias/interference, etc.) (Kahl et al. 2021).

Conclusions

Passive acoustic monitoring in general does present enormous opportunity in spite of its challenges and limitations. As data processing methods improve and our understanding of acoustic communities grows, the upfront investment in recording technology may pay off in the long run as long-term datasets accumulate and ways to automate their processing and analysis are developed. In the meantime, acoustic indices could provide researchers and land managers with a coarse picture of biodiversity patterns at their study locations given certain conditions are met. We identify the following scenarios in which acoustic indices could be useful:

1) When the research aim is explicitly temporal (describing patterns of change in vocal activity within a location over time). Within-site changes in acoustic indices are one of the most well-supported use cases of the tool and have been documented in the contexts of diel and seasonal environmental cycles, migration phenology, and time since restoration (Farina et al. 2015, Buxton et al. 2016, Borker et al. 2020). Comparing any type of acoustic data between sites introduces the issue of uneven detection space, caused by differences in hardware sensitivity, habitat (acoustical masking due to the presence of vegetation) and/or geophonic characteristics (proximity to running water, wind exposure), leading to can erroneous conclusions about between-site differences in vocal species richness or activity. These issues can be overcome by extensive spatial sampling or accounted for by explicitly measuring and modeling these differences; however, this is rarely done in studies employing acoustic monitoring technology (Yip et al. 2017, Royle 2018). However, quantifying changes in acoustic activity within a single site across years or sampling periods gets around these challenges and still provides extremely valuable information about seasonality, phenology, and habitat use, provided that microphones are cared for and tested regularly for degradation (Turgeon et al. 2017).

One major impetus for the current study was to provide Parks with constructive information about their natural resources: a data management plan that included an analysis plan employing acoustic indices was instrumental in getting the research approved in the first place. As a result, both Denali and Sequoia/Kings Canyon now have the precedent, equipment, and resources to apply acoustic monitoring to other areas of interest. Furthermore, the National Park Service Natural Sounds and Night Skies Division's development of standardized acoustic monitoring protocol can be applied to any Park in the nation to yield comparable data types at the continental scale. Other specific potential applications for acoustic recorders include Long-term Ecological Reserves (LTERs) and National Ecological Observatory Network (NEON) sites (Kampe 2010, Müller et al. 2010): massive data collection operations with wide spatio-temporal coverage and great ecological importance, but which are likely limited in resources and personnel specialized in bird species identification. The use of acoustic indices on audio recordings could be a significant contribution to these programs' understanding of ecological patterns over broad temporal and/or spatial scales.

2) When the habitat(s) or sites sampled are already known or strongly suspected to span a wide range of diversity values. As demonstrated here, suites of complementary acoustic indices can reliably distinguish between sites with differences in species richness of about 5 or more species, but not fewer. Thus, indices may sufficiently parse differences in richness in scenarios of dramatic landscape change such as before and after fire (Meyer et al. in prep.), or between sites with very different management practices such as clear-cuts and plantations versus integrated agroforestry landscapes (Hayashi et al. 2020). However, our finding that index values asymptote at higher levels of richness suggests an upper bound on the ability of indices to capture diversity within the most speciose recordings. Similar evidence of acoustic indices

“saturating” below the highest levels of richness has been found in other studies as discussed above. For example, two studies have found that acoustic indices are less useful in tropical areas, where hundreds of species from multiple taxonomic groups may be vocalizing simultaneously (Eldridge et al. 2018, Jorge et al. 2018). Therefore, strong prior knowledge of the study system in question should thus guide the practitioner in implementing an acoustic index approach.

3) When anthropogenic or geophonic noise is minimal across all sites and therefore unlikely to bias index values. Several widely-used acoustic indices are susceptible to bias when soundscapes contain anthropogenic noise (Gasc et al. 2015). These issues may be resolved by strategically placing recorders away from roads, streams, waterfalls, or areas where a non-target organism dominates the soundscape (e.g. Pacific tree frog chorus, cicada call). However, given the goals of a study, this may be impossible and/or lead to a bias away from sampling noisier environments despite ecological interest in them. Notably, noisy habitats where indices may fail include riparian habitats which are disproportionately vulnerable to climate-change and land-use impacts (Woodward et al. 2010), and the urban environment, which is a large and fascinating arena for the study of sensory ecology, animal behavior, and evolution, as well as critical to effective conservation in the Anthropocene (Grimm et al. 2008, Goddard et al. 2010, Sih et al. 2011, Pataki 2015, Lynn et al. 2018). When variation in ambient noise can either be minimized or controlled for, acoustic indices may still be useful.

In this paper, our aim was to compare output between human annotations and acoustic indices of units of 10-minute samples of audio to evaluate whether indices summarize biological information in a unit of time relevant to traditional bird surveyors (a 10-minute point count survey). However, any single 10-minute sample of the environment, whether by point count or audio recording, is unlikely to capture all the species present at that site. Other recent investigations of acoustic indices as biodiversity indicators recommend sampling sites for 120 hours minimum in order to adequately reduce within-site index variability, and also recommends sampling continuously rather than subsampling over time (Bradfer-Lawrence et al. 2019, Bradfer-Lawrence et al. 2020). The present analysis only summarizes between 13-68 hours of data per dataset from randomly extracted 10-minute chunks. Predictive power may increase if, instead of using 10-minute samples, acoustic indices are calculated over a longer, continuous period of time and compared with a rarefied estimate of species richness generated from the ground-truthed values, rather than reporting site means, which underestimate total richness and do not account for uneven sampling effort or variation in patchiness within and among habitats (Gotelli and Colwell 2001, Chao et al. 2014). In general, we agree that at least some of the inconsistency in performance is attributable to a lack of standardized methodology, and we welcome the development of a standardized approach to collecting and analyzing acoustic index data that is informed by its limitations.

Similar to the way that advances in sequencing technology have revolutionized the field of genomics and its application to conservation science, developments in passive acoustic monitoring promise to revolutionize the study of biodiversity. Studies that employ passive acoustic monitors in concert with traditional surveys and which specifically test assumptions about how acoustic data compare to traditional data, are highly valuable in advancing this exciting, rapidly burgeoning field toward generalizable best practices. While a recent meta-analysis reports that the majority of studies suggest similar or superior performance of acoustic recorders over human observers in detecting bird species present (Darras et al. 2018), results are still mixed, and many studies that found discrepancies between the approaches recommend a tandem approach rather than complete replacement of humans by recorders. Hybrid approaches involving in-person observers will be necessary for any studies for which relative abundance at the community level is of key interest. Recent contributions to the literature emphasize the importance of explicitly modeling of variables that affect sampling radius of the microphone, as estimates of diversity are strongly influenced by sampling area and effort (Leach et al. 2016, MacLaren et al. 2018, Sugai et al. 2019). For those seeking to adopt acoustic monitoring techniques in their research and monitoring efforts, we suggest considering acoustic methods such as acoustic indices as sophisticated tools that can expand the scope of wildlife study and which require time to learn how to use correctly, rather than ready-made, inexpensive replacements for humans altogether.

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CHAPTER 1 TABLES

Table 1.1. *Summary of avian vocal richness in audio recordings from three acoustic dataset.*

Dataset	Number of 10-min Recordings	# of Sites	Min. Richness	Median Richness	Max. Richness	Variance of Richness
Denali	409	23	1	4	16	10.1
Lakes	180	10	1	3	9	2.86
Sequoia	78	9	1	6	16	11.9

Table 1.2. *Summaries of Random Forest models* using a suite of acoustic indices to predict observed vocal avian diversity in acoustic recordings.

MSE	**R^2**	**Model**	**Response Type**	**Dataset**
3.52	0.585	RandomForest-Global	Richness	All Combined
2.47	0.103	RandomForest-Global	Richness	Lakes
6.26	0.435	RandomForest-Global	Richness	Sequoia
3.46	0.654	RandomForest-Global	Richness	Denali
3.49	0.603	RandomForest-Model Selection	Richness	All Combined
2.40	0.158	RandomForest-Model Selection	Richness	Lakes
5.46	0.533	RandomForest-Model Selection	Richness	Sequoia
3.47	0.662	RandomForest-Model Selection	Richness	Denali
0.164	0.123	RandomForest-Model Selection	Shannon	Lakes
0.205	0.505	RandomForest-Model Selection	Shannon	Sequoia

CHAPTER 1 FIGURES

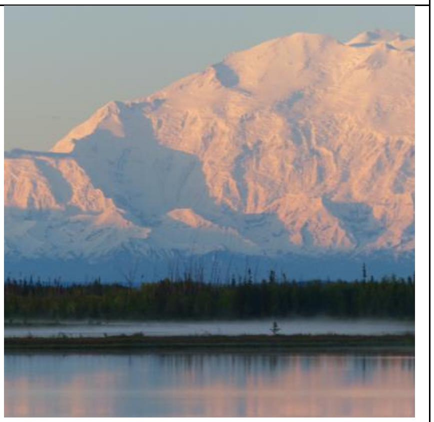
LAKES	SEQUOIA	DENALI
 © Mary Clapp	 (cc) Koan-Sin Tan	 © Hank Lentfer

Figure 1.1. Photographs of study locations.

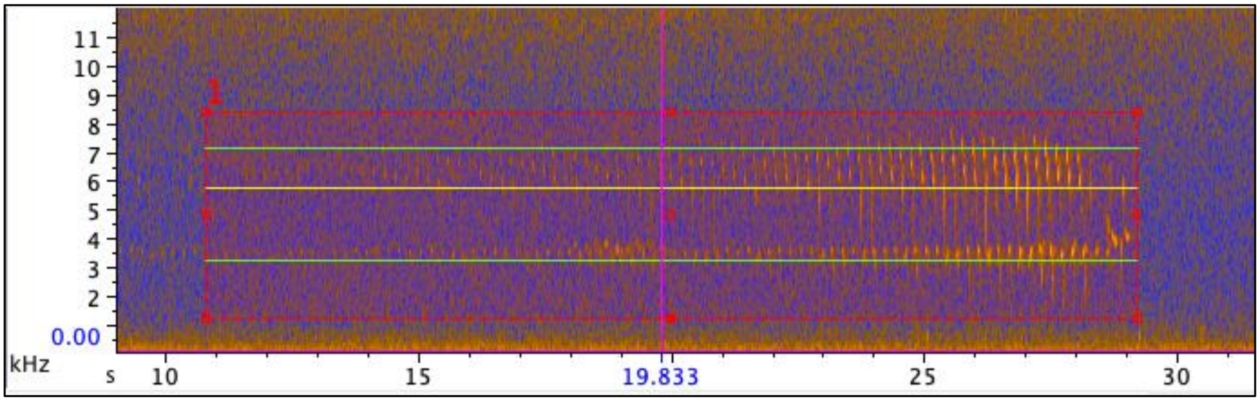


Figure 1.2. Spectrogram of an American Pipit (Anthus rubescens) flight call lasting several seconds. Green horizontal lines represent 5th and 95th frequency percentiles; yellow horizontal line represents Center Frequency. Spectrogram generated in RavenPro.

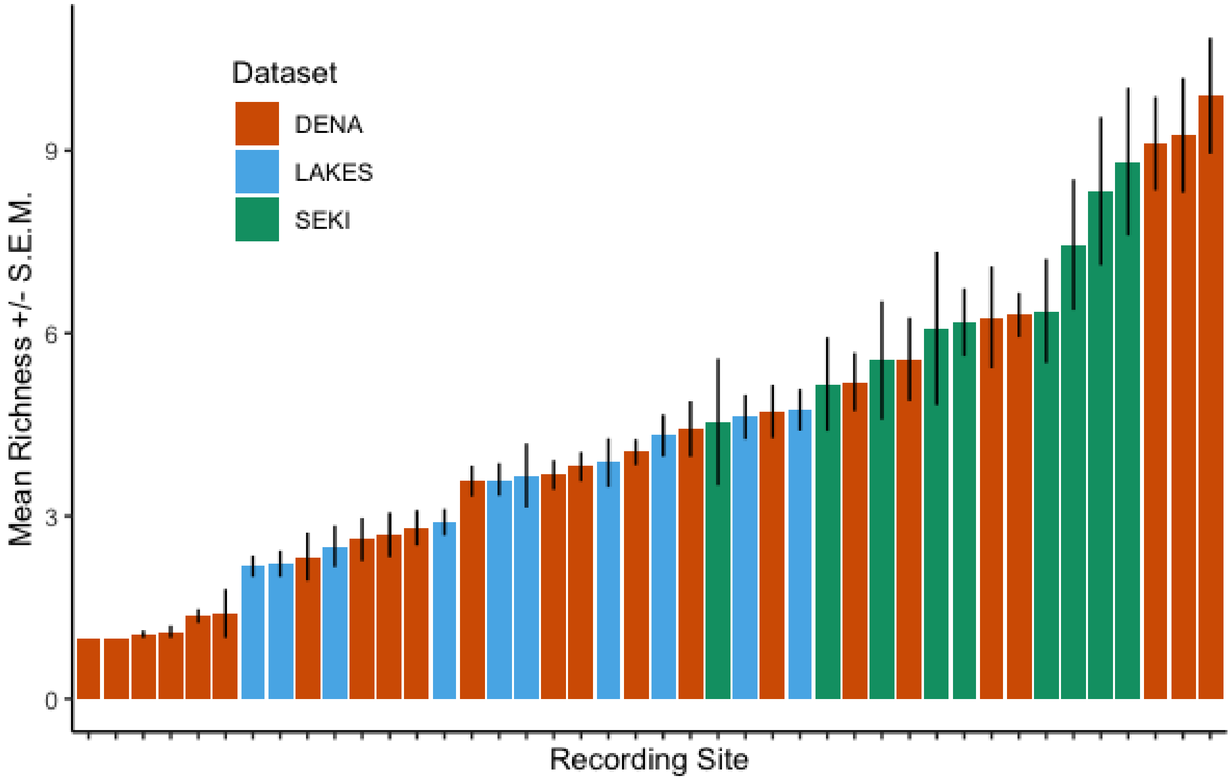


Figure 1.3. Mean of per-recording avian species richness organized by recording site, at each of three study locations. Study locations were along an elevational gradient in Denali National Park (DENA; orange bars), Sequoia forest in Sequoia National Park (SEKI; green), and at high-elevation lake basins in Sequoia/Kings Canyon National Park (LAKES; sky blue).

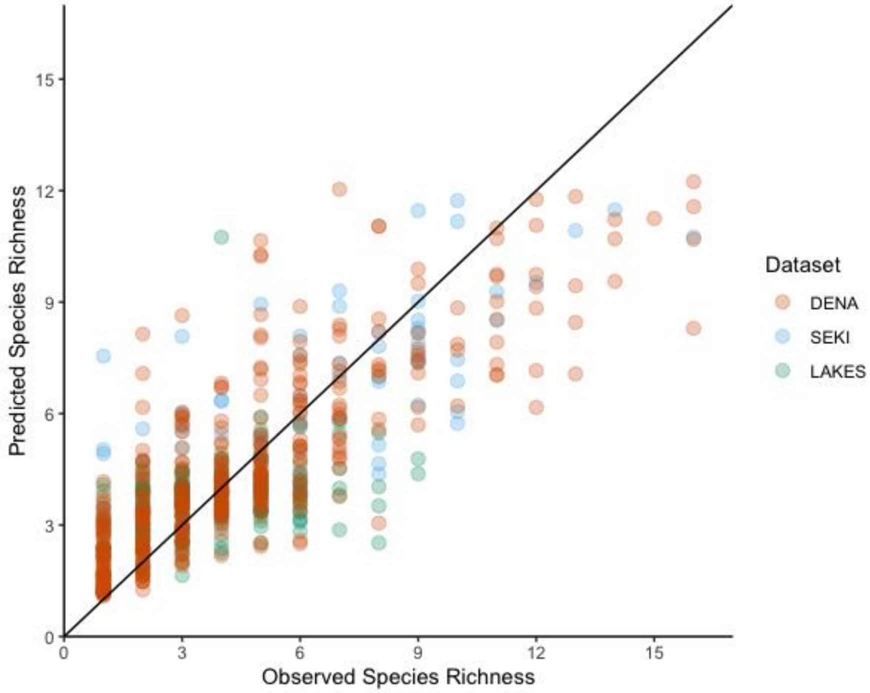
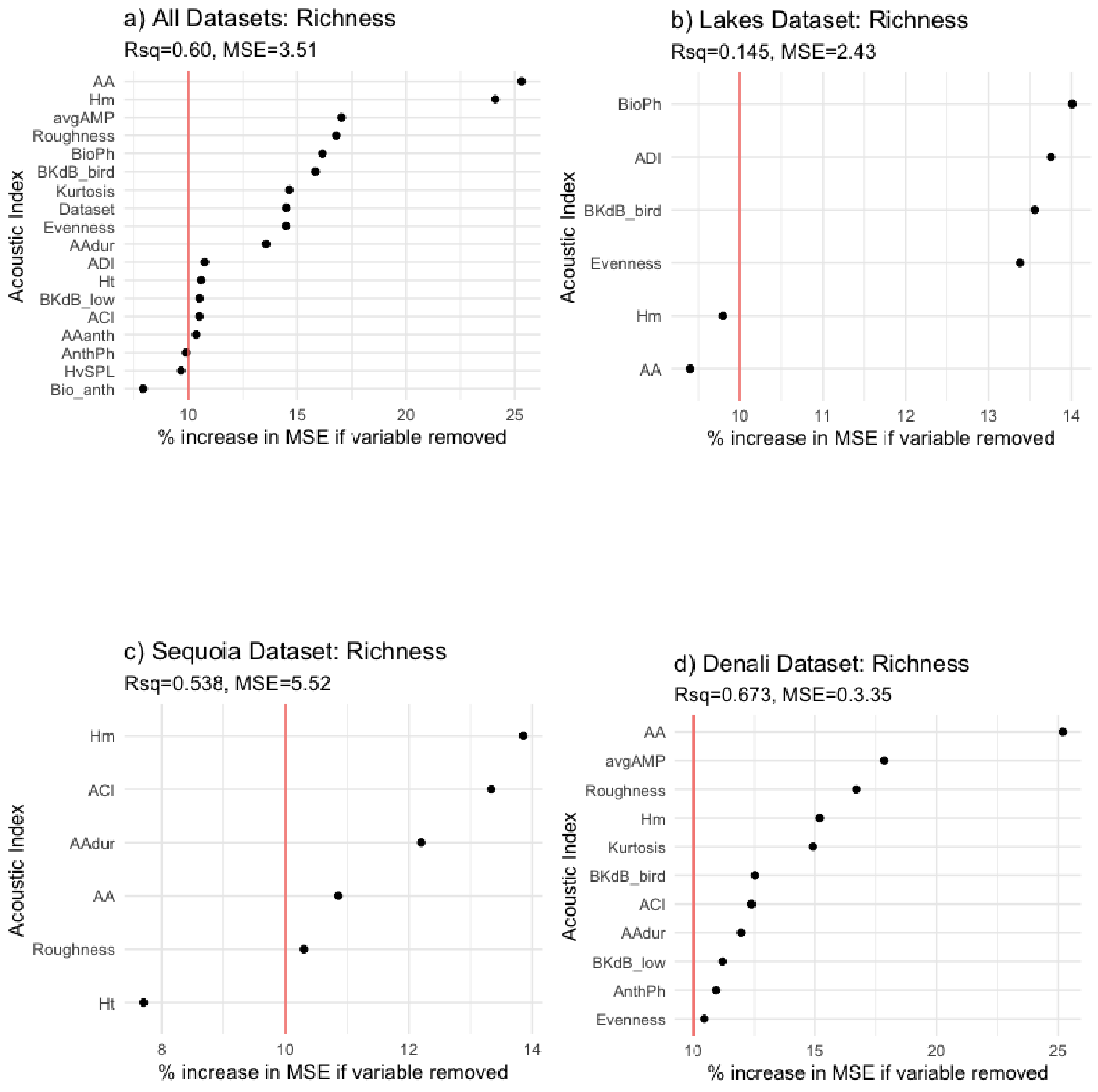


Figure 1.4. Observed versus predicted avian species richness from top Random Forest model using three acoustic datasets from U.S. National Parks. The black line represents a 1:1 relationship.



a) All Datasets: Richness

Rsq=0.60, MSE=3.51

b) Lakes Dataset: Richness

Rsq=0.145, MSE=2.43

c) Sequoia Dataset: Richness

Rsq=0.538, MSE=5.52

d) Denali Dataset: Richness

Rsq=0.673, MSE=0.3.35

Figure 1.5. Variable importance of each acoustic index in the top Random Forest model predicting avian vocal richness in acoustic recordings for **a)** all datasets combined, and **b-d)** each dataset separately. Higher % increase in MSE indicates that index has more predictive power.

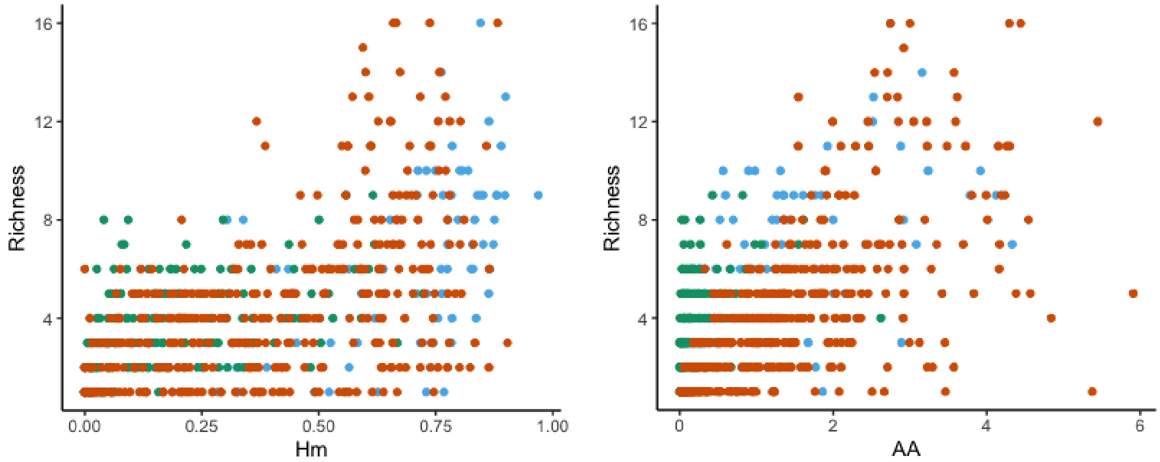
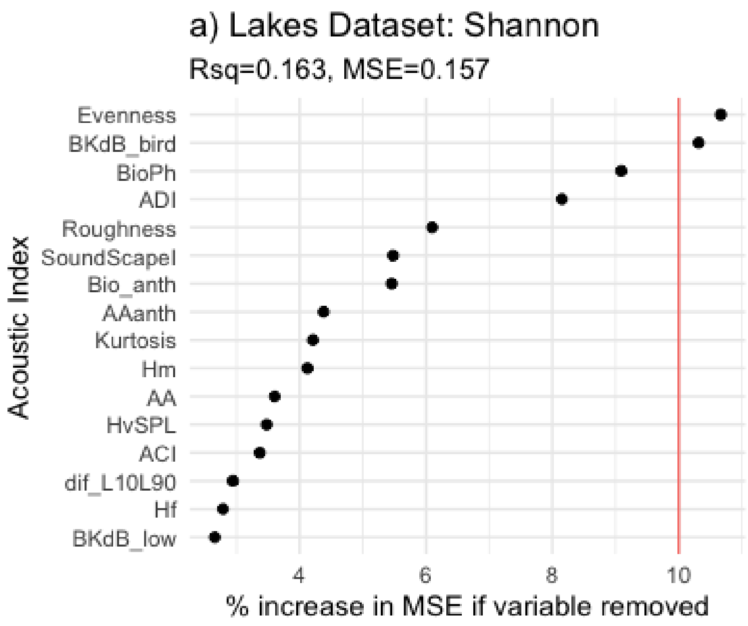


Figure 1.6. Relationships of two influential acoustic indices to the response variable Richness from the top Random Forest from all three datasets combined.



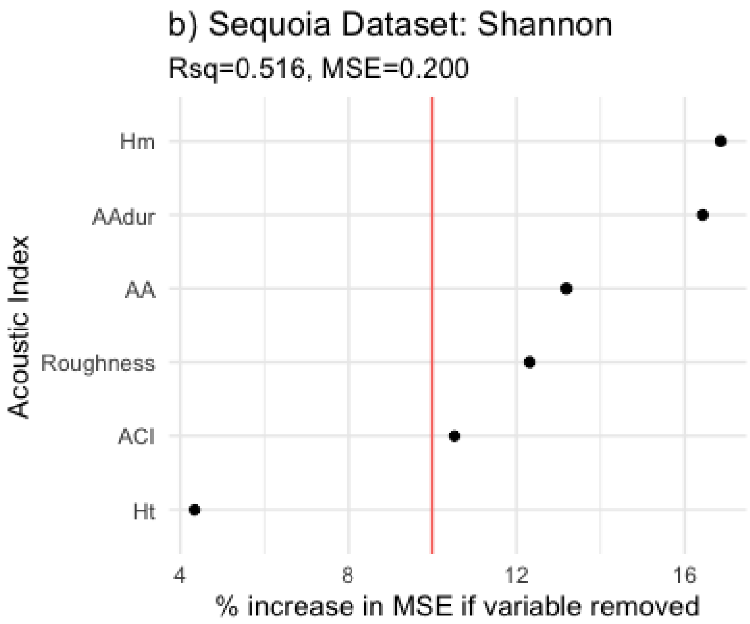
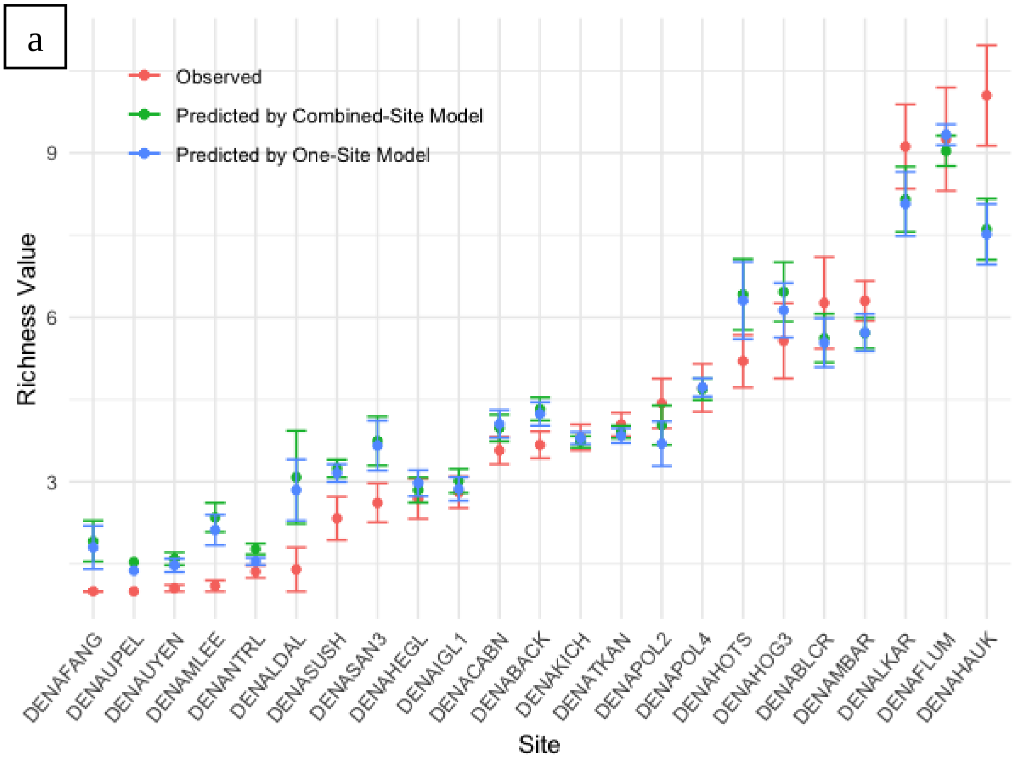
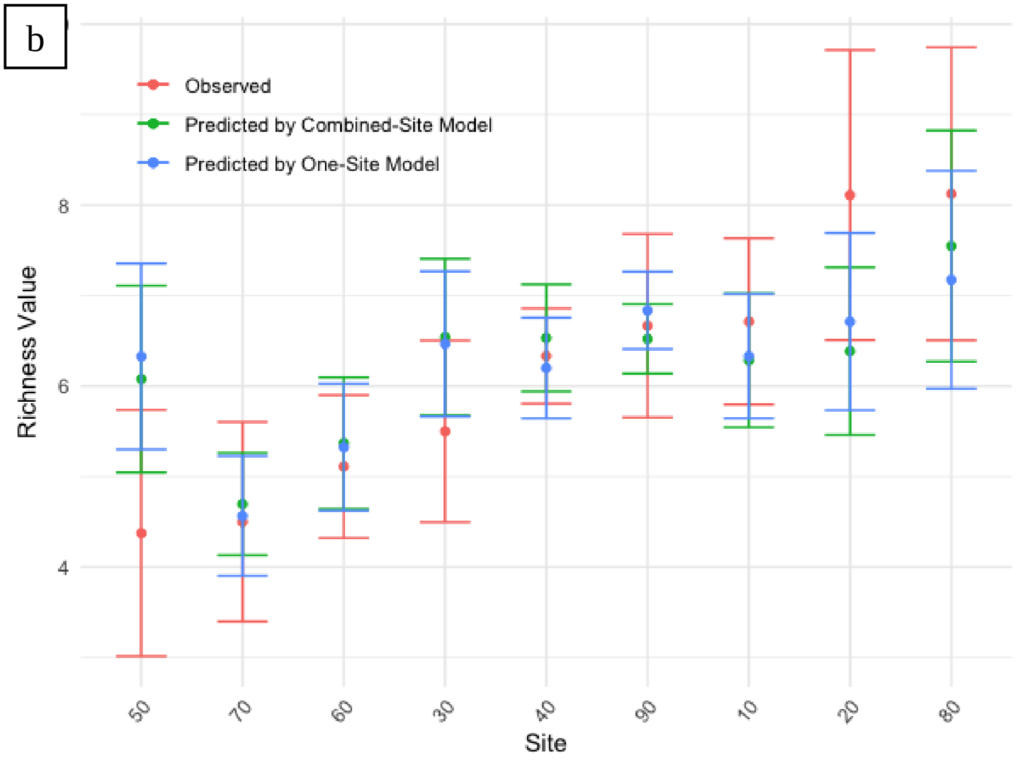


Figure 1.7. Variable importance of each acoustic index in the top Random Forest model predicting Shannon Vocal Activity for **a)** the Lakes dataset and **b)** the Sequoia dataset.

a


Observed
Predicted by Combined-Site Model
Predicted by One-Site Model
Richness Value
9
6
3
Site
DENAFANG
DENAUPEL
DENAUYEN
DENAMLEE
DENANTRL
DENALDAL
DENASUSH
DENASAN3
DENAHEGL
DENAIGL1
DENACABN
DENABACK
DENAKICH
DENATKAN
DENAPOL2
DENAPOL4
DENAHOTS
DENAHOG3
DENABLCR
DENAMBAR
DENALKAR
DENAFLUM
DENAHAUK

b


Observed
Predicted by Combined-Site Model
Predicted by One-Site Model
Richness Value
8
6
4
Site
50
70
60
30
40
90
10
20
80

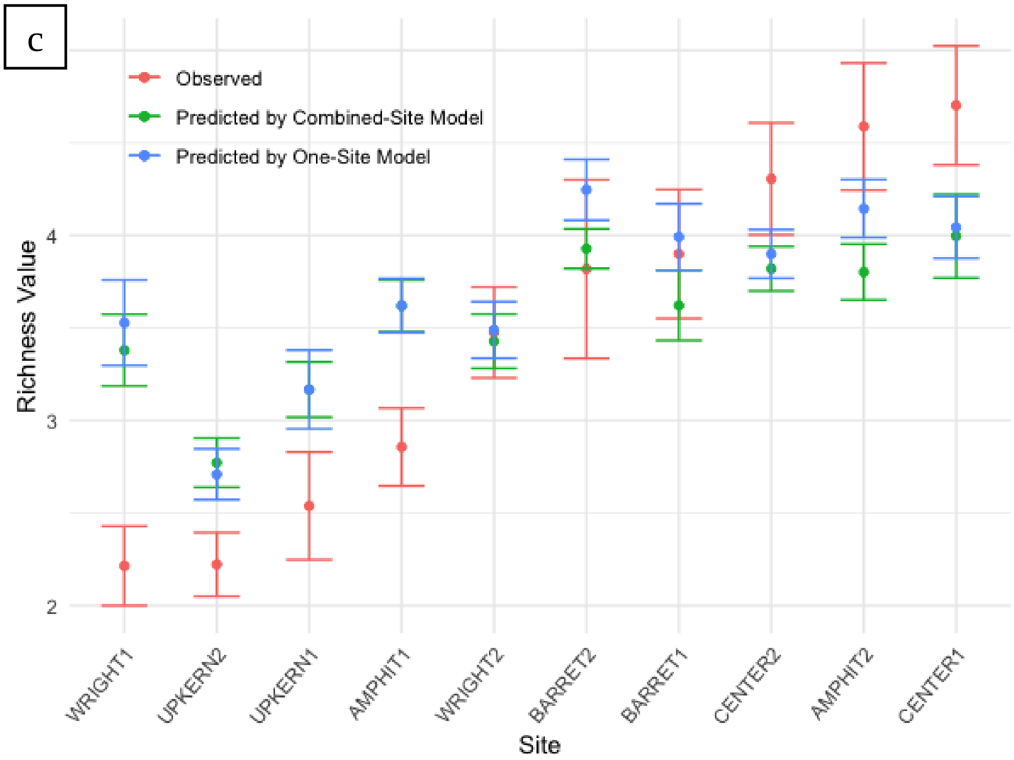


Figure 1.8. Mean per-recording richness as observed in annotated recordings (pink) compared with predicted richness of the top model for all sites combined (green) and top model for that site alone (blue) for the **(a)** Denali, **(b)** Sequoia, and **(c)** Lakes datasets.

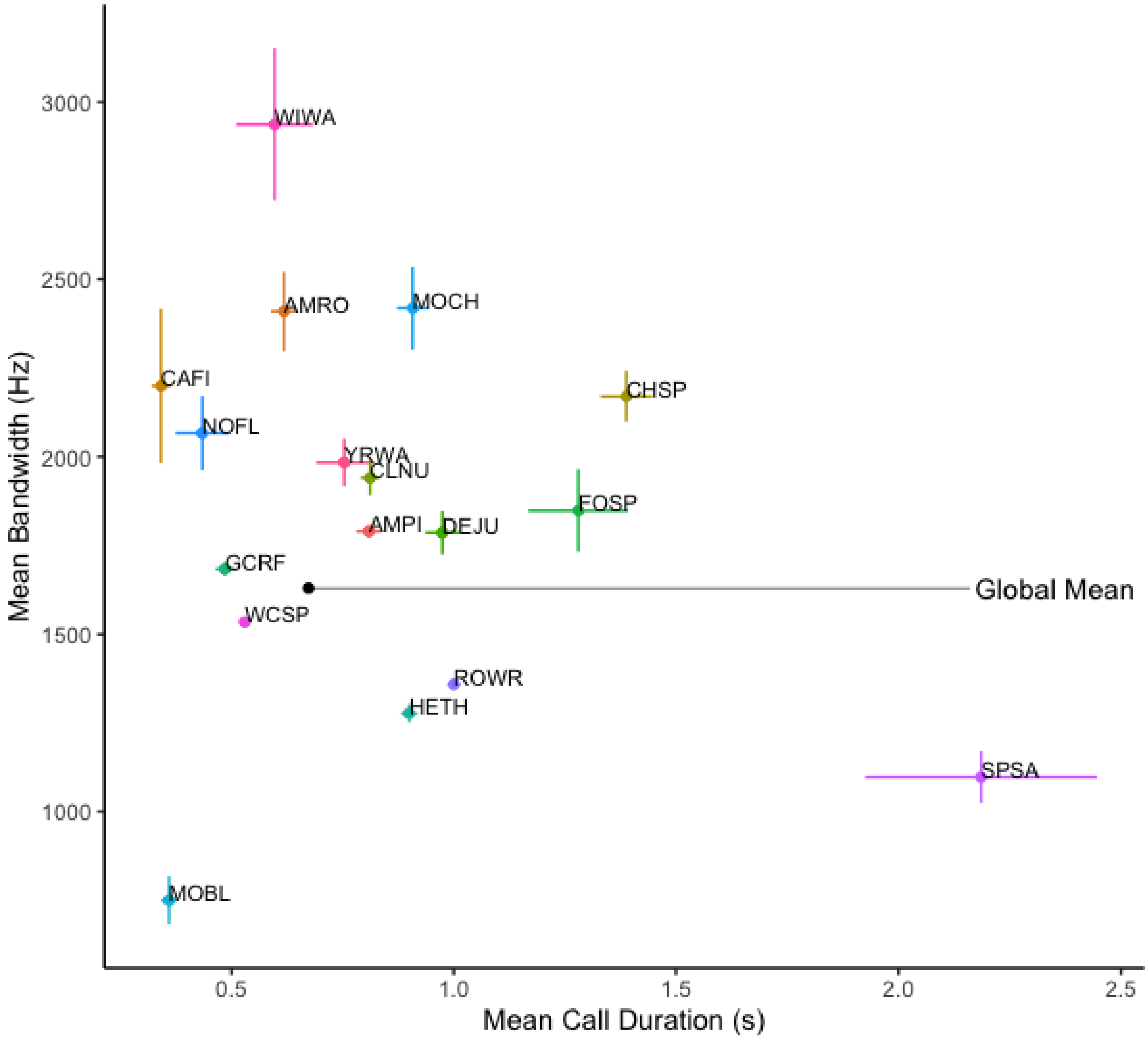


Figure 1.9. Variation in the mean bandwidth and duration of bird vocalizations in the Lakes dataset. Species toward the upper right of this graph likely over-weigh index values, whereas species toward the origin of the graph likely under-weigh index values.

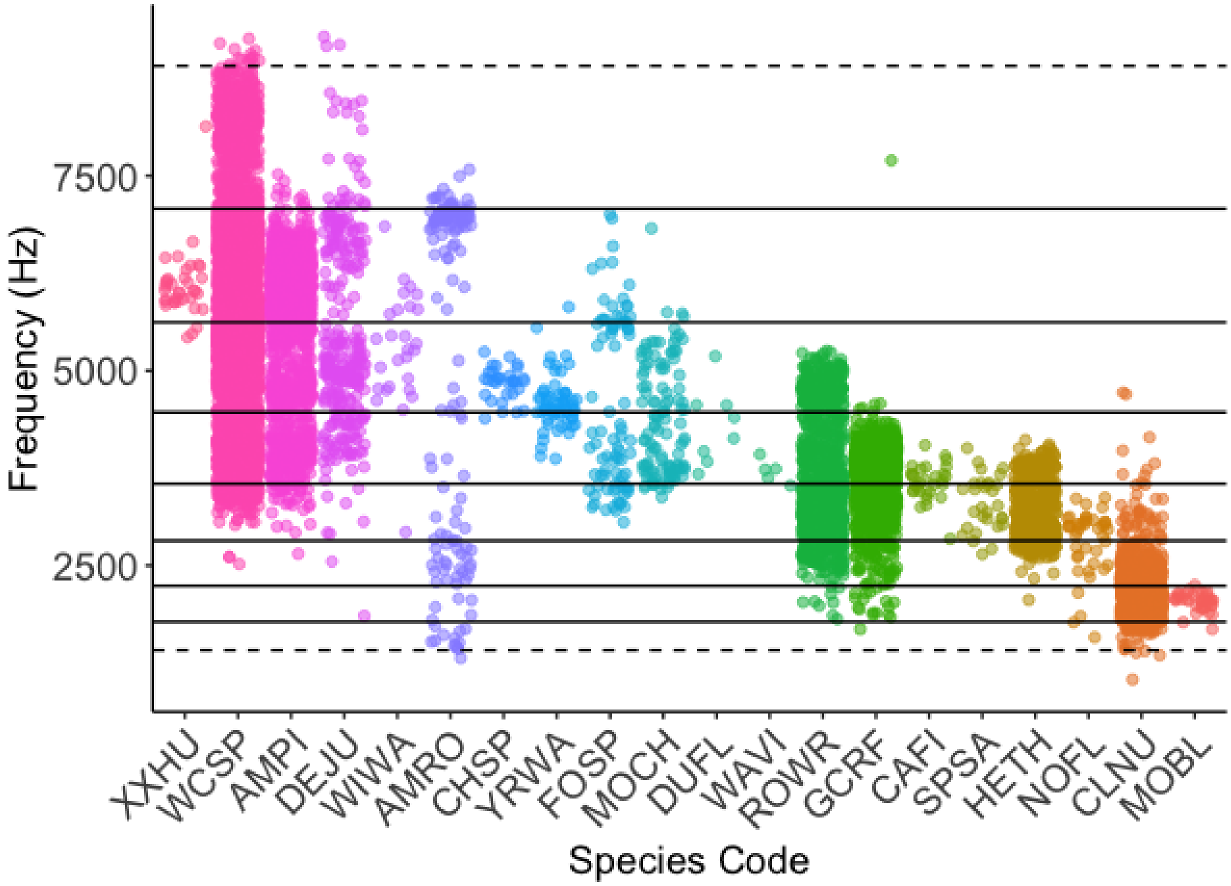


Figure 1.10. Center frequencies of bird calls present in the Lakes dataset. Horizontal lines indicate 1/3-octave bins used for acoustic index calculations; dashed lines represent the upper and lower bounds of those calculations. Some species occupy several frequency bins while others occupy only 1 or 2. These differences could unevenly weight indices by species, causing indices to underpredict species richness due to the unequal contributions of rarer &/or less garrulous species.

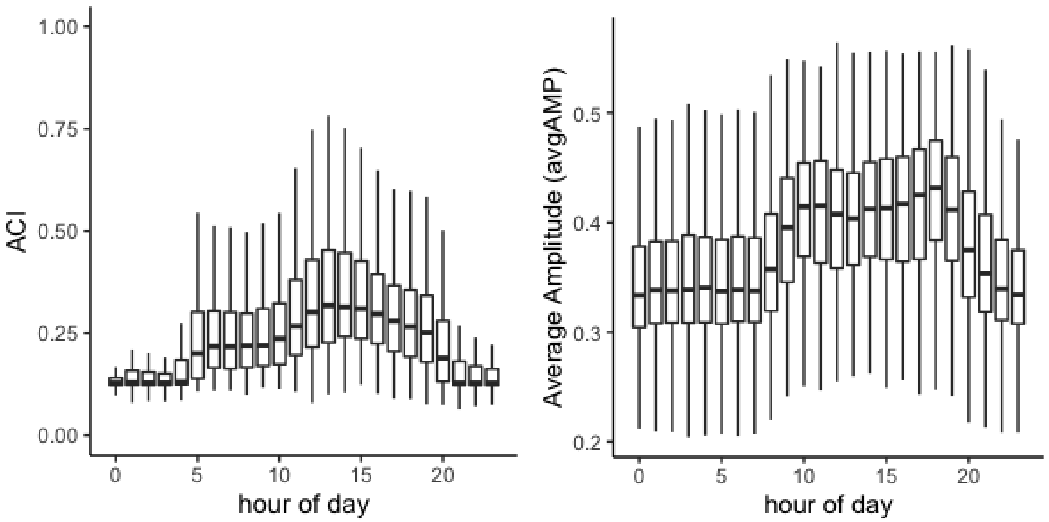


Figure 1.11. Examples of diel variation in 2 acoustic indices in the Lakes Dataset.

CHAPTER 1 SUPPLEMENTAL INFORMATION

The Sequoia data were collected after a large wildfire, the Rough Fire, burned in 2015 in order to describe post-fire community assembly across different forest management types (lead collector E.W.M.); the Lakes data were collected in order to describe the impacts of trout introductions in alpine lakes on lakeside terrestrial community (lead collector M.K.C.), and the Denali dataset is part of an ongoing acoustic inventory and monitoring effort at sites throughout the Park across an elevational gradient from 168 to 3327 meters (lead collector D.H.B.). Detailed information about equipment and recording schedules can be found in the table below.

Table 1.S1. Recording summaries for 3 datasets.

	Recording Equipment	**# Sites**	**Dates Data Collected** **(precise dates vary by site)**	**Sampling Specifications**	**Sampling Scheme**	**Total Minutes Annotated for Richness-Only**	**Total Minutes annotated for Richness-Activity**
Sequoia	SongMeter SM3 (Wildlife Acoustics)	9	June-Nov 2016	Single-channel WAV sampling rate=48kHz sampling rate and gain=35dB	Continuous recording for 4h beginning 1 hr < local sunrise and after sunset	780	0
Lakes	SongMeter SM2+ (Wildlife Acoustics)	10	June-Sept 2015	Single-channel WAV sampling rate=48kHz sampling rate and gain=35dB	Continuous recording 24h	1980	1220
Denali	Roland R05 + Larson-Davis SPL meter	23	April-July 2010-2014	Single-channel MP3 sampling rate = 64kbps	First 15 min of each hour, beginning 30 min before local sunrise to 6 hr after sunrise	4080	0
TOTAL						**6840**	**1220**

Table 1.S2. Species Lists for (a) Lakes, (b) Sequoia, and (c) Denali datasets

(a) LAKES		
4-Letter AOU Code	**Common Name**	**# of Sites Present**
AMPI	American Pipit	10
GCRF	Gray-crowned Rosy-Finch	10
ROWR	Rock Wren	10
WCSP	White-crowned Sparrow	10
CLNU	Clark's Nutcracker	9
DEJU	Dark-eyed Junco	7
MOCH	Mountain Chickadee	5
CAFI	Cassin's Finch	4
DUFL	Dusky Flycatcher	4
MOBL	Mountain Bluebird	4
HETH	Hermit Thrush	3
SPSA	Spotted Sandpiper	3
YRWA	Yellow-rumped Warbler	3
AMRO	American Robin	2
NOFL	Northern Flicker	2
BRBL	Brewer's Blackbird	1
CHSP	Chipping Sparrow	1
FOSP	Fox Sparrow	1
MALL	Mallard	1
WAVI	Warbling Vireo	1
WIWA	Wilson's Warbler	1
XXHU	Unknown Hummingbird	1

(b) SEQUOIA		
4-Letter AOU Code	**Common Name**	**# of Sites Present**
AMRO	American Robin	9
BRCR	Brown Creeper	9
GCKI	Golden-crowned Kinglet	9
MOCH	Mountain Chickadee	9
RBNU	Red-breasted Nuthatch	9
STJA	Steller's Jay	9
DEJU	Dark-eyed Junco	8
FOSP	Fox Sparrow	8
WBNU	White-breasted Nuthatch	8
WHWO	White-headed Woodpecker	8
BUSH	Bushtit	7
HAWO	Hairy Woodpecker	7
PIWO	Pileated Woodpecker	7
YRWA	Yellow-rumped Warbler	7
CORA	Common Raven	6
NOFL	Northern Flicker	6
PSFL	Pacific-slope Flycatcher	6
WETA	Western Tanager	6
HAFL	Hammond's Flycatcher	5
RBSA	Red-breasted Sapsucker	5
DUFL	Dusky Flycatcher	3

GTTO	Green-tailed Towhee	3
CAFI	Cassin's Finch	2
HOWR	House Wren	2
MOBL	Mountain Bluebird	2
WEWP	Western Wood-Pewee	2
WIWA	Wilson's Warbler	2
GHOW	Great Horned Owl	1
LISP	Lincoln's Sparrow	1
MGWA	MacGillivray's Warbler	1
NOGO	Northern Goshawk	1
PAWR	Pacific Wren	1
SPTO	Spotted Towhee	1
TOSO	Townsend's Solitaire	1
WESO	Western Screech-Owl	1

(c) DENALI		
4-Letter AOU Code	**Common Name**	**# of Sites Present**
REDP	Redpoll sp.	16
WCSP	White-crowned Sparrow	15
WIWA	Wilson's Warbler	13
FOSP	Fox Sparrow	11
CAJA	Canada Jay	10
DEJU	Dark-eyed Junco	10
AMRO	American Robin	9
HETH	Hermit Thrush	9
OCWA	Orange-crowned Warbler	9
SWTH	Swainson's Thrush	9
VATH	Varied Thrush	8
WIPT	Willow Ptarmigan	8
LEYE	Lesser Yellowlegs	7
MYWA	Myrtle Warbler	7
SAVS	Savannah Sparrow	7
WISN	Wilson's Snipe	7
WTPT	White-tailed Ptarmigan	7
GCSP	Golden-crowned Sparrow	6
GCTH	Gray-cheeked Thrush	6
RCKI	Ruby-crowned Kinglet	6
UNBI	Unidentified Bird	6
ATSP	American Tree Sparrow	5
BOCH	Boreal Chickadee	5
LISP	Lincoln's Sparrow	5
NOWA	Northern Waterthrush	5
ARWA	Arctic Warbler	4
OSFL	Olive-sided Flycatcher	4
BBMA	Black-billed Magpie	3
CANG	Canada Goose	3
WWCR	White-winged Crossbill	3
YEWA	Yellow Warbler	3
ALFL	Alder Flycatcher	2
BLPW	Blackpoll Warbler	2
CORA	Common Raven	2
MERL	Merlin	2

NOFL	Northern Flicker	2
SACR	Sandhill Crane	2
SOSA	Solitary Sandpiper	2
SURF	Surfbird	2
WHIM	Whimbrel	2
AMGP	American Golden-Plover	1
AMPI	American Pipit	1
ATTW	American Three-toed Woodpecker	1
BAEA	Bald Eagle	1
COLO	Common Loon	1
GCRF	Gray-crowned Rosy-Finch	1
GOEA	Golden Eagle	1
GRYE	Greater Yellowlegs	1
LALO	Lapland Longspur	1
LTDU	Long-tailed Duck	1
LTJA	Long-tailed Jaeger	1
MEGU	Mew Gull	1
PIGR	Pine Grosbeak	1
PISI	Pine Siskin	1
RUBL	Rusty Blackbird	1
RUGR	Ruffed Grouse	1
TRUS	Trumpeter Swan	1

CHAPTER 2: Introduced trout filter high-elevation lakeside bird communities in the Sierra Nevada, California

ABSTRACT

The headwaters of California's Sierra Nevada provide important resources for wildlife and humans alike and are increasingly imperiled by climate change and other human-induced stressors. The introduction of non-native fishes into these historically fishless waters has profoundly restructured the aquatic food web, resulting in lower invertebrate diversity and the endangerment of endemic taxa such as the mountain yellow-legged frog (*Rana sierrae/muscosa*). However, the extent to which the effects of trout introductions cascade into the terrestrial environment is poorly understood even though these habitats are tightly linked. We quantified avian community composition, diversity, and overall abundance at fish-containing and fishless lakes in the southern Sierra Nevada for four years (2014, 2015, 2016, and 2020). We documented a change in avian beta diversity between fish-containing and fishless lakes, driven largely by turnover, as well as a decrease in overall avian abundance at fish-containing lakes approaching statistical significance. A fish eradication project at one lake between 2016-2019 allowed us to conduct a BACI (Before, After, Control, Impact) case study to assess changes in the avian community following fish removal. We report a two-fold increase in overall avian abundance at the fish-removal relative to the control lake, including the detection of two insectivorous bird species that were not detected at any previous surveys at that lake. Our results highlight the importance of considering aquatic and terrestrial habitats as interdependent systems and further motivate the conservation of fishless lake habitat in the Sierra Nevada's alpine waters.

INTRODUCTION

As human-caused global climate change alters the world’s ecosystems, certain biomes experience accelerated change (Davis 2001, Loarie et al. 2009). Alpine areas make up roughly 2.4% (3.55 million km^2) of the earth’s surface and have already experienced shifts in community composition, shrinkage and turnover of endemic species’ ranges, and altered biogeochemical and hydrological processes (Parmesan and Yohe 2003, Tingley et al. 2009, Basagic and Fountain 2011, Huang et al. 2018). In the United States, a large majority of alpine habitat falls under governmental protection from intense development via the United States Wilderness Act of 1964. Protected wilderness areas are thus considered places where wild systems can thrive “untrammeled by man” in the absence of human modifications to the landscape (*Wilderness Act* 1964). However, climate change and other human-caused stressors such as air pollution and introduced species cause significant changes to even the so-called most “pristine” areas (Vitousek 1994). Research on these areas is critically important for informing management and policy, and mitigating impacts; however, the rugged and relatively undeveloped character of alpine areas adds to the challenge of collecting the necessary data to meet research needs.

One of the most significant threats to biodiversity and ecosystem function is the spread of introduced species (Mack and D’Antonio 1998, Pimentel et al. 2005). Post-industrial colonial human settlement across the globe has been characterized by the incidental and intentional spread of organisms to places outside their native and historical ranges, with a variety of socioecological impacts at scales far exceeding such activities by most precolonial human societies and by natural disturbances (Ricciardi 2007, Reo and Parker 2013, Cruz 2018). Of all species introductions, relatively few result in an invasive or ecosystem-changing outcome; however, the ones that do can radically alter biodiversity and habitat structure, drive native species extinctions, and create “no-analogue” ecological states (Vitousek et al. 1996, Williamson 2006, Strayer 2010, Boltovskoy et al. 2021). Species introductions thereby serve as powerful natural experiments that test fundamental evolutionary and ecological theories, as well as elucidate the feasibility and efficacy of restoration efforts (Vredenburg 2004, Sax et al. 2007). Understanding the impacts of introduced species on biodiversity and ecosystem function as we enter our planet’s sixth mass extinction event is paramount to conserving both (Ceballos et al. 2015).

Freshwater food webs are particularly vulnerable to species invasions compared to terrestrial or marine systems in part because they are more likely to contain prey that are evolutionarily naïve to new predator types (Cox and Lima 2006). One type of species introduction that is common in freshwater systems is intentional movement of commercially and recreationally valuable salmonids into water bodies outside those fishes’ natural range. There is ample evidence that introduced fish radically alter aquatic ecosystems at multiple levels of organization (Simon and Townsend 2003, Korsu et al. 2010). Fish introductions, especially into historically fishless water systems, can result in an alternative stable state with different (often simplified) food webs, altered predator-prey dynamics, and in some cases, extirpation of native biota (Holling 1973, Scheffer and Carpenter 2003, Eby et al. 2006). Introduced fish are a major contributor to amphibian declines worldwide: the suppression and/or local extirpation of native amphibian populations by introduced game fish has been documented in the Sierra Nevada and Cascades ranges of California (Knapp and Matthews 2000, Matthews et al. 2001, Joseph et al. 2011), the Rocky Mountains (Pilliod et al. 2010), the Andes (Martín-Torrijos et al. 2016), and la Sierra de Neila, Spain (Martínez-Solano et al. 2003). The mechanism of these declines is a combination of direct predation, usually on tadpoles, and competition with adult frogs for a shared prey base of aquatic insects.

The Sierra Nevada mountains of California provide a well-studied example of non-native introduction in a freshwater ecosystem. The Sierra Nevada's high-elevation headwaters and their montane tributaries were historically devoid of all fish above about 1800 m in elevation since the most recent Ice Age ended roughly 10,000 years ago (Knapp 1996, Rundel and Millar 2016). Glaciers carved deep valleys as they receded, resulting in steep gradients between headwater lake basins and the lowland valleys, which prevented low-elevation fish from populating the headwaters. In the late 1800's, settlers began stocking high-elevation areas with hatchery-raised trout, motivated largely by a desire to increase the recreational value of the mountains newly dispossessed of its native Numu people and in early development by Euro-Americans (Cowx 1994, Walker 2014, Lent 2020).

The ecological impacts of these trout introductions are profound. Trout significantly reduce the abundance, biomass and diversity of many large-bodied aquatic invertebrates that would otherwise emerge as winged adults and enter the terrestrial environment as prey for terrestrial consumers (Knapp et al. 2001, Vredenburg 2004a). Aside from the well-documented impacts of trout on amphibians (via direct predation as well as by competition for prey), the indirect impacts of trout introductions on terrestrial consumers are largely unknown, despite growing recognition that cross-system resource subsidies can play a major role in food web structure, community stability, and consumer abundance (Bartels et al. 2012, Wright et al. 2013).

The strength of a resource subsidy on the recipient food web varies by system and is predicted by the energy available in the donor subsidy relative to the total energy available in the recipient habitat, as well as its density and concentration in time &/or space (Yang et al. 2010).

Alpine ecosystems, characterized by extremely low terrestrial productivity (Figure 2.1) and highly temporally pulsed aquatic insect emergences, are a prime model system in which to study the effects of cross-system resource subsidies from the aquatic zone on terrestrial consumers (Piovia-Scott et al. 2016).

The importance of a subsidy also depends on animal behavior. In theory, cross-system resource subsidies can support more consumers in the recipient system than would normally be sustainable on in-situ-only resources, if consumers can switch nimbly enough to capitalize on the subsidy (Polis and Strong 1996). This has been demonstrated empirically in several systems. For example, in a well-studied forested riparian system in Japan, higher numbers of insectivorous birds and bats recruit to stream reaches in which aquatic insect emergence was unimpeded, compared with reaches within which emergence was experimentally restricted (Iwata et al. 2003, Fukui et al. 2006). Beyond increased abundance of consumers, allochthonous inputs to terrestrial systems also promote individual growth rates by increasing availability of more nutritious prey: in an island system, seasonal inputs of seaweed indirectly support individual growth rate and fecundity in brown anoles, which switch from terrestrial insect prey to the detritivores present on the seaweed (Wright et al. 2013).

Finally, the importance of a subsidy must depend on the nutritional content of the input material, such that it becomes preferred prey for terrestrial consumers when available (Krebs et al. 1977, Ostfeld and Keesing 2000). More protein-rich than seeds, insects are preferred prey for many bird species during the breeding season, when nutritional requirements are high for egg production and nestling provisioning. Gray-crowned rosy-finches and other bird species, such as the mountain white-crowned sparrows, exhibit seasonal increases in bill length as they switch from granivory to insectivory during the summer months (Johnson 1977, Morton and Morton

1987). Aquatically-derived insects in particular can be more nutritious than terrestrial prey due to the abundance of algal-derived highly-unsaturated fatty acids in their tissues (Schindler and Smits 2017). During their brief but intense emergence, adult mayflies (insect Order *Ephemeroptera*) comprise 22-38% of the diet of the gray-crowned rosy-finch, an alpine specialist songbird. Gray-crowned rosy-finches are less common at fish-containing lakes during summer, preferring to aggregate and forage at fishless lakes (Epanchin 2009).

It is not surprising that rosy-finch populations are affected by aquatic insect subsidies in this way. Rosy-finches are unusual among alpine birds in that they possess a gular sac, or an extendable pouch below the tongue that can be filled with prey items (Mowbray et al. 1941). This adaptation permits a much wider home range because they can collect an estimated 25 times more prey per foraging bout than typical songbirds without this anatomy (Twining 1940). Further, they are not territorial, and are semi-colonial during nesting, placing their nests in craggy areas high in alpine basins (MacDougall-Shackleton et al. 2020). Together, these characteristics likely facilitate their effective use of emerging aquatic insect resource pulses occurring at different specific localities in alpine lake basins, and for their populations to become particularly dense in the basins with the richest insect emergences. It is unknown whether these aquatic subsidies to the terrestrial environment also affect populations of more “typical” sub-alpine and alpine breeding songbirds that tend to make frequent, short-distance food collection trips within the confines of their all-purpose territories. Breeding birds that maintain small home ranges during the breeding season are likely more restricted in their ability to search for high-quality prey after settlement, and therefore their use of an aquatic insect subsidy may depend more strongly on their territory choice than, for example, a rosy-finch. Thus, the responses of birds to introduced trout are likely to vary across species.

In theory, animals should develop preferences for habitats where their reproductive success and survival are maximized over evolutionary time (Levins 1968). According to the Ideal Free Distribution, habitats of overall higher quality support a higher absolute number of individuals or breeding pairs compared to more marginal habitats (Fretwell and Lucas 1969). In this study, we tested the hypothesis that the resource subsidy of emerging aquatic insects at fishless lakes increases the quality of alpine lakeside habitat for birds. If this is the case, and if birds have reliable information about the quality of emerging aquatic insects at lakes, we predict that birds will follow an ideal free distribution relative to lake habitat, such that overall avian abundance and diversity will be higher at fishless lakes during the breeding season due to greater availability of high-quality prey items compared to fish-containing lakes. We further predict that the presence of fish in lakes serves as a filter on the bird community, and that bird communities will be dissimilar between fish-containing and fishless lakes.

METHODS

Study location

Sequoia and Kings Canyon National Parks (SEKI) are two contiguous National Parks on the southern end of the Sierra Nevada mountain range in California, USA. Ninety-six percent of the Parks’ 865,964 acres is federally designated wilderness, which affords the highest level of protection from human development. The focus of this study was the high-elevation region of the Parks; specifically, the headwater lake basins above 3000 meters in elevation. These lake basins are comprised primarily of perennial graminoid vegetation (wet grasses and forbs), sparse evergreen woodland (foxtail and whitebark pine), riparian scrub (primarily willow/*Salix* sp.), and talus or boulderfield (Figure 2.1). Alpine areas are highly seasonal, covered in deep snowpack for roughly half the year. The avian community is comprised mostly of short- and long-range migratory species that winter elsewhere and arrive to their breeding grounds in the spring (Siegel and Wilkerson 2005, Siegel et al. 2011). Post-breeding altitudinal migrations by several lower-montane species in the late summer occur regularly (Boyle 2017).

We identified study lakes with and without trout in headwater basins throughout SEKI using ArcGIS and a database containing eco-geomorphological information about the range's >8,000 water bodies (Knapp et al. 2020). In addition to choosing only lakes higher than 3,000 m in elevation, we restricted our search to lakes greater than 10,000 m^2 in area and deeper than 3 m in order to confine variation among fishless lakes to those which could possibly host trout populations if they were introduced (Armstrong and Knapp 2004). We located 6 pairs of fish-containing and fishless lakes (12 lakes total) within 6 basins (Amphitheater, Barrett, Center, East Lake, Upper Kern, and Wright) for the initial surveys in 2014-2016. In 2020, we expanded the study design to include multiple lakes per basin and added 4 new basins (Dumbbell, Gardiner, Observation, and Sixty Lakes) for a total of 39 lakes within 10 basins (Table 2.1, 2.2). A graphical summary of the environmental characteristics of study lakes can be found in the Supplementary Information (Figure 2.S1).

Avian surveys

We established points every 300m along the shoreline of each study lake as point count locations. Because lakes vary in size, the number of points at each lake also varies, with the smallest lakes containing 1 survey point and the largest containing 6 (Table 2.1). During the avian breeding season (June-July) and within the hours of 0530-1000, the first author (MKC) performed multi-species point counts at each point along the lakesides. The challenges of backcountry travel and the distances between the study sites limit the amount of data that can be collected in-person in such remote locations; therefore, number of surveys per season and basins visited vary by year (Table 2.1, 2.2). Survey protocol was based on standardized methods to aid in general replicability (Ralph et al. 1995, Matsuoka et al. 2014). MKC performed a 10-minute count at each point, recording every bird detected by sight or sound, the detection type(s) ("v" = visual, "c" = call, "s" = song), the estimated distance of the bird from the point, and whether the bird was counted previously (the second instance of each doubly counted bird was filtered from the data for analysis). Survey-level variables included wind (Beaufort scale), air temperature from a compact alcohol thermometer placed in the shade, Julian Day, and a binary variable for whether there was direct sun on the point.

Statistical Analyses

We used the avian point count data to test for the effect of fish presence on four response variables: i. total abundance; ii. alpha diversity (species richness), iii. beta diversity (pairwise dissimilarity), and iv. the abundance of the 6 most common species in the regional species pool.

i. Total abundance.

Total abundance of birds per point, regardless of species, was analyzed using generalized linear mixed models (GLMM) with a Poisson distribution and log link, which is suitable for count data (Bolker et al. 2009). We specified *fish* (categorical with two levels; fish-containing and fishless) and *elevation* (continuous, scaled and centered) as fixed effects, and a nested structure of *point* within *lake* within *basin* as random effects to account for nonindependence at the basin, lake, and count levels. For every survey point *i* at each lake *j* within each basin *k* , the count of birds is modeled as:

$$count \sim Poisson(\mu_{ijk});$$

$$\log(\mu_{ijk}) = Int. + Fish_j + Elevation_j + Year_{ijk} + \ Basin_k + \ \ Lake_{jk} + Point_{ijk},$$

$$Basin_k \sim N(0, \sigma^2_{Basin})$$

$$Lake_{jk} |\ Basin_k \sim N(Basin_k, \sigma^2_{Lake})$$

$$Point_{ijk} |\ Lake_{jk} \sim N\left(Lake_{jk}, \sigma^2_{Point}\right)$$

Model evaluation for GLMMs followed the recommendations in Zuur and Ieno (2016): to validate model assumptions, we inspected the residuals for homogeneity by plotting them against residuals and all model covariates. We calculated an approximate measure of overdispersion by comparing the sum of squared Pearson residuals with the residual degrees of freedom using a Chi-squared test (Bolker et al. 2009). We generated 95% confidence intervals for the model by parametric bootstrapping: simulating new data using the model estimates and variances and reporting the range within which 95% of the predicted values falls around each parameter estimate (Amrhein et al. 2017).

ii. Avian Diversity: Species Richness.

We modeled species richness using the same modeling procedure, structure, and evaluation as the abundance models above, but with species count (number of species detected) per point as the response variable.

iii. Avian Diversity: Beta diversity.

We used the Bray-Curtis index to estimate community dissimilarity at my sites from the 2020 survey data. The pairwise Bray-Curtis index reflects the dissimilarity in species composition between sites, weighted by species' abundances (Koleff et al. 2003, Anderson et al. 2011). Dissimilarity between two samples can be due to nestedness (when species are added or lost without replacement), turnover (when species are lost and replaced by other species), or both (Baselga 2010). Calculating total dissimilarity without investigating the contribution of each process separately can obscure the effects of either process on community dissimilarity (Tingley and Beissinger 2013, Soininen et al. 2018). Therefore, we decomposed both indices into these components using the R package `betapart` (Baselga and Orme 2012). To determine how fish presence influences avian beta diversity, we conducted a permutational multivariate analysis of variance (PERMANOVA) using the *adonis2* function in the R package vegan (Anderson 2017, Oksanen et al. 2019). We included the effects of fish presence and elevation, and set basin as blocking factor, because basin was the only random effect in any of the richness or abundance GLMMs whose variance deviated significantly from zero. To visualize differences in community composition between fish-containing and fishless lakes, we used nonmetric multidimensional scaling (NMDS) on abundance-weighted dissimilarity (Bray-Curtis). Dissimilarity measurements require even sampling, so only 2020 data were used for beta diversity analysis.

iv. Single-species abundance models.

Bird species within a community vary in their niche space (MacArthur and MacArthur 1961). This could drive differential responses to an environmental perturbation such as fish removal. Therefore, we built single-species abundance models for the five most common species in the dataset: Gray-crowned Rosy-finch (*Leucosticte tephrocotis*), White-crowned Sparrow (*Zonotrichia leucophrys oriantha*), Dark-eyed Junco (*Junco hyemalis*), American Pipit (*Anthus rubescens*), and Rock Wren (*Salpinctes obsoletus*). Counts of individual species often result in zero-inflation—more zeros in the data than is predicted by a Poisson distribution, the family typically used to model count data (Harrison 2014). This commonly occurs in counts of animals for which the probability of detecting an individual during a survey is less than one. One solution to the issue of incomplete detectability is to model the processes contributing to zero-inflation in count data using occupancy or n-mixture models, which require repeated counts within the season, ideally three or more (MacKenzie et al. 2003, Royle and Kéry 2007). In cases where multiple visits cannot be conducted, binomial zero-inflated Poisson models (ZIPs) can be used to model “false zeros” due to detection error or other covariates (Sólymos et al. 2012). The ZIP has a hierarchical structure with a log-link: a Bernoulli process is used to model the probability of getting a 0 on the count, and abundance is modeled like the GLMMs above using a Poisson distribution. We built ZIPs using the R package glmmTMB (Brooks et al. 2017) with two different structures for the extra-zero process: (1) intercept-only, and (2) detection-related covariates (Beaufort-scale estimation of wind speed, Julian day, and time of morning). Julian Day and Time of morning were scaled and centered to 0. We held the structure of the abundance portion of the model constant among the two models and included the same covariates as in the species-naïve abundance and richness models above (elevation and fish presence). Where AIC values of the two models were not significantly different, I chose the simpler model for bootstrapping.

v. Fish Removal.

Golden Bear Lake, in Center Basin, was a fish-containing lake at the start of the study but underwent trout removal by SEKI Aquatics personnel beginning in September 2016. By 2020, the trout population was estimated to be 95% reduced from its original numbers and was exhibiting signs of nearing a “functionally fishless” state, including a robust mayfly emergence and colonization by adult mountain yellow-legged frogs (*Rana muscosa*) (D. Boiano, personal communication). Golden Bear’s restoration presents a valuable experimental test of the hypothesis that trout suppress bird abundance. To estimate whether bird abundance or richness changed after trout removal, we used an M-BACI (Multiple Before, After, Control, Impact) design to assess the initial effect of trout removal of bird abundance and species richness while controlling for variation in count data both across the study period and other lakes (McDonald et al. 2000). Golden Bear served as the “Impact” lake, and three lakes (one fishless lake within Center Basin and a fishless and fish-containing lake each from Amphitheater Basin) served as Control lakes, as we collected count data at these locations at least once per year in all sampling years. (2020 data from this lake was not included in any previous analyses.) We used GLMMs with a Poisson distribution and log link to model the response variables of point-level avian abundance and richness, with a fixed-effects structure that included the factors “before-after” (whether the survey was pre- or post-trout removal at Golden Bear) and “control-impact” (whether the survey was at Golden Bear or at a control lake), and an interaction term between the two (a significant interaction term indicates a significant effect of the “impact”). We used a random-effects structure that nested point within location within basin within year to account for non-independence resulting from the spatially nested structure of the data.

RESULTS

Avian abundance

The abundance GLMM indicates a significant negative relationship between avian abundance and elevation (β=-0.18; s.e.=0.09; Wald’s z, p=0.038, Table 2.4, Figure 2.2), and a an effect of fish on avian abundance approaching statistical significance (β=-0.19; s.e.=0.11; p=0.089, Table 4, Figure 2.2). Model estimates of avian abundance per point were 4.393 birds at fish-containing lakes and 5.312 birds at fishless lakes, a difference of ~1 bird per 300m-radius. The model estimates a greater than twofold increase in abundance from the highest elevation sampled (~3,650 m, 3.58 birds) to the lowest (~3,100 meters, 8.1 birds) (Figure 2.2a).

Bootstrap-generated 95% CIs overlap substantially between lake types, likely due to low statistical power and poor sampling across the wide range of environmental variation present in this system. Model evaluation including the inspection of homogeneity in residual values and estimating overdispersion, indicated a satisfactory fit of the model to the data.

Avian diversity: species richness and beta diversity

A complete species list of birds detected during point counts can be found in Table 2.3. Observed avian species richness declined with elevation (β=-0.19; s.e.=0.07; Wald's z, p=0.011) and did not significantly differ by lake type (β=-0.13; s.e.=0.10; p=0.189; Figure 2.2b). Beta diversity between fish-containing and fishless lakes was explained by both fish presence and elevation (PERMANOVA, Table 2.5; visualized by NMDS, Figure 2.4). These differences can be attributed to turnover (the even replacement of individuals from one species by individuals from another species), not by nestedness (the loss of species without replacement) (Table 2.5).

Species-level patterns in abundance

The ZIP model with the Intercept-Only zero component did not differ in explanatory power from that containing environmental covariates (Table 2.S1); therefore I used the former, simpler model structure for each of the single-species models I built.

The five most common species in the regional species pool exhibited various responses to elevation and lake fish presence (Table 2.6a-e): Gray-crowned rosy-finch were counted in greater numbers at fishless lakes. Dark-eyed juncos also exhibited a negative response to fish presence, but the model suggests a lower effect size. Mountain white-crowned sparrows and rock wrens were counted in greater numbers at fish-containing lakes. Counts of American pipit did not differ significantly between lake types. Elevation was a significant predictor of abundance in four of the five species modeled: gray-crowned rosy-finch, rock wren, and American pipit (Table 2.6a, d, e) increased in abundance with increasing elevation, while dark-eyed junco declined (Table 2.6c). White-crowned sparrow abundance did not differ by elevation (Table 2.6b).

Effects of Fish Removal

In 2020, counts of both avian abundance and species richness at Golden Bear, the fish-removal lake, increased beyond the range of its historic (2014-2016) variation (mean +/- 1 standard deviation) and into the range of variation of the fishless reference lake within the basin (Figure 2.6). This positive effect of trout removal on abundance was highly significant after taking into spatio-temporal variation in counts using an M-BACI design ($ß_{\mathrm{BAxCI}} = 1.34$, s.e. = 0.38, $p < 0.001$; Table 2.7a; Figure 2.5). Avian richness was higher in 2020 at both impact and control lakes within Center Basin (but lower at both control lakes in Amphitheater Basin), and the interaction term in the M-BACI GLMM was not significant (Table 2.7b), indicating that trout removal did not influence species richness.

At Golden Bear Lake, eight out of 19 (42%) of all detected species increased beyond 1 standard deviation of the mean from previous surveys (Figure 2.6). Two species were detected in 2020 that had not previously been detected in surveys: American dipper (*Cinclus mexicanus*) and mountain bluebird (*Sialia currucoides*) (Figure 2.6). We detected four species in 2014-2016 that were not detected on this survey: chipping sparrow (*Spizella passerina*), fox sparrow (*Passerella iliaca*), Wilson’s warbler *Cardellina pusilla*), and yellow-rumped warbler (*Setophaga coronata*).

DISCUSSION

Patterns of avian abundance and diversity

The fishless lakes in this study supported more birds compared to lakes with fish (roughly 1 bird per 300m of shoreline), and hosted a different distribution of individuals among species, once abiotic factors such as elevation were controlled statistically. My results suggest that differences exist in the breeding avian community surrounding fish-containing versus fishless lakes in the Sierra Nevada alpine zone, thus providing support for the hypothesis that perturbations to the aquatic ecosystem have cascading impacts into the terrestrial zone. These results are consistent with a both comprehensive literature about the prevalence of aquatic subsidies to terrestrial consumers in nature (Polis et al. 1997, Bartels et al. 2012, Piovia-Scott et al. 2016), and with a growing literature about the potential for perturbations to one system to cause trophic cascades whose effects cross ecosystem boundaries to impact terrestrial consumers (Matthews et al. 2002, Sarnelle and Knapp 2005, Lawler and Pope 2006, Epanchin et al. 2010, Rudman et al. 2016, Koel et al. 2019). Beyond the study of a single terrestrial species, this study documents the effects of an aquatic trophic cascade on an entire community of terrestrial consumers: songbirds.

We did not detect any significant differences in avian species richness between fish-containing and fishless lakes. However, community composition can turn over in response to environmental perturbations even when richness does not differ, and this beta diversity is a crucial component of functional diversity (Socolar et al. 2016). Our beta diversity analysis suggests that fish-containing and fishless avian communities are significantly dissimilar, and that this difference is due to turnover (the balanced replacement of individuals of one species with individuals of another), rather than nestedness (species addition/loss without replacement) (Baselga 2010). Species-specific models reveal differential responses to lake fish presence: I detected a positive effect of fishlessness on gray-crowned rosy-finch and dark-eyed junco, and the opposite effect on white-crowned sparrows. Rock wren and American pipit, the other two relatively abundant species in the regional species pool, appeared not to differ in abundance between lake types.

With this point-count data alone, we cannot determine whether differences in abundance are due to an increased number of breeding pairs at fishless lakes (a numeric response), to opportunistic recruitment to an ephemeral resource (a functional response), or both. Bird species differ in home range size, dietary preferences, and nesting behavior, and these factors are all likely to control in which manner (numeric or functional) and to what extent a species is able or likely to respond to such a resource pulse. Some foraging guilds may more readily exploit aquatic insect emergences over others: in a study that investigated the degree to which different avian foraging guilds are associated with emergent aquatic insect biomass in Wisconsin, USA, aerial insectivores were four times more likely to be detected at points where aquatic insects are emerging, but other foraging guilds (e.g., gleaners, bark probers) did not exhibit a response (Schilke et al. 2020). Specialized anatomy may explain why gray-crowned rosy finches exhibit such a strong response to mayfly emergences: they possess malar pouches, or extendable “cheek” pouches that can be filled with prey items (Twining 1940). This adaptation facilitates a much wider home range because they can collect more prey per foraging bout than typical songbird species. In comparison, most other songbirds have smaller home ranges are thus potentially less likely to capitalize on a subsidy outside their home range, especially if they are not adapted to exploit it. We found a strong positive association between rosy-finch abundance and fishless status, which corroborates previous research on this species (Epanchin 2009). This suggests that our analyses are sufficiently powerful to detect differences in abundance between lake types when effect size is large; however, we may have not been able to detect more subtle differences in abundance in other species.

Differential species-specific responses to fish presence could also reflect an interaction between foraging strategy and interspecific competitive dynamics, in which species that can capitalize on the aquatic subsidy prefer to forage and/or nest at fishless lakes, and may open niche space or relax competition for food and/or nest sites at fish-containing lakes. Mountain white-crowned sparrows have been documented eating mosquitos in the high elevation Sierra Nevada, one of the few aquatic dipteran species that is actually more abundant at fish-containing lakes (Knapp et al. 2001, Morton 2002). Within the existing mosaic across the landscape, they (and individuals of other species still present at fish-containing lakes) may be able to utilize the available prey there and avoid competition for space or food at fishless ones. However, white-crowned sparrows are hardly ever completely absent from fishless lakes and have been observed foraging on emerging aquatic insects when they are available, suggesting that they are acceptable prey items at the least.

With respect to nest sites, alpine areas are characterized by low terrestrial primary productivity, so breeding birds that utilize vegetation structure for nest-building (e.g., dark-eyed juncos, white-crowned sparrows) may exhibit competition for that limited resource, and thus be further constrained in their ability to recruit to aquatic prey pulses if they are forced to nest elsewhere. The gray-crowned rosy-finch, on the other hand, nests in vertical cliffs and rock crevices—in the absence of competition for nest sites and with the ability to carry exceptionally large boluses of food for nestlings, this species represents a combination of traits that would make them most able to exploit a resource pulse both numerically (through territory selection near fishless lakes) and functionally (through the ability to find and travel to a resource pulse off-territory). If, for example, white-crowned sparrows preferred to nest at fishless lakes but were outcompeted (either by another ground/shrub-nesting species or by a more dominant white-crowned sparrow), one might predict a negative effect of nesting at the fish-containing lake on productivity or nestling quality. This prediction would be consistent with the theoretical framework of the Ideal Despotic Distribution (Fretwell 1972), an alternative to the Ideal Free Distribution, which we used as a guiding theory in this study.

Given the high nutritional value of aquatically-derived prey via polyunsaturated fatty acids, it is quite possible that a diet enriched in aquatic insects would impact bird consumers beyond simply their presence or abundance on the landscape, such as through differences in clutch size or nestling growth rate (Twining et al. 2016, Schindler and Smits 2017). The importance of consuming aquatically-derived prey for consumers is likely more pronounced for species adapted to live at or near areas characterized by these resource pulses, as they may have lost the ability to biochemically synthesize PUFA from shorter-chain fatty acids found in terrestrial prey items (Twining et al. 2019, 2021). These differences in productivity could result in source-sink dynamics, or in the most extreme, pose an ecological trap to birds, especially if they are naïve to the lower nutritional quality of fish-containing habitat. For example, in a lowland system in Ontario where lake acidification reduces emerging aquatic insect abundance, tree swallows nesting around acidified lakes laid smaller eggs and had nestlings in poorer condition, attributed to the reduction in calcium-rich insects in their diet during the time of egg production (St. Louis and Barlow 1993). It is currently unknown to what extent the unique nutritional contents of aquatic insects (e.g., calcium, highly-unsaturated fatty acids) are limited for terrestrial consumers in the alpine Sierra Nevada, but it is an important mechanistic link in understanding the dynamics of aquatic-terrestrial resource subsidies in this and other systems

(Schindler and Smits 2017). A study of the effects of diet on clutch size and nestling condition of birds at fish-containing versus fishless lakes would help to illuminate the mechanisms by which avian communities are structured there with respect to fish presence.

In addition to directly reducing available aquatic prey to terrestrial consumers, fish presence could also be filtering the avian community by reducing profitable terrestrial prey indirectly: in stream systems in the Rocky Mountains and in South Africa, riparian spider abundances declined at fish-containing stream reaches due to competition with trout for emerging aquatic prey (Benjamin et al. 2011, Jackson et al. 2016). In many systems, birds commonly prey upon spiders at the aquatic-terrestrial interface, especially during the breeding season to provision nestlings (Gunnarsson 2007, Jackson et al. 2020). A recent study from a forested riparian ecosystem in Brazil documented a profound impact of experimental suppression of emerging aquatic insects on the surrounding terrestrial food web: when emerging aquatic insects were experimentally excluded, riparian spider density declined due to increased predation pressure from birds and bats. This mesopredator control resulted in a twofold increase of the spiders' terrestrial insect prey. They conclude that the presence of the aquatic subsidy stabilizes the terrestrial food web by weakening interaction strengths among terrestrial mesopredators (spiders) and top predators (birds and bats).

If the presence of the aquatic insect subsidy functions similarly in this alpine study system, fish-containing and fishless lakes may differ in terrestrial insect community via differential top-down predation pressure. Lakes with greater abundances of riparian spiders, together with the ephemeral aquatic subsidy, could support greater numbers of birds and other terrestrial predators like bats, while fish-containing lakes may host fewer spiders but more terrestrial insects due to increased predation pressure on spiders from the birds that do nest there.

These differences in prey availability may in turn filter the regional bird community depending on the diet preferences of individual bird species. A more comprehensive analysis of the arthropod community at this aquatic-terrestrial interface that included a diet study of avian predators would shed light on the particular trophic interactions driving species-specific patterns of abundance at fish-containing and fishless lakes.

Some caveats must be considered relating to the experimental design of this study. Although the parameter estimate for the effect of fish in the overall abundance model is marginally significant, p-values are unreliable indicators of effect size significance when statistical power is low, as is common and at times unavoidable in ecological studies (Halsey et al. 2015). Bootstrap-derived 95% confidence intervals overlap between lake types, suggesting a considerable amount of uncertainty in that parameter estimate. This is likely due to unmodeled variation present in the system, including factors that influence bird detectability (such as wind speed, air temperature, etc.), as well as those influencing occupancy (such as land cover).

Furthermore, insect emergences at fishless lakes are highly pulsed in both time and space, and the likelihood of conducting a bird survey at any particular fishless lake during an insect emergence, either within the span of a morning or on the day(s) within the season, was low. The 10-minute surveys we conducted are specifically designed to estimate abundances of resident birds (birds with territories overlapping the point-count detection area), and therefore are biased toward measuring residents and not individuals that may opportunistically recruit to lakes from elsewhere. Anecdotally, when mayflies happened to be emerging during a bird survey, it was common to observe multiple species actively foraging over the lake surface and shoreline, sometimes without vocalizing. During one such survey at a small lake at ~3,237 meters on 26 June 2020, I observed nine individuals of four different species (75% of the total individuals detected on the survey) actively foraging on emerging mayflies. These species included gray-crowned rosy-finch (previously documented to capitalize on mayfly emergences) and yellow-rumped warbler (an insect specialist), as well as two generalists, dark-eyed junco and white-crowned sparrow. These emergences typically occur later in the morning (after avian surveys conclude around 0930-1000) once water temperature has increased. It is possible that the avian sampling protocol, while congruent with well-established standards for avian survey (Ralph et al. 1995) and fairly reliable in measuring patterns of avian residency at lakesides, did not fully capture the pulse in activity exhibited by songbirds exploiting the subsidy, especially if the mechanism behind the difference in bird abundance was opportunistic recruitment rather than a numerical response (an increase in recruitment of nesting pairs). The magnitude of specifically the opportunistic response to these resource pulses might be better measured with more targeted sampling of lakes at the time of aquatic insect emergence.

Fish Removal: Evidence for cross-trophic release from competition

A fish removal effort at one study lake served as an experimental test of how the bird community responds to fish removal as emerging aquatic insects rebound. Using an M-BACI design that included 3 reference lakes to serve as spatiotemporal controls for the removal lake, we found that in the short-term, mean bird abundance per survey doubled after fish were removed, after accounting for year effects. These data represent only a single survey visit post-trout-removal and should be interpreted with much caution; that said, they are consistent with a strong suppressive effect of fish on bird abundance.

If the observed increase in abundance at this lake is directly related to the return of the insect subsidy, its magnitude is much greater than the estimate of the predicted effect of fish on bird abundance in the overall abundance model generated from the observational study (Table

4a). These 2020 counts thus may reflect a temporary recruitment response (the increase in prey availability attracting consumers from a greater area), rather than a stabilized numerical response (the patch supporting greater numbers of breeding animals). It is possible that over time, the magnitude of the increased bird abundance will become more subtle as the food-web stabilizes into its reverted fishless stable state. However tentative these data are, they do reflect one replicate of a direct experimental perturbation, compared to the correlational study I present in this paper, and provides compelling evidence in support of the collection of avian data pre- and post-fish-removal at additional lakes slated for restoration in the future.

Field research on the effects of predatory fish introductions on terrestrial systems is ongoing in several systems and continues to yield rare and valuable empirical tests of theory about community structure, food web stability, and animal behavioral ecology. For example, Koel and colleagues (2019) recently reported that invasion of Yellowstone Lake by non-native lake trout reduced nutrient transport across the aquatic-terrestrial boundary, with effects on multiple higher-order terrestrial consumers. Researchers documented shifts in the diets of black and grizzly bears, as well as a decrease in eagle fecundity, as their preferred prey, the native Yellowstone cutthroat trout, declined in response to lake trout invasion (Koel et al. 2019). This study took place at a single lake but utilized a 40-year dataset to uncover the effects they reported, which speaks to the volume of data (as well as the observational acumen and ecological knowledge) needed to elucidate these nuanced but profound connections. While the availability of data limits what we know about the impacts of trout introductions on native fauna, the accumulating research that does exist suggests that impacts of trout beyond the aquatic boundary are numerous.

One implication of this study is that preserving and restoring fishless habitat in the alpine is important for the larger community beyond the aquatic zone. One of the major justifications for trout removal projects in California's National Parks and Forests is to restore habitat specifically for the mountain yellow-legged frog (*Rana sierrae/muscosa*), now a federally endangered species. Mountain yellow-legged frog populations recover successfully at restored fishless lakes; however, they are doubly threatened by the spread of *Batrachochytrium dendrobatidis*, or Bd, a fungal pathogen that has resulted in extensive die-offs of frogs across the Sierra Nevada and worldwide (Vredenburg 2004, Knapp et al. 2011). The extinction probability of *Rana sierrae/muscosa* is sadly uncertain; however, conservation and management are increasingly interested in moving away from a single-species paradigm into a more holistic one that prioritizes ecological stability, overall biodiversity, and ecosystem services (Kremen and Ostfeld 2010, Wenny et al. 2011, White et al. 2013). This study lends legitimacy to efforts to continue funding trout removal projects that restore habitat to its fishless condition by demonstrating a wider community-level effect.

Limitations of ecological study in wilderness

A major limitation of this study is the challenging tradeoff between extensive spatial replication and intensive temporal resurvey, both extremely important to establishing sufficient statistical power to detect ecological patterns in data of species that are mobile or cryptic, &/or where detection-given-presence is not a guarantee. Methodological advances in point count data analysis over the past two decades allow for imperfect detection to be modeled with amendments to classic standardized protocols (MacKenzie et al. 2003, Royle and Kéry 2007, Zipkin et al. 2010). These amendments typically involve longer &/or more frequent visits to point locations, making the fieldwork more time-consuming, especially in wilderness areas that must be accessed by traveling for multiple days on foot. This study involved 5-10 day backpacking trips where surveyors traveled on average 8.2 miles between study basins, often off-trail and over rugged, mountainous terrain. Devising ways to increase sampling capacity in data-deficient remote wilderness areas such as the alpine would have profound impacts on our understanding of and our ability to forecast changes to these socio-ecologically important places.

Conclusions

Mountaintops and alpine areas are one of the most quickly changing biomes in the world. They are already critically important areas for many bird species throughout their annual cycle, as many birds migrate upslope after breeding to track resource availability (Boyle and Martin 2015, Boyle 2017). As the pace of climate change quickens, recent research suggests that alpine areas may become even more important, acting as refugia for both endemic specialists and for biodiversity at large, “sheltering” many lowland species into the future as they track their niches upslope (Loarie et al. 2009, Morelli et al. 2020). As a result, upper montane and alpine areas are likely to increase in species richness and host novel species assemblages. The consequences of these no-analogue communities are largely unknown, especially at the food-web level, and will likely be mixed (Urban et al. 2012, HilleRisLambers et al. 2013, Wallingford et al. 2020). Previous work on interspecific aggression in montane tropical songbirds along elevational replacement zones shows that novel competition can restrict species ranges, with subordinate species yielding their range to better competitors (Jankowski et al. 2010). If high-elevation endemics are poorer competitors, they could face increased risk of extinction.

Multiple stressors to ecosystems can interact to have impacts greater than the sum of each stressor alone (Mainka and Howard 2010). Alpine headwaters will become even more crucially valuable areas for the persistence of several species and for ecosystem services to humans into the future. Advancing our knowledge of how alpine communities function now will aid in our ability to mitigate biodiversity loss and steward our ecosystems forward through the so-called Anthropocene.

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CHAPTER 2 TABLES

Table 2.1. Locations and sampling effort for avian point counts at alpine lakes with or without fish, in California's Sierra Nevada mountains. were established every 300m along the shore of each lake, except where terrain precluded safe travel to the location. Therefore, lakes differ in the number of point count locations as a function of their size. 39 lakes (25 fishless and 14 fish-containing) within 10 basins were sampled over the course of the study (2014-2020).

Basin	Lake Name	Lake Type	# points	Area (m^2)	Elevation (m)
Amphitheater	AMPHIT2	fish	5	238,544	3,272
	AMPHIT1	fishless	4	137,772	3,447
	AMPHIT1B	fishless	1	25,207	3,469
Barrett Lakes	BARRET2	fish	4	118,430	3,512
	BARRET1	fishless	2	28,515	3,493
Center	CENTER2	fish	4	73,241	3,405
	CENTER1	fishless	2	22,970	3,395
Dumbbell	UD	fish	5	159,511	3,386
	SD2	fish	1	9,994	3,310
	DBLONG	fish	3	41,713	3,341
	DUMBLL1	fishless	1	13,374	3,231
	SD1	fishless	1	19,080	3,310
East Lake	EASTLA2	fish	1	17,188	3,270
	EASTLA1	fishless	1	15,550	3,410
Gardiner	GARDNR2A	fish	3	95,833	3,214
	GARDNR2B	fish	1	13,351	3,210
	GARDNR2C	fish	1	18,076	3,110
	GARDNR1A	fishless	2	113,507	3,223
	GARDNR1B	fishless	2	27,896	3,130
	GARDNR1C	fishless	1	15,600	3,130
Observation	UM1	fishless	2	23,180	3,322
	UM2	fishless	1	10,480	3,237
	A	fishless	5	101,241	3,220

	A.4	fishless	1	19,083	3,225
	UMLONG	fishless	2	23,561	3,335
	MAGICALTARN	fishless	1	6,792	3,213
Sixty Lakes	FJORD	fishless	3	57,057	3,303
	ISLAND	fishless	2	80,000	3,300
Upper Kern	UPKERN2	fish	1	14,024	3,530
	SOUTHAM	fish	3	108,609	3,640
	UKLONG	fish	2	59,874	3,570
	UPKERN2B	fish	1	22,410	3,470
	UPKERN1	fishless	1	11,040	3,590
	UPKERN1B	fishless	2	30,109	3,650
	SAMUP	fishless	1	10,391	3,650
Wright Lakes	WRIGHT2B	fish	1	19,825	3,530
	WRIGHT2	fish	1	22,507	3,490
	WRIGHT1B	fishless	2	21,623	3,530
	WRIGHT1	fishless	2	21,591	3,510

Table 2.2. Temporal sampling effort of avian point counts around lake basins in the Sierra Nevada mountains. Years vary by the number of visits (rounds of point count sampling) to each place.

Basin	**Lake Name**	**2014**	**2015**	**2016**	**2020**
Amphitheater	AMPHIT1	8-Jul	9-Jun, 7-Jul		28-Jun
	AMPHIT1B				28-Jun
	AMPHIT2	8-Jul	8-Jun, 6-Jul		28-Jun
Barrett	BARRET1		7-Jun, 4-Jul		29-Jun
	BARRET2		4-Jul		29-Jun
Center	CENTER1	25-Jun	23-Jun, 17-Jul	7-Jun, 5-Jul	4-Jul
	CENTER2			7-Jun	
	CENTER2	25-Jun	23-Jun, 18-Jul	7-Jun, 6-Jul	4-Jul
Dumbbell	DBLONG				27-Jun
	DUMBLL1				27-Jun
	SD1				27-Jun
	SD2				27-Jun
	UD				27-Jun
East Lake	EASTLA1	21-Jun			7-Jul
	EASTLA2	22-Jun			7-Jul
Gardiner	GARDNR1A				11-Jul
	GARDNR1B				11-Jul
	GARDNR1C				11-Jul
	GARDNR2A				10-Jul
	GARDNR2B				10-Jul
	GARDNR2C				10-Jul
Observation	A				25-Jun
	A.4				25-Jun
	MAGICALTARN				26-Jun
	UM1				26-Jun
	UM2				26-Jun
	UMLONG				26-Jun

Sixty Lakes	FJORD				8-Jul
	ISLAND				8-Jul
Upper Kern	SAMUP				6-Jul
	SOUTHAM				6-Jul
	UKLONG				6-Jul
	UPKERN1		22-Jun, 21-Jul		6-Jul
	UPKERN1B				6-Jul
	UPKERN2		22-Jun, 21-Jul		6-Jul
	UPKERN2B				6-Jul
Wright Lakes	WRIGHT1		20-Jun, 22-Jul		5-Jul
	WRIGHT1B				5-Jul
	WRIGHT2		20-Jun, 22-Jul		5-Jul
	WRIGHT2B				5-Jul

Table 2.3. List of species detected during point count surveys at high elevation lakes in the Sierra Nevada, in order of commonness. Total species = 27 species over 150 surveys.

AOU Code	**Common Name**	**# of times detected**	**Fraction of surveys detected**
ROWR	Rock Wren	83	0.553
WCSP	White-crowned Sparrow	79	0.527
GCRF	Gray-crowned Rosy-Finch	69	0.460
DEJU	Dark-eyed Junco	68	0.453
AMPI	American Pipit	42	0.280
CLNU	Clark's Nutcracker	37	0.247
DUFL	Dusky Flycatcher	37	0.247
HETH	Hermit Thrush	30	0.200
YRWA	Yellow-rumped Warbler	22	0.147
AMRO	American Robin	13	0.087
MOCH	Mountain Chickadee	13	0.087
WIWA	Wilson's Warbler	13	0.087
FOSP	Fox Sparrow	11	0.073
CAFI	Cassin's Finch	6	0.040
SPSA	Spotted Sandpiper	6	0.040
AMDI	American Dipper	3	0.020
MOBL	Mountain Bluebird	3	0.020
RBNU	Red-breasted Nuthatch	3	0.020
NOFL	Northern Flicker	2	0.013
WTPT	White-tailed Ptarmigan	2	0.013
XXHU	Unidentified Hummingbird	2	0.013
BRBL	Brewer's Blackbird	1	0.007
BRSP	Brewer's Sparrow	1	0.007
CHSP	Chipping Sparrow	1	0.007
EAGR	Eared Grebe	1	0.007
OSFL	Olive-sided Flycatcher	1	0.007
TOSO	Townsend's Solitaire	1	0.007

Table 2.4. Summary tables for GLMMs predicting avian abundance and species richness at high-elevation lakes. Estimates are untransformed from the log scale. Elevation is a significant predictor of both abundance (p=0.038) and species richness (p=0.011). The effect of fish on abundance is marginally significant (Wald's z, p=0.090).

	Abundance Model				**Richness Model**			
Fixed Effects	*Estimate*	*SE*	*95% CI*	*p*	*Estimate*	*SE*	*95% CI*	*p*
Intercept	1.67	0.16	1.36 – 1.98	**<0.001**	1.13	0.17	0.80 – 1.47	**<0.001**
Fish	-0.19	0.11	-0.42 – 0.03	0.090	-0.13	0.10	-0.32 – 0.06	0.189
Elevation	-0.18	0.09	-0.35 – -0.01	**0.038**	-0.19	0.07	-0.33 – -0.04	**0.011**
[yr] 2015	0.22	0.13	-0.05 – 0.48	0.104	0.22	0.16	-0.10 – 0.54	0.179
[yr] 2016	0.13	0.17	-0.21 – 0.47	0.452	0.19	0.21	-0.23 – 0.61	0.382
[yr] 2020	0.18	0.14	-0.09 – 0.46	0.190	0.25	0.17	-0.07 – 0.58	0.129
Random Effects								
σ^2	0.15				0.24			
τ_{00}	$0.05_{\text{point:(location:basin)}}$				$0.00_{\text{point:(location:basin)}}$			
	$0.00_{\text{location:basin}}$				$0.00_{\text{location:basin}}$			
	0.05_{basin}				0.05_{basin}			
N	6_{point}				6_{point}			
	39_{location}				39_{location}			
	10_{basin}				10_{basin}			
Observations	150				150			
Marginal R^2 / Conditional R^2	0.150 / 0.488				0.143 / 0.285			

Table 2.5. PERMANOVA testing the effects of fish presence and elevation on avian beta diversity (pairwise Bray-Curtis similarity and its nestedness and turnover components). Beta diversity is explained by both fish presence and elevation, and is attributable to species turnover.

Dissimilarity Measure	**Fish Presence**				**Elevation**			
	SS	R^2	*F*	*P*	*SS*	R^2	*F*	*P*
Bray **(Total)**	1.1065	0.05443	4.8774	0.045 *	3.1163	0.15329	13.7369	0.0001 ***
Bray (Nestedness)	0.01	0.0053	0.3179	0.434	-0.35488	-0.188	-11.268	0.999
Bray (Turnover)	1.1	0.07162	7.1688	0.042 *	3.3638	0.21902	21.9224	0.0001 ***

Table 2.6. ZIP models for the lakeside abundance of five alpine bird species with respect to elevation and fish condition. Poisson model estimates are untransformed from the log-scale. Bolded p-values indicate a parameter estimate significantly different from 0 (Wald's z, α = 0.05).

a) Gray-crowned rosy-finch

	Estimate	*SE*	*95% CI*	*p*
Count Model				
Intercept	0.58	0.2	0.17 – 0.98	**0.005**
Fish	-0.55	0.24	-1.02 – -0.09	**0.019**
Elevation	0.29	0.14	0.01 – 0.57	**0.046**
[yr] 2015	-0.36	0.57	-1.47 – 0.75	0.527
[yr] 2016	0.03	0.25	-0.47 – 0.53	0.906
[yr] 2020	0.03	0.4	-0.75 – 0.80	0.943
Zero-Inflated Model				
(Intercept)	-0.82	0.37	-1.54 – -0.11	0.025
Random Effects				
σ^2	0.49			
$\tau_{00\ \text{locpoint:(location:basin)}}$	0			
$\tau_{00\ \text{location:basin}}$	0			
$\tau_{00\ \text{basin}}$	0.1			
N_{locpoint}	75			
N_{location}	36			
N_{basin}	10			
Observations	120			
Marginal R^2	0.258			
AIC	349.044			
log-Likelihood	-164.522			

b) White-crowned sparrow				
	Estimate	*SE*	*95% CI*	*p*
Count Model				
Intercept	-0.46	0.21	-0.87 – -0.05	**0.029**
Fish	0.57	0.25	0.09 – 1.05	**0.02**
Elevation	-0.22	0.12	-0.45 – 0.02	0.076
[yr] 2015	0.63	0.42	-0.19 – 1.45	0.131
[yr] 2016	0.06	0.25	-0.43 – 0.55	0.813
[yr] 2020	-0.83	0.4	-1.62 – -0.04	**0.039**
Zero-Inflated Model				
(Intercept)	-19.92	8741.73	-17153.41 – 17113.56	0.998
Random Effects				
σ^2	0.8			
$\tau_{00\ \text{locpoint:(location:basin)}}$	0.3			
$\tau_{00\ \text{location:basin}}$	0			
$\tau_{00\ \text{basin}}$	0			
N_{locpoint}	75			
N_{location}	36			
N_{basin}	10			
Observations	120			
Marginal R^2	0.222			
AIC	323.358			
log-Likelihood	-151.679			

c) Dark-eyed junco				
	Estimate	*SE*	*95% CI*	*p*
Count Model				
Intercept	-0.78	0.32	-1.40 – -0.15	**0.015**
Fish	-0.48	0.27	-1.01 – 0.05	0.077
Elevation	-1.1	0.21	-1.52 – -0.69	**<0.001**
[yr] 2015	1.38	0.52	0.37 – 2.39	**0.007**
[yr] 2016	1.2	0.41	0.40 – 1.99	**0.003**
[yr] 2020	-0.01	0.44	-0.87 – 0.84	0.977
Zero-Inflated Model				
(Intercept)	-2.75	1.38	-5.45 – -0.05	**0.046**
Random Effects				
σ^2	1.09			
$\tau_{00\ \text{locpoint:(location:basin)}}$	0			
$\tau_{00\ \text{location:basin}}$	0			
$\tau_{00\ \text{basin}}$	0.32			
N_{locpoint}	74			
N_{location}	35			
N_{basin}	10			
Observations	119			
Marginal R^2	0.552			
AIC	255.531			
log-Likelihood	-117.766			

d) American pipit

	Estimate	*SE*	*95% CI*	*p*
Count Model				
Intercept	-1.41	0.36	-2.11 – -0.71	**<0.001**
Fish	0.04	0.34	-0.63 – 0.72	0.898
Elevation	0.86	0.24	0.40 – 1.32	**<0.001**
[yr] 2015	1	0.77	-0.51 – 2.52	0.194
[yr] 2016	0.03	0.34	-0.64 – 0.71	0.924
[yr] 2020	0.24	0.53	-0.81 – 1.28	0.656
Zero-Inflated Model				
(Intercept)	-18.9	9549.86	-18736.28 – 18698.49	0.998
Random Effects				
σ^2	1.5			
$\tau_{00\ \text{locpoint:(location:basin)}}$	0.35			
$\tau_{00\ \text{location:basin}}$	0			
$\tau_{00\ \text{basin}}$	0.1			
N_{locpoint}	75			
N_{location}	36			
N_{basin}	10			
Observations	120			
Marginal R^2	0.343			
AIC	219.136			
log-Likelihood	-99.568			

e) Rock wren				
	Estimate	*SE*	*95% CI*	*p*
Count Model				
Intercept	-0.36	0.2	-0.75 – 0.02	0.062
Fish	0.19	0.23	-0.26 – 0.63	0.407
Elevation	0.28	0.11	0.06 – 0.50	**0.011**
[yr] 2015	-1.59	1.02	-3.59 – 0.41	0.118
[yr] 2016	-0.16	0.28	-0.71 – 0.40	0.578
[yr] 2020	0.21	0.3	-0.38 – 0.80	0.48
Zero-Inflated Model				
(Intercept)	-20.78	8574.13	-16825.77 – 16784.21	0.998
Random Effects				
σ^2	0.85			
τ_{00} locpoint:(location:basin)	0.02			
τ_{00} location:basin	0.03			
τ_{00} basin	0			
N locpoint	75			
N location	36			
N basin	10			
Observations	120			
Marginal R^2	0.192			
AIC	281.732			
log-Likelihood	-130.866			

Table 2.7. Results of an M-BACI analysis (3 control lakes, 1 treatment lake) of experimental trout removal on lakeside bird count data using GLMMs demonstrate a strong positive effect of trout removal on bird abundance (a) but not species richness (b).

	a) Abundance Model				**b) Richness Model**			
Predictors	*Estimate*	*SE*	*95% CI*	*p*	*Estimate*	*SE*	*95% CI*	*p*
Intercept	1.73	0.21	1.32 – 2.13	**<0.001**	1.26	0.17	0.93 – 1.58	**<0.001**
Before-After	-0.09	0.38	-0.85 – 0.66	0.809	0.09	0.32	-0.53 – 0.72	0.766
Control-Impact	-0.34	0.21	-0.75 – 0.07	0.104	-0.06	0.19	-0.44 – 0.32	0.758
BA*CI	1.34	0.38	0.60 – 2.09	**<0.001**	0.19	0.38	-0.56 – 0.94	0.62
Random Effects								
σ2	0.17				0.25			
τ00	0.07 loc.pt:(location:(basin:year))				0.00 loc.pt:(location:(basin:year))			
	0.00 location:(basin:year)				0.00 location:(basin:year)			
	0.15 basin:year				0.08 basin:year			
	0.00 year				0.00 year			
N	15 loc.pt				15 loc.pt			
	4 location				4 location			
	2 basin				2 basin			
	4 year				4 year			
Observations	69				69			
Marginal R^2	0.169				0.021			
Conditional R^2	0.642				NA			
Deviance	330.614				268.17			
AIC	346.614				284.17			
log-Likelihood	-165.307				-134.085			

CHAPTER 2 FIGURES

Figure 2.1. A typical alpine lake at 3300 m elevation in Sixty Lakes Basin, surrounded by a mix of talus, bare rock, and sparse graminoid, willow, and stunted conifer vegetation. Photo M. Clapp

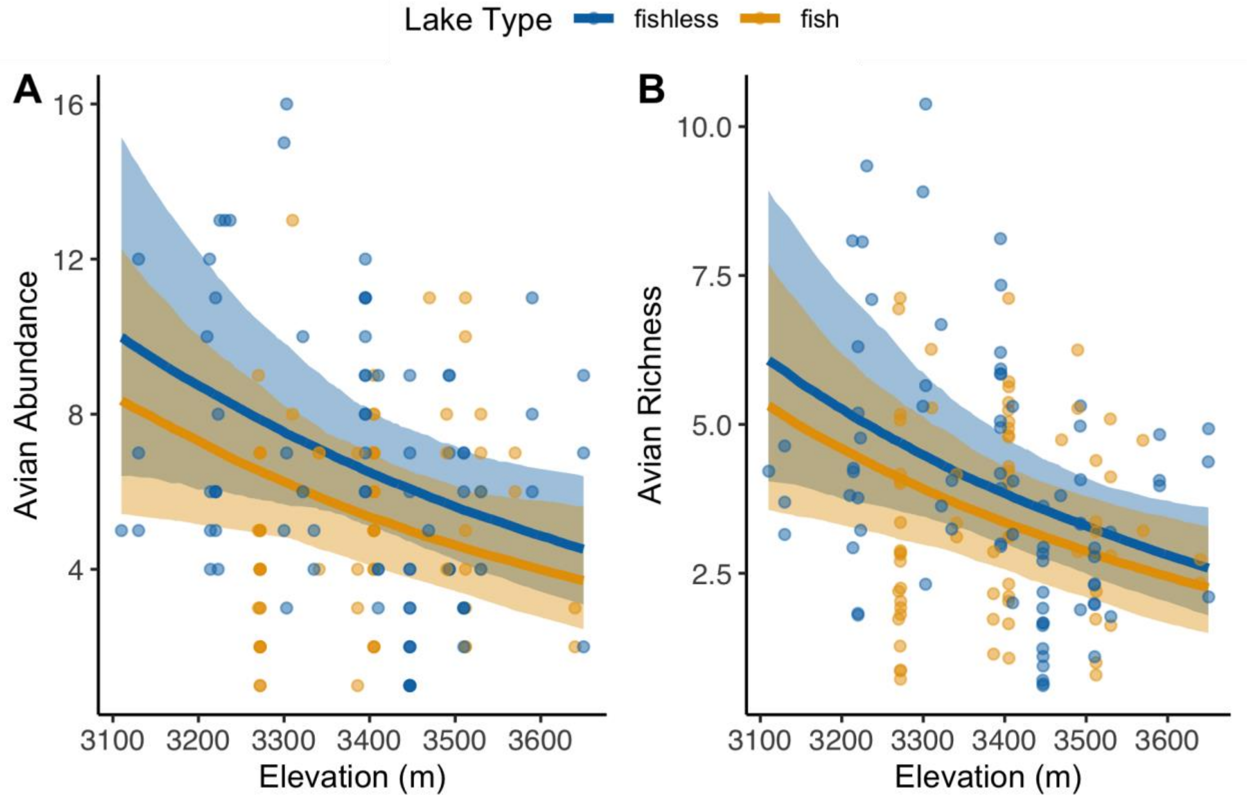

Figure 2.2. GLMM predictions for (A) avian abundance and (B) avian richness at point counts of fish-containing and fishless lakes across elevations. Elevation has a significantly negative effect on both abundance (Wald's z, p = 0.375) and richness (Wald's z, p = 0.011). The presence of fish has a marginally significant negative effect on overall avian abundance (Wald's z, p = 0.089) but not richness (Wald's z, p = 0.189). 95% confidence intervals are from model predictions of bootstrapped data. Points reflect raw counts and species counts, respectively. See model summary tables for more details.

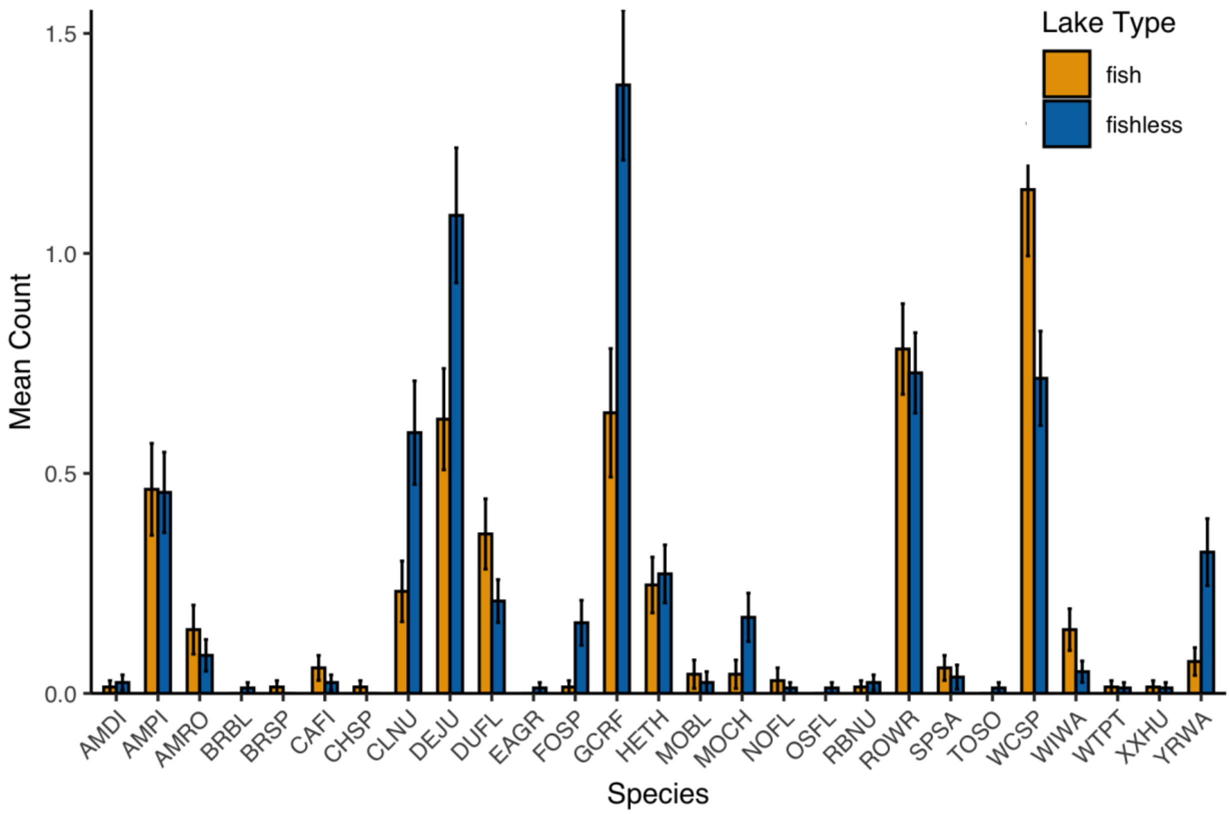

Figure 2.3. Bird species differ in their relative abundances at fish-containing (gold) and fishless (blue) lakes. Bars represent mean counts per species per survey point +/- standard error.

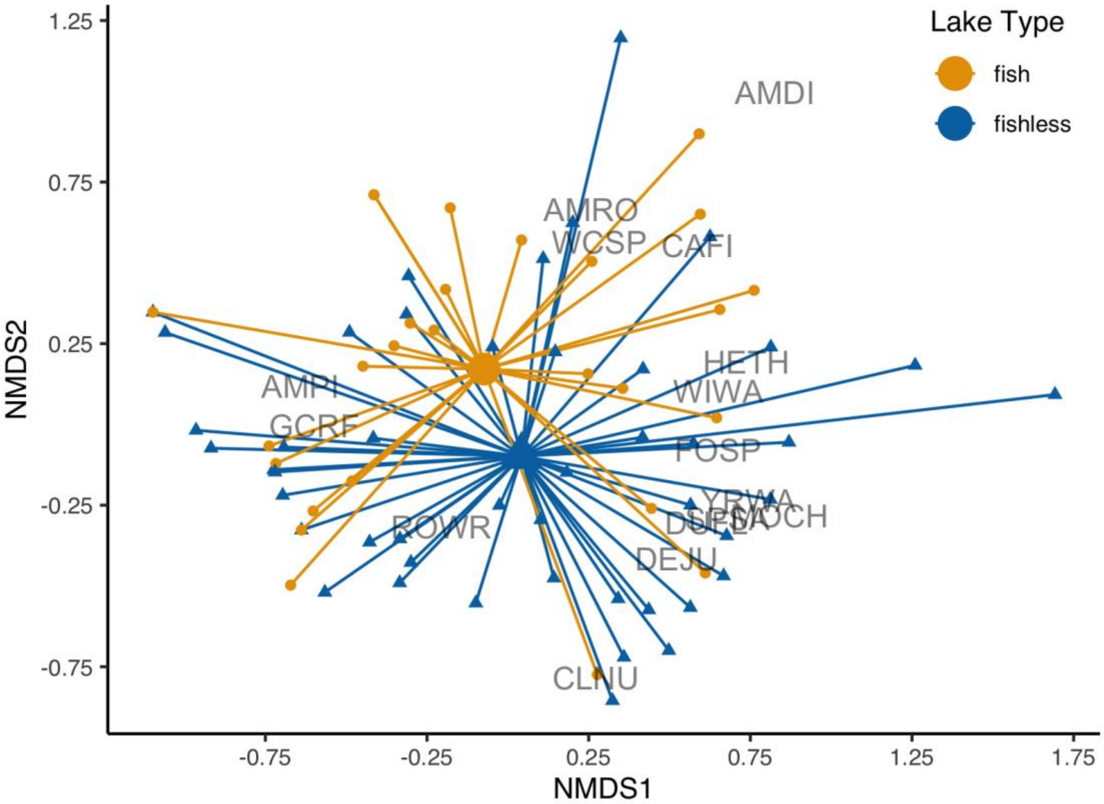

Figure 2.4. Spider plot for ordination analysis (NMDS) of Bray-Curtis dissimilarity illustrates differences in community composition between fish-containing and fishless lakes (k=3, stress=0.136). Each point represents a single survey point.

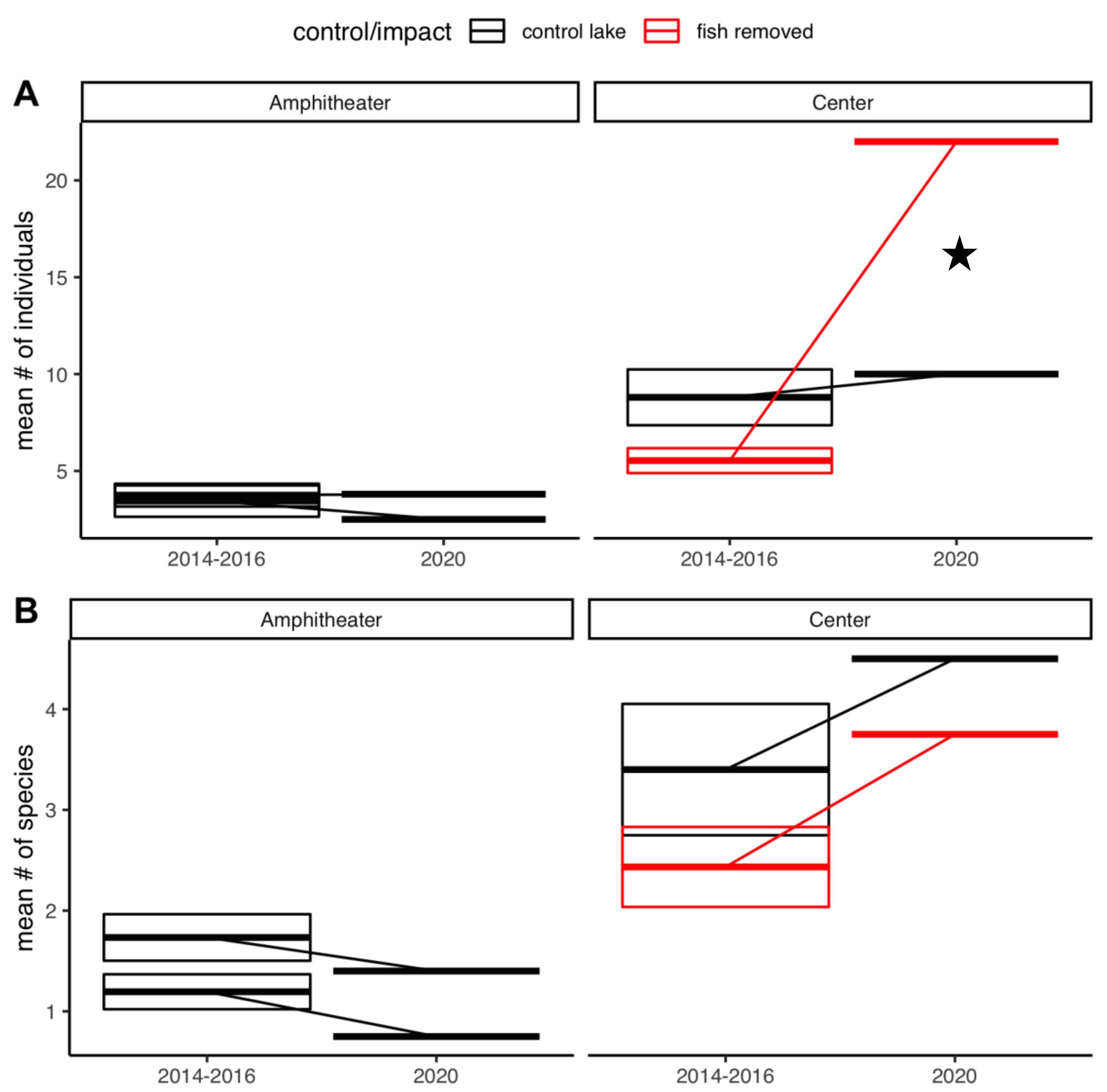

Figure 2.5. Initial results from the M-BACI (Multiple Before-After, Control-Impact) study of single-lake fish removal on (A) bird abundance and (B) species richness. The lake represented by red underwent trout removal between the two time periods depicted on the x-axis. The lakes represented by black are control lakes whose fish state did not change over the course of the study. The boxplots for 2014-2016 represent standardized point-level means +/- standard deviation (mean lake-level abundance per visit divided by the number of survey points at each lake), which facilitates direct comparison between the two lakes. The star indicates a significant effect of trout removal on bird abundance (a significant interaction term in the BACI GLMM; see Table 7). Avian species richness (B) was not affected by trout removal.

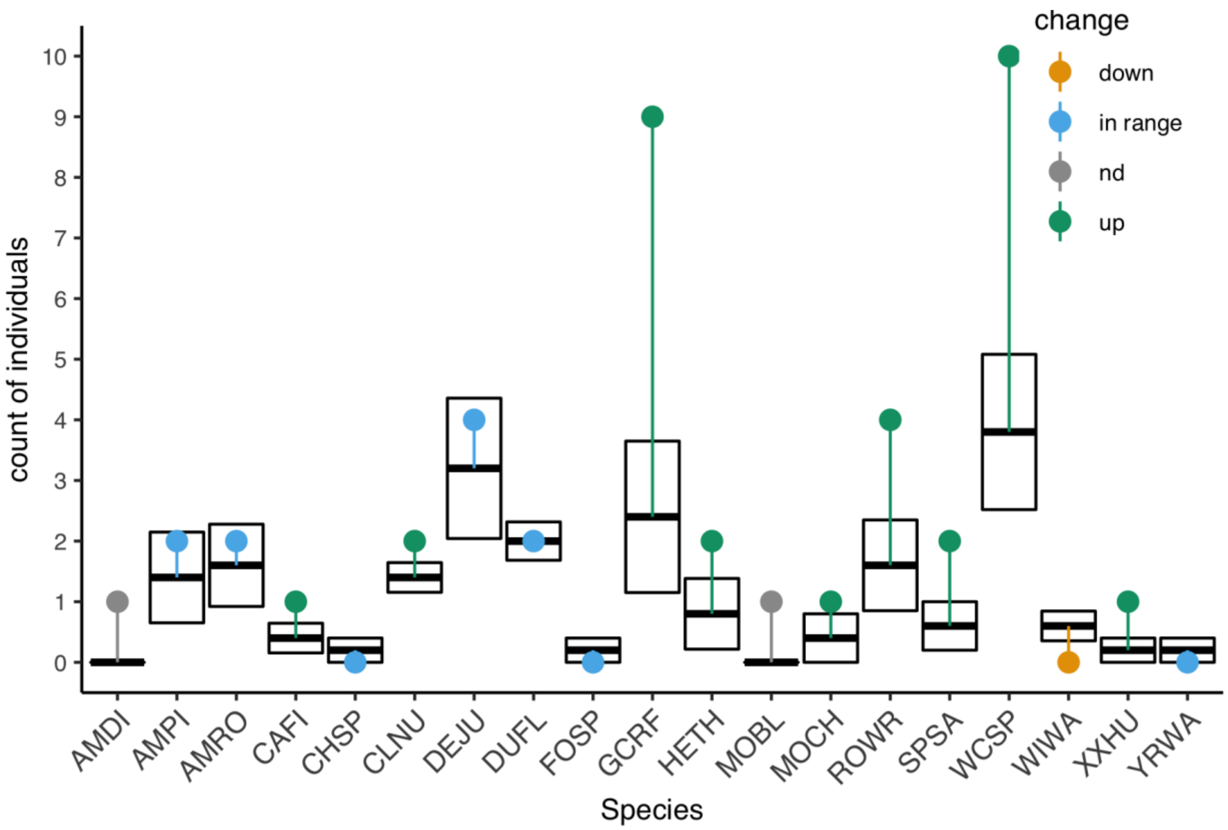

Figure 2.6. Changes in counts by species at Golden Bear Lake pre- (crossbar boxes) and post- (colored dots) fish removal. Crossbar boxes represent the mean lake-level totals per species of all surveys conducted 2014-2016 +/- S.E.M. Colored dots represent lake-level totals per species in the 2020 survey. AMDI (American Dipper) and MOBL (Mountain Bluebird) were never detected at this lake prior to trout removal so we have no variance data (“nd”) to evaluate whether these counts are within the range of variation pre-fish-removal.

CHAPTER 2 SUPPLEMENTAL INFORMATION

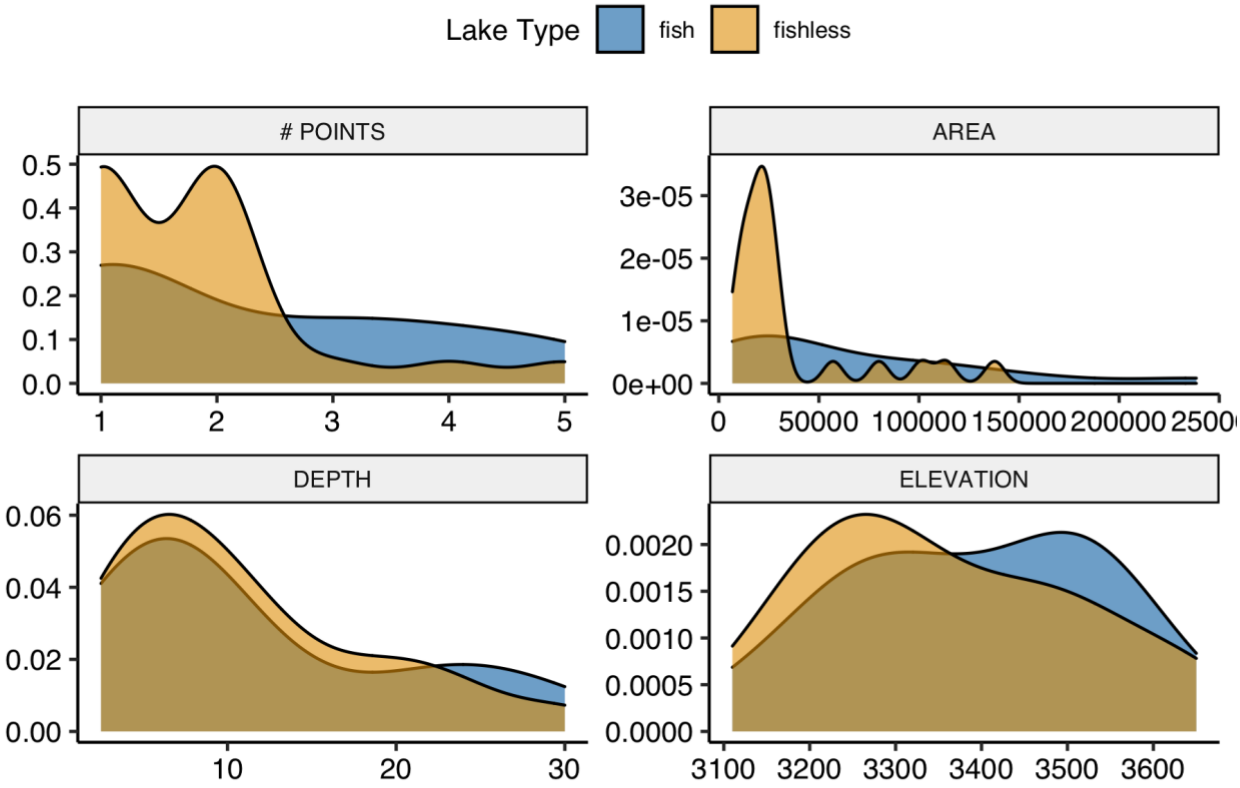

Figure 2.S1. Density plots of environmental characteristics of sample lakes (n = 39), grouped by fish condition (1 = fishless, 2 = fish-containing). Overall, depth and elevation of lakes were similar between lake types. Density plots reveal the fishless study lakes to be smaller than the fish-containing ones; therefore, the number of avian survey points around each lake also differed.

Table 2.S1. Candidate ZIP models for gray-crowned rosy finch abundance**.** Poisson model estimates are untransformed from the log-scale. Bolded p-values indicate a parameter estimate significantly different from 0 (Wald's z, $\alpha = 0.05$).

	Intercept-Only				**Env. Covariates**			
Conditional Model	*Estimate*	*SE*	*95% CI*	*p*	*Estimate*	*SE*	*95% CI*	*p*
Intercept	0.6	0.55	-0.48 – 1.67	0.277	0.8	0.63	-0.44 – 2.04	0.205
Fish	-0.57	0.24	-1.03 – -0.10	**0.016**	-0.64	0.24	-1.12 – -0.17	**0.008**
Elevation	0.31	0.14	0.04 – 0.59	**0.027**	0.27	0.13	0.02 – 0.52	**0.037**
[yr] 2015	0.02	0.54	-1.05 – 1.08	0.973	-0.16	0.62	-1.37 – 1.06	0.801
[yr] 2016	-0.72	0.69	-2.08 – 0.64	0.303	-0.89	0.72	-2.30 – 0.51	0.213
[yr] 2020	-0.05	0.54	-1.11 – 1.02	0.93	-0.17	0.62	-1.38 – 1.05	0.785
Zero-Inflated Model								
Intercept	-0.71	0.35	-1.40 – -0.03	**0.041**	-0.36	0.42	-1.18 – 0.46	0.392
Wind					-0.3	0.28	-0.86 – 0.26	0.292
Julian Day					0.19	0.39	-0.57 – 0.94	0.626
Time					-0.27	0.3	-0.86 – 0.32	0.376
Random Effects								
σ^2	0.54				0.49			
τ_{00}	0.01 $_{\text{locpoint:(location:basin)}}$				0.00 $_{\text{locpoint:(location:basin)}}$			
	0.00 $_{\text{location:basin}}$				0.00 $_{\text{location:basin}}$			
	0.09 $_{\text{basin}}$				0.06 $_{\text{basin}}$			
N	80 $_{\text{locpoint}}$				80 $_{\text{locpoint}}$			
	39 $_{\text{location}}$				39 $_{\text{location}}$			
	10 $_{\text{basin}}$				10 $_{\text{basin}}$			
Observations	144				144			
Marginal R^2/Cond'l R^2	0.286 / NA				0.301 /NA			
AIC	400.48				403.546			
log-Likelihood	-190.24				-188.773			

CHAPTER 3: Environmental variation influences the importance of aquatic prey in the nestling diet of a montane sparrow

ABSTRACT

A growing body of research suggests that aquatic subsidies can strongly influence recipient terrestrial systems at multiple levels of organization, including individual body condition of terrestrial consumers, population carrying capacity, and food web structure. However, the ultimate importance of a subsidy to a consumer depends on its availability to consumers in space and time. Environmental drivers such as snowpack and spring weather determine the magnitude of aquatic resource pulses and thus, their availability to terrestrial consumers, but there is a dearth of empirical study on how variation in space (distance to subsidy) and time (seasonal changes in abundance) modulate a subsidy's importance to consumers. We studied the diets of nestling mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*) relative to seasonal availability of aquatic resources in a year where snowpack was 213% of average. We used Bayesian stable isotope mixing models to estimate the proportion of diet derived from aquatic versus terrestrial sources. We found no evidence that diet source proportions in the nestlings of this species varied over distances of up to 160 m from water. However, both the proportion of aquatically derived energy and the trophic position of nestling diets decreased with respect to hatch date, with late-season nestlings feeding at half a trophic level lower than early-season nestlings. Future work across multiple years will clarify the dynamics of the relationship between interannual environmental variability and foraging behavioral flexibility.

INTRODUCTION

Water, in its various forms and quantities, circumscribes the rules of life in the high Sierra. The Pleistocene epoch's glaciers retreated for the last time over 10,000 years ago, polishing bedrock, carving out high peaks, and leaving in their wake the moraines and lowlands that would become the meadows and headwaters we now know as the high country of the Sierra Nevada (Glazner and Stock 2010). In this late Holocene, our current epoch, the high country is a strikingly seasonal place where a deep winter snowpack mutes the land for half the year, then infuses it with life as it melts with the lengthening days of spring. Snowmelt and sun invigorate the ponds, streams, lakes, and meadows where willows break bud, wildflowers bloom, mushrooms appear, ground squirrels emerge from hibernation, and all manner of fauna, butterfly and bird and human alike, seasonally gather for a brief and lively summer. The primacy of water in shaping life on land—through providing drinking water, promoting plant growth, and hosting a diverse aquatic community—is undeniable with one glance at an alpine meadow in summer. This observation in fact belies a dearth of knowledge about what role this pulse of aquatic productivity plays in the diets of terrestrial consumers, like birds.

Navigating uncertainty in the environmental conditions of breeding grounds during the brief summer season is critical to an animal's survival and reproductive success. Depending on the snowpack and on spring daily temperatures, spring green-up may begin as early as May or late into July at high elevations and latitudes—this extreme variability in environmental conditions both seasonally and interannually has thus shaped the reproductive strategies and behavioral ecology of the animals that breed there (Martin and Wiebe 2004). For example, to cope with a shorter overall season, many bird species high on the elevational gradient exhibit a slower life-history strategy than lower-elevation relatives, trading off annual fecundity with higher paternal investment on smaller clutches with higher fledging probability (Badyaev and Ghalambor 2001, Bears et al. 2009). Successfully syncing the timing of nesting with peaks in resource abundance is a major driver of reproductive success, sometimes explaining more variability in annual fecundity than nest predation (Nagy and Holmes 2004). Food abundance also been implicated as a potentially more important proximate driver of habitat selection and settlement than predation risk (Chalfoun and Martin 2007). While many factors influence the settlement heuristics of birds, the ability to assess and/or predict the availability of their food sources over space and time is one of the most important to their fitness.

The availability of highly profitable prey plays a critical role in meeting the energetic needs of both adults and offspring during the breeding season. The nestling-provisioning period is one of the most energetically demanding in a bird's life cycle, as adults must balance self-nutrition (investment in survival of self and future reproduction) with offspring survival (investment in current reproductive success) (Martin 1987). The nestlings of altricial bird species are nearly always food-limited due to constraints on the abilities of parents to supply food (Biermann and Sealy 1982, Perrig et al. 2014, Orłowski et al. 2017). Several experimental and observational studies document a direct positive relationship between local food abundance and the nutrition, growth rate, and survival probability of nestlings (Quinney et al. 1986, Perrig et al. 2014). Larger nestlings typically have better survival and recruitment rates (Tinbergen and Boerlijst 1990, Both et al. 1999). Abundant food resources within a bird's territory also benefit them indirectly: in resource-rich territories, central-place foragers spend less time off the nest foraging and benefit by reduced nest exposure to predation (Duncan Rastogi et al. 2006) and/or better control over incubation temperature (Martin 1987). Conversely, and beyond survival, nutritional stress during development has strong negative impacts on brain development. This results in lifelong deleterious effects on adrenocortical function (Pravosudov and Kitaysky 2006), learning ability (Kitaysky et al. 2006), spatial memory (Pravosudov et al. 2005), and song development (Nowicki et al. 2000, 2002) in birds. Directly or indirectly, the effects of food abundance on nestling quality and survival are likely to be especially important in alpine environments, where nestling survival is prioritized over annual fecundity.

Where a bird's nest is tucked into the temporal landscape of food availability can also have strong implications for the lives of its nestlings. Synchrony between peak arthropod abundance and consumer reproduction has been observed in many bird species, reflecting an evolutionary strategy to time the energetic needs of nestling provisioning with maximum available biomass of nutritionally dense prey (Lack 1968, Perrins 1970, Norment 1992, Van Noordwijk et al. 1995, Eeva et al. 2000, Epanchin et al. 2010). One recent study in a high-elevation sagebrush ecosystem documented an increase in the body condition of sympatric sparrows (Brewer's sparrow, *Spizella breweri*; and vesper sparrow, *Poocetes gramineus*) following a seasonal pulse in insect availability, suggesting that the abilities of birds to capitalize on short pulses of productivity is beneficial (Cutting et al. 2016). Further, experimentally delaying of the timing of clutch initiation in great tits (*Parus major*) resulted in smaller clutch sizes and nestling weights compared to unmanipulated clutches, suggesting that the quality of nestlings suffers when adult birds are unable to match reproductive timing with seasonal prey abundance (Verhulst and Tinbergen 1991).

In temperate environments, and especially in highly seasonal alpine environments, consumers must rely on proximate cues that predict future environmental condition to sync their reproductive schedules optimally, as many arrive and settle on their breeding grounds in advance of the peak in food biomass. Interannual environmental variation such as snowpack impacts the timing of both insect prey availability and onset of nesting, but not necessarily uniformly, introducing phenological mismatches between the peak of nestling provisioning and peak food abundance (Visser et al. 1998; Harper and Peckarsky 2006; Day and Kokko 2015; Everall et al. 2015). This mismatch makes optimal habitat selection more challenging, likely because snow masks visual cues of habitat quality. In heavy snow years, the date of peak nesting for dusky flycatchers (*Empidonax oberholseri*) at Tioga Pass Meadow was more mismatched with peak insect biomass (more delayed relative to the insect biomass peak) than in normal or light snow years (Pereyra 2011).

Beyond the general importance of pulses of arthropod prey to birds during the breeding season (Ricklefs 1998), it is becoming increasingly well understood that aquatic systems can provide important subsidies to terrestrial consumers by contributing an additional pulse of biomass to the recipient environment (Polis et al. 1997). Depending on their magnitude and availability in space and time, these subsidies can influence consumer growth rates, consumer population carrying capacity, and recipient food web structure and stability (Nakano and Murakami 2001, Sabo and Power 2002, Yang et al. 2008, Wright et al. 2013). However, the extent to which allochthonous *inputs* (input from external sources) are actualized as *subsidies* (measurable changes to trophic structure, consumer fitness, etc.) to the recipient environment, remains poorly understood. Work that quantifies the timing and magnitude of subsidies to recipient consumers across dynamic environmental conditions is needed to make more general inferences about when and how subsidies are likely to influence ecosystem processes (Subalusky and Post 2019).

Stable isotope analysis (SIA) of consumer diets is one important tool that can address this research need: SIA of consumer tissue can quantify both the composition and origins of their diets using ratios of natural variability in stable isotopes of carbon and nitrogen between aquatic and terrestrial sources and across trophic levels (Post 2002, Inger and Bearhop 2008). Typically, smaller (more negative) values of $\delta^{13}C$ correspond to the C3 photosynthetic pathway and a greater terrestrial carbon signature, while enriched $\delta^{13}C$ values reflect preferential uptake of heavy carbon (^{13}C) from the photosynthetic pathway of algae (DeNiro and Epstein 1978). With regards to trophic position, values of $\delta^{15}N$ are typically enriched with each trophic step, so larger values correspond to higher trophic levels (Deniro and Epstein 1981, Post 2002).

SIA's quantitative estimates of diet are less prone to the biases of traditional methods such as the differential digestion of diet items (in boluses, feces or stomach contents) or visual occlusion (from video or in-person observations of diet). The use of SIA to investigate subsidies has yielded surprises in the importance of aquatic prey to terrestrial consumers. When aquatic and terrestrial systems are tightly coupled, as they are in riparian corridors or headwater environments, terrestrial consumers such as riparian-associated birds have been estimated to derive over 50% of their energy from the aquatic system, occupying a isotopic signature space similar to fish (Jackson et al. 2020). Measured over time and across environmental conditions, SIA has the power to reveal dynamics in the importance of aquatic subsidies to terrestrial consumer diets that are currently poorly understood (Schindler and Smits 2017). It also provides a quantitative basis for determining an animal's association with aquatic habitat specifically as a function of diet, as opposed to association due to nesting structure, cover, and/or reliance on water itself. Giving texture to the way we define which animals are "riparian associated" or reliant on aquatic systems will aid in management and conservation efforts that target the specific needs of consumers.

How might the trophic *origin* of prey (aquatic or terrestrial) impact their value to terrestrial consumers? The nutritional content of aquatically-derived food may actually exceed that of terrestrially-derived food due to the presence of certain compounds specific to algae-based food chains, such as polyunsaturated fatty acids (Martin-Creuzburg et al. 2017, Twining et al. 2019). In the same way that salmon are highly desirable to humans due to their high concentrations of omega-3 fatty acids, these compounds are essential elements of the diets of wild animals and have been found to positively influence important proxies of fitness, such as growth rate. One recent study compared the diets of prothonotary warbler (*Protonotaria citrea*) nestlings between river sites that naturally varied in aquatic prey (mayfly) densities. They found that adults provisioned nestlings with prey items in accordance to their local availability and that the nestlings that were fed more mayflies grew more rapidly than those fed caterpillars (Dodson et al. 2016). Even though the number of fledged young did not differ between sites, there appear to be nutritional benefits to consuming aquatic prey. Indeed, body condition and growth rate of nestlings may be more evolutionary useful measures for reproductive success than fledging success, as they better predict fledgling survival to independence and recruitment into the breeding population (Tinbergen and Boerlijst 1990, Both et al. 1999, Streby et al. 2014). Thus, understanding the role of aquatically derived prey in terrestrial consumer nutrition, body condition, and survival is emerging as an important development in foraging ecology research.

The aim of this study was to integrate emerging knowledge about the importance of aquatic subsidies to terrestrial consumer diets with the growing literature on how different species cope with environmental variation. Using SIA, we explore diet flexibility in a model system, the mountain white-crowned sparrow (*Z. l. oriantha,* hereafter “MWCS”), relative to spatial and temporal variation in prey abundance. We hypothesized that, as central-place foragers, MWCS adults are limited spatially in foraging during breeding and will take prey in accordance with their local availability at the territory level. Under this **Local Availability Hypothesis,** we predicted that isotopic patterns of MWCS nestling diet will match the spatial and temporal availability of insect prey on the study site, where birds nesting closer to aquatic habitat (the source of the subsidy) will provision their nestlings a greater proportion of aquatic insects (exhibit $\delta^{13}C$ enrichment) than birds nesting further away from the subsidy source.

Alternatively, birds may exhibit strong preferences for aquatic prey, and compensate behaviorally for spatial and temporal variation in its availability. Where sufficiently strong preferences exist, birds may increase search time and/or search distance for the payoff of more profitable prey. Under this alternative **Aquatic Preference Hypothesis**, we would predict there to be no relationship between a nest's distance to water and the proportion of aquatically derived diet in nestling MWCS.

Seasonality in the trophic positions of avian consumers is currently poorly understood. We therefore also examined patterns in trophic position (measured by $\delta^{15}N$ enrichment) relative to environmental variables. Over the course of a summer season, $\delta^{15}N$ is known to increase in insect tissues due to isotopic enrichment during ontogenetic shifts between life stages (Tibbets et al. 2008). Furthermore, seasonal succession in the aquatic insect community in the relative abundances of grazers/shredders (abundant in the early season) towards predators (abundant late-season) has been documented in small, intermittent streams similar to the one in this study (Beche et al. 2006, Bogan and Lytle 2007). We thus predicted that nestlings hatching later in the season will be fed a diet at a higher trophic level (enriched in $\delta^{15}N$) compared to earlier-season nestlings.

METHODS

Study Location and System

Tioga Pass Meadow is a subalpine meadow located along the boundary between Yosemite National Park and Inyo National Forest at 2,940-3,010 m elevation (Figure 3.1). It is bounded to the west by a two-lane highway, and to the east by encroaching lodgepole pine forest and Mount Dana (3,981 m elevation). One small seasonal stream bisects the meadow and drains into Tioga Lake to the north. In 2017, the April 1 snowpack at Tioga Pass was 213% of average. April 1 snowpack is generally close to the annual peak, and it is therefore a good indicator of water availability across the following summer (Morton 1994). Snow cover exceeded 50% on 1 July, and the bisecting stream flowed throughout the course of the study season. In addition to this stream and Tioga Lake, other water sources include a pond on the meadow's forested southeastern edge, ephemeral seeps from accumulated snowpack on the meadow's southern edge, and drainage from two culverts entering the meadow from the west under Tioga Pass Road. These water sources create heterogeneity in the foraging landscape of the nesting birds both by shaping the terrestrial plant community and, in the perennial supply of water, as a source of emerging aquatic insects.

Mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*) are a subspecies of migratory songbird that winters in Mexico and breeds at high elevations in the Sierra Nevada (Chilton et al. 2020). Adult white-crowned sparrows are considered granivorous but, like many songbirds, switch to almost complete insectivory when provisioning young (Morton and Morton 1987, Ricklefs 1998). Compared to their sister subspecies, *Z. l. nuttalli*, which reside year-round in the far more constant climate of coastal California, *oriantha* typically produce only one brood per year (Morton 2002). Males assume greater parental care in *oriantha* compared to *nuttalli*, and fledging success is high: on average, 94% of *oriantha* nests fledge, with 86% of those fledging all nestlings successfully (Mead and Morton 1985). The natural history, physiology, behavior and breeding ecology of the Tioga Pass Meadow population of *oriantha* has been studied extensively since 1968, making them a model system for studying the interaction of environment and foraging behavior (Morton 2002).

Nest Searching and Nestling Body Measurements

In July 2017, we searched for the nests of MWCS at Tioga Pass Meadow. We found 18 nests between 30 June and 19 July, between the hours of 0600 and 1100 following well-established protocols designed to minimize disturbance and predation risk (Martin and Geupel 1993). Upon discovery of the nest, the status, number, and stage of eggs &/or nestlings was noted. If nestlings had not hatched yet, the nest was visited every 1-2 days to determine hatch date as precisely as possible. Consistent with previous work on this population, “Day 0” or hatch date was considered to be the day the first nestling hatched (Morton 2002). Nestlings within a clutch sometimes hatch over the course of up to 3 days, so hatch date does not necessarily reflect the exact hatch date of all nestlings within the clutch in these cases. On Day 6 or 7 post-hatching, they were removed from the nest for body measurements and feather sampling for SIA.

On all nestlings, we measured mass with a Pesola scale to the nearest gram, and tarsus length (true tarsus) with calipers. Because hatching asynchrony is common in MWCS and we were not able to determine the exact hatch date and time of each individual nestling, we use the nest-level mean nestling mass for comparison with diet data.

We also took feather samples (4-5 contour feathers from the ventral side of the sparrow) from 36 white-crowned sparrow nestlings from 12 nests between 15 July and 1 August. The feathers were placed immediately in clean plastic bags and kept at constant room temperature until washing and analysis took place. We photographed each nestling before returning them to the nest. We tracked the survival of each nest every day over the course of the nestling period and documented whether the nest fledged or failed. We used the presence of parents making scolding calls and visual confirmation of fledgling provisioning as evidence of fledging success.

Insect Sampling

i. Insect abundance

We used sticky traps to collect data on the abundance and diversity of insects at Tioga Pass Meadow. Each trap was made of two 150-mm petri dish halves painted on the inside with a coat of Tanglefoot coating and mounted to a 1m yardstick stuck into the ground (Smith et al. 2014). In 2017, we sampled for insects using sticky traps along each of 3 transect lines of 3 traps each in the upper, middle, and lower meadow running east-west with the “streamside” trap (“C”) directly next to the main stream and the “forest-meadow” (“E”) and “mid-meadow” (“W”) traps placed 100 m directly east and west from the main stream, respectively (Figure 3.2). We deployed sticky traps in two rounds, one from to 15-25 July and one from 25 July–1 August. Total sampling time between the two rounds differed by 3 days.

We identified insects to the taxonomic level of Family using a dissecting scope and categorized them as Aquatic (A) or Terrestrial (T), using expert knowledge and a dichotomous key. Six out of the 502 insect specimens could not be categorized as A or T (being semiaquatic or belonging to a Family with both A and T species); these specimens were omitted from analysis. To address the possibility that differences in insect abundance between sampling rounds could be due to inconsistent sampling effort, a per-day insect count for each source type (A or T) was calculated by dividing the total number of insects by the number of days the trap was out. This assumes that traps accumulate insects in a linear fashion.

ii. Insect size

No single method of insect sampling holistically characterizes the community. In particular, sticky trap sampling can be biased against nonvolant organisms such as grasshoppers and lepidopteran larvae (Hoback et al. 1999, Kent et al. 2019). Therefore, between 18-24 July, we also conducted a single round of sweep net surveys at each sticky trap location to gather data on insect body size and to collect insects for future SIA. We randomly determined a direction for the sample by spinning the bezel of a compass for 5 seconds and reading the resulting bearing. Starting from the sticky trap, we kicked a sweep net in front of us as we walked a single 10-meter transect. All insects were identified in the field to taxonomic Order, measured lengthwise to the nearest mm, and collected for future use in stable isotope analysis. Insects were immediately placed into a sampling tray on snow in a cooler, and then transferred to a freezer upon returning from the field.

Stable Isotope Analysis

We processed nestling feathers for natural-abundance isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$). We washed all feathers by agitating them in a small jar with a 0.25% solution of detergent (Alconox powder) for 1 minute, followed by two 1-minute deionized water rinses in separate jars. We used sewing scissors and/or a razor and forceps to cut the feather into small enough pieces to fit inside a 5x8mm tin capsule. We weighed the sample to 1 +/- 0.2 mg using a microbalance at the Stable Isotope Facility at Davis, CA.

The tin-encapsulated feather samples were analyzed using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) at the UC Davis Stable Isotope Facility. Stable isotope values are reported in parts per thousand (‰ or δ) notation relative to international standards VPDB (Vienna Pee Dee

Belemnite) for carbon, and Air for nitrogen. Long-term standard deviation of the analytical procedure is 0.2 ‰ for ^{13}C and 0.3 ‰ for ^{15}N.

Statistics

i. Insect Data

We tested differences in aquatic and terrestrial insect abundance both across space (by trap location) and time (by sampling round) using an additive two-factor ANOVA. We performed two additional ANOVAs; one including a blocking variable for Site (1, 2, or 3) and the other including an interaction term between Location and Round. We compared model fit using AICc in the Rpackage 'MuMIn' and chose a final model using Akaike's Information Criterion corrected for small sample sizes (AICc). We chose the model with the greatest weight and the lowest AICc by >3 points. To further assess the differences between means between groups, we conducted a Tukey's post-hoc test for multiple comparisons of means.

In addition to overall insect abundance, we also visualized and described differences in insect community composition between sampling periods (1 and 2) and meadow locations (streamside, forest-meadow, and mid-meadow). At both taxonomic levels of Order and Family, we calculated pairwise Bray-Curtis dissimilarity of traps, which weighs dissimilarities by relative abundance (Koleff et al. 2003). We conducted a PERMANOVA to test the overall effects of sampling round and location on dissimilarity, using the *adonis2* function in the R package 'vegan' (Anderson 2017, Oksanen et al. 2019). Within each sampling round, we used a pairwise PERMANOVA to assess dissimilarity among sampling locations (C/ "streamside", E/ "forest/meadow", W/ "mid-meadow") using the R package 'pairwiseAdonis' (Martinez Arbizu 2020). We visualized these differences using the *metaMDS* function in vegan, setting k = 3. We also estimated insect diversity using Hill numbers (Chao et al. 2014). We used individual-based interpolation and extrapolation to account for differences in sample abundance using the R package ‘iNEXT’ (Hsieh et al. 2016).

We compared average body size of insects between meadow locations using a one-way ANOVA with Tukey’s post-hoc test for multiple comparisons of means. Body size was log-transformed to meet model assumptions of homoscedasticity.

ii. Nestling Data

To calculate a standardized score of body condition, we calculated the mean nestling mass for each nest on the day they were banded and subtracted the population-level mean mass of nestlings for the age they were banded. Positive scores thus represent a mean nestling mass greater than the population-level mean, and negative scores represent mean nestling mass less than the population-level mean. Population-level means by age were derived from the growth curve from the long-term dataset for this population (Morton 2002).

We investigated the relationship between diet and nestling condition at the nest level using linear models, with standardized mean nestling mass as a response variable and mean $\delta^{15}N$, mean $\delta^{13}C$, and clutch size as predictor variables.

iii. Diet Analysis with BSIMMs

We estimated the relative contributions of aquatically- and terrestrially-derived energy sources to nestling diets using Bayesian stable isotope mixing models (BSIMMS) using the R package MixSIAR (Parnell et al. 2013, Stock et al. 2018). We used the two-element, two-end-member model with terrestrial and aquatic basal resources as end members described by Post 2002, and followed published guidance on best practices for using BSIMMs in studies of trophic ecology given the constraints of my study design (Post 2002, Phillips et al. 2014). The only covariate included in the model was Nest ID as a fixed effect, as our primary goal was to estimate nest-level proportions of aquatically versus terrestrially derived diet.

In this model, isotope values for the terrestrial and aquatic basal sources (or "end members"), respectively, are needed to estimate the relative contributions of each to consumer diets. Ideally, end-member data are collected *in situ* and reflect the temporal and spatial variation relevant to the consumers in the food web. However, the collection and processing of source materials for isotope analysis can be unfeasible; in this case, proxies from the literature for similar locations/systems are used. Using a published dataset from headwater lake systems throughout the Sierra Nevada, we calculated mean $\delta^{15}N$ and $\delta^{13}C$ ± S.D. for terrestrial (terrestrial vegetation, wetland vegetation) and aquatic (submerged aquatic vegetation, littoral sediment) basal resources from a subset of sites between 3,154-3,389 m elevation— a similar elevation to Tioga Pass Meadow taking into account latitudinal differences across the mountain range (Smits et al. 2021).

The exact ratio of isotopes (e.g., 13C:12C aka $\delta^{13}C$) within the tissue of a diet item is not faithfully incorporated into the consumer's tissues. Isotopic discrimination is the process by which the heavy and light isotopes of elements are differentially incorporated into consumer tissue along trophic steps. Although $\delta^{15}N$ and $\delta^{13}C$ are generally enriched along trophic steps, the magnitude of their enrichment varies depending by element, consumer identity, consumer tissue, and on the elemental concentration of the diet items themselves (DeNiro and Epstein 1978, Deniro and Epstein 1981). Therefore, mixing models require data on the trophic discrimination factors (TDFs), that are as specific as possible to the study system to make accurate estimates of diet composition (Phillips et al. 2014).

Trophic discrimination factors for most wild animals are not described, as they involve extensive laboratory work on captive animals; thus, literature values are used in lieu of species-specific TDFs. In my model, I used TDF values of 1‰ ± 0.5‰ for δ^{13}C, and 6‰ ± 1‰ for δ15N, which are based on a study employing a similar two-end-member mixing model to estimate the diet composition and trophic position of riparian swallows (Kautza and Sullivan 2016).

Another potential source of bias in using literature-derived TDFs is the concentrations of C and N in different diet items; for example, insects are typically enriched in nitrogen relative to plant material and result in higher TDFs (Phillips and Koch 2002, Pearson et al. 2003). Concentration-dependent mixing models can accommodate diet-item-specific TDFs when consumer diets are expected to consist of both animal and plant matter. We opted against using a concentration-dependent mixing model based on personal observation and literature review indicating that the diets of white-crowned sparrow nestlings consist almost entirely of insect matter (Chilton et al. 2020).

BSIMMs can be more precise when informed by previous information on consumer diets such as stomach contents, video footage or quantitative observations of feeding, bolus capture, etc. In the absence of such data for this population, I employed uninformative priors for all models. I used 300,000 MCMC iterations with a burn-in of 200,000, and chains were thinned every 100 iterations (the “long” setting in MixSIAR’s `run_model` function). We reviewed the Gelman diagnostic criteria for sufficient chain mixing and model convergence. We considered a model adequately converged if the Gelman diagnostic for all variables was < 1.05.

We tested the relationship between diet source and 1) distance to water and 2) hatch date by extracting the nest-level posterior values for proportion of aquatically derived diet from the

BSIMM and performing two separate linear regressions on those posterior values with hatch date and distance to water as continuous variables and nest as a random effect.

iv. Trophic Position

I estimated the trophic position of each nest using the two-source equation in Post 2002:

$$TP = TL + \{\delta_c - \frac{[\delta_{b1} * \alpha + \delta_{b2} * (1 - \alpha)]}{\Delta_N}\}$$

where TP = trophic position; TL = trophic level of the basal resource (e.g., 1 for primary producers); δ_{b1}= δ^{15}N of basal resource 1 (in this case, literature-derived mean for the aquatic base); α = the proportion of consumer diet derived from basal resource 1 (in this case, mean posterior estimate from the Bayesian mixing model described above); δ_{b2}= δ^{15}N of basal resource 2 (in this case, literature-derived mean of the terrestrial base); and Δ_N = fractionation factor per trophic level (here, 3.4‰ from Post 2002).

RESULTS

Insects

Overall, insect abundance, body size, and community composition differed depending on where in the meadow the traps were set. Specifically, trap locations differed in the overall abundance of aquatic (but not terrestrial) insects captured. There were twice as many aquatic insects in the streamside (C) traps compared with either the mid-meadow (W) or forest-meadow (E) traps (ANOVA with Tukey's post-hoc test; Table 3.1, Figure 3.3). Terrestrial insect abundance did not differ significantly between trap locations, although the mid-meadow traps (W) had marginally fewer insects than those of other two locations. There was no significant difference in insect abundance of either aquatic or terrestrial insects over time, once the difference in number of days within each sampling round was taken into account (i.e., sampling round was not significant in either the Aquatic or Terrestrial ANOVA; Table 3.1). Regardless of location, terrestrial insects had greater mean abundances in traps than did aquatic insects.

Insect community composition at both the Family and Order levels differed by sampling round and by location (Figure 3.5, Table 3.4; only Family-level analyses shown). All contrasts were significant, meaning that community composition varied significantly across all sites and sampling rounds (Pairwise PERMANOVA, Table 3.4). The most abundant Order across all sampling locations and rounds was Diptera, mostly represented by terrestrial dipterans from the families Sciaridae (fungus gnats) and Phoridae (small hump-backed flies) (Table 3.3). Both taxa declined in abundance in Round 2. The most common taxa that increased in abundance between rounds were dipterans Mycetophilidae (another type of fungus gnat) and Scathophagidae (dung flies), hymenopteran Ichneumonidae (Ichneumon wasps), and to a lesser extent lepidopteran Pterophoridae (a type of moth) and neuropteran Hemerobiidae (lacewings) (Table 3). All aquatic taxa decreased between sampling rounds, except caddisfly Family Phryganeidae (Order Trichoptera) staying constant in number (Table 3.3). In Round 1, the most abundant aquatic taxon was Chironomidae, the non-biting midges (Order Diptera).

Mean body size of insects was greater at the streamside (C) and mid-meadow (W) locations compared to the forest-meadow (E) location (ANOVA with Tukey's post-hoc test; Table 3.2, Figure 3.4).

Individual-based species accumulation plots indicate that insect diversity at the Family and Order levels were adequately sampled using sticky traps, with only rare insect Families continuing to accumulate with the addition of new individuals (Figures 3.S1 & 3.S2).

Nestling Diet

Nests were generally isotopically distinct, revealing nest-level variation in diet across both C and N isotopes as well as in dietary breadth (Figure 3.6). Visual inspection of the isospace plot validated that the source values used for analysis adequately covered the dietary breadth of MWCS nestlings, because the nestling biplot values fell within the isospace of the source values (Figure 3.7).

Model-derived posterior means of the proportion of the diet derived from aquatic pathways ranged from 0.50 to 0.82 (global mean = 0.697), suggesting an overall strong reliance on diet items derived from the aquatic food web (Figure 3.8). The 2.5% and 95% Bayesian credible intervals around the posterior means ranged between 0.07 and 0.94, which indicate considerable uncertainty in these estimates, likely due to the use of literature-derived values for basal resources, which are not specific to the study location and represent greater variability in isotopic signatures.

Nests varied in the proportion of aquatically derived food in their diets (Figure 3.6). There was no relationship between diet and distance to water (Table 3.5; Figure 3.8). However, there was a negative relationship between proportion of diet aquatically derived and hatch date ($ß = -0.068 \pm 0.035$; $p< 0.01$; Table 3.5; Figure 3.9), with chicks hatching later receiving less aquatically derived food.

The mean trophic position of nests also declined with hatch date, with the earliest-hatching nest (July 8) being provisioned a diet greater than half a trophic level higher than the latest-hatching nest (July 26) ($ß = -0.03 \pm 0.01$; $p = 0.002$; Table 3.6; Figure 3.10).

Nestling Condition

We did not detect any significant correlations between either trophic position or diet source on nestling condition (Table 3.7, Figure 3.11).

DISCUSSION

Our insect data from both sticky traps and sweep net samples demonstrate that the insect community available as prey for MWCS varied spatially and temporally. Consistent with our hypotheses and previous studies about the horizontal reach of aquatic insect availability into adjacent terrestrial habitat (Muehlbauer et al. 2014, Schindler and Smits 2017, Schilke et al. 2020), insects of aquatic origin were more likely to be found at the sampling locations next to the main tributary stream bisecting the meadow than at any other location. Overall abundance of terrestrial insects did not vary spatially or between sampling rounds, but in general were more abundant than aquatic insects. Insect community composition did also vary across both space and time, laying a mosaic of potential prey availability for MWCS consumers during their breeding season.

Temporal trends in nestling diet

We present evidence that the diet of this population of MWCS nestlings varies within the temporal span of a single breeding season, with nestlings that hatch later in the season being provisioned a diet lower in aquatic origin and at a lower trophic level than nestlings hatching earlier in the season.

The difference in mean trophic level over the span of 3 weeks was roughly one-half of a step. This could be explained in two ways: first, adult MWCS could be selecting the same diet items over the course of the season, but those items themselves are becoming depleted in N over time. This is unlikely, given that adult stages of insects should enrich in $\delta^{15}N$ over the season, resulting in the opposite pattern (Tibbets et al. 2008). Second, and more likely, the pattern may be a result of nestlings being fed diet items from a lower trophic level later in the season. Very few studies have investigated whether and how avian trophic position changes over the course of the season. However, one unpublished study of gray-crowned rosy-finch diet using SIA also documented a seasonal decrease in nestling trophic position (Epanchin 2009). The author suggested that a late-season switch in prey away from lowland insects deposited on snow from aeolian processes, which are enriched in $\delta^{15}N$ due to crop fertilizers used at their origin, and toward mayflies (aquatic insects that are non-consumers as adults), could explain this apparent drop in trophic position. Contrary to Epanchin's findings on rosy-finches, we documented a shift in diet origin over the course of the season *away from*, rather than *toward*, aquatically derived prey. However, MWCS nestlings in our study may similarly be experiencing a switch in prey to insects of a lower trophic level. Insect sampling at a finer temporal scale, as well as SIA on likely diet items, would allow us to build a BSIMM with specific diet items instead of basal resources as end members, and shed light on what diet shifts might explain a drop in trophic position late in the season.

We document a negative relationship between reliance on the aquatic pathway and hatch date, indicating that earlier-season MWCS nestlings were fed an aquatically enriched diet relative to nestlings later in the season. Our result is consistent with other recent studies on the use of an aquatic prey subsidy both as provisioning material for nestlings and in adult diet of several bird species (Dodson et al. 2016, Jackson et al. 2020, 2021).

The implications of these two seasonal trends—a shift away from aquatically derived prey and a drop in trophic position—are unclear with respect to the success of MWCS nests. We did not detect any statistically significant relationships between nestling condition and either trophic position or dietary source. However, with a sample size of only 12 nests and some uncertainty about each nestling's exact age, we may simply lack the statistical power here to detect an effect. An ample literature describes seasonal declines in nesting success across many bird species, usually describing negative trends in clutch size, nestling size, survival, and recruitment to the breeding population the following year (Van Noordwijk et al. 1995, Both et al. 1999, Thomas et al. 2001). These studies often implicate a decline in prey abundance as the driver of reduced reproductive success in late- compared to early-season, but none directly link trophic position or aquatic reliance with seasonal declines in reproductive success. Below we review what is known about those links.

Many studies have documented positive effects of aquatic subsidies on the body condition of terrestrial consumers such as lizards and warblers, specifically on growth rate (Sabo and Power 2002, Wright et al. 2013, Dodson et al. 2016). The biochemical mechanisms for this nutritional benefit are beginning to be explored in wild animal populations. There is evidence that a diet high in aquatically-derived polyunsaturated fatty acids (PUFA) is positively correlated with growth rate and body condition in two common riparian birds, the Eastern phoebe (*Sayornis phoebe*) and the tree swallow (*Tachicineta bicolor*), in both laboratory-based diet studies and in wild populations (Twining et al. 2016, 2018, 2019). These fatty acids are essential for development and cell function, and are highly concentrated in aquatic insects but undetectable in most terrestrial ones because they originate in algae (Hanson et al. 1985, Hixson et al. 2015, Twining et al. 2018).

Birds can obtain PUFAs either behaviorally through foraging on PUFA-rich aquatic prey, or by internally synthesizing PUFAs from precursor short-chain fatty acids abundant in terrestrial food webs (Twining et al. 2021a). However, animals differ by foraging strategy in their efficiency in synthesizing PUFA: the expression of genes controlling these biochemical pathways appears to be suppressed or lost in groups that evolved in habitats naturally abundant in aquatic prey, suggesting that dietary reliance on aquatic prey for PUFA may be more important for riparian and water-associated species than for upland, dryland, or generalist species that have retained efficiency in these biomechanical pathways. Twining et al. (2021*b*) found that a population of blue tits (*Cyanistes caeruleus*), which are generalists, did not vary aquatic prey intake with the distance of their nests to water, and that nestlings were able to synthesize the PUFA they need from the precursors found in the terrestrial prey they were provisioned (Twining et al. 2021b). White-crowned sparrows are similar to blue tits in their generalist dietary habits, so the lack of strong aquatic signature across space may be explained by a weak energetic need for aquatically sourced PUFA. Alternatively, it could suggest support for the Aquatic Preference Hypothesis, which predicted that nests would not differ in proportion of aquatic pretty in the diet relative to distance, because adults nesting farther away from water will incur the cost of increased travel in order to provision their young with aquatic prey. Investigation into whether WCSP can synthesize PUFA from precursor materials would help disentangle these two possibilities, with significantly different implications regarding MWCS' reliance on aquatic resource pulses.

Comparatively very little work has been done on the direct links between diet trophic position and correlates of fitness. Some work on this has been done in marine systems, but data are lacking for terrestrial and freshwater systems. In a seabird system, consumption of high-trophic-level prey (anchovies), combined with high diet diversity (the presence of alternative prey), was correlated with high reproductive success in little penguins (*Eudyptula minor*) (Kowalczyk et al. 2014). However, the data on the relationship between prey trophic level and diet quality is mixed; others have found that historic shifts in prey trophic position in penguins (eating more zooplankton-based diet versus a fish-based diet) did not correlate with mass in adult rockhopper penguins (*Eudyptes chrysocome*) (Morrison et al. 2014). One study on tree swallows (*Tachicineta bicolor*) reported no link between variation in δ^{15}N and correlates of nestling body condition, but this study was done in an agricultural system, where nitrate-rich agricultural runoff alters the isotopic enrichment δ^{15}N independent of trophic position, thus complicating inferences about trophic position (Moore et al. 2014). A study on wood thrush (*Hylocichla mustelina*) diet in the Eastern US reported that adults and nestlings associated with nests *without* brood parasitism by Brown-headed cowbirds (*Molothrus ater*) were enriched in both δ^{15}N and δ^{13}C relative to parasitized nests. Enrichment of δ^{15}N was attributable to a high proportion of spiders in the diet, a preferred prey item for wood thrushes. The authors concluded that, in parasitized nests, cowbird chicks outcompeted wood thrush nestlings for their preferred prey (protein- and calcium-rich spiders), resulting in a wood thrush diet lower in trophic position compared with nestlings in unparasitized nests (Ladin et al. 2015). In cases where trophic position of prey correlates with abundance of key nutrients (protein, calcium) in their tissues, a drop in trophic level of a consumer may be indicative of increased nutritional stress and have ramifications on nestling development consistent with the nutritional stress hypothesis (Nowicki et al. 2002). However, it is unclear whether trophic level alone is a reliable indicator of nutritional quality or value; this likely depends on the consumer's needs, niche, and foraging strategy.

Spatial patterns in nestling diet

Contrary to the predictions of our resource limitation hypothesis, we did not detect an increased aquatic signature in nests close to the tributary stream (or any source of water), regardless of the evidence that aquatic insects were in higher abundance at streamside locations. This suggests that MWCS at Tioga Pass Meadow are not taking prey in proportion to their availability, as was documented in other studies of riparian subsidy on avian diet (Dodson et al. 2016). This could be explained by a homogenous level of preference for aquatic prey across the population. Combined with model estimates of population-level reliance on aquatic prey >50%, this result suggests support for the Aquatic Preference Hypothesis. However, while the nest farthest away from the stream was 163m away, but most nests were within 50m of the stream. Color-banded MWCS adults with known nest locations were routinely spotted at distances greater than 100m from their nests, suggesting that the range in distances from the stream we sampled is not great enough to detect an effect of water. If aquatic prey are desirable diet items for sparrows, differences in flight distances up to ~150 meters may be trivial for foraging sparrows feeding young. Future work could specifically increase nest-searching efforts to places much farther away from water sources: this would better describe the nesting niche of MWCS relative to water, as well as give us the potential to test our hypotheses regarding diet and distance to water more robustly.

The lack of relationship between reliance on aquatically derived diet and distance to water could also reflect an ability of parents to behaviorally offset prey availability to meet the energetic and nutritional needs of their nestlings with greater foraging effort. Indeed, the primacy of maintaining nestling body condition despite environmental stress or food limitation appears to have shaped the evolution of parental care in some passerines: adults trade off their own body condition (mass, stress physiology) to maintain provisioning rates in food-scarce landscapes to maximize the survival probability of their nestlings. For example, when preferred prey are scarce during the breeding season, adult spotted flycatchers (*Muscicapa striata*) have been documented to prioritize the energetic value of the diets of their nestlings over their own, consuming less profitable prey themselves while provisioning their young the preferred prey in order to keep nestling body condition constant (Davies 1977). Similarly, blue tit adults nesting in territories where their preferred prey, caterpillars, are scarce, increase foraging distance and search time to provision nestlings with large caterpillars in order to optimize nestling diet (Tremblay et al. 2004). These examples suggest an exquisite ability of adult birds to respond behaviorally to variation in prey abundance with little detriment to nestling quality. However, this offset is likely to hold only to a certain threshold of food limitation, after which point the energetic costs would exceed the energy available and reproductive success would suffer. The abundant literature on the consequences of food limitation on reproductive success and survival illustrate this point (see Introduction).

The timing of reproductive events relative to local phenology is also likely to account for unexplained variation in diet composition. The prediction that reliance on aquatic prey declines with distance to subsidy may still be expected in “average” water years, when birds are theoretically optimally poised to nest relative to environmental conditions. However, these relationships may change in very wet or very dry years. In wet conditions (more snowpack, later snowmelt), we expect aquatic insect emergence to be delayed relative to normal years, but more abundant and diverse overall due to habitat persistence through the late summer (Finn and Poff 2008). In dry, warm conditions, aquatic insects adapted to cold flow emerge earlier, in fewer numbers, and smaller than in normal to wet years (Harper and Peckarsky 2006, Giersch et al. 2017, Hotaling et al. 2017). As a result, we hypothesize that the population mean reliance on aquatically sourced prey would be lower in dry years relative to normal years, but potentially that the slope of the relationship between distance to water and amount of aquatically derived diet would be steeper, with only the closest nests to water being able to provision nestlings with aquatic prey.

Future Directions for Study

We must also make some caveats about the uncertainty presented by our BSIMMS in this study. Because isotopic signatures of basal resources vary widely across time and space, and because herbivores and primary consumers (the diet items of the sparrows, in most cases) differ in which basal resources they use, a two-end-member model without in-situ sources such as the one presented here is still fraught with a great deal of uncertainty in its estimates of MWCS diet. Source samples specific to our study site and/or isotopic analysis of likely prey items for MWCS in this meadow, would improve estimates. Augmenting the models with informative priors on likely diet items using cameras at nests, for example, would also decrease uncertainty (Robinson et al. 2018, Swan et al. 2020). Other studies have had success complementing stable isotope analysis with DNA metabarcoding of source and/or prey items to make more holistic estimates of diet contributions (Soininen et al. 2014, Compson et al. 2019, Whitaker et al. 2019). This approach would likely cost more than traditional or camera surveys but would undoubtedly improve the inferential power of the BSIMMs. However, regardless of which TDFs and basal resource values were used in the mixing models, the general patterns we uncovered—of lower δ13C and δ15N relative to hatch date—were consistent across all models, even if their absolute estimates differed substantially.

Conclusions

Taken together, the results of this study demonstrate that MWCS display behavioral flexibility in diet in response to variable environmental conditions within a season without major impacts to measures of reproductive success, such as nestling body condition. We focused on a common generalist species as a model for how animals may successfully navigate environmental variability and find evidence that they are able to do so successfully. However, we also review evidence from other studies that suggest this ability may vary with foraging strategy and evolutionary history. The strategies of MWCS are unlikely to represent all alpine-associated bird species. Future work could investigate the diets of bird species from multiple foraging guilds for a more holistic understanding of how bird communities respond to environmental variability in resource availability.

We build important links between environmental variation and prey assimilation into the diets of wild animals in a highly dynamic system. With this study, we also begin to answer recent calls for more research that investigates how aquatic-terrestrial connectivity differs in different biomes (Burdon 2021). This study took place during an extraordinarily wet season where snowpack was 213% of normal, and lays the groundwork for future study over different seasons to complement the 50+ years of data that have already been collected on this population. Work that more intensively samples insect prey, characterizes changes in diet over multiple seasons, and tracks measures of fitness (nestling quality, fledging success and survival to independence) could help build mechanistic understanding of how one widely-distributed species responds to the environmental uncertainty we can expect to accompany our changing climate.

The role of aquatic subsidies in a changing climate

Early hypotheses of the impacts of projected climate change scenarios on montane birds predicted that many species' ranges would shrink as they track their niche upward (Tingley et al. 2009). Recent studies have revealed a more heterogeneous response to climate, with more nuanced predictions about how niche space for birds has and will continue to change (Tingley et al. 2012, Elsen and Tingley 2015, Socolar et al. 2017). A few long-term datasets from the Sierra Nevada and the Great Basin have found that warmer, drier breeding seasons result in constant or greater productivity and population estimates for some bird species (Saracco et al. 2019; DeSante and Saracco 2021, Zillig et al. in prep). This could potentially result from thermally driven increases in insect prey activity and abundance. However, the effects of future climate conditions on birds are likely to be variable. For MWCS in particular, a negative correlation was found between spring temperature and both fledging success and population size across a 32-year study period for a population of MWCS only a few kilometers from the TPM study area (DeSante and Saracco 2021). Warmer temperatures may increase the density of major nest predators like Belding’s ground squirrels, which may offset whatever benefits MWCS accrue from greater insect prey densities (Morton et al. 1993).

Thus, while correlations between abiotic factors (e.g., temperature and precipitation) and avian productivity have laid a strong foundation for predicting bird responses to climate change, integrating biotic interactions into our work will help us explain these heterogenous shifts and more effectively manage climate-sensitive species and ecosystems. A recent study employing a large set of Breeding Bird Survey data found that life history is an important predictor of a bird species’ sensitivity to climate-driven phenological advancement of green-up. Their results suggest that species that migrate early, more slowly, and/or migrate a shorter distance, are better able to track the onset of spring than others (Youngflesh et al. 2021). Complementing large-scale studies like this with in-depth studies of the mechanistic drivers of these mismatches (such as food availability and diet composition) will strengthen our understanding of how birds respond to climate change.

While positive correlations between dry conditions and bird productivity have been documented in the short-term, at longer time scales, extensive periods of drought may impact bird populations differently by restructuring the food web from the bottom-up. Headwater aquatic insect communities are generally fairly resistant to interannual variability in water flow, but multi-year drought conditions erode the resilience of these communities, resulting in community turnover (favoring stress-tolerant species and seeing declines in large-bodied clinger and swimmer taxa) and loss of species diversity largely due to drying-caused habitat fractionation and increasing volatility of interannual snow conditions (Bogan et al. 2015, Herbst et al. 2019). There appears to be a nonlinear response to drought, where richness and abundance will sharply decline after a certain amount of decline in flow—this puts small, intermittent and headwater streams, such as the one in this meadow, at greatest position of change.

A 30-year multi-species study of avian demography found strong evidence that increasingly earlier snowmelt and warmer springs may lead to more diverse breeding bird communities and higher breeding bird densities in subalpine habitat, probably driven by recruitment of lower-elevation species into the upper edge of their species range (DeSante and Saracco 2021). If breeding bird communities become denser and more diverse at higher elevations, while aquatic insect communities become less abundant due to drier headwaters, food resources for birds during the breeding season may become a limiting resource and engender novel competitive dynamics (Jankowski et al. 2010, Urban et al. 2012). We posit that the strength and composition of the aquatic subsidy is likely to play a large role in the productivity of an increasingly diverse and dense avian community into our warmer, drier future.

Meadows are early-successional habitat, a transitional state between lake beds and forest mediated by groundwater (Rundel and Millar 2016). Meadow cover in the Sierra Nevada has decreased in the past century due to a combination of fire suppression and long-term increases in minimum temperature (Millar et al. 2004). The proportion of current meadow habitat projected to remain into the next century is likely to decline drastically (between 0.5-<0.1, depending on the climate variables taken into consideration), with only the most highly connected meadows remaining (Maher et al. 2017). Alpine and subalpine meadows have thus been identified as a top priority in recent work on prioritizing the identification and management of climate refugia for habitats of ecological and cultural importance (Balantic et al. 2021). Prior to European settlement of the Sierra Nevada, the Southern Sierra Miwok and Northern Mono/Paiute people actively managed meadows by burning to slow succession and promote the growth of plants important for food and basketry materials, as well as to maintain habitat for bear, deer, and other animals (Anderson 2005). Reviving the land management practices of native people in meadow areas could be one way to buffer the impacts of a changing climate on ecologically important landscapes, while also supporting native people in the regrowth of their cultural practices and nurturing a more sustainable land stewardship ethic focused on connection and reciprocity.

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CHAPTER 3 TABLES

Table 3.1. Terrestrial and aquatic insect abundance from sticky traps in Tioga Pass Meadow differs among sampling locations (E = east/forest-meadow, W = west/mid-meadow, C = central/streamside) but not between sampling period (1 = 15-25 July; 2 = 25 July-1 Aug), according to a Tukey's post-hoc comparison of multiple (with 95% confidence intervals).

Terrestrial

Term	**Contrast**	**Estimate**	**Conf. Low**	**Conf.High**	**P (adj.)**
Sampling Period		-0.600	-3.985	2.785	0.710
Location	*E-C*	1.674	-3.385	6.733	0.670
	W-C	-3.233	-8.292	1.826	0.250
	W-E	-4.907	-9.966	0.152	**0.058**

Aquatic

Term	**Contrast**	**Estimate**	**Conf. Low**	**Conf.High**	**P (adj.)**
Sampling Period		-0.387	-1.042	0.268	0.225
Location	*E-C*	-1.386	-2.365	-0.407	**0.006**
	W-C	-1.726	-2.705	-0.747	**0.001**
	W-E	-0.340	-1.319	0.638	0.643

Table 3.2. a) ANOVA and b) Tukey’s post-hoc comparison of multiple means of insect body size among different meadow locations**.** Insect body size was log-transformed to meet model assumptions of homoscedasticity.

a) ANOVA Summary (formula = log(body size) ~ Location)

Term	**df**	**Sum Sq.**	**Mean Sq**	**F statistic**	**P**
Location	2	5.18824971	2.59412486	15.5264673	**8.05E-07**
Residuals	141	23.5579413	0.1670776		

b) Tukey’s post-hoc comparisons of multiple means of insect body size among different meadow locations, with 95% confidence intervals.

Term	**Contrast**	**Est. Difference**	**Conf. Low**	**Conf. High**	**P (adjusted)**
Location	forest-meadow: streamside	-0.39092	-0.60071	-0.18112	**0.00006**
	mid-meadow: streamside	-0.00050	-0.26165	0.26066	0.99999
	mid-meadow: forest-meadow	0.39042	0.17769	0.60315	**0.00008**

Table 3.3. Insect Orders and Families represented in sticky trap collections by Round, including the difference in individuals caught between sampling rounds (positive numbers represent Families that increased in abundance on the sticky traps from Round 1 to Round 2. “Source” refers to A (Aquatic), T (Terrestrial), or U (Unknown).

Order	Family	Source	Round 1 (n)	Round 2 (n)	Difference
Coleoptera	Cerambycidae	T	21	30	9
Coleoptera	Tenebrionidae	T	8	0	-8
Diptera	Cecidomyiidae	T	103	0	-103
Diptera	Chironomidae	A	66	29	-37
Diptera	Dolichopodidae	T	52	18	-34
Diptera	Muscidae	T	28	0	-28
Diptera	Mycetophilidae	T	9	60	51
Diptera	Phoridae	T	169	52	-117
Diptera	Rhagionidae	T	7	6	-1
Diptera	Scathophagidae	T	46	76	30
Diptera	Sciaridae	T	265	205	-60
Diptera	Tabanidae	T	6	0	-6
Diptera	Tipulidae	A	9	0	-9
Hemiptera	Delphacidae	T	86	44	-42
Hemiptera	Psyllidae	T	119	58	-61
Hymenoptera	Braconidae	T	17	6	-11
Hymenoptera	Ceraphronidae	T	0	8	8
Hymenoptera	Encyrtidae	T	0	7	7
Hymenoptera	Ichneumonidae	T	72	104	32
Hymenoptera	Pteromalidae	T	10	0	-10
Hymenoptera	Tenthredinidae	T	47	34	-13
Lepidoptera	Pterophoridae	T	6	14	8
Neuroptera	Hemerobiidae	T	0	9	9
Plecoptera	Nemouridae	A	18	0	-18
Thysanoptera	Phlaeothripidae	T	86	34	-52
Trichoptera	Phryganeidae	A	14	15	1

Table 3.4. PERMANOVA results based on Bray-Curtis dissimilarities using abundance data of insects at Tioga Pass Meadow. Insect community composition differs by (a) Round and (b, c) Location within Round. See Figure 5 for a visualization of community composition using NMDS.

a) PERMANOVA, all data					
Term	**df**	**SumOfSqs**	**R^2**	**F-stat**	**p.value**
Round	1	0.656	0.108	4.888	**0.001**
Location	2	1.113	0.183	4.144	**0.001**
Residual	32	4.296	0.708		
Total	35	6.064	1.000		
b) Pairwise PERMANOVA, Round 1					
Term	**df**	**SumOfSqs**	**R^2**	**Pseudo-F**	**p.value**
C vs E (Round 1)					
Location	1	0.559	0.331	4.940	**0.004**
Residual	10	1.131	0.669		
Total	11	1.690	1.000		
C vs W (Round 1)					
Location	1	0.449	0.231	2.997	**0.006**
Residual	10	1.500	0.769		
Total	11	1.949	1.000		
E vs W (Round 1)					
Location	1	0.203	0.149	1.749	**0.035**
Residual	10	1.163	0.851		
Total	11	1.366	1.000		
c) Pairwise PERMANOVA, Round 2					
Term	**df**	**SumOfSqs**	**R^2**	**Pseudo-F**	**p.value**
C vs E (Round 2)					
Location	1	0.349	0.272	3.745	**0.006**
Residual	10	0.932	0.728		
Total	11	1.281	1.000		
C vs W (Round 2)					

Location	1	0.510	0.250	3.333	**0.007**
Residual	10	1.531	0.750		
Total	11	2.041	1.000		
E vs W (Round 2)					
Location	1	0.329	0.205	2.585	**0.006**
Residual	10	1.271	0.795		
Total	11	1.600	1.000		

Table 3.5. Output for linear models predicting posterior estimates of proportion of aquatically derived diet with hatch day and distance to water, respectively. The effect of hatch day is significantly negative (later-hatching nests were provisioned less aquatically derived diets). We did not detect an effect of the distance to water. Nest ID is included as a random effect in both models.

	Hatch Day Model	***Water Model***
(Intercept)	0.76	0.76
[CI]	[0.720, 0.800]	[0.694, 0.826]
Hatch Day	**-0.08**	
[Hatch Day CI]	[-0.123, -0.044]	
Dist. to Water		0.00
[Dist. to Water CI]		[-0.069, 0.062]
N	36000	36000
N (nests)	12	12
AIC	-27684.40	-27674.46
BIC	-27650.43	-27640.49
R2 (fixed)	0.18	0.00
R2 (total)	0.31	0.33

Table 3.6. Hatch date is negatively related to trophic position in MWCS nestlings.

	Trophic Position			
Predictors	*Estimate*	*SE*	*95% CI*	*p*
(Intercept)	8.42	1.67	4.64 – 12.19	**0.001**
hatchday	-0.03	0.01	-0.05 – -0.01	**0.004**
clutchsize	0.05	0.08	-0.13 – 0.24	0.523
Observations	12			
R^2 / R^2 adjusted	0.657 / 0.581			

Table 3.7. Results of a linear model predicting standardized mean nestling mass in MWCS, predicted by C and N isotopes, and accounting for clutch size. Average standardized nestling mass is not significantly related to either d13C or d15N.

	Standardized Mean Nestling Mass			
Predictors	*Estimate*	*SE*	*95% CI*	*p*
(Intercept)	44.19	38.42	-46.66 – 135.04	0.288
mean_d13C	1.89	1.56	-1.79 – 5.57	0.263
mean_d15N	0.40	1.01	-1.98 – 2.78	0.703
clutchsize	-0.96	1.31	-4.05 – 2.13	0.485
Observations	11			
R^2 / R^2 adjusted	0.233 / -0.096			

CHAPTER 3 FIGURES

Figure 3.1. Tioga Pass Meadow**,** looking north from the Yosemite National Park Boundary towards Tioga Peak on July 21, 2017. Photo M. Clapp

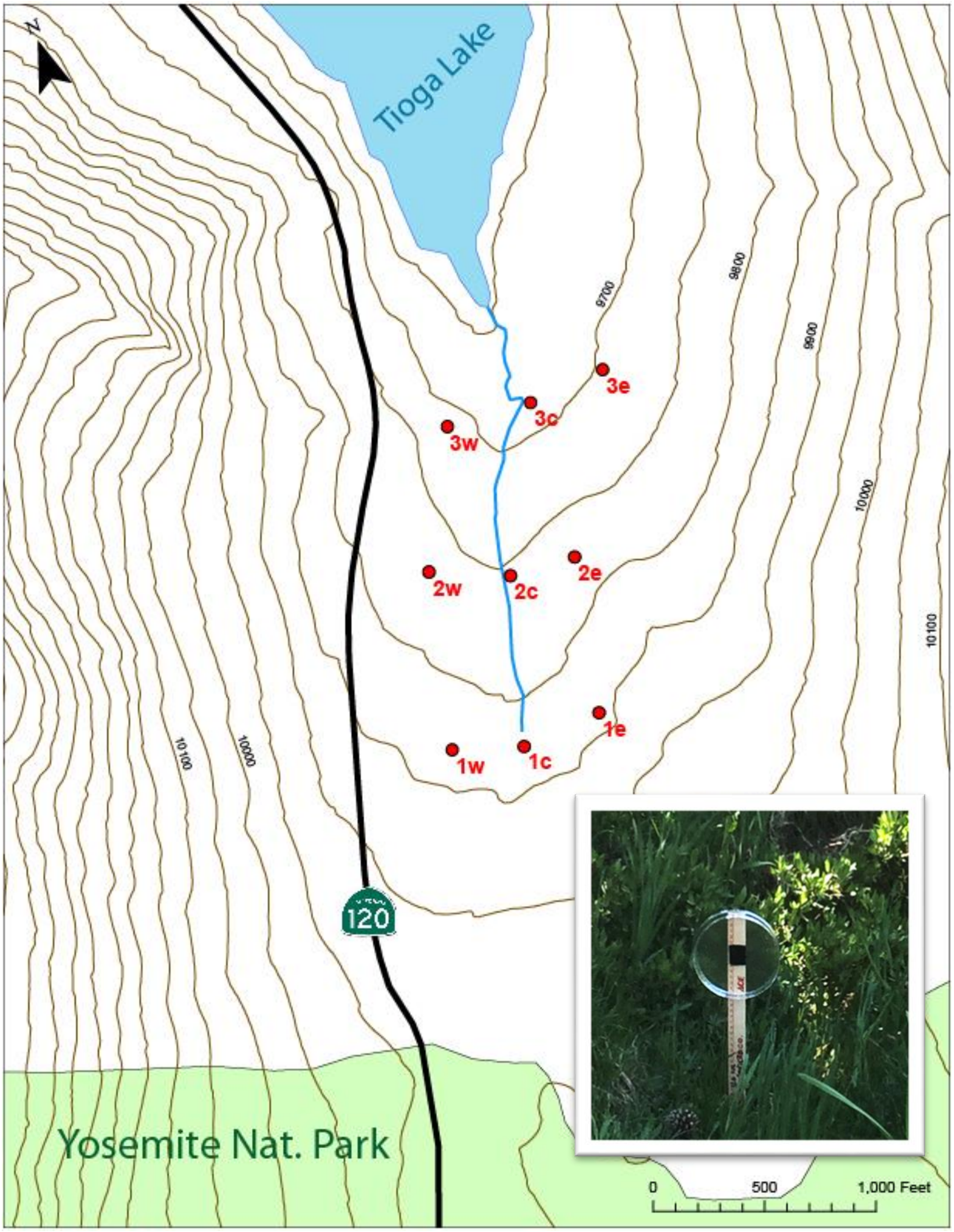

Figure 3.2. Spatial organization of insect sampling protocol at Tioga Pass Meadow**.** Traplines 1-3 are placed 250m apart, beginning with the "C" (streamside) trap. The E and W traps labeled "W" fell within typical meadow habitat (forbs, grasses, and shrubs). Traps labeled C were placed directly adjacent to the tributary stream. "E" traps fell within the encroaching lodgepole pine forest cline. One sweep net survey was also performed at each trap. Inset photo depicts one sticky trap. Map by R. DiPaolo, photo by M. Clapp.

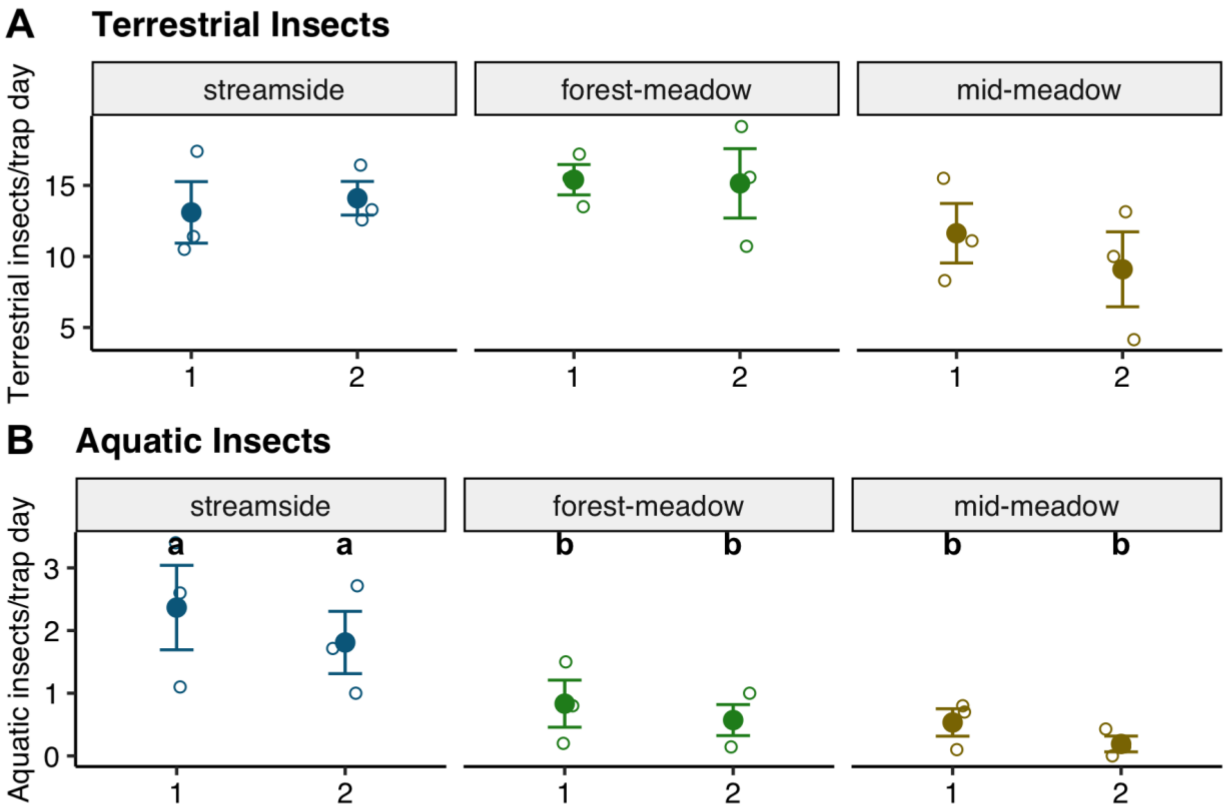

Figure 3.3. Insect abundance in Tioga Pass Meadow by (A) terrestrial and (B) aquatic origin, sticky trap location (streamside, in the forest-meadow cline, and mid-meadow), and sampling period (1 = 15-25 July; 2 = 25 July-1 Aug). There is no significant difference in terrestrial insect abundance between trap locations or rounds. The streamside traps contained significantly more aquatic insects than did the other two groups, but did not differ by sampling round.

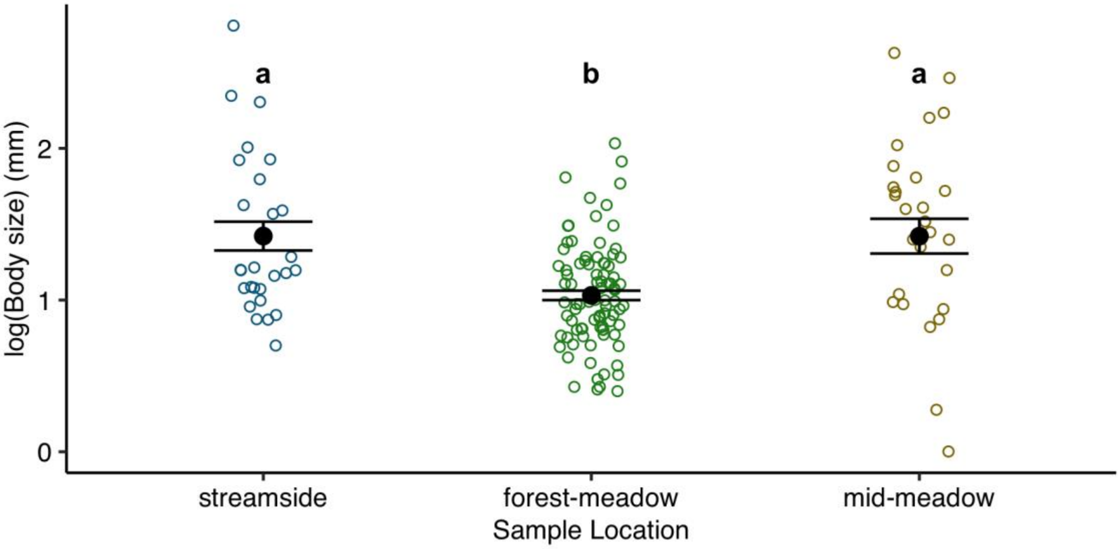

Figure 3.4. Mean body size of insects differs among sampling locations, based on sweep-net samples. We captured smaller-sized insects in the forest-meadow ecotone (n=89 insects), compared with the streamside (n=28) and mid-meadow (n=27) microhabitats.

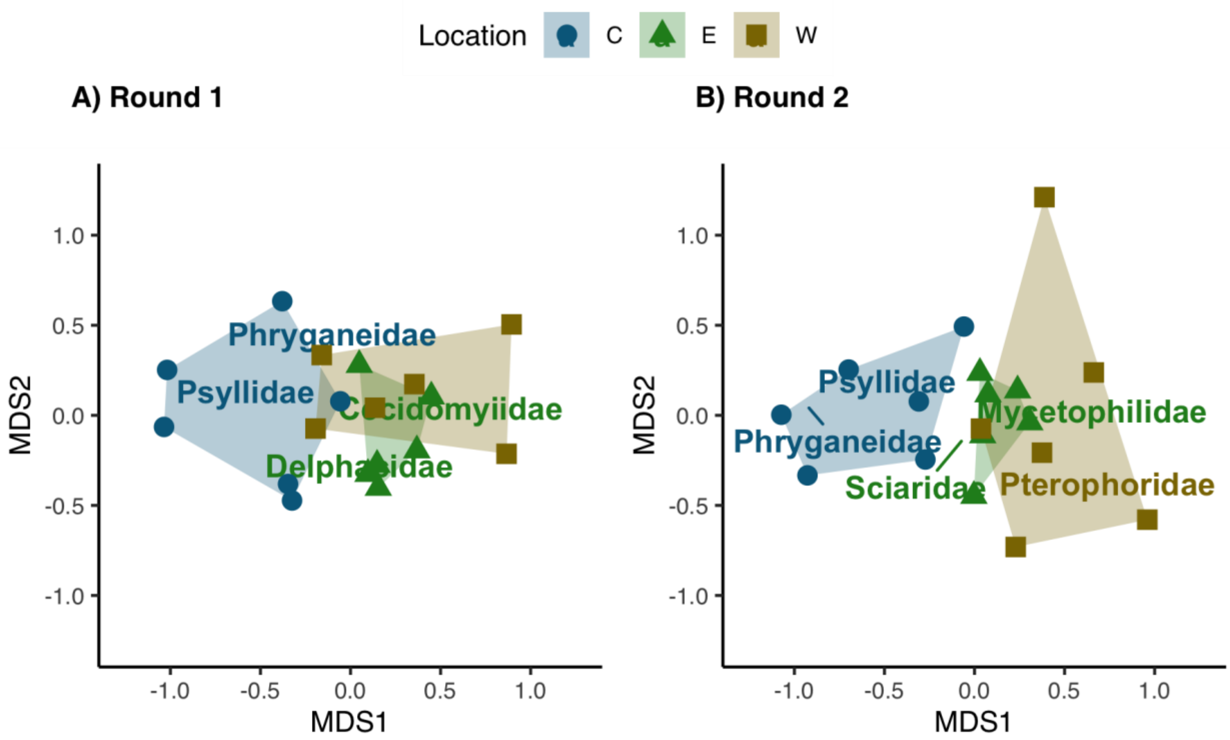

Figure 3.5. NMDS visualization of insect community composition as captured by sticky traps indicates differences by trap location (colors) and by sampling round (panels A and B). Bolded taxonomic family groups represent families that are significantly (alpha = 0.05) correlated with each sampling location as defined by the correlation index r.g (De Caceres and Legendre 2009). Many more families were present but are not represented here for legibility. Differences between groups and sampling rounds are summarized in a PERMANOVA (Table 3).

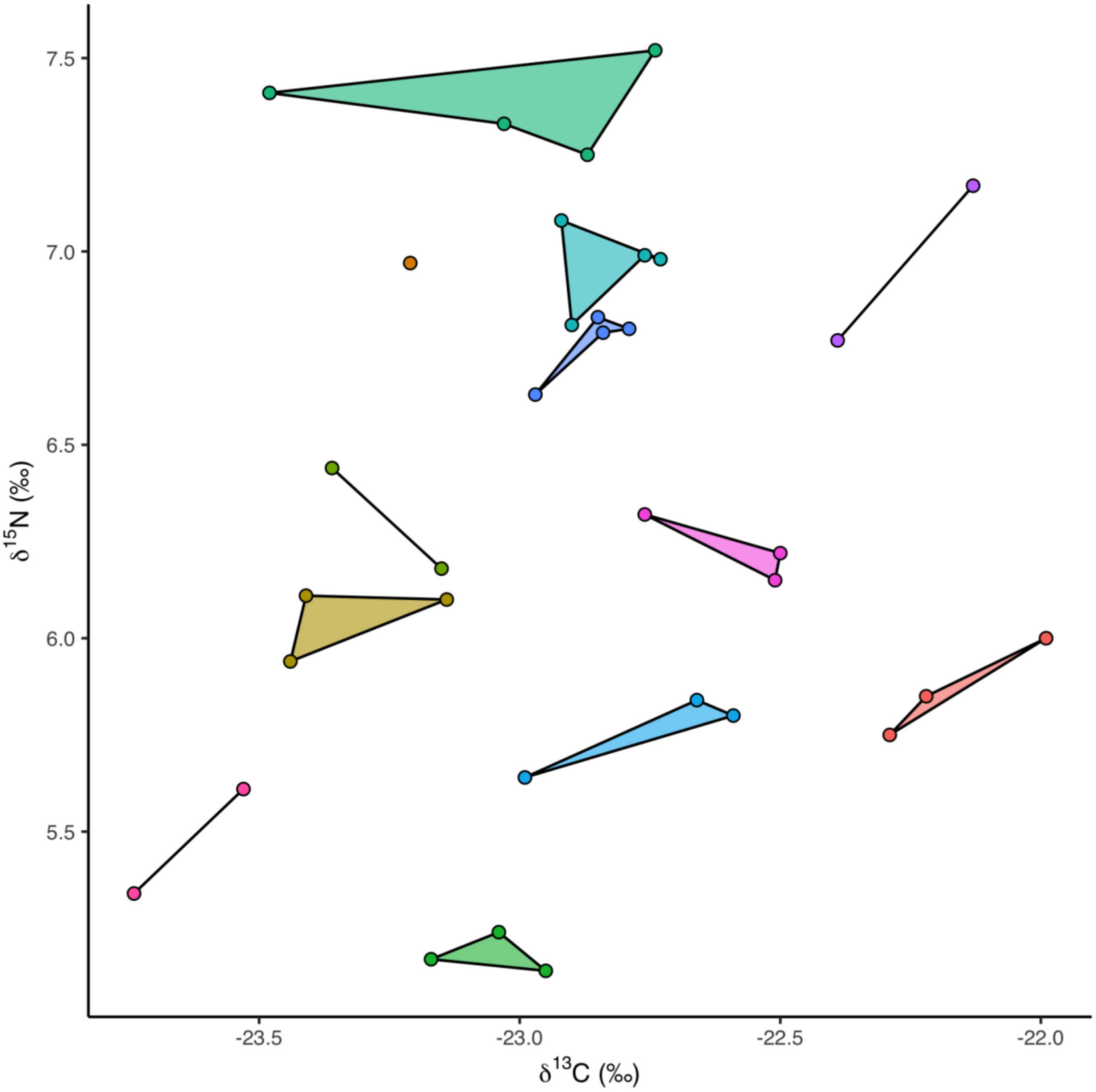

Figure 3.6. Two-source (carbon-nitrogen) stable isotope biplot for individual nestlings (feathers) grouped by nest (colored polygons). Nests vary in dietary breadth, but not significantly by any explanatory variable measured in this study. Less negative values of δ^{13}C indicate greater reliance on a diet derived from the aquatic food web; greater values of δ^{15}N indicate a higher trophic position of the consumer.

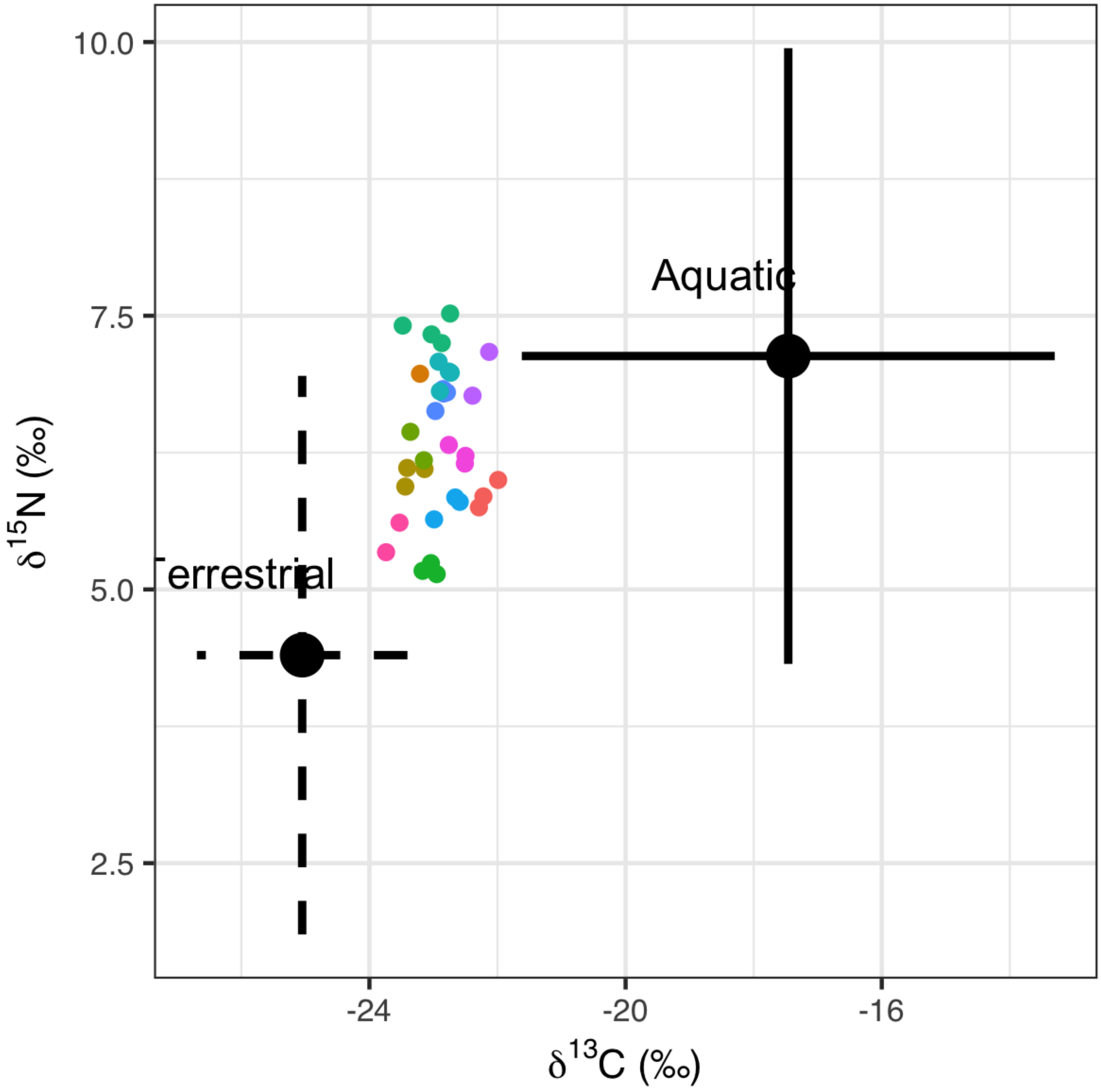

Figure 3.7. Isospace plot for stable isotopes of C and N in MWCS nestling feathers (each dot representing 1 nestling colored by nest). Means +/- SD of basal resources are corrected for trophic discrimination factors (TDFs) (see methods). Visual inspection of this plot confirms that the consumer data fall within the geometric space of the (TDF-corrected) basal resource data and thus represent both adequate isotopic coverage and separation of dietary origin.

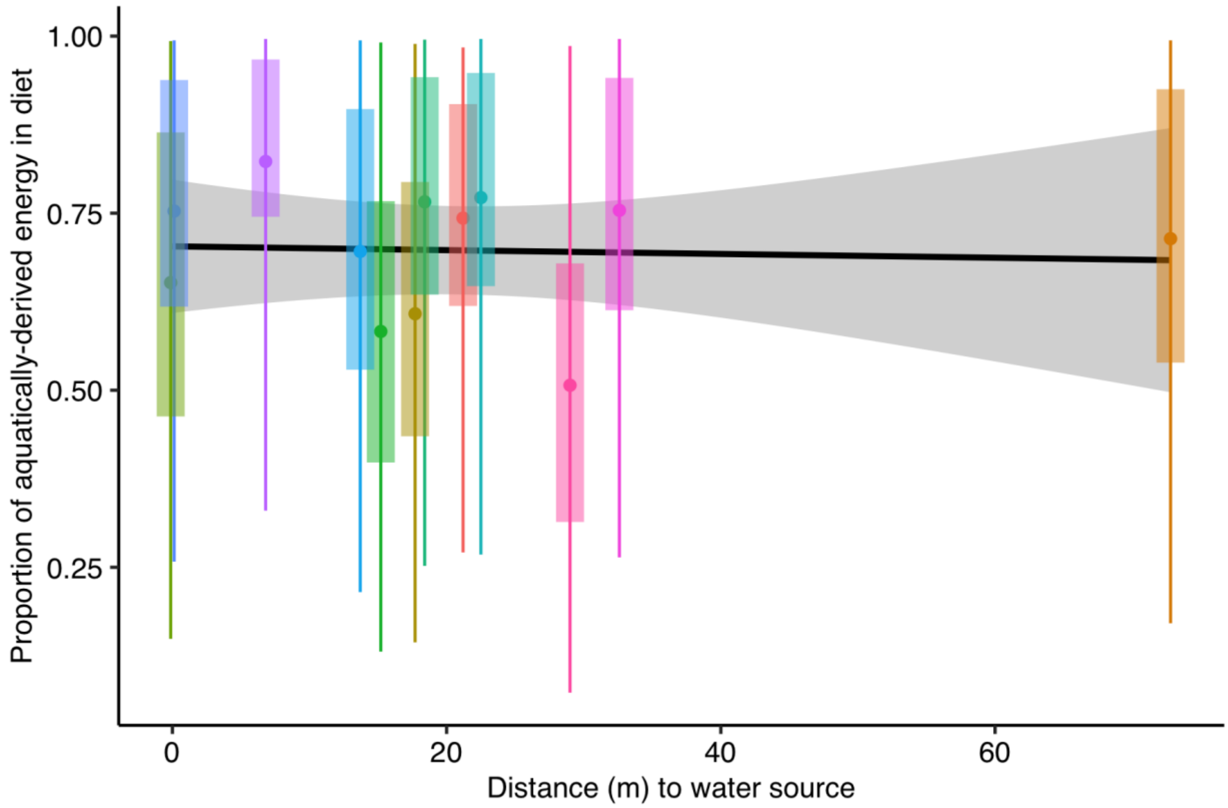

Figure 3.8. The proportion of MWCS nestling diet does not vary with respect to the nest's distance from a water source**.** Nest-level posterior means and 50% Bayesian credible intervals are represented by dots and shaded rectangles respectively, and vertical lines represent 95% Bayesian credible intervals. Colors represent individual nests.

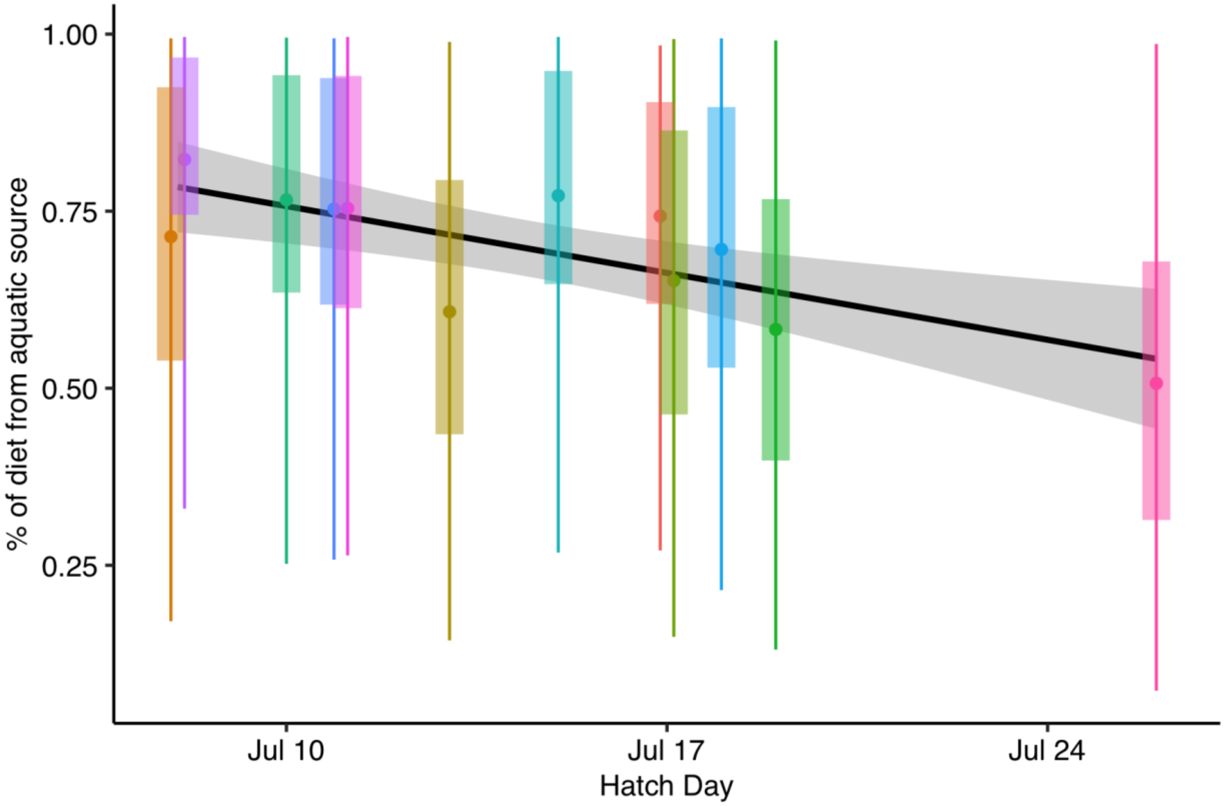

Figure 3.9. The proportion of MWCS nestling diet derived from the aquatic pathway decreases with later hatch date**.** Nest-level posterior means and 50% Bayesian credible intervals are represented by dots and dotted lines respectively, and vertical lines represent 95% Bayesian credible intervals. Colors represent individual nests.

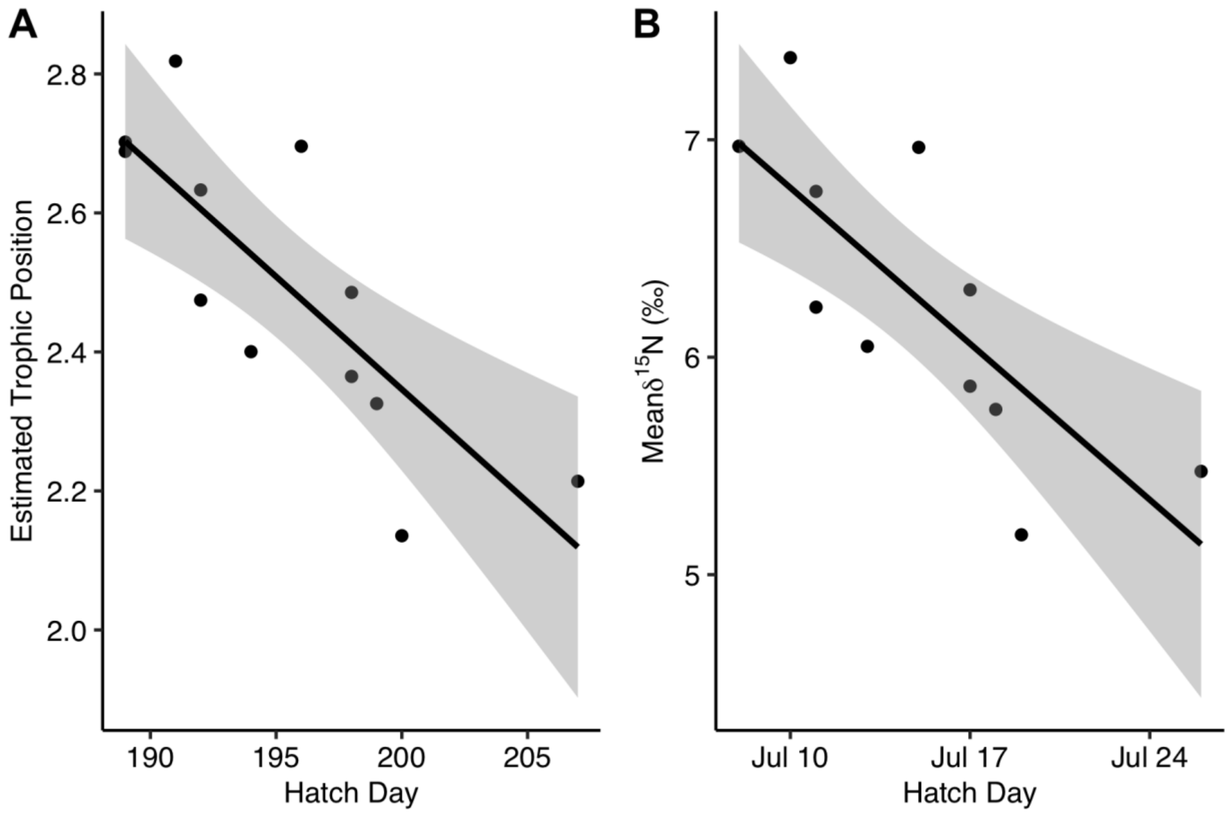

Figure 3.10. Estimated trophic position (A) and mean δ15N values (B) of MWCS nests decline as a function of hatch date**.**

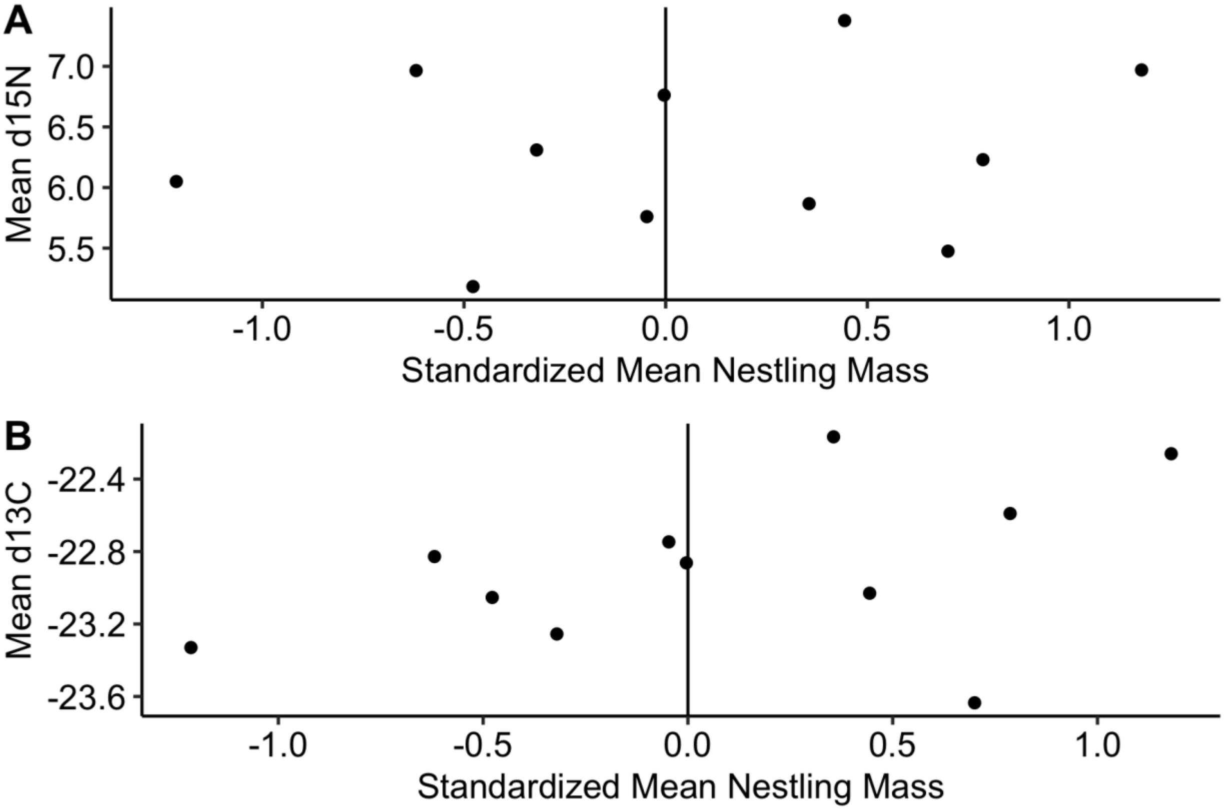

Figure 3.11. Average standardized nestling mass per nest is not significantly related to either A) δ^{15}N or B) δ^{13}C in MWCS nestlings.

CHAPTER 3 SUPPLEMENTAL INFORMATION

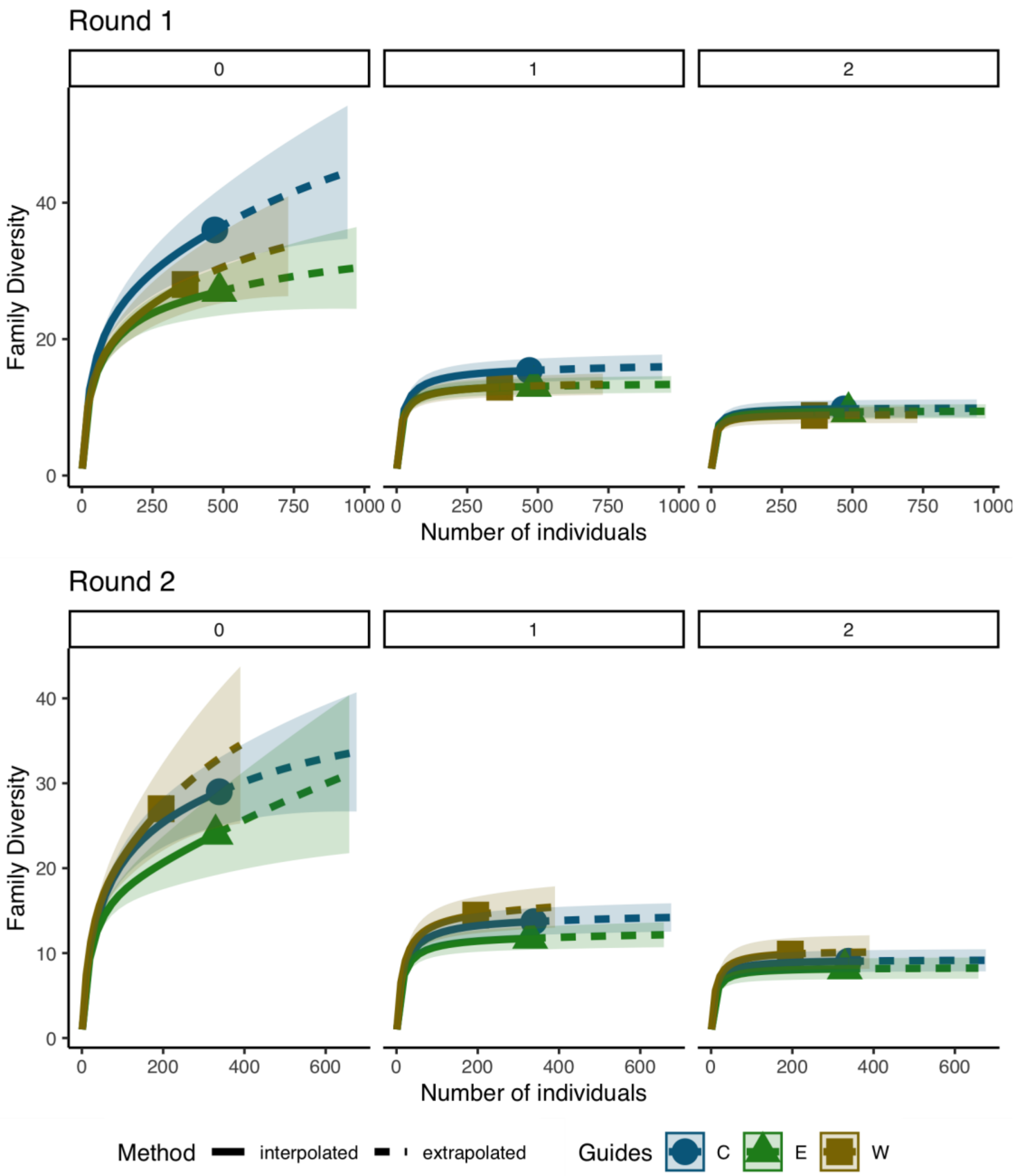

Figure 3.S1. Interpolated and extrapolated insect diversity at the Family level using Hill numbers 0 (richness), 1 (Shannon diversity index), and 2 (Simpson evenness index) by round and sampling location in Tioga Pass Meadow. The presence of an asymptote indicates sufficient sampling of the diversity present. Although family richness does not completely asymptote, the asymptotes for Hill = 1 suggests that the most abundant insect families are sufficiently sampled. Fewer total individuals were captured in Round 2 compared with Round 1.

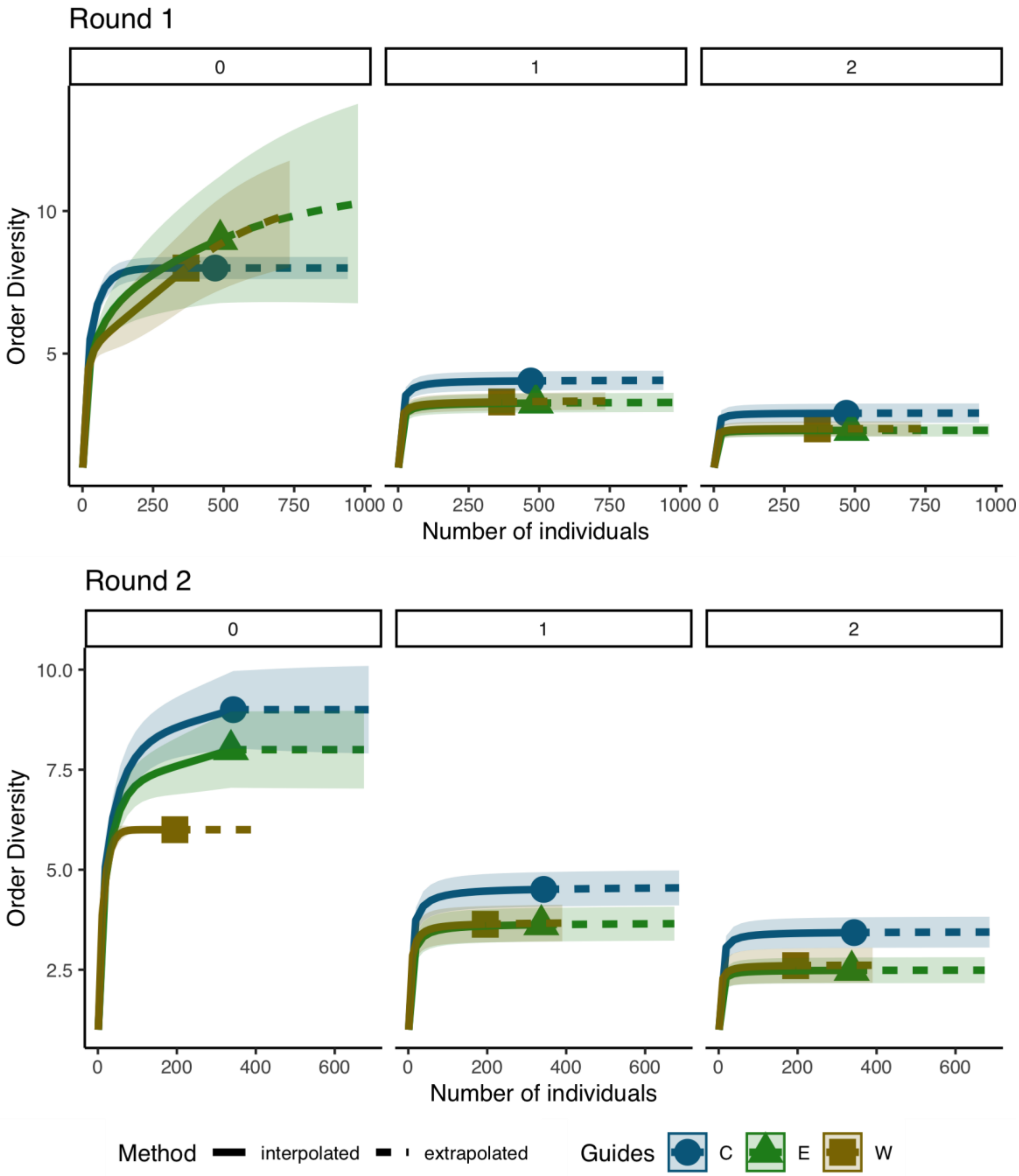

Figure 3.S2. Interpolated and extrapolated insect diversity at the Order level using Hill numbers 0 (richness), 1 (Shannon diversity index), and 2 (Simpson evenness index) by round and sampling location in Tioga Pass Meadow. The presence of an asymptote indicates sufficient sampling of the diversity present. Although richness does not completely asymptote for Round 1, the asymptotes for Hill = 1 suggests that the most abundant insect Orders are sufficiently sampled. Fewer total individuals were captured in Round 2 compared with Round 1.

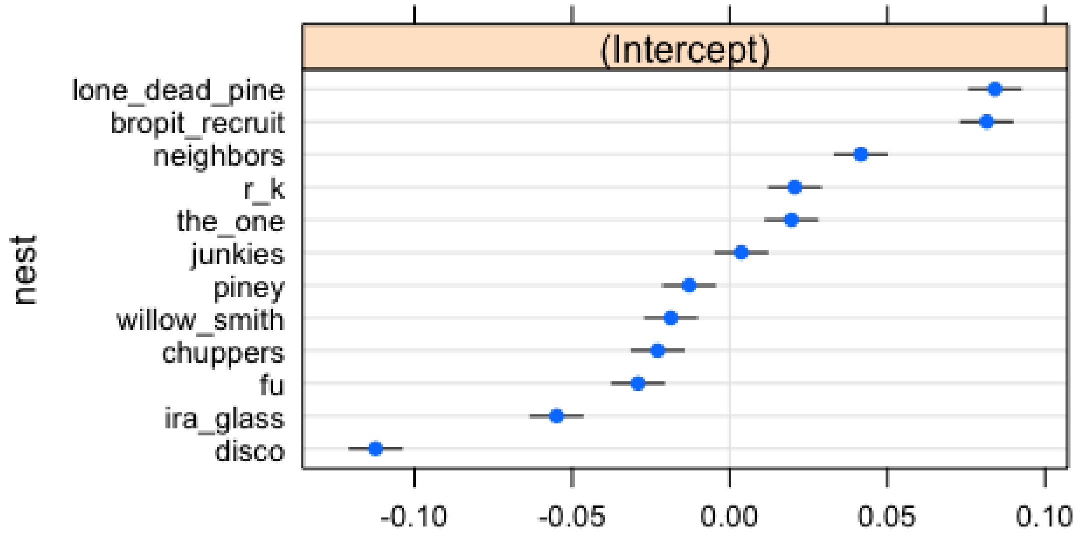

Figure 3.S3. Random effects dotplot shows that nests differ in the proportion of diet derived from aquatic sources (see Table 4 for full model output).

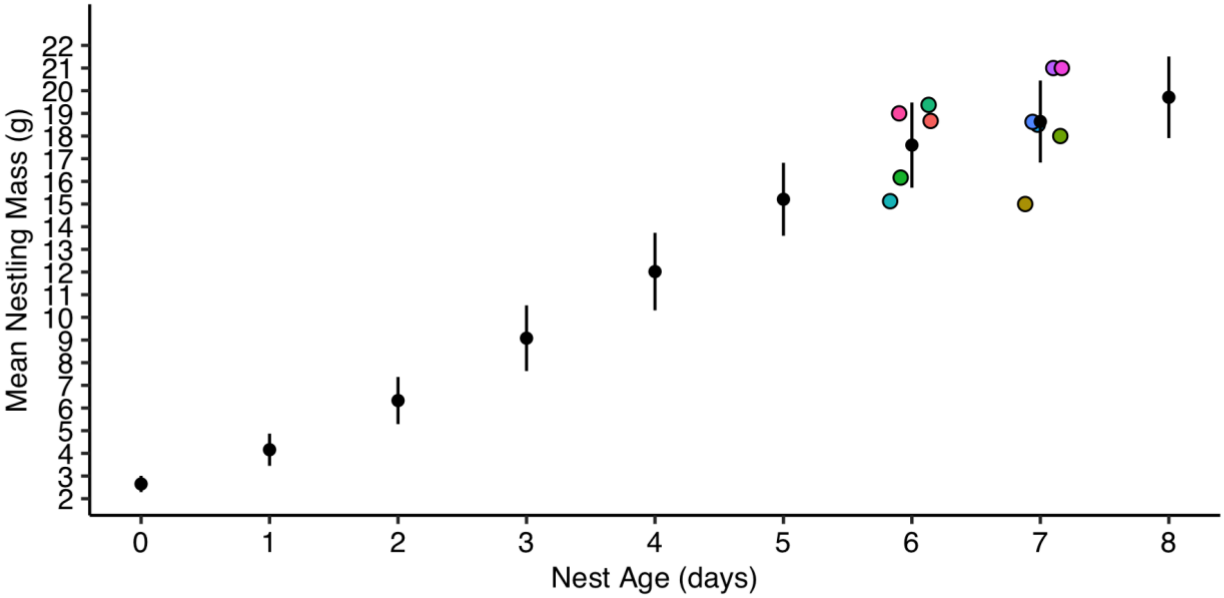

Figure 3.S4. Mean nestling mass on the day of feather sampling**.** Black dots and lines represent population-level mean and standard deviation of nestling mass by day, adapted from Morton 2002.