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AMERICAN KESTREL (*FALCO SPARVERIUS*) BREEDING PRODUCTIVITY AND DIET IN A VERNAL POOLS AND GRASSLAND HABITAT

A Thesis submitted in partial satisfaction of the requirements for the degree of Master of Science

in

Environmental Systems

by

Joy Marie McDermot

Committee in charge:
Marilyn L. Fogel, Ph.D, Chair
Danielle L. Edwards, Ph.D
Jessica L. Blois, Ph.D

2016

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The Thesis of Joy Marie McDermot is approved:

_____
Danielle L. Edwards, Ph.D

_____
Jessica L. Blois, Ph.D

_____
Marilyn L. Fogel, Ph.D
Committee Chair

University of California, Merced
2016

Dedication

For my husband,
Donald L. Stewart III who has shown me love and support.

ACKNOWLEDGEMENTS

I must express my deepest gratitude to Dr. Marilyn Fogel for allowing me to join her lab and learn from her. I would also like to thank Dr. Fogel for her endless support throughout this process. I would like to acknowledge Dr. Jessica Blois and Dr. Danielle Edwards for sharing their advice and wisdom; their input has been invaluable. I would also like to thank, tremendously, Mr. Steve Simmons who supported this project by providing time, effort, and resources. I would like to acknowledge the University of California, Merced Reserve System for their funding support for this project. I would like to thank and acknowledge Christopher Swarth, previous Reserve director, for his assistance, knowledge, and support. I would also like to acknowledge Dr. Elizabeth Williams, Dr. Christina Bradley, and David Araiza for their assistance and guidance. This project would not have been possible without the assistance from Isabel Lawrence and Andrew Ho. I would like to acknowledge my fellow lab members Daniel Toews, Bobby Nakamoto, and Jonathan Nye. I would like to thank my husband, Donald Stewart, and my parents, Cindy and Mark McDermot, for their love and support. I would also like to thank Kimber Moreland and Rebecca Abney for being an excellent support system during this journey.

ABSTRACT

American Kestrel (*Falco Sparverius*) breeding productivity and diet in a vernal pools and grassland habitat

by
Joy Marie McDermot

Master of Science, Environmental Systems
University of California, Merced

Committee Chair: Marilyn Fogel

American Kestrel populations have declined since the 1960s, and the cause has yet to be identified. To further comprehend the decline of the American Kestrel, my study examined kestrel breeding productivity including occupancy, hatching success, and fledging success in nest boxes in conjunction with the identification of dietary resources. In this thesis, I monitored and documented the breeding success of the American Kestrel from nest boxes on the UC Merced's Vernal Pools and Grassland Reserve from 2014-2016. I also analyzed food resources of the population and of individuals to quantify intraspecific and temporal dietary variation. I employed a multi-faceted approach to fully examine diet composition, breadth, and variation within a population. I used pellet and prey remain analysis as well as stable isotope analysis of carbon, nitrogen, and hydrogen in feathers and prey items. Nest box occupancy increased over the three-year study period from 60% to 80%. In 2016, the hatching and fledging success decreased drastically from 68% to 44% and 100% to 69%, respectively. Predation and nest failures occurred more frequently in 2016 compared to 2015 and 2014. Based on examination of prey and pellet remains diet composition was similar in 2015 and 2016, kestrel's consumed mostly spiders, orthopterans, and small birds. In 2016, late nesting kestrels (May and June) consumed a greater number of orthopterans compared to kestrels that nested earlier in the season who ate spiders. Stable isotope analyses revealed that adults may feed at a higher trophic level than nestlings. Stable isotope mixing models indicated that adult diets in 2015 and 2016 were composed principally of orthopterans (2015 = 25-59%, 2016 = 18-60%) and birds (2015 = 28-58%, 2016 = 15-60%). In 2015, nestling diets were similar to adult diet with slightly different proportions of orthopterans (18-72%) and birds (17-47%). In 2016 nestlings, diets were comprised of orthopterans (15-58%) and mammals (9-56%). Overall, American Kestrels colonized the nest boxes rapidly, however, reducing predation of eggs and nestlings by mitigating predator access to nest boxes is crucial to increasing hatching and fledging success on the Merced Vernal Pools and Grassland Reserve. In terms of dietary resources, invertebrates are the largest proportion of the kestrel diet. Vertebrate consumption could also be an important factor in kestrel diet due to the higher amount of biomass in vertebrate prey. Preservation of key prey items is crucial to the conservation of the American Kestrel population. Changes in dietary resource abundance could be a predominant factor influencing the decline of the species.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS v

ABSTRACT vi

LIST OF FIGURES viii

LIST OF TABLES x

CHAPTER 1: BACKGROUND AND INTRODUCTION 1

CHAPTER 2: AMERICAN KESTREL BREEDING PRODUCTIVY FROM A VERNAL POOLS AND GRASSLAND HABITAT NEST BOX PROGRAM 12
- Introduction 12
- Methods 13
- Results 14
- Discussion 15

CHAPTER 3: DETERMINING AMERICAN KESTREL DIET BREADTH AND VARIATION USING PREY REMAINS AND STABLE ISOTOPE ANALYSIS OF $\delta^{15}N$, $\delta^{13}C$, AND $\delta^{2}H$ 25
- Introduction 25
- Methods 27
- Results 32
- Discussion 37

CHAPTER 4: CONCLUSIONS 61

REFERENCES 68

APPENDIX A: RAW DATA 76

LIST OF FIGURES

Figure 1.1. American Kestrels at various ages 6

Figure 1.2. Merced Vernal Pools and Grassland Reserve (MVPGR) study site in March 2016....7

Figure 1.3. Location of all 30 nest boxes on the MVPGR in 2016 indicated by red dots ...8

Figure 1.4. Expected food niche breadth of kestrels in 2015 compared to expected food niche breadth in 2016 9

Figure 1.5. Expected food niche overlap of individual nest boxes A-F during a dry breeding season (2015) 10

Figure 1.6. Expected food niche overlap of individual nest boxes A-F during a wet breeding season (2016) 11

Figure 2.1. The hatching success by month for 2015 and 2016 indicated that 2015 had greater success in March and April.....22

Figure 2.2. Fledging success for 2015 and 2016 by nest initiation month 23

Figure 2.3. The distribution of nest failures through the breeding season for all three years (2014-2016) 24

Figure 3.1. Average proportions of vertebrate prey found within nest boxes for 2015 and 2016.....49

Figure 3.2. The average proportions of invertebrate prey types found within nest boxes for 2015 and 2016 50

Figure 3.3. Proportions of each major prey type by occupied nest boxes in 2015 51

Figure 3.4. Proportions of each major prey type by occupied nest boxes in 2016 52

Figure 3.5. Distribution of stable isotopic values for adults and nestlings from both sampling years 53

Figure 3.6. Distribution of δ^2H for adults and nestlings sampled from both years 54

Figure 3.7. Bayesian standard ellipses area (SEA_B) for adults and nestlings in 2015 and 2016.....55

LIST OF FIGURES (cont.)

Figure 3.8. Bayesian standard ellipses area (SEA_B) of prey items collected in 2015 with diet corrected nestlings from 2015.....56

Figure 3.9. Bayesian standard ellipses area (SEA_B) of prey items collected in 2015 with diet corrected nestlings from 2016.....57

Figure 3.10. Bayesian standard ellipses area (SEA_B) of prey items collected in 2015 compared to diet corrected adults from 2015 (A) and 2016 (B).....58

Figure 3.11. SIAR mixing model results for adults sampled in 2015 and in 2016.....59

Figure 3.12. SIAR mixing model results for nestlings sampled in 2015 and in 2016.....60

Figure 4.1. Representative diet breadth in 2015 and 2016 65

Figure 4.2. Representation of measured individual niche breadth and variation between nest boxes in 2015.....66

Figure 4.3 Representation of measured individual niche breadth and variation between nest boxes in 2016.....67

LIST OF TABLES

Table 2.1. Banding summary for 2014-2016 adult and nestling American Kestrels.....18

Table 2.2. Summary of American Kestrel productivity results (2014-2016) 19

Table 2.3. Breeding productivity results by nest initiation month (2015-2016).....20

Table 2.4. Productivity of second clutch attempts (2015-2016).....21

Table 3.1. Types of prey consumed by American Kestrels occupying man-made nest boxes and number of individuals (2015 and 2016) 44

Table 3.2. Summary statistics for dietary Pairwise Overlap, Population Similarity Index, and Niche Breadth.....45

Table 3.3. Average isotope values for major prey groups (2015-2016) 46

Table 3.4. American Kestrel stable isotope averages for 2015 and 2016 adults and nestlings 47

Table 3.5. Small sample size corrected standard ellipses area (SEA_C) and Bayesian Standard ellipses (SEA_B) for prey, adult kestrels, and nestlings in 2015 and 2016.....48

CHAPTER 1: BACKGROUND AND INTRODUCTION

The American Kestrel (*Falco sparverius*) is a widely distributed species that is common in a multitude of landscapes, yet a decrease in population throughout North American has been documented since the 1960s (Farmer and Smith 2009, Smallwood et al. 2009). American Kestrels (Figure 1.1) are the smallest falcon species in North America and are dispersed throughout North America, Central America, and parts of South America. This species has an expansive distribution and is abundant in several habitats including open grasslands, areas with low tree density, and deserts (Smallwood and Bird 2002). Principally, there have been reported declines in the Northeast and Midwest (Hoffman and Smith 2003, Farmer et al. 2008), however, more recently the western United States has reported population losses of 1.5 to 2.7% per year (Farmer and Smith 2009, Smallwood et al. 2009). Reasons for the decline in kestrel populations have not been thoroughly examined in all regions. Most research has been focused on the Midwest and the East while much of the Western populations in Washington, Oregon, and California have not been investigated.

West Nile Virus (WNV) and predation by Cooper's Hawks have been thought to contribute to the decline of the kestrel populations (Farmer et al. 2008). However, in Northeastern regions of the U.S. and parts of Canada, where WNV is found in kestrels, population reductions occurred before WNV was prevalent (Smallwood et al. 2009). Furthermore, relationships between increased Cooper's Hawk populations and American Kestrel population loss has not been shown in all areas of kestrel decline (Smallwood et al. 2009). Habitat degradation and changes in land use has reduced the number of available nesting sites for kestrels (Smallwood et al. 2009). Since kestrels are secondary cavity nesters, they rely heavily on natural cavities in trees and cliffs to have higher nesting success. In the Western United States, kestrel population losses are thought to be linked to variations in land use and long periods of drought (Bird 2009, Farmer and Smith 2009), but speculation regarding these factors has not been proven. The conversion of open grassland to agriculture reduces foraging sites and potential nesting sites. Kestrels prefer to forage in less dense vegetation or in open grasslands compared to densely vegetated areas (Sheffield et al. 2001). One of the many challenges in discovering the underlying causes of the degradation of the American Kestrel population is the variation in the landscapes that kestrels occupy. Regional and local habitat conditions are likely to be influencing kestrel populations through combinations of disease, predation, habitat loss, changes in land-use, climate change, and prey availability.

Efforts have been made to alleviate the stresses of habitat degradation and a reduction in natural nest cavities for kestrels since the 1970s. Construction of man-made nest structures, nest boxes, has provided additional nest sites for kestrels across North America (Nagy 1963, Hamerstrom, Hamerstrom, and Hart 1973, Bloom and Hawks 1983, Toland and Elder 1987, Smallwood and Collopy 2009). Nest box programs offer unique opportunities to examine and monitor the breeding success and productivity while assisting in the conservation of a declining species. Long-term nest box programs for

American Kestrels have contributed information on breeding productivity as well as habitat use. However, nest boxes alone have not proven successful at boosting populations over time (Smallwood et al. 2009). Long-term monitoring studies have documented drops in nest box occupancy rates over long periods of time, 10+ years (Smallwood et al. 2009).

Long-term monitoring across several habitat types and climate regions is necessary due to the kestrels' expansive range. Minimal data have been published on nest box use and success in western United States, including California. More specifically, there are even fewer long-term reports or publications on the breeding productivity of kestrels nesting in Central California. Central California's unique mixture of natural and human-modified landscapes provides an interesting opportunity to study American Kestrel productivity. Monitoring nest boxes in this region will contribute knowledge of how land use and regional characteristics (e.g., habitat type, drought, diet) play a role in kestrel populations. It is important to explore American Kestrels at the population level to identify decreases in population size as well as to learn what drives successful and unsuccessful populations.

Diet breadth and composition of a population and of individuals may contribute to American Kestrel success and breeding productivity. The amount and type of prey nestlings consume influences growth and can dictate fledging success in some avian species (Killpack et al. 2015). The diet composition of opportunistic raptors is dependent on habitat characteristics and prey abundance (Steenhof and Kochert 1988, Korpimaki 1992, Rodriguez et al. 2010). In drier climates, several raptor species experience an increase in diet breadth and in invertebrate prey compared to raptors in cooler temperatures (Carmona and Rivadeneira 2006). Areas with intense agricultural practices and prolonged drought, such as Central California, could have reduced prey abundance during key breeding months, affecting diet composition and breadth of both adult and nestling birds (Britschgi, Spaar, and Arlettaz 2006). Examining how the American Kestrel population diet varies on the Merced Vernal Pools and Grassland Reserve (MVPGR) between years with fluctuating environmental conditions (e.g., drought verses increased precipitation) can indicate how the population may be influenced by long-term climate changes.

The diet breadth and composition of an opportunistic raptor species has the potential to vary between individuals. Individual diet variation is influenced by an assortment of factors, including foraging ability, individual preference for specific prey, and territory (Bolnick et al. 2003, Resano-Mayor et al. 2014). American Kestrel diet has the potential to consist of a variety of prey types including invertebrates, small mammals, birds, reptiles, and amphibians (Smallwood and Bird 2002). The diet breadth and composition of an individual influences the individual's fitness levels (Golet et al. 2000, Katzner et al. 2005). Evidence supports that adults who feed nestlings a specialized diet have greater reproductive success compared to adults who feed nestlings more generalized diets (Golet et al. 2000, Katzner et al. 2005). The link between reproductive output and specialized diet is not true for all avian species (Whitfield et al. 2009).

There are several ways to determine diet in avian species, for example, by examining gut contents, pellet analysis, and nest cameras. In addition, stable isotope analysis (SIA) of carbon, nitrogen, and hydrogen can assist in identifying diet composition, trophic position, integration of diet into tissues, and habitat locations (i.e., migration routes and breeding grounds) in animals, including birds (DeNiro and Epstein 1978 and 1981, Estep and Dabrowski 1980, Hobson and Clark 1992, Inger and Bearhop 2008, Hobson 2011). Tissues, such as feathers or blood, can reflect the diet and trophic position of the individual during the time that particular tissue was synthesized. By using stable isotopic values from individuals and of their potential prey items, diet can be thoroughly investigated (Hobson 1990, Hobson and Clark 1992).

SIA provides insight into environmental conditions and nutrient use in organisms through analysis of the incorporation of diet items into specific tissues. Information on vegetation can be determined by SIA of carbon. More positive $\delta^{13}C$ values are associated with C_4 photosynthetic plants and more negative $\delta^{13}C$ are associated with the C_3 photosynthetic pathway (Farquhar, Ehleringer, and Hubick 1989). Changes in $\delta^{13}C$ in C_3 plants can indicate water-use efficiency patterns in vegetation, which can provide information on environmental conditions (Farquhar, Ehleringer, and Hubick 1989). Stable isotope analysis of both nitrogen and carbon have also been useful in understanding nutrient use in animals. For example, an animal's protein source (e.g., animal protein or plant protein) can influence the degree of carbon and nitrogen isotopic fractionation for blood, liver, muscle, and feather tissues (Hobson and Clark 1992). A higher enrichment in ^{15}N occurs in adult birds with low nutrient intake, due to a greater proportion of recycled nitrogen from catabolism (Hobson, Alisauskas, and Clark 1993).

SIA has contributed to the successful identification of the trophic position, diets, resource use variation, and migratory patterns of avian species in multiple studies (Mizutani et al. 1990, Hobson Piatt, and Pitocchelli 1994, Hobson 1999, Barea and Herrera 2009, Symes and Woodborne 2010, Weiser and Powell 2011). Mitzutani and colleagues (1990) were able to identify differences in feeding behaviors of Great Cormorants (*Phalacrocorax carbo*) by examining $\delta^{13}C$ in feathers and prey items. By utilizing both carbon and nitrogen isotopes, Hobson, Piatt, and Pitocchelli (1994) displayed how trophic position and foraging locations can be determined in seabird populations. Stable isotopes have also been useful for determining the true feeding guild and protein sources of avian species. For example, Barea and Herrera (2009) provided evidence that a frugivore specialist was also consuming a variety of arthropods. Additionally, SIA has been used to identify resource portioning between and within species in communities (Symes and Woodbourne 2010).

For this study, stable isotopes of feather tissue combined with data on pellet and prey remains provided a well-rounded view of the American Kestrel diet and dietary differences within a population. In addition to providing insight on environment, trophic position, and diet incorporation, SIA is a less invasive way to examine diet compared to conventional methods, such as examination of gut contents, and can be less labor intensive compared to pellet dissection and cameras. One feather can take days to a week

to fully form and will reflect the diet of an individual during the time the feather was being formed (Bearhop et al. 2002).

The continuing issue of American Kestrel population loss in North America and the lack of understanding of causes indicates that more research is needed on American Kestrel population status and breeding biology. More specifically, a lack of current, published literature has led to limited knowledge of American Kestrel breeding productivity in man-made nest boxes in California, therefore in Chapter two, I have examined and documented the breeding productivity of American Kestrels inhabiting man-made nest box structures on the University of California, Merced Vernal Pools and Grassland Reserve (MVPGR) (Figure 1.2, Figure 1.3). The objectives were to quantify the breeding productivity from three years of data and to compare the overall breeding productivity results to other nest box programs. Breeding productivity was quantified using occupancy rates, clutch size, hatching success, fledging success, and nesting success. This research will provide insight on the successes of nest box use in an arid environment and highlight future research and conservation needs.

Chapter three will address the gaps in knowledge of kestrel diet breadth, composition, and diet variation within a population which has not yet been examined in the Central California. The goal of this chapter is to examine diet niche breadth and variation between American Kestrels occupying nest boxes on the MVPGR using prey analysis and SIA. Using a dual technique approach to determine diet has allowed me to address questions related to population diet breadth, individual diet specialization, differences between age classes, and annual differences in prey composition.

The first objective was to examine diet composition and breadth of the population by analyzing pellets and nest box prey remains. I hypothesized that diet breadth and composition will reflect environmental conditions and will vary from 2015 to 2016 depending on environmental changes (Figure 1.4). Other raptors have experienced changes in diet due to environmental conditions, such as increases in temperature or decreases in rainfall (Dawson and Bortolotti 2000). Diet breadth tends to increase in drier climates, and the composition of invertebrate prey also increases with warmer conditions (Carmona and Rivadeneira 2006, Santillan et al. 2009). Therefore, in a dry year on MVPGR the diet breadth of kestrels should be greater in comparison to years with increased precipitation.

The second objective was to examine food niche variation between occupied nest boxes by using prey data and stable isotope analysis of feather tissue. I expected that there would be some level of diet variation experienced between nest boxes in both 2015 and 2016 due to the opportunistic nature of American Kestrels. When food resources are limited, an increase in opportunism in predatory birds is predicted (Emlen 1973). If opportunism is greater, then the food niche of individuals would be larger. Increased food niche would result in more overlap between individuals. Therefore, I hypothesized that 2015 would have more overlap and less diet variation because prey is likely to be more limited during a dry year (Figure 1.5). In comparison, I expected 2016 to have

more diet variation and less overlap in diet between nest boxes due to the increased rainfall during the 2016 breeding season.

The final objective was to determine diet variation between different age classes (adults and nestlings). Stable isotope analyses of feather tissue were used since adult and nestling diets cannot be distinguished by using pellet and prey remain data. I hypothesized that the stable isotopic composition and diet of adults would differ from nestling American Kestrels during breeding season. Dietary differences have been documented in other American Kestrel populations as well as other small falcon species (Sarasola, Santillan, and Galmes 2003, Santillan et al. 2009, Catry et al. 2016).

Understanding how diets differ within a population could assist in identifying variation in foraging strategies and habitat characteristics. This research on diet and breeding productivity provides knowledge of how diet may contribute to an individual's fitness and identifies what factors influence population success.

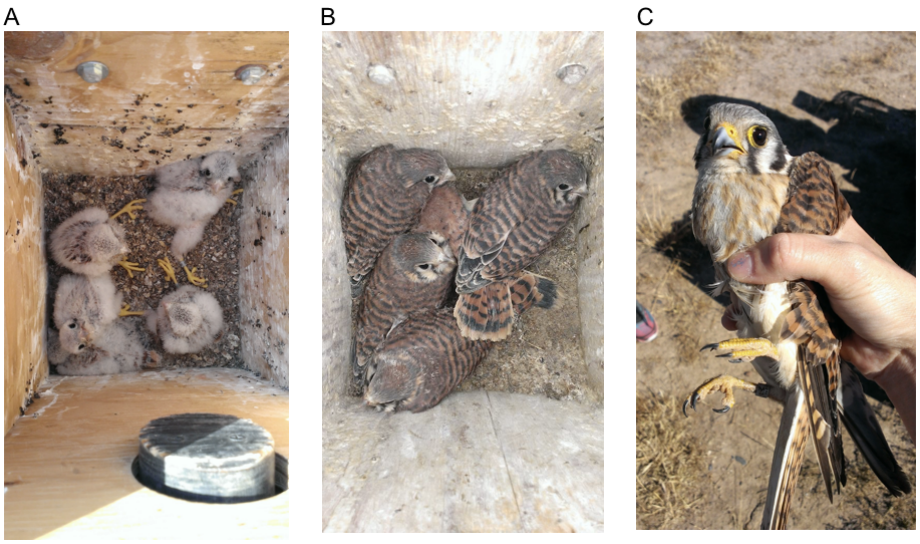

Figure 1.1. American Kestrels at various ages. A) American Kestrel nestlings at approximately 1-2 weeks of age. B) Nestlings at approximately 3-4 weeks of age, just prior to fledging the nests. C) An adult female American Kestrel breeding on the Merced Vernal Pools and Grassland Reserve in 2016.

Figure 1.2. Merced Vernal Pools and Grassland Reserve (MVPGR) study site in March 2016.

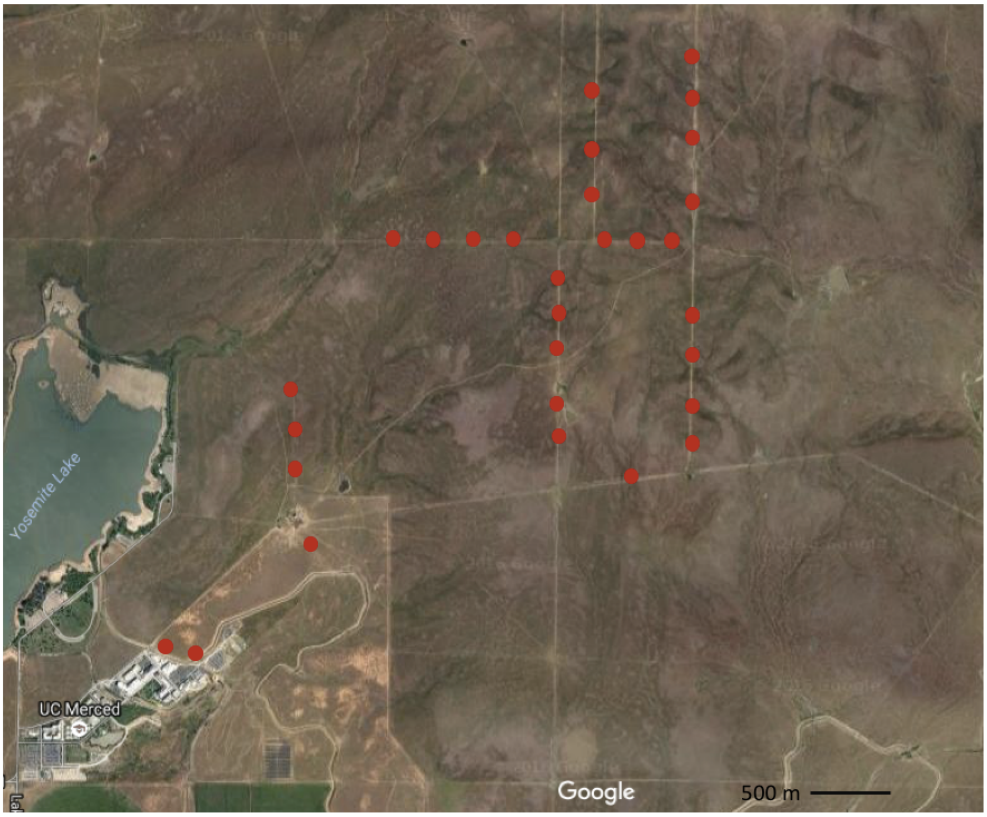

Figure 1.3. Location of all 30 nest boxes on the MVPGR in 2016 are indicated by red dots.

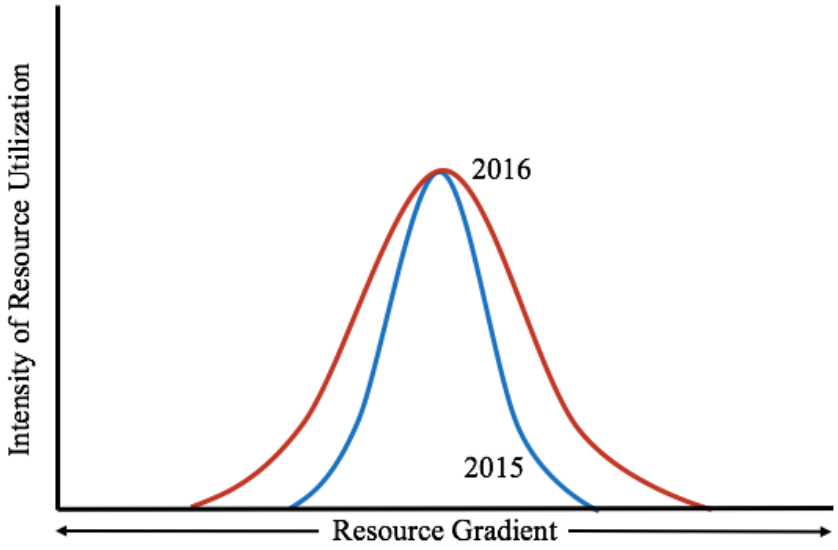

Figure 1.4. Expected food niche breadth of kestrels in 2015 compared to expected food niche breadth in 2016. Food niche breadth will be greater in the dry year (2015), because limited preferred prey will cause expansion in kestrel diet range.

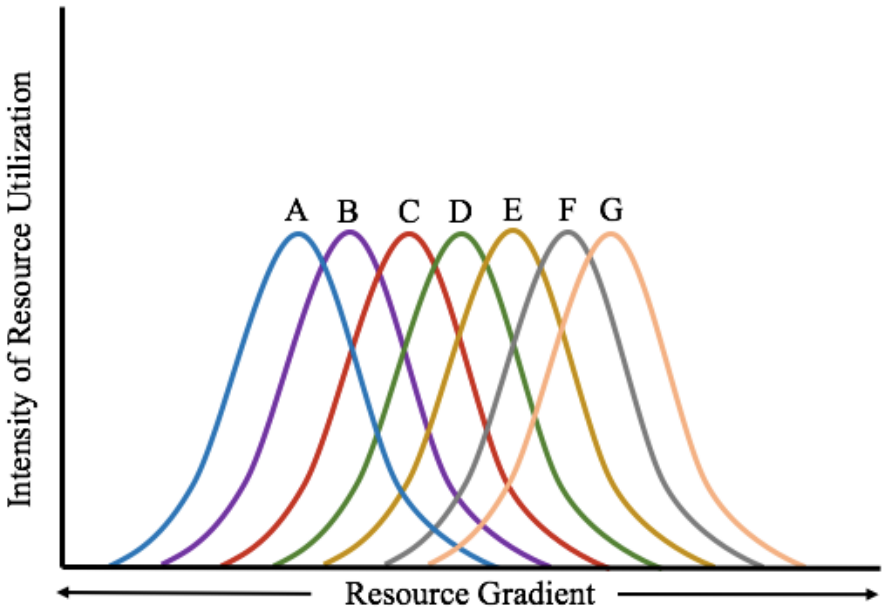

Figure 1.5. Expected food niche overlap of individual nest boxes A-F during a dry breeding season (2015). There will be high overlap in food resources, because prey is likely to be limited during periods of water stress increasing diet niche of individuals.

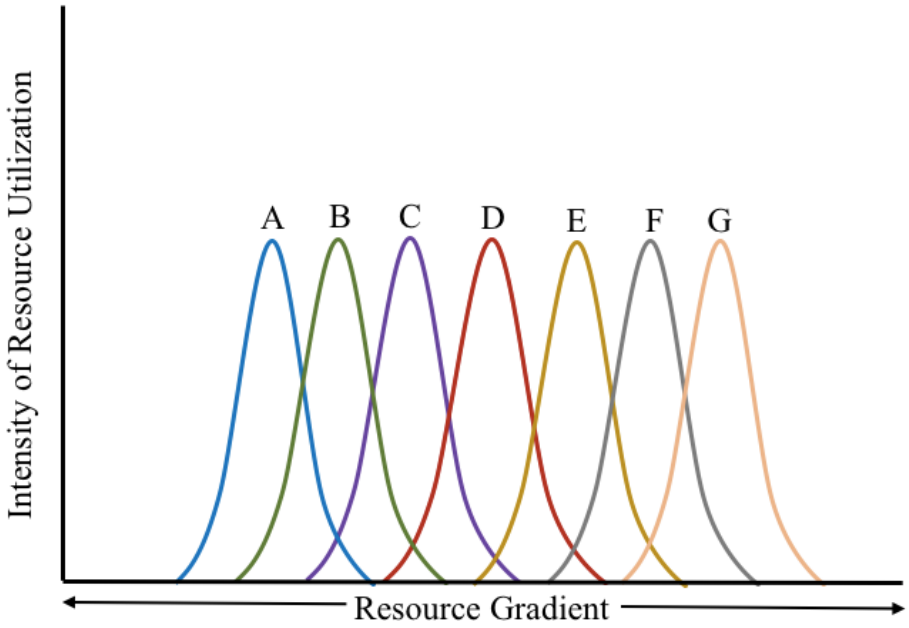

Figure 1.6. Expected food niche overlap of individual nest boxes A-F during a wet breeding season (2016). There will be low food niche overlap of individuals, because prey is likely to be more abundant in years with increased precipitation compared to drier years.

CHAPTER 2: AMERICAN KESTREL BREEDING PRODUCTIVITY FROM A VERNAL POOLS AND GRASSLAND HABITAT NEST BOX PROGRAM

Introduction

Habitat loss and land use changes have negatively influenced many raptor species (Donazar, Negro, and Hiraldo 1993), including the American Kestrel (*Falco sparverius*) (Steenhof and Peterson 2009, Brown and Collopy 2013). Minimal availability of nesting sites is thought of as a contributor to the large scale and widespread decline in American Kestrel populations across North America (Hamerstrom, Hamerstrom, and Hart 1973, Sauer et al. 1997, Farmer et al. 2009, Smallwood et al. 2009). To combat the effects of habitat and nest site loss, programs involving man-made nest structures have been established in many regions of North America, primarily Eastern and Mid-West regions, as early as the 1950s (Hamerstrom, Hamerstrom, and Hart 1973, Craig and Trost 1979, Varland and Loughin 1993). These nest box monitoring programs have helped to ameliorate the decline of the kestrel population and provide insight in to kestrel breeding productivity.

Nest boxes offer sites for breeding pairs in areas that have few natural nesting cavities to help boost populations (Katzner et al. 2005). It has become increasingly important to not only establish nest box programs for declining populations, but to monitor nesting success within man-made nest structures. Despite the success of many nest box programs, population decline is still occurring in many regions of North America (Smallwood et al. 2009). The continued population decline indicates other mechanisms are influencing kestrel populations. Further examination and documentation of American Kestrels via nest box programs can assist in understanding aspects that may contribute to kestrel breeding productivity. In California, existing published data on kestrel populations and documentation of kestrel nest box program success is minimal (Bloom and Hawks 1983). Documenting nest initiation, hatching success, clutch size, fledging success, and nesting success will assist in quantifying the productivity of kestrels occupying nest boxes.

In 2014, the University of California, Merced Vernal Pools and Grassland Reserve (MVPGR) established a nest box monitoring program to contribute to American Kestrel conservation. The University's nest box program offers a unique opportunity to study breeding productivity in kestrels in a region where documentation of kestrel populations is sparse. In the first year of the study, kestrels occupied six of ten nest boxes and 15 chicks fledged (Swarth et al. 2014). After the first year of the program, 20 more nest structures were added to the landscape and more frequent monitoring was conducted. This chapter describes and assesses the results from a three-year (2014-2016) study of American Kestrel breeding productivity at the MVPGR in Merced, California. The goals of this project were to document and analyze breeding productivity in nest boxes, as well as document banding and recapture rates of adults and nestling kestrels. The objectives were to quantify breeding productivity to make comparisons between years and to compare the overall breeding productivity results to other nest box programs.

Methods

Study Area

This study took place at the University of California, Merced Vernal Pools and Grassland Reserve, adjacent to the University of California, Merced campus. The MVPGR is primarily an open grassland habitat with seasonal vernal pool coverage during winter and early spring. The vegetation consists of annual grasses and forbs with little tree cover, which includes mostly willow species (*Salix spp*.). The MVPGR is approximately 2,656 ha in size and largely borders private land that contains similar ecological characteristics. The study area was chosen for its accessibility to nest box structures from the University of California, Merced campus.

Nest Boxes

In January of 2014, MVPGR erected 10 American Kestrel nest box structures. In 2015, an additional 20 nest structures were added to the MVPGR boundaries. Following Bird and Palmer (1988), all nest boxes are bolted to the top of steel poles that are approximately three meters tall. Nest boxes are 45.72 cm by 20.32 cm by 20.32 cm, and are spaced at least 200 meters apart. All nest boxes contain four to six centimeters of wood shavings to protect eggs from breaking.

Data Collection

This study took place over the course of three breeding seasons from 2014 to 2016. In 2014, boxes were monitored for nest initiations from May through June and were examined every two weeks. In 2015 and 2016, nest boxes were checked weekly beginning in early March for occupancy to determine an approximate nest initiation date. The alteration in method allowed for determination of a more accurate nest initiation date. To check for nest initiations, the entrance hole to the nest box was covered and the lid of the box was removed slightly to determine if eggs or an incubating female or male inhabited the box. The date of the first egg sighting was recorded if the box contained eggs or if an incubating female or male was present.

Two weeks after the first sighting of incubation or eggs, females and/or males were banded. While banding the adult, the number of eggs were counted and recorded. In 2014 and 2015, boxes were only visited once during the incubation period for banding purposes and were not visited again until suspected hatching in order to limit disturbance. In 2016, after banding the incubating adult, the occupied boxes were then monitored weekly to determine an accurate hatching date. Each year, approximately 1-2 weeks after the nestlings hatched, they were banded. During this time, the number of nestlings hatched was recorded and the box was examined for any unhatched or missing eggs. After banding the nestlings, general observations were made on a weekly basis at each occupied box to determine an estimated fledging date. All birds were banded using United States Geological Survey (USGS) aluminum bands (USGS Permit #20416), unless previously banded. All capturing procedures for adults and nestlings followed the

Animal Care Protocol guidelines approved by the University of California, Merced (IACUC #AUP14-0002).

All nest boxes were examined for predation, if eggs, nestlings, and/or adults were missing. Records were kept on whether a box was abandoned by an adult before the incubation period began, predation occurred, or whether all eggs went unhatched despite incubation. Breeding productivity was quantified using occupancy rates, clutch size, hatching success, fledging success, and nesting success.

Results

Banding Success

The number of newly banded adults increased from 2014 (n = 3) to 2015 (n = 8) (Table 2.1). The increase in banding is likely due to the increase in number of boxes placed on the MVPGR. In 2016, the number of newly banded adults (n = 13) increased from 2015 (n = 8) (Table 2.1), indicating that there is immigration into the MVPGR's breeding population of kestrels. Recaptured females and males was highest in 2015 (n = 3 Female, n = 5 Male) (Table 2.1). There were more females than males captured and recaptured over the three-year period. Females typically incubate longer and are more likely to be captured for banding compared to males. No new males were banded in 2014 and 2015, but six were banded in 2016 (Table 2.1). This increase in newly banded males can be attributed to the fact that nests were checked more frequently; therefore, the likelihood of finding a male in the nest was greater. The number of nestlings banded increased from 2014 (n = 15) to 2015 (n = 44) (Table 2.1). However, in 2016 only 38 nestlings were banded (Table 2.1).

Breeding Productivity

The percent occupancy was variable over the course of the three-year study period from 60% (n = 6 in 2014, n = 18 in 2015) to 80% (n = 24) of the nest boxes occupied, with an average of 67% occupancy (Table 2.2). Occupancy over two years (2015-2016) varied across months, with the majority of nest initiations occurring in March and April (Table 2.3). Productivity by month could not be examined in 2014 due to sampling methods and lack of nest initiation dates. For both 2015 and 2016, there were only a total of ten nest initiations per year in May, June, and July combined (Table 2.3).

The average clutch size also increased over the three-year period, with an average clutch size for three years of 4.09 eggs per clutch (Table 2.2). Clutch size is highest in March (mean = 4.54) and May (mean = 4.50) (Table 2.3). Clutch size mean decreased in June (mean = 3.33) and July (mean = 3.50) (Table 2.3).

In 2014, there were a total of 22 eggs produced, with 68% hatching success (Table 2.2). From 2015 to 2016, there was a large increase in the number of eggs produced (n = 73 verse n = 110) (Table 2.2), however, the percent of successfully hatched eggs drastically decreased in 2016 (44%) compared to 2015 (70%). In 2016, there was an increase in predation of eggs by raccoons (*Procyon lotor*) and snakes, contributing to a lower

hatching success in those years. Overall, March and April were the most productive months for hatching success (Figure 2.1) (Table 2.3). In 2015, hatching success was greater in March and April compared to 2016 (Figure 2.1). However, in 2016 there were successfully hatched eggs later in the breeding season (May and June) (Figure 2.1).

The average fledging success over three years was 85% (Table 2.2). Fledging success was 100% in 2014, but dropped in subsequent years to 86% in 2015 and to 69% in 2016 (Table 2.2). In 2015, nests that initiation in March and April had the greatest fledging success (83% and 88%) (Figure 2.2). In 2016, fledging success increased from March through June (Figure 2.2). The average percent of successful nests was 56% for all three years (Table 2.2). Overall, the most successful months were March and April with percent successful nests at 54% and 63% (Table 2.3).

In both 2015 and 2016, some females that attempted to have a second clutch (Table 2.4), while in 2014, there were no known second clutch attempts. Nesting success of second nest attempts was greater in 2016 compared to 2015 by 67% (Table 2.4). In 2015, none of the eggs hatched, whereas in 2016 17% of all second clutch eggs hatched (Table 2.4). Additionally, the clutch size increased from 3.67 (2015) to 4.67 (2016) (Table 2.4). A factor that may have influenced the second clutch success in 2016 is the increase in rainfall during the breeding season.

Nest Failures

Across all three years, there was a total of 22 nest failures (i.e., unsuccessful at fledging at least one nestling) (Figure 2.3). Seven of the failed nests can be attributed to predation by raccoons or snakes, likely gopher snakes (*Pituophis catenifer*). Nine of the failure events were due to un-hatched eggs, where adults completed the incubation period, but the eggs did not hatch. Lastly, six of the failures were due to the adults abandoning the eggs before beginning incubation. All the nest abandonments took place during April (100%) (Figure 2.3). Most predation events occurred in May (86%) with the rest occurring in April (14%) (Figure 2.3). The clutches that did not hatch were scattered throughout the season (Figure 2.3). However, un-hatched clutches were greatest in June and July (Figure 2.3).

Discussion

Overall, the MVPGR's monitoring program banded of 30 new adults, 97 young, and recaptured of 16 kestrels. The increase in nest boxes on the MVPGR led to an increase in the number of young and banded adults. Banding will assist in furthering the examination of immigration patterns, return rates, and dispersal in kestrels on the MVPGR. For example, three females banded in 2012 and 2013 at the nearby Flying M Ranch were captured on the MVPGR. Additionally, two female siblings that were also banded at the Flying M Ranch in 2013 both nested as adults on the MVPGR in 2015 and 2016. These findings indicate that some adults will nest in the same general area where they hatched and that dispersal of young from their natal origin is minimal.

The nest box occupancy on the MVPGR for three years is comparable to other nest box studies, which vary from 45% to 75% (Varland and Loughin 1993, Breen and Parrish 1997, Smallwood and Collopy 2009). In Iowa, nest box occupancy averaged 45.1% (Varland and Loughlin 1993) and in Florida ranged from 55.9% to 75% with yearly fluctuations (Smallwood and Collopy 2009). Occupancy rates are known to fluctuate annually due to climate variation and changes in prey availability (Varland and Loughin 1993, Breen and Parrish 1997, Dawson and Bortolotti 2000). Some nest box studies have shown a long term trend of declining occupancy (Smallwood et al. 2009), while other studies have found that nest box occupancy has increased overtime (Smallwood and Collopy 2009, Steenhof and Peterson 2009). The increasing trends are likely due to locally hatched birds returning to their natal area as adults to nest. In this study, there has yet to be a recaptured adult that was banded on the MVPGR as a nestling, but returning kestrels that were banded in other local nest box programs were found. It is too early to determine any long term occupancy trends for the MVPGR program.

Reports on average clutch size range from 4.3 to 5.0 (Varland and Loughin 1993). The average clutch size in this study was 4.09. Environmental factors, such as food availability, population density, and climate have been known to influence clutch size in birds (Lloyd 1999). The MVPGR kestrels also showed seasonal variation in clutch size, where clutch size was higher in earlier months compared to later in the breeding season. Seasonal shifts in clutch size from high to low are common in other bird species depending on when the climate and resources are optimal (Crick et al. 1993). The optimal nest initiation time for greater clutch size appears to be in March, April, and May for the American Kestrel.

The average hatching rate over the three-year period is on the lower end of what has been found in other studies. Other studies conducted in North America varied from 62% to 89% (Varland and Loughlin 1993, Smallwood and Bird 2002, Smallwood and Collopy 2009), while the MVPGR is at 61%. One factor that may influence the hatching success is the age and size of the female. Younger and smaller females may not be capable of fully covering their clutch during the incubation period, resulting in lower hatching success (Bortolotti and Wiebe 1993). Future examination of size and age in adult females on the MVPGR may provide more insight on hatching success. Additionally, predation of eggs contributed to low hatching success on the MVPGR. Preventing predation will help to increase hatching success in future studies.

The average percentage of nestlings fledged on the MVPGR is comparable with reports from other studies. The MVPGR experienced an average of 85% fledging rate, whereas other studies reported between 85% and 98% (Varland and Loughin 1993, Smallwood et al. 2009). The drop-in fledging success over the three-year period (2014-2016) could be a result of an increase in predation. In 2016, there were more predation events on eggs and nestlings compared to previous years. Predators in the Merced area that are capable of preying on nestling kestrels include raccoons and gopher snakes. It is possible that there was an increase in the number of active predators in 2016 resulting in more predation events at nest boxes.

Although an increase in predator numbers is possible, it may well be that local predators are learning to associate nest boxes with prey. Predators learning to utilize artificial nest boxes for prey has been demonstrated in other cavity nesting birds (Nilsson, Johnsson, Tjernberg 1991, Martin and Li 1992, Martin 1993, Miller 2002). Predators can become more aware of nest sites that are older; an increase in predation risk is correlated to an increase in age of a nest sites (Martin and Li 1992). Tree Swallows (*Tachycineta bicolor*) in artificial nest boxes experience a reduction in nesting success overtime due to increases in predation by raccoons and snakes (Robertson and Rendell 1990), similar to what has been found in this study. In a study on Common Goldeneyes (*Bucephala clangula*), nesting in man-made structures, predation events on the same nest box in successive years was common (Dow and Fredga 1983). At the MVPGR one nest box experienced predation in 2014 and again in 2016, where eggs went missing in both years. Evidence indicates that predation may occur more frequently in kestrel nest boxes at the MVPGR in future years if not addressed.

Predation does not account for all nestling deaths and disappearances in this study. For example, in 2016 there were two nests that experienced unexplained deaths of nestlings. In the two nests, a total of five nestlings were found dead and were being consumed by their siblings. It is unknown if the cause of death was from siblings' attack or from other causes, such as starvation. It is not uncommon for kestrel nestlings to practice and experience cannibalism (Bortolotti, Wiebe, and Iko 1991). Cannibalism has been linked to the abundance of small mammals: when prey is low there is a higher frequency of cannibalism by parents and nestlings (Bortolotti, Wiebe, and Iko 1991).

Breeding productivity was the lowest in 2016 compared to the previous two years, due to a high number of nest failures. There was variation between years in the breeding productivity on the MVPGR, which could be influenced by climate, weather, and prey availability (Dawson and Bortolotti 2000). The increase in rainfall in 2016 compared to the previous years may have contributed to the increase in early nest abandonment and possibly the death of nestlings prior to fledging. However, it is difficult to determine any long-term trends regarding environmental conditions in relation to nesting success as this nest box program has only been in place for three years.

The results of the kestrel nest box occupancy and productivity study are similar to studies in various regions across the United States, indicating that breeding kestrels will occupy and be can be successful in a range of landscapes. This multi-year examination of kestrel productivity and the nest box program has provided insight in to areas of success and areas in which the project could improve. In the future, management of nest boxes should be focused on preventing predation and understanding reasons for unhatched eggs to increase nesting success.

Table 2.1. Banding summary for 2014-2016 adult and nestling American Kestrels. New adults, male and female, refer to adults that were captured for the first time and were not previously banded. Recaptured adult refers to adults that have been previously banded from this study or another.

Year	New Adult Females	Recaptured Adult Females	New Adult Males	Recaptured Adult Males	Nestlings Banded	Number of Boxes
2014	3	1	0	3	15	10
2015	8	3	0	5	44	30
2016	13	1	6	3	38	30

Table 2.2. Summary of American Kestrel productivity results (2014-2016). Hatching success refers to the percentage of eggs that hatch from the number of eggs laid. Fledging success refers to the percentage of nestlings that are suspected to have successfully fledged the nest. Percent success is the percentage of nests that were successful at fledging at least one young.

	2014	2015	2016	Averages
Number of Boxes	10	30	30	-
Number Occupied	6	18	24	-
Percent Occupied	60%	60%	80%	67%
Average Clutch Size	3.67	4.05	4.56	4.09
Total Eggs (n)	22	73	110	-
Total Hatched (n)	15	51	48	-
Hatching Success	68%	70%	44%	61%
Total Fledglings (n)	15	44	33	-
Fledging Success	100%	86%	69%	85%
Percent Successful	60%	61%	46%	56%

Table 2.3. Breeding productivity results by nest initiation month (2015 - 2016). Nest initiation month refers to the month in which the first egg was laid.

Nest Initiation Month	Number of Nests	Average Clutch Size	Hatching Success	Fledging Success	Percent Successful
March	13	4.54	63%	73%	54%
April	19	4.31	66%	80%	63%
May	4	4.50	11%	100%	25%
June	3	3.33	10%	100%	33%
July	2	3.50	0%	-	-

Table 2.4. Productivity of second clutch attempts (2015-2016). Results from females that had a first clutch earlier in the season and then attempted to have a second clutch later in the season. It was not determined if females had the same male mate in the second clutch as the first.

	Number of Nests	Average Clutch Size	Percent Hatched	Percent Successful
2015	3	3.67	0%	0%
2016	3	4.67	17%	67%

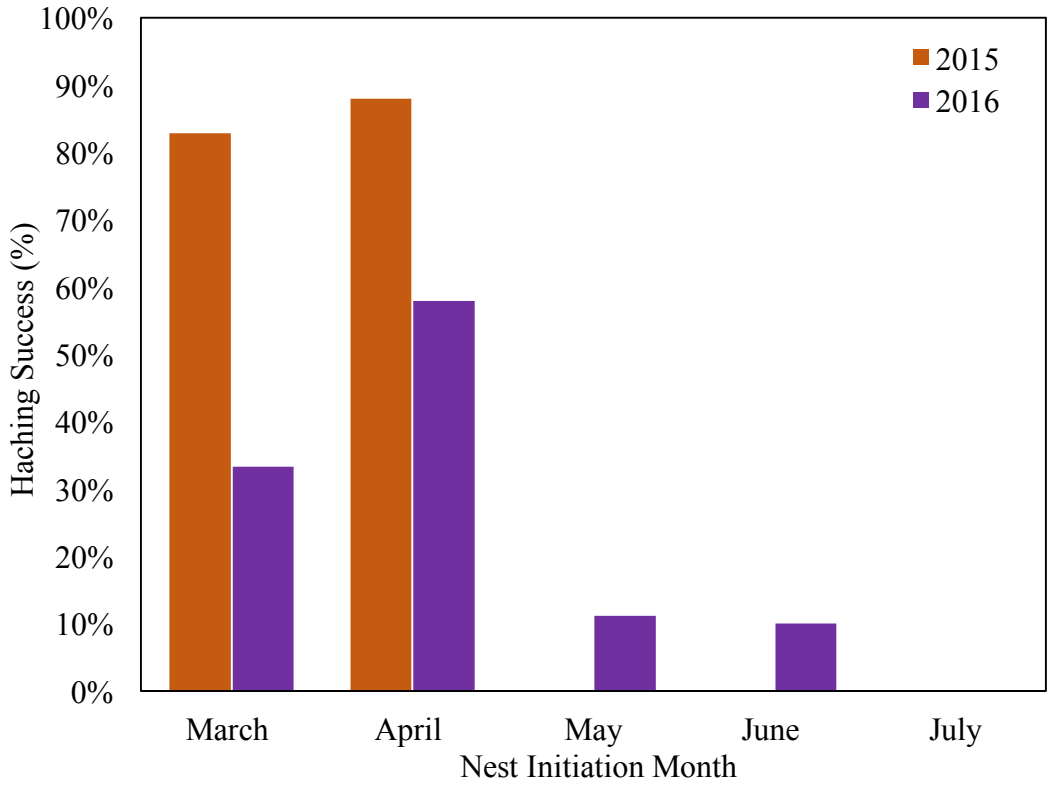

Figure 2.1. The hatching success by month for 2015 and 2016 indicated that 2015 had greater success in March and April. Although the hatching success in 2016 was lower overall there was hatching success observed in later months, May and June. In 2015, there were nest attempts in July; however, none of those attempts were successful.

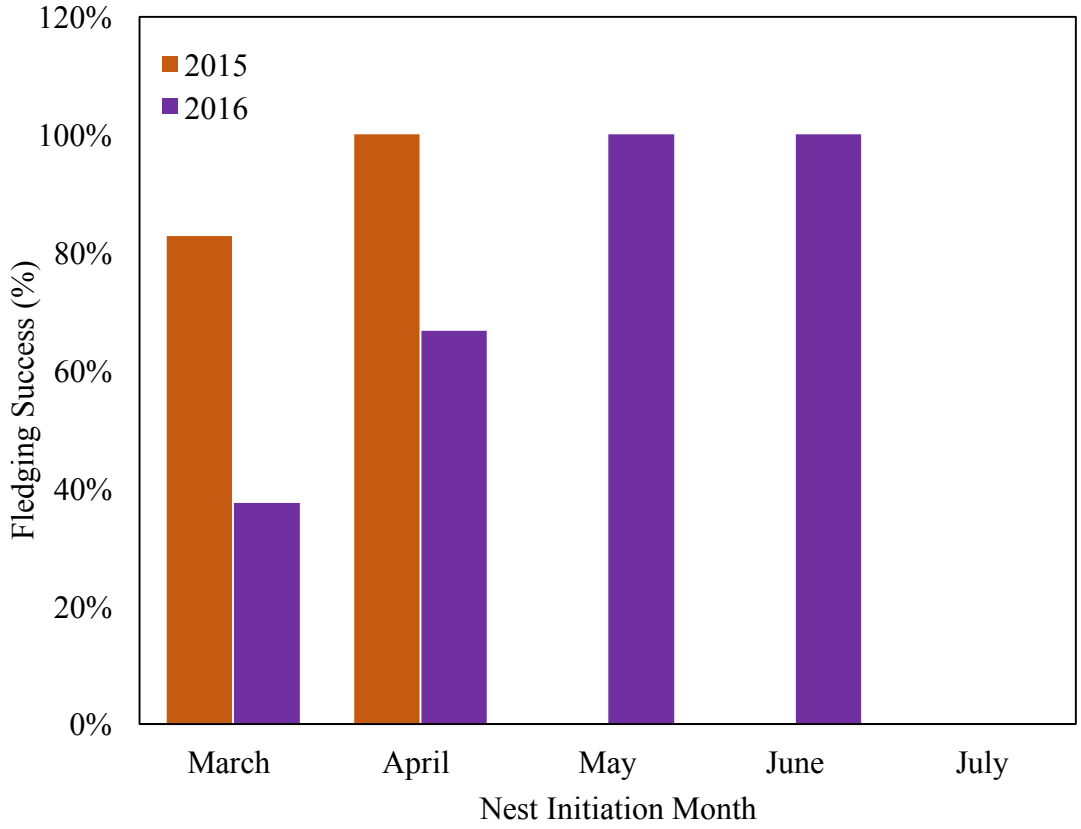

Figure 2.2. Fledging success for 2015 and 2016 by nest initiation month. In 2015, the fledging success was greater for nests that had earlier nest initiation dates than nests that began in March and April. None of the nests initiated in May and June were successful in 2015 at fledging nestlings. In 2016, there was 100% fledging success in both May and June.

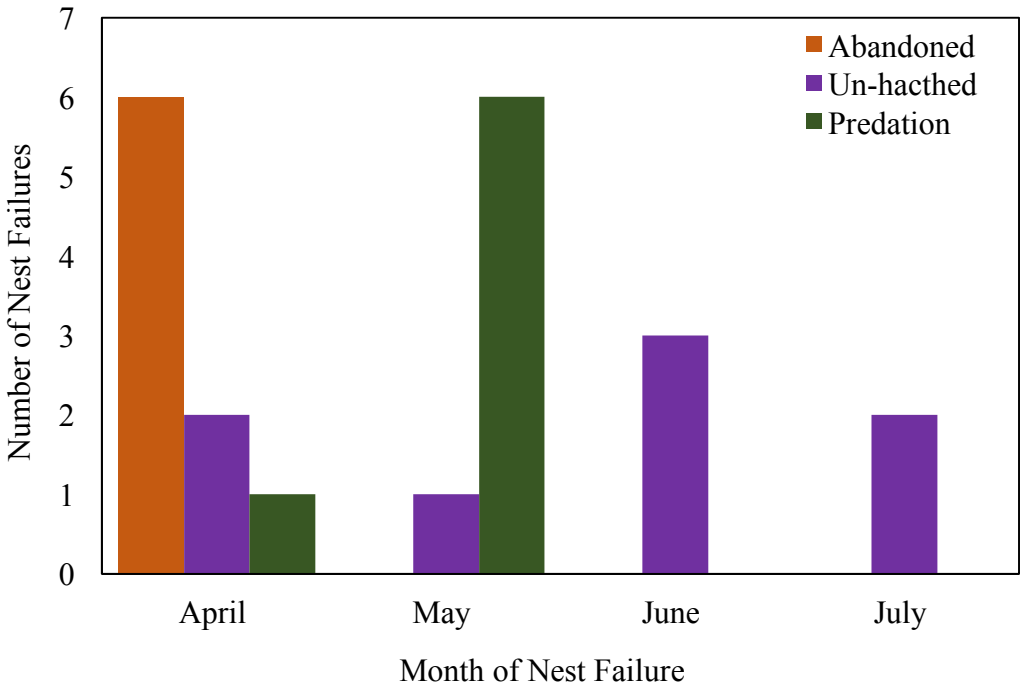

Figure 2.3. The distribution of nest failures through the breeding season for all three years (2014-2016). Abandoned nest (n=6) refers to nests with eggs that were not seen with an incubating adult. The unhatched eggs (n=9) are eggs that were observed being incubated by adults on more than one occasion. Most predation events occurred primarily in May (n=7) and were determined to be either from raccoons or snakes. Abandoned nests are only seen in April and contribute significantly to the number of failures observed during April. Unhatched eggs were witnessed in all months, however, June and July have more compared to April and May. This is likely due to the failures of second clutch attempts. For abandoned nests and nest with all unhatched eggs the nest initiation month was used.

CHAPTER 3: DETERMINING AMERICAN KESTREL DIET BREADTH AND VARIATION USNG PREY REMAINS AND STABLE ISOTOPE ANALYSIS OF $\delta^{15}N$, $\delta^{13}C$, AND $\delta^{2}H$

Introduction

Diet and food availability are closely linked to reproductive success in avian species (Simons and Martin 1990, Richner 1992, Wiehn and Korpomaki 1997), with prey abundance and prey availability often acting as the most important limiting factors (Vali, 2012). Additional factors such as food resource type (i.e., vertebrate versus invertebrates) can influence nestling development and survival in raptor species (Wiehn and Korpomaki 1997), ultimately affecting species success. During periods of low prey abundance, diet breadth and composition will change (Roughgarden 1972, Thompson and Colgan 1990) with the potential to influence reproductive output and nestling fledging success (Lacombe, Bird, and Hibbard 1994). In birds, food resource use, food niche breadth, and trophic position can vary between individuals and temporally within a population (Resano-Mayor 2014). Examining how diet changes through time and within a population is essential to gaining insight on reproductive success, growth, and survival.

It is common to find variation in diet composition and food niche width within and between populations (Jaksic and Braker 1982). For generalist species, diet breadth and composition are heavily influenced by habitat type, the availability of prey, yearly and seasonal climate, and foraging behaviors (Dawson and Bortolotti 2000). In a wide-ranging species, such as the American Kestrel, diet has the potential to differ across landscapes. Diet variation in American Kestrel has been documented in different habitat types in South America (Sarasola, Santillan, and Galmes 2003, Santillan et al. 2009). Santillan and colleagues (2009) found that kestrel diets differed across different landscapes in Argentine Patagonia and differed between years depending on environmental conditions. Environmental conditions, such as severe drought, may influence diet composition and variation in kestrel populations. By determining the diet breadth and composition under varying environmental conditions key prey resources of a population can be identified.

Different prey resources may contribute to differential breeding success of American Kestrels. In Argentine Patagonia, it was determined that vertebrate species were major biomass contributors to diet despite even though, numerically, invertebrates dominated kestrel diets (Santillan et al. 2009). In many regions, the biomass of vertebrate prey changes seasonally, contributing to a seasonal shift in predator diets (Nilsson 1981, Ben-David, Flynn, and Shell 1997). Changes in seasonal density or abundance in prey could influence the diet composition of kestrels and ultimately their breeding success. For example, kestrels that nest earlier in the spring season, when it is cooler, may have more vertebrates in their diet compared to late nesting kestrels. Changes in diet due to nest timing may give early nesting birds an advantage over birds nesting later in the year due to the availability of prey resources.

Diets of raptors and other bird species are typically examined by identifying animal remains found in pellets and in nests or by using trigger cameras at nest sites. A few caveats exist with using these standard diet practices (Garcia-Salgado et al. 2015). For example, with raptors that do not swallow their prey whole, like the kestrel, it is difficult to estimate the number of vertebrate prey in pellets (Marti, Bechard, and Jaksic 2007). In prey remains, it is often difficult to identify species of small mammals and birds, because parents often pluck, skin, and tear up the prey away from the nests (Redpath et al. 2001). Nest cameras allow for better identification and totals compared to pellets and prey remains. Smaller prey items such as small birds and invertebrates are often too small to see in camera pictures (Garcia-Salgado et al. 2015). Additionally, using these common methods does not always allow for determining variation among individuals. For example, there may be diet variation between the male and female of a breeding pair, between nestlings and adults, or variation between nestlings in the same brood. Stable isotope analysis (SIA) in conjunction with standard diet analysis practices has the potential to offer more insight on population and individual diet variation.

Using SIA of feather tissue in birds is a less invasive way to examine diet compared to gut content analyses and is less labor intensive compared to pellet dissection and prey identification. One feather can take days to a week to fully form and can reflect the diet of an individual from a specific point in time (Bearhop et al. 2002). To use feathers in SIA, the molt pattern of the species needs to be well known, because the timing of when different feathers grow (i.e., primary vs. body feathers) is important for determining diet at a particular time and location. For adult kestrels, molting begins at the start of the breeding season (Pyle 2005), therefore, molted feathers collected will reflect the diet from the previous year. For nestlings, juvenile plumage begins to form approximately two weeks after hatching (Bird and Clark 1983).

Stable isotopes of nitrogen and carbon are commonly used to examine diet and trophic position. The $\delta^{15}N$ composition of an animal is generally an indicator of trophic level, where an enrichment of $\delta^{15}N$ designates a higher trophic position (DeNiro and Epstein 1981, Minagawa and Wada 1984). The $\delta^{13}C$ of plants and animals can also help track energy flow through food webs (Jones et al. 1979) and is used to detect photosynthetic pathways in plants (Farquhar, Ehleringer, and Hubick 1989). C_3 and C_4 plants have distinct carbon isotopic compositions ($\delta^{13}C$) in which $\delta^{13}C$ of C_3 plants are more negative (e.g., -23 to -30‰) relative to the $\delta^{13}C$ values of C_4 plants (e.g., -10 to -14‰) (Farquhar, Ehleringer, and Hubick 1989). Stable isotopes of hydrogen ($\delta^{2}H$) have primarily been used in migratory studies in ecology and less frequently to examine diets and trophic positions in animals (Estep and Dabrowski 1980, Hobson, Atwell, and Wassenaar 1999, Birchall et al. 2005, Doucett et al. 2007, Finlay et al. 2010, Vander Zaden et al. 2016). Studies on various animals have shown that 70-90% of tissue hydrogen originates from an individual's diet, rather than drinking water (Podlesak et al. 2008, Wolf et al. 2011). Hydrogen isotopes can be particularly useful in tracking trophic level when combined with $\delta^{15}N$ and $\delta^{13}C$. Adding an additional diet tracer allows one to run more expansive models of diet composition such as adding more prey items (Phillips et al. 2014). The

addition of an added isotope system (e.g., δ^2H) is even more important in landscapes dominated by all C_3 plants, as is the case in Central California.

The goal of chapter three was to examine diet niche breadth and variation between American Kestrels occupying nest boxes on the Merced Vernal Pools and Grassland Reserve (MVPGR) using prey analysis and SIA. The first objective was to examine diet composition and breadth. I hypothesized that diet breadth and composition due to environmental conditions and will vary from 2015 to 2016 depending on environmental changes. The second objective was to examine dietary niche variation between occupied nest boxes. I hypothesized that, in 2015, nest boxes would have more overlap and less diet variation, because prey is likely to be more limited during a dry year. In contrast, I expected 2016 nest boxes to have more diet variation and less overlap in diet between nest boxes. Lastly, I hypothesized that there would be dietary differences between adult and nestling American Kestrels during the breeding season. Understanding how diets differ within a population could assist in identifying variation in foraging strategies and provide insight on habitat characteristics.

Methods

Study Site

The Merced Vernal Pools and Grassland Reserve (MVPGR) is a 2,656-ha protected reserve adjacent to the University of California Merced campus located in Merced County, California. The MVPGR is an open grassland habitat that contains seasonal vernal pool coverage during winter and early spring with minimal tree coverage. The vegetation consists of annual grasses and forbs with willow species (*Salix spp*.). Ten American Kestrel nest boxes were placed along pre-existing fence posts in 2014 and an additional 20 nest structures were added in 2015.

Pellet Collection and Analysis

Pellet collection took place at occupied kestrel nest boxes during the breeding season months (March through July) in 2015 and 2016 on the MVPGR. Pellets were collected from underneath nest boxes bi-weekly from the start of incubation until all young had fledged. Additionally, pellets were collected from within the nest box during times when adults and nestlings were banded. In 2015, there were 90 pellets collected from 11 occupied nest boxes. In 2016, there were 84 pellets collected from 11 occupied nest boxes.

All pellets were taken to the Stable Isotope Laboratory at the University of California, Merced for dissection and analysis. Pellets were broken apart by hand and with forceps, then the remains of prey items were separated for identification. Invertebrates were identified down to the lowest possible taxonomic group using distinguishable characteristics such as mandibles, heads, legs, and elytra. Using the identifiable invertebrate body parts, a minimum number of individuals (MNI) was estimated for each pellet. Mandibles and hind tibia were counted to estimate MNI of orthopterans, elytra were counted to estimate MNI of beetles, and chelicerae were counted to estimate MNI

of spiders. For vertebrate species, it was only possible to determine the presence or absence of major groups of prey (e.g., birds, mammals, reptiles), because American kestrels do not swallow their prey whole and only remnants of birds and mammals are found in pellets.

Prey Remains

Prey remains from inside the boxes were collected while banding adults, banding nestlings, and after all young had fledged from occupied kestrel boxes with successful clutches.

All prey remains collected from occupied boxes were identified down to the lowest possible taxonomic group and the number of individuals consumed was estimated based on identifiable body parts. Similar to pellets, invertebrates were identified using distinguishable characteristics such as mandibles, heads, legs, and elytra. Using the identifiable invertebrate body parts, a minimum number of prey individuals was estimated for each nest box.

To determine species and quantity of avian prey, box contents were carefully examined for feathers, beaks, legs, wings, and other bone structures. Feathers from non-kestrel avian species found inside nest boxes were compared to known feathers to determine species. For mammals, the skulls or dentaries were used to identify the prey down to genus. When dentaries or skulls were not present, other characteristics were used to determine genus, for example, limb length and shape, tail length, and fur color. For reptilian prey, the number of tails found within a box were used to determine quantity, however, the specific species were not identified.

Feather Collection from Kestrels

For adult American Kestrels, feathers were collected opportunistically from inside occupied nest boxes during 2015 and 2016. Feathers were identified to be male (n = 3) or female (n = 18) by examining coloration. In 2015, nestling pinfeathers (n = 9) were collected opportunistically from inside occupied nest boxes. Due to the size and lack of formation of the pinfeathers sex was unidentifiable. During the 2016 breeding season, feathers were collected directly from individual nestlings after juvenile plumage appeared at approximately 20 days of age. Three breast or body feathers were collected from two nestlings from each successful nest, one male (n = 8) and one female (n = 7) if both sexes were present. Three to four feathers were necessary for replication and to examine possible variation in stable isotopes of an individual. Variation was not found within individuals (Appendix A Table A.1). All American Kestrel nesting feathers were collected under United States Geological Survey (USGS) Permit number 20416 and California Scientific Collecting Permit number SC-13366. All capturing procedures followed the Animal Care Protocol guidelines approved by the University of California, Merced (IACUC #AUP14-0002).

Stable Isotope Analysis

All feathers from American Kestrels and avian prey (n = 41) were first rinsed in deionized water, then rinsed in 2:1 chloroform methanol, followed by a final rinse in deionized water. Feathers were then left to air-dry for 24 to 48 hours in a fume hood, until dry. Then feathers were placed inside clean whorl pack bags and left open for two to three weeks until prepped for SIA. Approximately 0.650 mg +/- 0.100 of feather was cut from mid-feather across the vein for SIA of carbon and nitrogen. For hydrogen isotopes 0.150 mg +/- .05 of feather tissue was cut from mid-feather across the vein.

To investigate the proper cleaning procedure for arthropods, chitin was collected from kestrel nest boxes in 2015 and four initial treatments were applied prior to stable isotope analysis of carbon and nitrogen. Members from Order Orthoptera (n = 9), Araneae (n = 9), and Odonata (n = 9) were included in each treatment. Treatment A was to grind chitin with no rinsing, treatment B was grinding chitin and rinsing three times in deionized water, treatment C was to rinse whole pieces of chitin three times in deionized water, and treatment D was whole un-rinsed chitin pieces. All treatments were dried in an oven at 50°C for 24 to 48 hours, until completely dried. The exoskeletal pieces were left in clean 2 ml micro-centrifuge tubes for approximately one week until stable isotope analysis preparation. Approximately 0.500mg +/- .100 of material was used for carbon and nitrogen isotope analysis. After analyzing the four treatments it was determined that whole chitin pieces rinsed well in deionized water worked best to limit variability.

For Order Orthoptera (n = 56), the hind tibias were used from families of Tettigoniidae (katydids), Caelifera (grasshoppers), and Gryllidae (crickets). For the Order Araneae (n = 29), a combination of chelicerae, tibia, metatarsus, and tarsus were selected for analysis, whereas the elytra from Order Coleoptera (n = 15) were analyzed. All pieces of invertebrate exoskeleton were rinsed three times in deionized water and were dried in an oven at 50°C for 24 to 48 hours, until fully dried. Once exoskeletal pieces were dry, they were left in clean 2 ml micro-centrifuge tubes for two to three weeks until stable isotope analysis preparation. For SIA, 0.500mg +/- .100 of material was used for carbon and nitrogen isotopes. For hydrogen isotopes 0.150 mg +/- .05 of material was used.

For stable isotopes of mammals, bone collagen was selected from mammal nest box prey remains. Between 30-60 mg of bone from *Thomomys* (n = 4), *Dipodomys* (n = 4), *Microtus* (n = 1), and *Peromyscus* (n = 1) were placed in micro-centrifuge tubes with 1.5 ml of 1N HCl at 4°C for 24 hours. After 24 hours, the HCl was decanted, and the collagen samples were rinsed in deionized water five times to neutrality. The collagen was then freeze-dried for 24-48 hours, until fully dried. When dry, collagen becomes opaque and hard. For stable isotopes of carbon and nitrogen between 0.400 - 0.600 mg of material was used. For hydrogen isotope analysis, 0.150 - 0.200 mg of material was cut from the collagen and weighed into a silver boat. Stable isotope analysis was replicated two more times for each individual to investigate within individual variation. No individual variation was found for mammal collagen.

Tails of lizards (n = 13) found within kestrel nest boxes were lipid extracted prior to SIA by first rinsing in deionized water to remove any bird excrement or debris. Approximately 1-2 mg were cut an inch up from the tip of the tail and placed in a 2 ml glass vial in which 2:1 chloroform methanol was poured until tissue was completely covered. The tissues were left for 24 hours in a fume hood. After the 24-hour period, the 2:1 chloroform methanol was decanted, then remaining tissue was rinsed using deionized water. Tails were placed in 2 ml plastic centrifuge tubes and freeze dried until tissues were completely dry, approximately 12 hours. Samples were left inside 2 ml centrifuge tubes until stable isotope analysis preparation. Approximately, 0.500mg +/- .100 of material was used for SIA of carbon and nitrogen and 0.150 mg +/- 0.05 of material was used for hydrogen.

All American Kestrel and prey tissue samples were weighed into 5 x 3.5 mm tin boats (carbon and nitrogen isotopes) and analyzed using a Costech Instruments elemental combustion system (EA) coupled to a ThermoFisher Delta V Plus isotope ratio-mass spectrometer via a Conflo IV interface. All samples were analyzed with a series of standards of known values, which include Acetanilide ($\delta^{15}N$ = -0.75‰ and $\delta^{13}C$ = -27.86‰), peach leaf ($\delta^{15}N$ = 1.98‰ and $\delta^{13}C$ = -25.99‰), and glycine ($\delta^{15}N$ = 11.25‰ and $\delta^{13}C$ = -36.57‰) for carbon and nitrogen. For hydrogen isotope ratios, all samples were weighed into 5 x 3.5 mm silver boats for reaction in a Thermo-scientific TC/EA and a ThermoFisher Delta V Plus isotope ratio-mass spectrometer. For hydrogen, all samples were run with the following standards: stearic acid ($\delta^{2}H$ = -233‰), chicken feather ($\delta^{2}H$ = -93.4‰), turkey feather ($\delta^{2}H$ = -53.9‰), mineral oil ($\delta^{2}H$ = -110‰), and pump oil ($\delta^{2}H$ = -112‰). Stable isotope ratios are reported in the δ notation:

$$\delta X = \left[\left(\frac{R_{sample}}{R_{standard}}\right) - 1\right] * 1000\ (‰)$$

where, δX refers to either $\delta^{15}N$, $\delta^{13}C$, and $\delta^{2}H$, R is the ratio of heavy to light isotopes for nitrogen, carbon, and hydrogen for the sample and the international standards. The measurements of precision of Acetanilide were $\delta^{15}N$ = -0.61‰ ± 0.3 and $\delta^{13}C$ = -28.2‰ ± 0.3, peach leaf $\delta^{15}N$ = 2.43‰ ± 0.3 and $\delta^{13}C$ = -25.9‰ ± 0.4, and for Glycine $\delta^{15}N$ = 11.6‰ ± 0.3 and $\delta^{13}C$ = -36.6‰ ± 0.5. The measurements of precision of stearic acid were $\delta^{2}H$ = -231‰ ± 5, mineral oil $\delta^{2}H$ = -109‰ ± 3, pimp oil $\delta^{2}H$ = -107‰ ± 3, chicken $\delta^{2}H$ = -88‰ ± 3, and for turkey $\delta^{2}H$ = -57‰ ± 3.

Statistical Analyses

To quantify dietary niche breadth for each of the two years, the Levins' index of food niche breadth (Colwell and Futuyma 1971) was used:

$$B = 1/\Sigma p_i^2$$

where p_i represents the proportion of prey type i of the diet from all nest boxes. Then, the B for each year was standardized using:

$$B_{sta} = \frac{B - B_{\min}}{B_{max} - B_{min}}$$

where B_{sta} is the standardized niche breadth (a value between 0 and 1), B_{min} is the minimum possible niche breadth or the minimum number of diet items a population could consume ($B_{min} = 1$), and B_{max} is the maximum number of individuals found in the nest box populations diet each year.

A Two-way Analysis of Variance (ANOVA) was used to test for statistical significance between the proportions of vertebrate prey per box in 2015 compared to 2016. An ANOVA was also used to test the statistical significance in invertebrate prey per box in the populations diet between 2015 and 2016.

To investigate individual specialization (specialization of each nest box) the Proportional Similarity Index (PS_i) was calculated using the R package RInSp (Zaccarelli, Bolnick, and Mancinelli 2015). To determine PS_i, first the populations diet in 2015 and 2016 was calculated by averaging the proportions of prey type found at each individual box (Bolnick et al. 2002). Then PS_i was calculated:

$$PS_i = 1 - 0.5 \sum_j |p_{ij} - q_i|$$

where, p_{ij} is the proportion of prey type j in clutch i's diet and q_i is the proportion of prey type j in the population's diet. PS_i values are reported on a scale from 0 to 1, where 0 indicates a diet completely dissimilar from the population and 1 represents an identical diet to the populations. To compare between the two year, the average PS_i was also calculated for the population for each year (Zaccarelli, Bolnick, Mancinelli 2015):

$$IS = \frac{\sum_i (PS_i)}{N}$$

Additionally, the standardized likelihood of an observed diet being pulled from the populations (λ_i) and the associated p-value, as described by Petraitis (1979), was used to test significance of an individual's diet. The λ_i was used to test the null hypothesis that individuals do not have a significant deviation from the population using a 0.05 significance level (Bolnick et al. 2002). The probability of the likelihood of an observed diet being pulled from the population (λ_i) was calculated:

$$(\lambda i) = \prod_j (q_j / p_{ij})^n$$

Where q_j is the populations proportion of resource j, p_{ij} is proportion of resource j in an individual's diet, and n represents n is the number of items for individual i and resource the resource j (Zaccarelli, Bolnick, Mancinelli 2015). Petraitis' W value was then calculated for each nest box to determine an individual's niche width, which is given on a

0 to 1 scale where 0 represents complete specialization and 1 represents no specialization (Petraitis 1979):

$$W_i = \lambda_i^{(\frac{1}{D})}$$

where D is the number of diet items recorded in an individual's diet. All λ_i measurements, hypothesis testing, and W_i values were completed using the R package RInSp Likelihood function (Zaccarelli, Bolnick, and Mancinelli 2015).

Two-way t-tests were used to examine variation in $\delta^{15}N$, $\delta^{13}C$, and $\delta^{2}H$ of adults and nestlings as well as variation between 2015 and 2016. Two-way t-tests were also used to explore variation in $\delta^{15}N$, $\delta^{13}C$, and $\delta^{2}H$ of prey items between the two study years.

To compare isotopic niche space and examine isotopic variation in prey items and American Kestrels, I estimated Bayesian standard ellipse areas (SEA_B) using $\delta^{15}N$ and $\delta^{13}C$ (Jackson et al. 2011). Additionally, the small sample size-corrected standard ellipse areas (SEA_C) was also calculated and used to compare the different groups of prey to one another. The SEA_C of the kestrel groups was also calculated. All Bayesian standard ellipses data was calculated using the SIBER package in R (Jackson et al. 2011).

Once the isotopic composition of prey is known, we can then use these values along with the isotopic composition of kestrels to estimate the diet composition. To examine the diet composition of adults and nestling between two years Bayesian mixing models in the SIAR package of R were used (Parnell and Jackson 2013). The top proportions of vertebrate and invertebrate prey items from each year, obtained from pellet and prey remain analysis, were used as diet sources. Species were grouped into larger orders (i.e. Aves, Mammalia, and Orthoptera) for the SIAR analyses. For 2015, mammals, birds, orthopterans, and spiders were used to determine diet proportions of nestlings and adults collected in 2015. For adults collected in 2016, the 2015 data from mammals, birds, orthopterans, and spiders were used, because feathers molted and collected in 2016 would reflect adult diets in 2015. For 2016 nestlings, the groups used were mammals, birds, orthopterans, and spiders. Mean (± SD) discrimination factors for $\delta^{15}N$ and $\delta^{13}C$ were estimated using reports on avian species from Hobson and Clark (1992) and Caut, Angulo, and Courchamp (2009). For $\delta^{15}N$, a discrimination factor of 2.8‰ ± 1.25 and for $\delta^{13}C$ 1.25‰ ± 0.98 was used. For $\delta^{2}H$, a discrimination factor of 30‰ ± 10 was used.

Results

Diet Breadth and Composition

A total of 906 prey items were identified in 2015 from analyzing pellets and prey remains from 11 occupied nest boxes (Table 3.1). Of the vertebrate prey, birds were the most abundant, which included unknown species (n=13), *Eremophila alpestris* (horned lark) (n=4), and *Petrochelidon sp.* (cliff swallow) (n=1) (Table 3.1). *Thomomys sp.* (pocket

gopher) were the most abundant mammalian prey; *Peromyscus sp.* and *Microtus sp.* (Vole) were also present. Lizards were the least prevalent vertebrate in 2015 (Table 3.1) (Figure 3.1). Five different orders of invertebrates were identified in 2015: Orthoptera (grasshoppers, katydids, crickets), Araneae (spiders), Coleoptera (beetles), and Chilopoda. Spiders were the most numerous invertebrate prey (n=415) followed by grasshoppers and katydids (n=342) (Table 3.1).

For 2016, there was a total of 1609 prey items identified from 11 nest boxes (Table 3.1). Birds, mammals, and lizards made up the vertebrate prey composition with birds being the most predominant vertebrate prey (Table 3.1). Two nests had instances of cannibalism, where nestlings consumed their siblings (Table 3.1). *Dipodomys sp.* (kangaroo rat) were the only identified mammals (n=2) and there were five unknown mammalian species (Table 3.1). The invertebrate prey was comprised of spiders, orthopterans, dragonflies, chilopods, and one hymenopteran (Table 3.1). Spiders (n=900) were the most abundant prey in 2016 followed by grasshoppers and katydids (n=595) (Table 3.1).

The average proportion of vertebrate prey per nest box did not vary in 2015 compared to 2016 (Figure 3.1). The total number of mammals in each year was the same (n=8). The number of individuals consumed for avian prey increased in 2016 (Table 3.1, Figure 3.1). Lizards were consumed in both years but increased in number from 2015 to 2016 (Table 3.1, Figure 3.1). There was no significant difference between the total proportions of all vertebrate prey per box in 2015 compared to 2016 (ANOVA, F Stat = 1.561, df = 20, p-value > 0.05).

Of the seven orders or sub-orders of invertebrates identified over the two years, all orders were present in both years except for Hymenoptera (Table 3.1). For both years, the majority of invertebrate prey was comprised of orthopterans, primarily grasshoppers, and spiders (Table 3.1, Figure 3.2). The number of invertebrate prey was greater in 2016 (n = 1560) compared to 2015 (n = 876), although the average proportions per box were similar (Figure 3.2). No significant difference was found between the total proportions of all invertebrate prey per box consumed in 2015 compared to 2016 (ANOVA, F Stat = 1.560, df = 20, p-value > 0.05) (Figure 3.2).

Diet breadth in 2015 (B_{sta} = 0.15) was slightly greater compared to 2016 (B_{sta} = 0.10). In 2015 there were 16 different types of prey identified and only 14 different types in 2016. Overall, diet breadth in both years was on the low.

Nest Box Diet Variation

Of the 11 nest boxes sampled from in 2015, most of the boxes contained fundamentally the same types of prey (Appendix A Table A.2) (Figure 3.3). All the nest boxes in 2015 contained some proportions of spiders and orthopterans (Figure 3.3), a few nests contained almost all grasshoppers (nest box 20) or all spiders (nest box 2 and 16) (Figure 3.3). Vertebrate prey, which was always at very low abundance relative to invertebrate prey, was absent from five nest boxes (Figure 3.3) and only one nest box had lizard

remains (nest box 25) in 2015. Bird prey items were found at all nests except for one (box 20) (Table 3.3) (Appendix A Table A.2).

Prey proportions differed more dramatically between nest boxes (n = 11) in the 2016 breeding season (Figure 3.4) (Appendix A Table A.2) though spiders and orthopterans were found at all nests, three nests contained extremely high proportions of spiders and another three contained high proportions of orthopterans (Figure 3.4) (Appendix A Table A.2). Beetles were found in minimal proportions in nine of eleven kestrel boxes. Avian prey was found at all nest boxes. The proportions of avian prey varied between nests (Figure 3.4). Mammal prey was present in seven boxes, while lizards were present in only five (Appendix A Table A.2).

Evidence for seasonal variation was estimated in 2016 prey proportions (Figure 3.4). In 2016, spider prey abundance decreased in nests that were initiated at later dates (Figure 3.4). The amount of orthopteran prey increased in nest boxes that were initiated in later months compared to earlier nest initiations for 2016 (Figure 3.3, Figure 3.4). Avian and mammalian dietary components varied throughout the season and lizards were only present in later nests in both years (Figure 3.3, Figure 3.4).

Overall, diet analyses indicated that prey found in kestrel nest boxes in 2016 was slightly more variable compared to 2015 (Table 3.2, Figure 3.3, Figure 3.4). The average Proportional Similarity Index (PS_i) of the 2015 population was 0.687 and was 0.669 in 2016, indicating there was more similarity in prey in nest boxes in 2015 than 2016 (Table 3.2). The average Pairwise Overlap between nest boxes was slightly greater in 2015 (0.567) compared to 2016 (0.527). Lastly, the average individual food niche breadth (W_i) values indicated that niche breadth in 2015 ($W_i = 0.712$) was greater than in 2016 ($W_i = 0.697$) (Table 3.2).

Fewer nest boxes showed diet variability in 2015 compared to 2016. In 2015, none of the nest boxes had proportional similarity index values less 0.500 and only three nest boxes (# 2, 20, and 29) had low Pairwise Overlap values less than 0.500 (Table 3.2). Only one nest box in 2015 had a low diet breadth (W_i) of 0.163, which indicates more generalists in the population (Table 3.2). In comparison, there were six nest boxes (# 3, 6, 7, 12, 14, 29) that had diets that overlapped less with one another, having Pairwise Overlap values less than 0.500 (Table 3.2). Boxes that had low overlap had high proportions of only one type of invertebrate (Figure 3.4). Two (#3 and #7) of the six boxes had Proportional Similarity Index values less than 0.500 indicating that they are more dissimilar from the population (Table 3.2, Figure 3.4). There were two nest boxes (# 7 and #29) that small food niche breadth (W_i) less than 0.500 (Table 3.2).

Stable Isotope Analysis

For stable isotope analysis, prey items were grouped by major classifications of mammals, birds, lizards, Araneae (spiders), Coleoptera (beetles), and Orthopterans (grasshoppers, katydids, and crickets). In general, variation in stable isotopes of prey was seen within various prey groups for $\delta^{15}N$, $\delta^{13}C$, and $\delta^{2}H$ (Table 3.3) (Appendix A Table

A.3, Table A.4, Table A.5, Table A.6). Variation between years was seen within some groups, though there was no consistent trend in variation between all three isotopes ($\delta^{15}N$, $\delta^{13}C$, and $\delta^{2}H$).

There were four different feeding guilds identified amongst the prey: herbivores, omnivores, carnivores, and detritivores. Herbivores, such as orthopterans, had mean $\delta^{15}N$ values 3.7‰ ± 1.9 in 2015 and 4.3‰ ± 1.5 in 2016 (Table 3.3). Other herbivores in 2015 included individuals from the small mammal group (mean $\delta^{15}N$ = 4.8‰ and 5.3‰). Higher $\delta^{15}N$ values of small mammals in 2016 indicated some herbivorous as well as omnivorous individuals within the population ($\delta^{15}N$ range = 2.5‰ to 7.3‰). Order Coleoptera is comprised of various species of herbivores, detritivores, and omnivores, and their $\delta^{15}N$ values ranged from 2.1‰ to 5.9‰ in 2015 and 2.3‰ to 10.7‰ in 2016 (Table 3.3). Initially, birds were identified as omnivores, but mean $\delta^{15}N$ values of 9.5‰ ± 0.70 in 2015 shows evidence for insectivorous species within the bird group (Table 3.3). In 2016, mean $\delta^{15}N$ for birds was 6.6‰ ± 1.7 (Table 3.3), perhaps indicating more herbivorous horned larks in their diet. Lizards ($\delta^{15}N$ = 5.9‰ ± 0.64 in 2015, 7.2‰ ± 0.73 in 2016) and spiders (Araneae) ($\delta^{15}N$ = 8.1‰ ± 1.7 in 2015, 6.9‰ ± 1.5 in 2016) (Table 3.3) are both carnivores. For $\delta^{15}N$, there was little variation in prey values between years, except for the avian group ($t = 7.8$, $df = 38$, $p < 0.05$) and lizards ($t = -3.3$, $df = 9.60$, $p < 0.05$).

The mean $\delta^{13}C$ values in 2015 were -25.7‰ ± 0.80 and -24.3‰ ± 2.4 for orthopterans and small mammals (Table 3.3). For 2016, the mean $\delta^{13}C$ values for orthopterans decreased to -27.5‰ ± 0.66, but mammals showed no change (mean $\delta^{13}C$ = -24.4‰ ± 1.3) (Table 3.3). Across year variation for $\delta^{13}C$ in beetles was not seen: mean $\delta^{13}C$ values were -26.6 ± 0.61 in 2015 and -27.7‰ ± 1.1 in 2016 (Table 3.3). For birds, variation within 2015 was low (range = -19.9‰ to -22.7‰) and in 2016 the range was larger (-21.4‰ to -25.4‰). For spiders, variation was seen within 2015 (mean $\delta^{13}C$ = -25.3‰ ± 1.5), but not in 2016 (mean $\delta^{13}C$ = -28.0‰ ± 0.49) (Table 2.3). The range of $\delta^{13}C$ in spiders was large for 2015: -22.7‰ to -26.7‰. Conversely, lizards were more variable in 2016 (mean $\delta^{13}C$ = -22.4‰ ± 1.6) compared to 2015 (mean $\delta^{13}C$ = -24.2‰ ± 0.27) (Table 3.3). More prey groups experienced variation between years in $\delta^{13}C$ values then in $\delta^{15}N$ values. Lizards, orthopterans, spiders, and bird $\delta^{13}C$ all differed significantly (t-test, $p < 0.05$) between 2015 and 2016.

All prey groups displayed low within year variation for $\delta^{2}H$ with majority having a standard deviation (SD) less than 15‰ except for mammals (Table 3.3). Orthopterans mean $\delta^{2}H$ in 2015 was -68.5‰ ± 8.2 and -73.8‰ ± 9.4 in 2016. Lizards showed no within year variation (Table 3.3). Birds, beetles, and spiders showed very little variation within a year (Table 3.3). Mammalian bone collagen, conversely, displayed a large amount of variation in $\delta^{2}H$ values with high standard deviations in 2015 (SD = 27.2) and in 2016 (SD = 24.2). The range for $\delta^{2}H$ in mammals for 2015 was between -39.5‰ to -106.3‰ and was -79.1‰ to -116.8‰ in 2016. I found no indication that this variation was related to species differences. For example, *Dipodomys* $\delta^{2}H$ ranged from -41.7‰ to -87.5‰, while $\delta^{2}H$ in *Thomomys sp.* bone material ranged from -39.5‰ to -85.8‰

(Appendix A Table A.3, Table A.5). *Microtus sp.* (vole) and an unknown mammal had the most negative δ^2H values (-106.3‰ and -116.8‰) (Appendix A Table A.3, Table A.5). For δ^2H, orthopterans were the only group that was statistically significantly different between years ($t = 2.1$, $df = 37.8$, $p < 0.05$).

The average $\delta^{15}N$ and $\delta^{13}C$ values in 2015 adults and 2016 adults were no statistically significant another (Table 3.4) ($t = -0.465$, $df = 19$, $p > 0.05$ and $t = -0.6761$, $df = 19$, $p > 0.05$) (Figure 3.5) (Appendix A Table A.7, Table A.8). The average $\delta^{15}N$ values for nestlings in 2015 and 2016 were both 7.1‰ ($t = 0.036$, $df = 22$, $p > 0.05$). In 2015, there appears to be more variation in $\delta^{15}N$ of nestlings (Table 3.4). The two age groups (adults and nestlings) differed significantly between the two years ($t = 5.07$, $df = 43$, $p < 0.05$) with adults having a greater mean $\delta^{15}N$ than nestlings (Table 3.4, Figure 3.5). The $\delta^{13}C$ averages in nestlings were significantly different between 2015 and 2016 ($t = 7.29$, $df = 22$, $p < 0.05$) (Table 3.4, Figure 3.5). Adults and nestling $\delta^{13}C$ values were also statistically significant ($t = 7.37$, $df = 43$, $p < 0.05$).

For δ^2H there was a significant difference between 2015 (mean = -0.5‰ ± 10.7) and 2016 (mean = -32.8‰ ± 13.8) for adults ($t = 6.02$, $df = 19$, $p < 0.05$) (Appendix A Table A.7, Table A.8). Nestlings in 2015 (mean = -46.3‰ ± 15.1) and 2016 (mean = -63.2‰ ± 6.7) also differed significantly from one another ($t = 3.79$, $df = 22$, $p < 0.05$) (Table 3.4, Figure 3.6). Adults were much more enriched in ^2H (range = +14‰ to -62‰) compared to nestlings for the two-year period (Range = -22‰ to -79‰) ($t = 8.09$, $df = 43$, $p < 0.05$).

Isotopic Niche Width (SEA)

American Kestrel nestlings in 2015 had a slightly larger isotopic niche width ($SEA_C = 2.14$) compared to adults ($SEA_C = 2.00$) (Table 3.4, Figure 3.7). In 2016 adults, isotopic niche width ($SEA_C = 1.59$) was smaller compared to 2015 (Table 3.5). Adults in 2015 and 2016 occupied similar isotopic niche space (Figure 3.8A), whereas nestlings in 2015 and 2016 appear to occupy different isotopic space (Figure 3.7). The 2015 nestlings also have greater isotopic niche width ($SEA_C = 2.14$) compared to 2016 nestlings ($SEA_C = 0.93$) (Table 2.5, Figure 2.7).

The Bayesian standard ellipses for $\delta^{15}N$ and $\delta^{13}C$ revealed that mammals contained the largest isotopic niche width in 2015 prey ($SEA_C = 15.4$) followed by spiders ($SEA_C = 7.90$) (Table 3.5, Figure 3.8, 3.10). In 2016, birds had the highest SEA_C at 8.03 (Table 3.5) occupying the greatest isotopic niche width (Figure 3.9). The orthopterans in 2016 had the second highest SEA_C at 3.10 (Table 3.5). In general, standard area ellipses of prey in 2015 displayed greater isotopic niche width for $\delta^{15}N$ and $\delta^{13}C$ compared to 2016 (Table 3.5, Figure 3.8, 3.9).

Diet Reconstruction

Avian prey and orthopterans contributed to adult isotopic composition in 2015 (Figure 3.11A-B). Minimal proportions of spiders and mammals contributed to 2015 adult kestrel isotopic compositions (Figure 3.11A). For 2015, the 95% confidence interval

(C.I.) proportions was 0.28 to 0.58 for birds and 0.25 to 0.59 for orthopterans. The SIAR analysis revealed similar dietary proportions in 2015 and 2016. In 2016 adults, bird (95% C.I. = 0.15 to 0.60) and orthopteran (95% C.I. = 0.18 to 0.60) proportions were similar to one another (Figure 3.11B). Adult feathers collected in 2016 should reflect the diet consumed in 2015 owing to the fact that kestrels molt their feathers at the start of the breeding season in May.

Orthopteran prey (95% C.I. = 0.0.18 to 0.72) were found to be the most likely prey item influencing isotopic compositions in 2015 nestlings (Figure 3.12A). Birds (95% C.I. = 0.17 upper = 0.47) were also detected in 2015 nestlings (Figure 6A). This is similar to what was found in adults in 2015 and 2016. Orthopterans (95% C.I. = 0.15 upper = 0.58) and mammals (95% C.I. = 0.085 to 0.56) were the highest contributors to nestling isotopic compositions in 2016 (Figure 3.12B). For nestlings, SIAR results indicated that vertebrate prey resources differed slightly in 2015 compared to 2016 (Figure 3.12A-B). Interestingly, spiders were predicted to be contributing the least to nestling, isotopically (Figure 3.12A-B).

Discussion

Diet Breadth and Variability

The American Kestrel diet at the time of breeding season, contained a diverse number of vertebrates and invertebrates, but the calculated diet breadths (B) were low in both 2015 (B=2.8) and 2016 (B=2.2) due to the high number of invertebrate prey remains in their boxes and pellets. Results of diet breadth are fairly consistent with a similar opportunistic raptor, the lesser kestrel (*Falco tinnunculus*) where diet breath (B) was between 2.85 – 3.75 (Korpimaki 1987). Studies of diverse bird species have found that opportunistic consumers will often have a smaller range in diet breadth when food is not limited (Weins and Rotenberry 1979, Steenhof and Kochert 1988). In one study, the diet of specialists deviated to other prey resources when preferred prey was limited, whereas generalist raptors chose prey based on what was most abundant (Steenhof and Kochert 1988). The diet of American Kestrels on the MVPGR may indicate which type of prey is abundant, because they are considered generalist predators (Rudolph 1982). In this study, birds comprised the greatest proportion of vertebrate prey in kestrel diet. Orthopterans (grasshoppers, crickets, and katydids) and spiders were the majority of invertebrate prey, likely due to the abundance of these prey groups on the MVPGR during the kestrel breeding season.

The initial hypothesis of this study proposed that diet breadth will differ between years as a result of variations in environmental conditions. Although in 2015 there were two more prey items found in the kestrel's diet compared to 2016, diet breadth (B) values were similar. Despite the greater amount of precipitation in 2016 compared to 2015, the differences in rainfall do not appear to have influenced diet breadth of kestrels in this study. For the MVPGR, the 2015 average monthly precipitation for March through June was 7.62 mm and in 2016 it was 46.9 mm (California Dept. of Water Resources). In contrast, the diet breadth of an opportunistic raptor (barn owl) has been shown to increase

in drier habitats compared to wetter habitats (Carmona and Rivadeneira 2006). Carmona and Rivadeneira (2006) also found that the barn owl diet in an arid climate was comprised of more invertebrate prey while wetter areas contained more mammals. The differences found in diet composition of barn owls was related to the small mammal diversity and abundance at their study sites (Carmona and Rivadeneira 2006). Abundance of prey species was outside the scope of this study, however, based on prey abundances in diet, the increased precipitation at MVPGR in 2016 did not change prey composition. Furthermore, the high proportions of invertebrates in kestrel diets could be explained by low small mammal diversity and/or abundance.

Kestrels have been found to consume immense numbers of invertebrates in other locations, but biomass of vertebrates could be just as important in diet (Santillan et al. 2009), with high prey densities influencing foraging behavior. Gard and Bird (1990) showed that in manipulated populations of kestrels, parents spent less time foraging for prey when prey abundance was high. Additionally, the prey delivery rates were greater for kestrels when prey density was high (Gard and Bird 1990). Gard and Bird (1990) also concluded that nestlings that received less food from parents, due to low prey density, were smaller in size at the fledging stage.

Although diet breadth did not differ from 2015 to 2016, more prey was found in 2016. A likely cause of variation in prey proportions and the amount of prey in 2016 is the increase in primary productivity due to precipitation. Studies conducted in grassland habitats have drawn similar conclusions regarding prey abundance linkage to variation in primary productivity (Boyer et al. 2003, Macias-Duarte et al. 2004). More specifically, Macias-Duarte and colleagues (2004) showed that small birds feeding on seeds increased in abundance proportionally with precipitation. Similar trends have been found in grassland arthropods, where both carnivorous and herbivorous arthropod populations increased with the addition of water (Boyer et al. 2003). These studies imply a possible bottom-up trophic effect at the MVPGR site, where increases in primary productivity result in greater abundances of higher trophic level organisms.

Overall, low dietary variation was determined within the population. However, there were more individuals in 2016 that had variable diets compared to kestrels nesting in 2015. In 2016, Mean Pairwise Overlap and PS_i appear to be driven by the proportions of invertebrate prey, with nest boxes that contained elevated proportions of only one type of invertebrate having lower overlap and PS_i values. Kestrels with earlier nest initiation dates had more spiders remains in their nest boxes compared to kestrels nesting later which had more orthopteran remains. Diet variability among individuals of a population is common in various types of animals and has long been thought that individual diet specialization and variation in food niche width reduces intraspecific competition (Roughgarden 1972, Polis 1984, Smith 1990, Bolnick 2001). Diet analyses in this study indicate that some kestrels have specialized diets while most have more generalized diets. Results from this study may not necessarily relate to environmental conditions, rather variation seen between the two years may reflect natural year to year fluctuations in kestrel diet regardless of the environmental conditions.

Dietary differences within the population and food niche specialization seen in 2016 could be related to nest initiation timing. The decrease in the dietary proportions of spiders later in the season, with increased orthopteran proportions later in the season, could be explained by the timing of grasshopper hatching dates. Grasshopper hatching is linked to ambient air temperature, soil temperature, and soil moisture (Hewitt 1979, Guo et al. 2009). As temperatures increase and precipitation decreases through the kestrel breeding season, orthopteran abundance increases, thereby providing food for late nesting kestrels.

For vertebrate prey, seasonal variability was much more difficult to discern, although there was evidence that seasonal timing played a role in the proportions of vertebrate prey within the diet. Increased avian prey in early to mid-season (late March to May) is possibly related to the timing of the horned lark breeding season, a major source of avian prey. Horned lark females begin building nests in late March through mid-May and incubate eggs for 11 days (Beason and Franks 1974). In horned larks, a ground dwelling species, nestlings and foraging adults could be more at risk of predation by kestrels during breeding months (Beason and Franks 1974). For small mammals, reports from other raptor diet studies revealed seasonal changes in small mammal availability (Dawson and Bortolotti 2000, Rodriguez et al. 2010). The lesser kestrel diet had similar changes in vertebrate prey proportions during the breeding season, in which mammals contribute to food resources earlier in the season compared to later (Rodriguez et al. 2010).

Stable Isotope Variation

The $\delta^{13}C$ of American Kestrels and associated prey measured at the MVPGR indicate an all C_3 plant environment: no $\delta^{13}C$ values associated with C_4 photosynthesis were found. The $\delta^{13}C$ values in American Kestrels and some of the prey items were significantly different between years. Differences of 1.0 to 1.5‰ in $\delta^{13}C$ in the kestrel population can be explained by trophic level variations in the kestrel population (Caut, Angulo, and Courchamp 2009). The greater enrichment of ^{13}C found in 2015 kestrels is likely due to changes in the baseline (vegetation) $\delta^{13}C$. More positive $\delta^{13}C$ values in 2015 can be related to lower precipitation amounts, which is due to water-use efficiency patterns in vegetation (Smedley et al. 1991). With less precipitation, water-use patterns become more conservative resulting in more fractionation and plant tissues that are more enriched in ^{13}C (Farquhar, Ehleringer, and Hubick 1989). Both 2014 and 2015 were extremely dry years in Central California, whereas 2016 had substantially more rainfall. Increased precipitation in 2016 resulted in more negative $\delta^{13}C$ values in 2016 nestlings.

Nitrogen stable isotopes were consistent within years and between years for various prey groups and kestrels, although beetles (Coleoptera) had greater variation within a year. The variation in beetle $\delta^{15}N$ seen in this study is likely related to the diversity of the beetle group. The order Coleoptera is a very diverse group consisting of detritivores, herbivores, and carnivores. For American Kestrels, differences in $\delta^{15}N$ between years were not witnessed; however, adults were more positive compared to nestlings, indicating

that adults may feed at a higher trophic level than nestlings. The difference in $\delta^{15}N$ between adults and nestlings can be attributed to dietary differences and possibly also to the timing of feather tissue development. The examination of pellets and prey remains revealed that prey composition varied through the season with spiders most abundant in diet within earlier months and orthopterans most abundant in later months. Adults typically begin molting feathers and growing new feathers during the incubation period, which can begin in March (Pyle 2005) when spider prey was most frequent in kestrel diet. Nestlings do not develop feathers until two weeks after hatching (Bird and Clark 1983), which is typically in May or June, but depends on timing of nest initiation. Nestling feathers would be forming when orthopterans were found most frequently in diet.

Small mammal $\delta^{2}H$ variation was extreme within both years, while other prey groups displayed only small amounts of inter-year variation. The differences in $\delta^{2}H$ values was not limited to discrepancies between different species, but was also seen within a single species. Differences in $\delta^{2}H$ could be linked to body size and metabolic rate. A study that examined $\delta^{2}H$ in lab reared rodents found that $\delta^{2}H$ in bone collagen changed with body size, with larger individuals being more enriched in ^{2}H than smaller and younger individuals (Kirsanow and Tuross 2011). In birds, it was identified that increased metabolic rate due to changes in temperature influenced $\delta^{2}H$ in blood and feather tissue of individuals of the same species, with cold temperatures and higher metabolic rates resulting in lower $\delta^{2}H$ values (Storm-Suke et al. 2012). For mammals, metabolic rate increases with body size (Nagy 1987), thus variances in metabolic rates in individuals could be the underlying cause for differing $\delta^{2}H$ values seen in mammal bone collagen. For invertebrates, within group variation of $\delta^{2}H$ was low for each year. The $\delta^{2}H$ of 2015 were higher in spiders, beetles, and orthopterans compared to $\delta^{2}H$ values measured in 2016, a trend that was also seen in American Kestrels.

Alternatively, variation in kestrel $\delta^{2}H$ found in this study can be explained by a combination of dietary differences, trophic position, new migrants into the population, and isotopic routing. Variation in $\delta^{2}H$ of 9‰ or less measured within nestlings in 2015 and 2016 is likely due to slight changes in diet composition. Hydrogen that becomes incorporated into animal tissues is a combination of water derived from an individual's diet (70-100%) and water derived from drinking (0-30%) (Estep and Dabrowski 1980, Hobson, Atwell, and Wassenaar 1999, Langin et al. 2007). Hobson, Atwell, and Wassenaar (1999) determined that 60-70% of hydrogen in feather tissue can be explained by diet, thus proportions of different prey items in an individual's diet will result in different isotopic composition. Dietary differences measured in pellet and prey remains corroborate the $\delta^{2}H$ variation is seen in feather tissue. Larger changes in $\delta^{2}H$ measured between adults and nestlings most likely results from trophic level differences. For hydrogen, trophic level fractionation can range from 30‰ to 50‰ (Birchall et al. 2005). Adults from 2015 on average were isotopically heavier by +30‰ compared to nestlings, indicating that adults in 2015 were feeding at a higher trophic level.

Another factor that may have influenced the δ^2H in adult kestrels is the potential for new migrants entering the population. Outlier δ^2H values of individuals indicate that the feather may not have been synthesized at the MVPGR or surrounding area. The δ^2H values of water varies across the earth, with lower latitudes generally having higher δ^2H compared to higher latitudes (Rozanski, Araguas-Araguas, and Gonfiantini 1993). The global δ^2H of water is also influenced by a continental gradient, where inland δ^2H are more negative compared to coastal values (Rozanski, Araguas-Araguas, and Gonfiantini 1993, Marshall, Brookes, and Lajitha 2007). Other factors that influence δ^2H across landscapes are temperature and altitude (Rozanski, Araguas-Araguas, and Gonfiantini 1993). The variation in δ^2H across the global and continental gradients is seen in vegetation as well as in higher trophic level organisms (Hobson and Wassenaar 1997, Marshall, Brookes, and Lajitha 2007). Adults emigrating into the population from a different region would have feather tissue δ^2H values that would reflect the previous regional δ^2H water values, which is possible for the MVPGR adult kestrels. Although several adult kestrels have been recaptured in nest boxes on the MVPGR, new adults make up a greater proportion of the population nesting in the boxes (refer to Chapter 2).

Isotopic routing contributes to variation in diet to tissue fractionation and influences the isotopic composition of individuals. Isotopic routing occurs when molecules from the diet are routed directly into synthesizing tissue without substantial isotopic fractionation. Isotopic routing is thought to occur during periods of rapid growth of individuals or in tissues undergoing rapid growth (Oelbermann and Scheu 2002, Trueman, McGill, and Guyard 2005). It was determined that the $\delta^{15}N$ values in growing salmon decreased as the growth rate increased (Trueman, McGill, and Guyard 2005). Similarly, in a study conducted on spiders, researchers found that adults were 2.1‰ heavier in $\delta^{15}N$ compared to their growing young (Oelbermann and Scheu 2002), supporting the concept that during periods of intense growth less fractionation occurs. In an individual that is growing there is less metabolic activity of molecules before being routed into tissue, resulting in less ^{15}N in tissues (Oelbermann and Scheu 2002). The ^{14}N is preferentially used in metabolic reactions, therefore highly metabolized molecules would result in more ^{15}N within tissue (DeNiro and Epstein 1981). American Kestrel nestlings undergo 30 days of rapid growth in body size and feather formation, which could lead to different fractionation values than adults. The differences measured between adult and nestling hydrogen isotopic composition could be due to isotopic routing occurring in nestlings.

Meehan and colleagues (2003) have proposed other hypotheses to explain differences in δ^2H between adults and nestlings in migratory raptors. The first is that adult primaries grown early in the breeding season have proteins derived from muscle tissue that formed from prey on wintering grounds (Meehan et al. 2003). A second hypothesis from Meehan et al. (2003) is that evaporative cooling is greater in adults compared to nestlings. Increased evaporative cooling in animals results in more positive δ^2H values in body water (Wolf and Martinez del Rio 2000). Although it is possible that wintering ground diet and evaporative cooling influenced δ^2H of adult kestrels in this study, these mechanisms fail to explain the variation seen between 2015 and 2016 amongst adults as well as variation amongst nestlings. Differences seen in δ^2H of the MVPGR population

are better explained by isotopic routing, trophic position, and adult migrants from other locations.

SIAR mixing model results were partially inconsistent with pellet and prey remains found within next boxes. Although orthopterans and birds did make up a significant proportion of kestrel prey found in nest boxes in 2015, the mixing model predicted that spiders were minimal proportions of kestrel diets. Spiders remains were in high abundance within kestrel boxes in 2015. In nestling from 2016, models indicated high proportions of orthopterans, birds, and mammals. Again, the mixing model failed to detect spiders as a large portion of kestrel diets in 2016 despite finding high proportion in kestrel nest boxes.

There are several plausible explanations for the inconsistency between prey remains and SIAR results. First, isotope prey values were shown to have overlap and could have made it difficult for the model to decipher between prey items due to isotopic similarity. Second, prey counts may not be the best comparison to SIAR outputs; instead, biomass could be a better predictor. Biomass of mammals and birds is much greater than invertebrate prey. For example, the pocket gopher body size can range from 60-200 g depending on sex and age (Daly and Patton 1986). The kangaroo rat (*Dipodomys sp*.) body size ranges from 130 to 180 g and horned lark average body size ranges from 28 to 48 g (Beason 1995). In comparison, the average weight of a grasshopper at the study site was 0.54 g. Therefore, one small mammal could be equivalent to 100+ individual grasshoppers.

The disparity between prey counts of spiders and isotopic composition of kestrels could be due to biomass as well as the diet quality of spiders or isotopic routing in nestlings. Diet quality can be described by the amount of protein that it contains, where low protein is associated with low quality. Spiders have been categorized as low quality diet items to other arthropod predators (Toft and Wise 1999). The effect of prey quality on the stable isotope composition of the consumer has been examined in several species. A study conducted on multiple large, mammalian herbivores revealed that higher protein diets had larger diet to tissue fractionation values compared to lower protein diets (Sponheimer et al. 2003). Similarly, various tissues from crows raised on animal protein had less nitrogen isotope fractionation compared to crows raised on plant protein (Hobson and Clark 1992). A study on tilapia found similar results and determined that both $\delta^{13}C$ and $\delta^{15}N$ were influenced by diet composition and the amount of food consumed (Gaye-Siessegger et al. 2003).

A more recent study on lesser kestrels used a similar approach to assessing diet variation based on SIAR mixing models (Catry et al. 2016). Additionally, the researchers collected pellets to determine if SIAR results were consistent with prey found in pellets. Catry and colleagues found that SIAR modeled results from blood samples compared well with pellet analyses. However, this study only examined crickets and grasshoppers from pellets, no other prey types (i.e., mammals) were quantified, and prey remains were not examined. Furthermore, when using SIAR mixing models to examine the diet of males, females, and young, the researchers used five or more types of prey (Catry et al. 2016),

but it is not mathematically possible to calculate accurate proportions of prey in an organism's diet consisting of more than three prey items (Phillips 2001). It is important to realize the limitations of diet reconstruction models to avoid obtaining inaccurate results. Although, Catry et al.'s (2016) assessment that variation in stable isotope values indicated variation between sexes and age groups, their modeled diets should be more realistically based on prey items.

In conclusion, the examination of pellets and prey remains revealed that the American Kestrel diet is variable during the breeding season. The fluctuation in the kestrel diet could be dependent upon the seasonal availability of prey items during the spring and the beginning of summer. Increased prey amounts in 2016 provides evidence of bottom-up driven forces at the MVPGR. Furthermore, stable isotope analysis of carbon, nitrogen, and hydrogen was crucial to the discovery of diet and trophic distinction in kestrel adults and nestlings. Measureable shifts in $\delta^{2}H$ and $\delta^{13}C$ in American Kestrels from 2015 to 2016 highlighted the ability of climate to alter isotopic composition at higher trophic positions due to variations at the primary producer level. This finding illuminates the importance of understanding the timing and origin of tissue formation in the multi-year, isotopic study of animals. The underestimation of spiders in SIAR results further emphasizes the need for enhanced examination of factors (e.g., prey quality) that influence fractionation in generalist raptor species.

Table 3.1. Types of prey consumed by American Kestrels occupying man-made nest boxes and number of individuals (2015 and 2016).

Prey Type	2015	2016	Total
Number of Nest Boxes	11	11	-
Thomomys sp.	4	1	5
Microtus sp.	1	-	1
Peromyscus sp.	1	-	1
Dipodomys sp.	-	2	2
Unknown Mammal	2	5	7
Horned Lark	4	16	20
American Kestrel	-	5	5
Cliff Swallow	1	-	1
Unknown Avian	13	11	24
Lizard	6	9	15
Coleoptera	71	43	114
Caelifera (grasshoppers) and Tettigoniidae (katydids)	342	595	937
Gryllidae (crickets)	19	12	31
Araneae (spiders)	415	900	1315
Odonata (dragonflies)	23	5	28
Chilopoda	4	4	8
Hymenoptera	-	1	1
Total Prey	902	1609	2511

Table 3.2. Summary statistics for dietary Pairwise Overlap, Population Similarity Index, and Niche Breadth. Mean Pairwise Overlap is the average diet overlap a single box has with other boxes in that same year. PS_i or proportional similarity index, is a representation of the diet of box compared to the overall diet of the population. W_i represents an individual's food niche breadth. The p-value tested for significance of diet breadth of an individual being pulled from the population.

Box ID	Mean Pairwise Overlap	PS_i	W_i	p
2015				
2	0.500	0.613	0.670	**
7	0.641	0.780	0.891	*
10	0.562	0.708	0.559	**
12	0.650	0.813	0.751	**
15	0.661	0.764	0.872	**
16	0.615	0.709	0.791	*
20	0.457	0.517	0.627	**
21	0.663	0.796	0.892	**
24	0.597	0.749	0.612	**
25	0.657	0.801	0.839	**
29	0.469	0.563	0.162	*
Population Mean	0.567	0.687	0.712	-
2016				
2	0.628	0.890	0.939	**
3	0.437	0.500	0.616	**
5	0.639	0.885	0.977	**
6	0.486	0.562	0.746	**
7	0.437	0.493	0.451	0.15
12	0.500	0.589	0.561	0.057
14	0.469	0.534	0.712	**
24	0.596	0.782	0.772	**
26	0.544	0.743	0.648	**
28	0.597	0.852	0.750	**
29	0.473	0.538	0.492	**
Population Mean	0.527	0.669	0.697	-

* = $p < 0.05$

** = $p < 0.01$

Table 3.3. Average isotope values for major prey groups (2015-2016).

	n	$\delta^{15}N$ (‰) ± SD	$\delta^{13}C$ (‰) ± SD	$\delta^{2}H$ (‰) ± SD
Small Mammals				
2015	5	4.8 ± 1.6	-24.3 ± 2.4	-74.2 ± 27.2
2016	5	5.3 ± 1.2	-24.4 ± 1.3	-83.3 ± 24.2
Birds				
2015	13	9.5 ± 0.70	-21.3 ± 1.1	-86.7 ± 15.8
2016	28	6.6 ± 1.7	-23.6 ± 1.5	-78.7 ± 10.0
Lizards				
2015	5	5.9 ± 0.64	-24.2 ± 0.27	-83.5 ± 9.9
2016	8	7.2 ± 0.73	-22.4 ± 1.6	-78.2 ± 7.6
Araneae				
2015	8	8.1 ± 1.7	-25.3 ± 1.5	-75.1 ± 12.0
2016	20	6.9 ± 1.5	-28.0 ± 0.49	-83.1 ± 11.1
Coleoptera				
2015	3	4.3 ± 2.0	-26.6 ± 0.61	-60.6 ± 13.0
2016	12	6.8 ± 2.7	-27.7 ± 1.1	-75.9 ± 10.8
Orthoptera				
2015	18	3.7 ± 1.9	-25.7 ± 0.80	-68.5 ± 8.2
2016	38	4.3 ± 1.5	-27.5 ± 0.66	-73.8 ± 9.4

Table 3.4. American Kestrel stable isotope averages for 2015 and 2016 adults and nestlings.

	n	$\delta^{15}N$ (‰) ± SD	$\delta^{13}C$ (‰) ± SD	$\delta^{2}H$ (‰) ± SD
Adults 2015	11	8.4 ± 1.0	-21.8 ± 0.6	-0.5 ± 10.7
Adults 2016	10	8.7 ± 1.3	-21.6 ± 1.0	-32.8 ± 13.8
Nestlings 2015	9	7.1 ± 1.3	-22.7 ± 0.6	-46.3 ± 15.1
Nestlings 2016	15	7.1 ± 0.4	-25.0 ± 0.8	-63.2 ± 6.7

Table 3.5. Small sample size corrected standard ellipses area (SEA_C) and Bayesian standard ellipses (SEA_B) for prey, adult kestrels, and nestlings in 2015 and 2016.

	Group	SEA_C	SEA_B
2015			
	Orthopterans	5.01	4.72
	Mammals	15.4	11.5
	Birds	2.26	2.07
	Spiders	7.90	6.77
	Adult kestrels	2.00	1.81
	Nestling kestrels	2.14	1.88
2016			
	Orthopterans	3.10	3.02
	Mammals	2.42	1.82
	Birds	8.03	7.73
	Spiders	2.25	2.13
	Adult kestrels	1.59	1.41
	Nestling kestrels	0.93	0.87

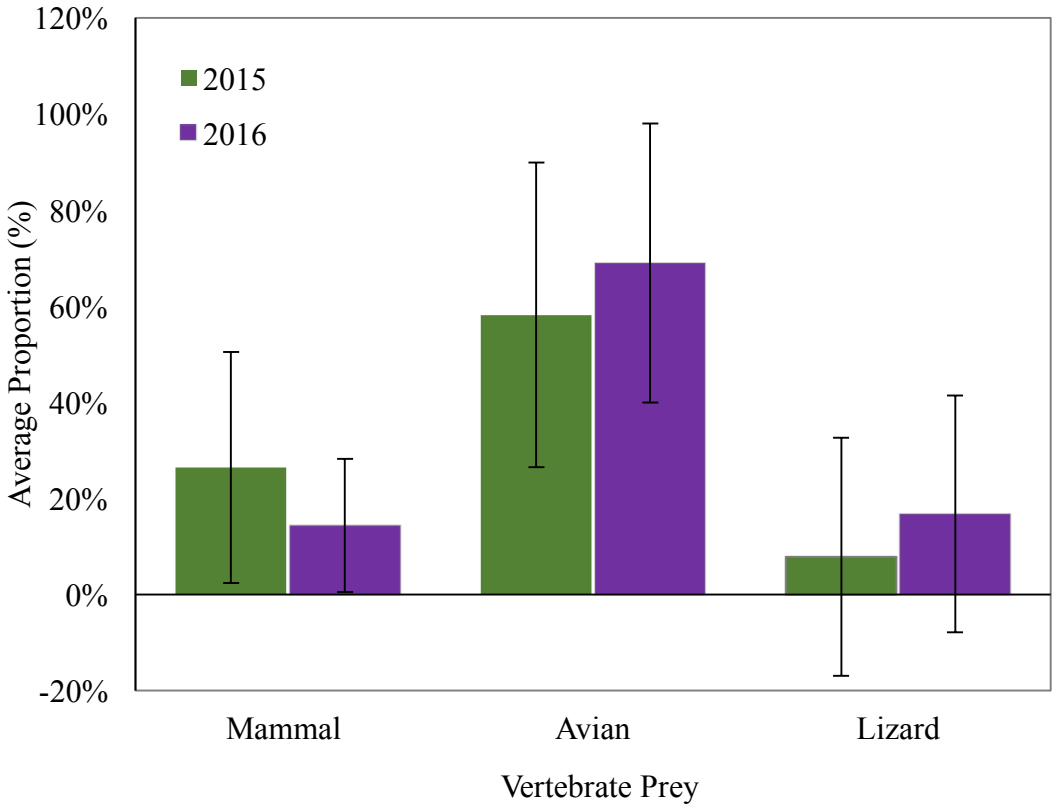

Figure 3.1. Average proportions of vertebrate prey found within nest boxes for 2015 and 2016. Error bars are represented by the standard deviation. In general, mammal prey decreased from 2015 to 2016, while lizard prey increased from 2015 to 2016. Avian prey makes up much of the vertebrate prey found within nest boxes for both years. Overall, the average proportion of vertebrate prey found per box did not significantly differ between 2015 and 2016 (ANOVA, F Stat = 1.561, df = 20, p-value > 0.05).

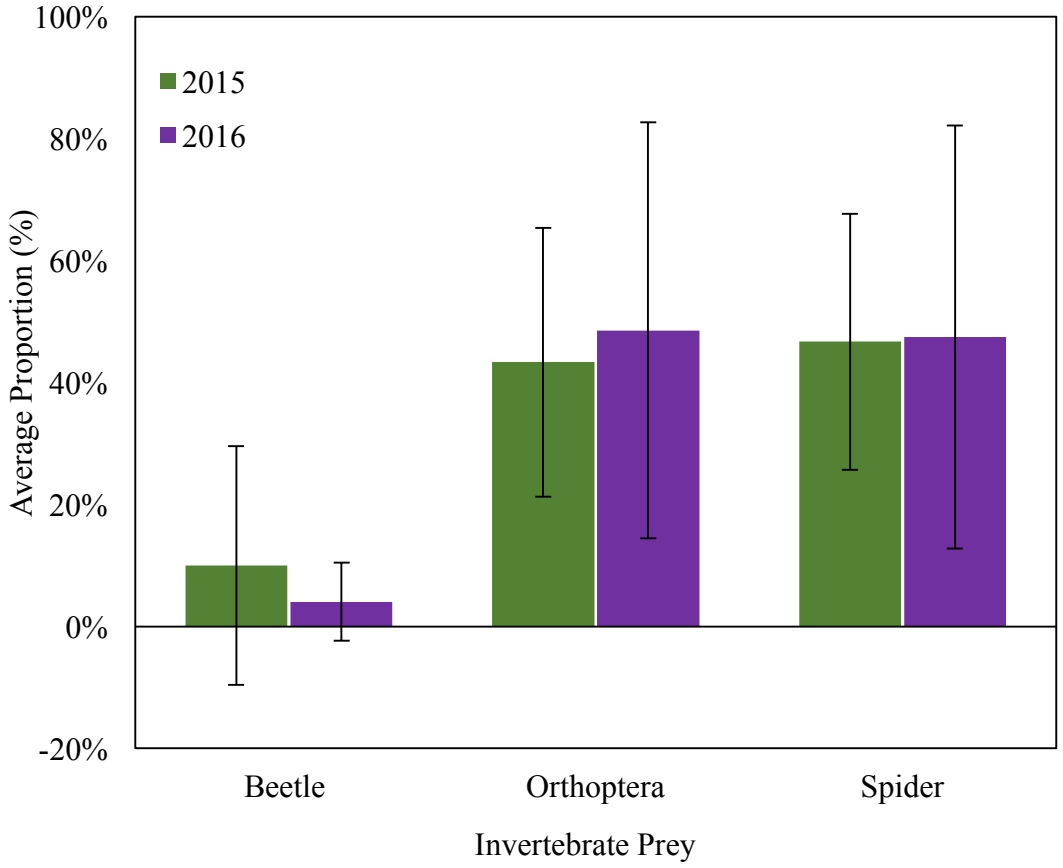

Figure 3.2. The average proportions of invertebrate prey types found within nest boxes for 2015 and 2016. The Orthoptera group includes all crickets, katydids, and grasshoppers. Error bars are represented by the standard deviations. There were similar average proportions of spiders and orthopterans for both years. No significant difference was found between the proportions of invertebrate prey per box in 2015 compared to 2016 (ANOVA, F Stat = 1.560, df = 20, p-value > 0.05).

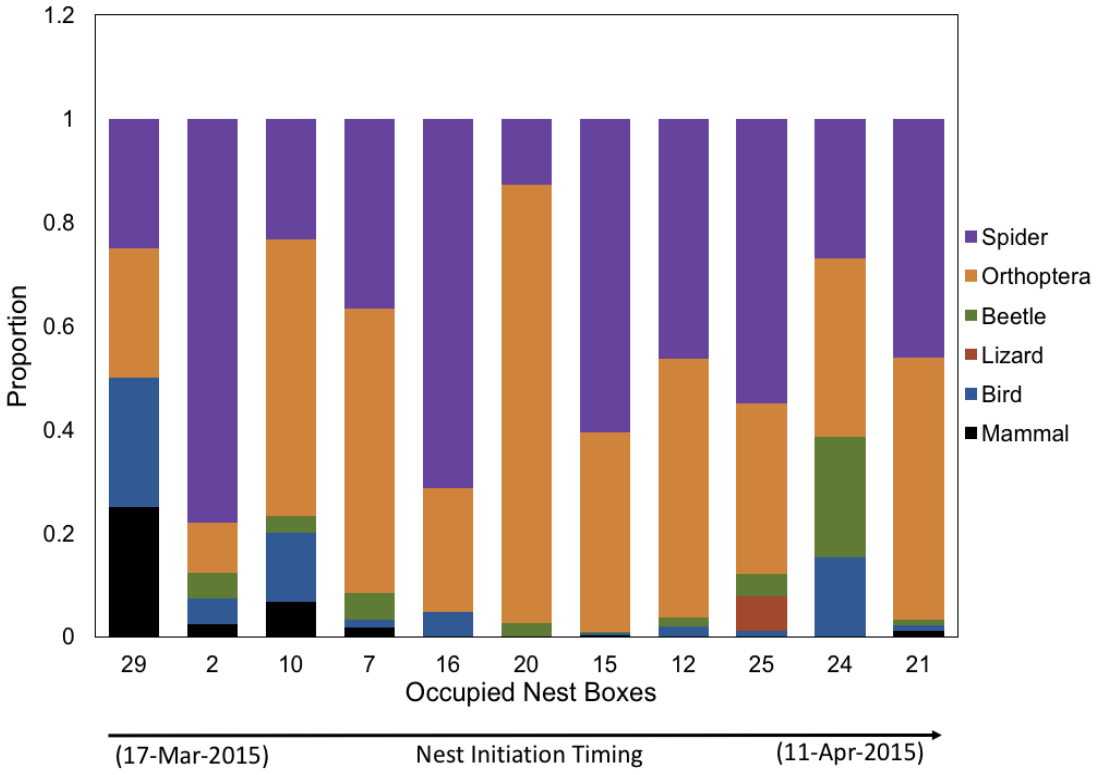

Figure 3.3. Proportions of each major prey type by occupied nest boxes in 2015. Nest boxes are arranged by nest initiation date (early season → late season). All nest boxes contained spiders and members of the order Orthopteran. The number of vertebrates varied across nest boxes, for example, box 10 diet composition was 13.3% for birds and box 20 had 0% bird prey. Birds were more common across nest boxes compared to other vertebrate species.

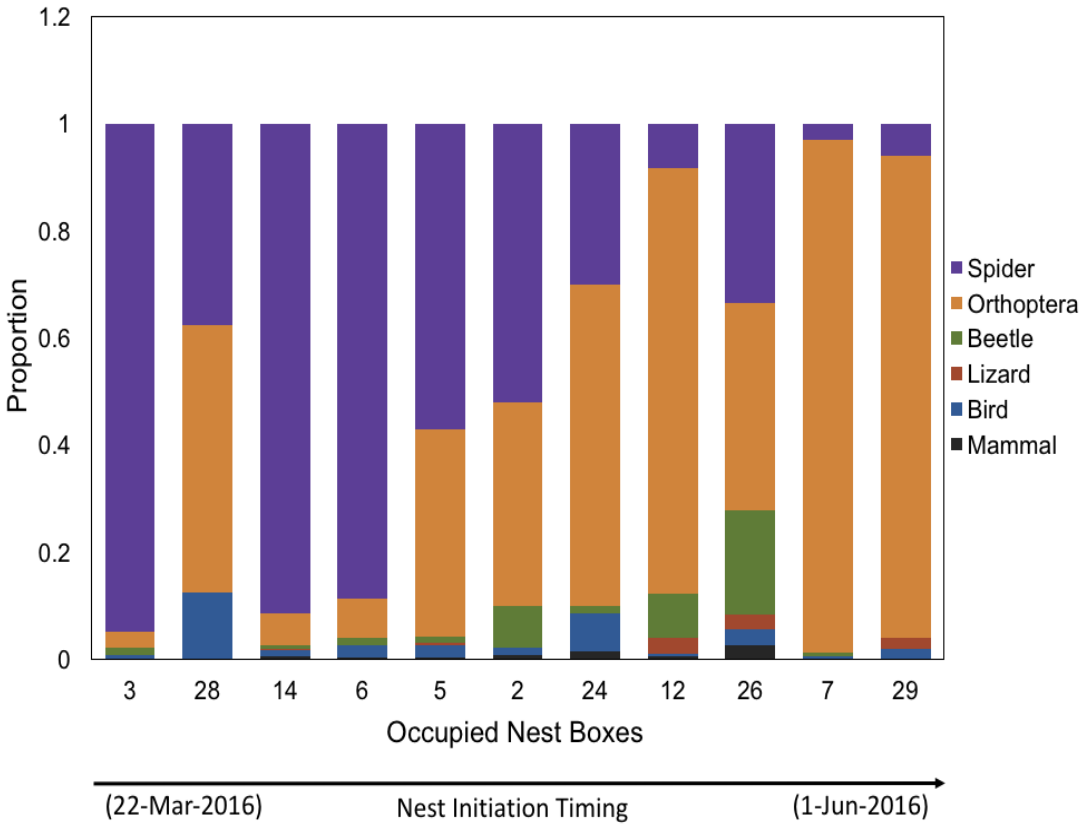

Figure 3.4. Proportions of each major prey type by occupied nest boxes in 2016. Nest boxes are arranged by nest initiation date (early season → late season). All nest boxes contained spiders and members from the order orthopteran. The proportions of spider and Orthoptera changed over time. Lizards were present in late season nests, but were absent from earlier nests.

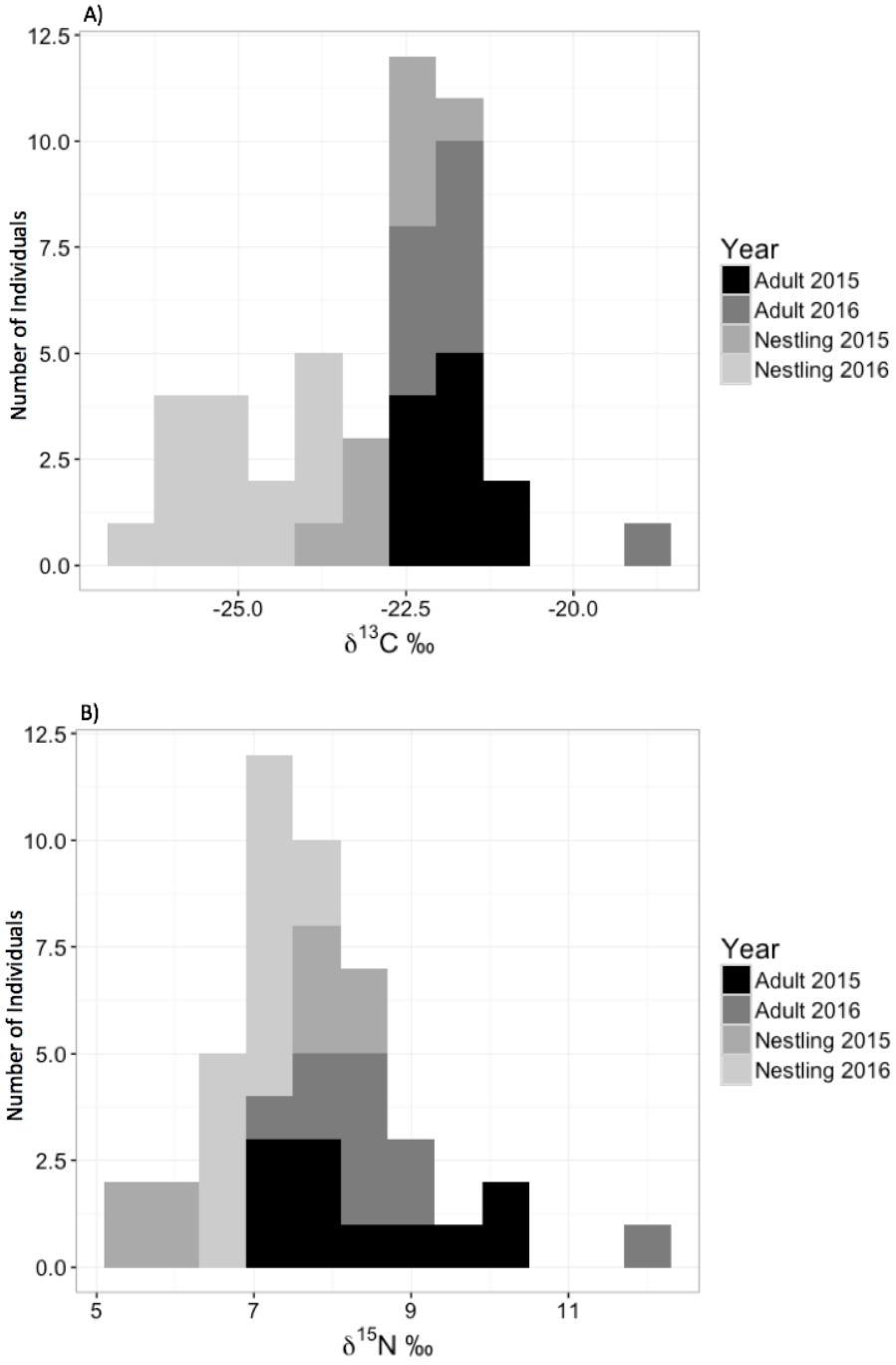

Figure 3.5. Distribution of stable isotopic values for adults and nestlings from both sampling years. (A) The distribution of $\delta^{13}C$ for year and age group. There was not a significant difference between years for adults, but, there was for nestlings ($p < 0.05$). There was also a significant difference between the two age groups ($p < 0.05$). (B) For $\delta^{15}N$, there was no significant difference between 2015 and 2016 for both adults and nestlings. A significant difference was measured between age groups ($p < 0.05$).

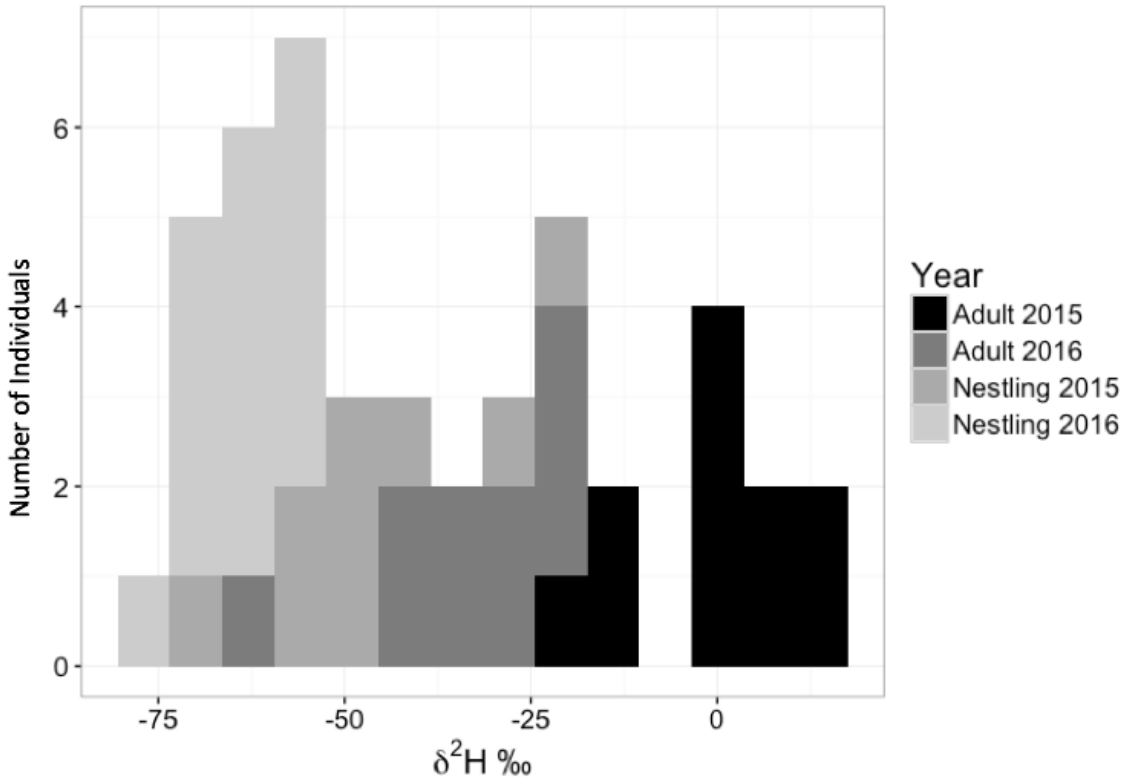

Figure 3.6. Distribution of δ^2H for adults and nestlings sampled from both years. Significant differences were found between adults and nestlings ($p < 0.05$), as well as, between years for both adults ($p < 0.05$) and nestlings ($p < 0.05$).

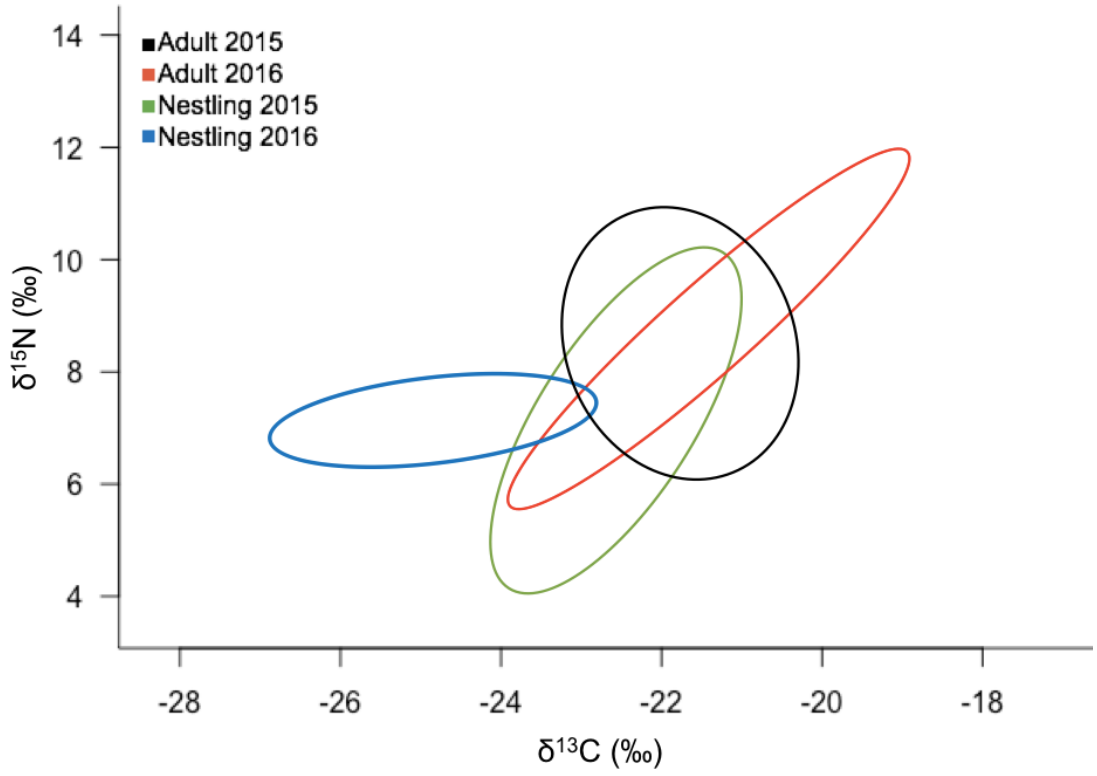

Figure 3.7. Bayesian standard ellipses area (SEA_B) for adults and nestlings in 2015 and 2016. The isotopic niche width was slightly greater in 2015 (SEA_B = 1.81) compared to 2016(SEA_B = 1.41) molted adult feathers. Nestlings in 2015 had greater niche width (SEA_B = 1.88) compared to 2016 (SEA_B = 0.87) and both occupied different isotopic space.

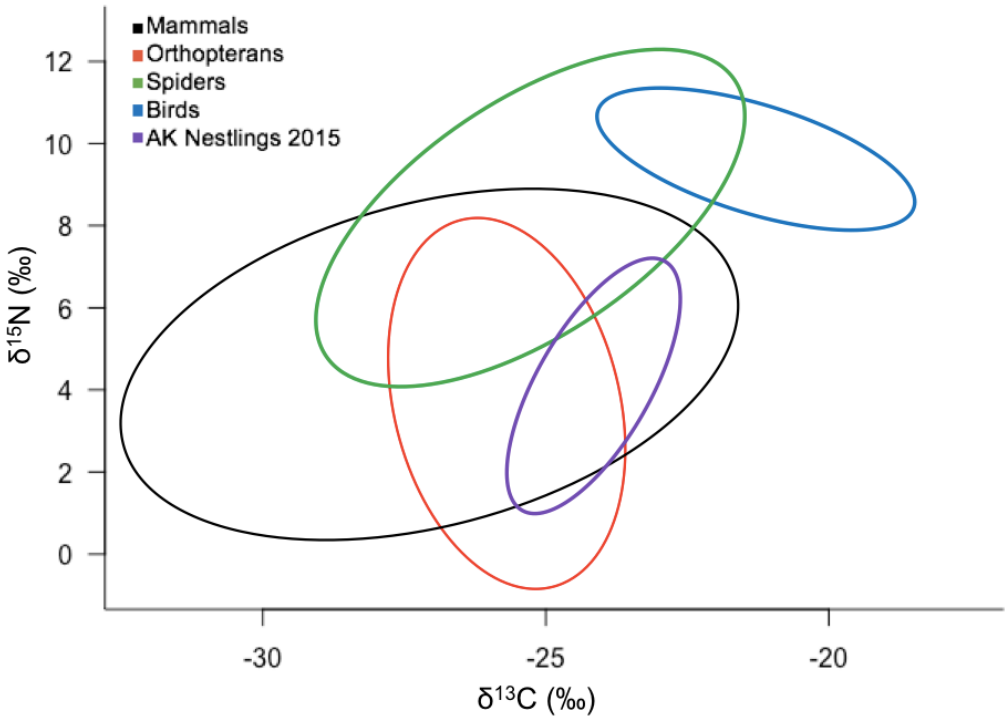

Figure 3.8. Bayesian standard ellipses area (SEA_B) of prey items collected in 2015 with diet corrected nestlings from 2015. Diet corrections for $\delta^{13}C$ was 1.25‰ and was 2.5‰ for $\delta^{15}N$. Kestrel nestling SEA_B was 1.88. Mammals had the greatest SEA_B at 11.5 followed by spiders, $SEA_B = 6.75$. Avian prey had the lowest SEA_B of all 2015 prey items ($SEA_B = 2.07$).

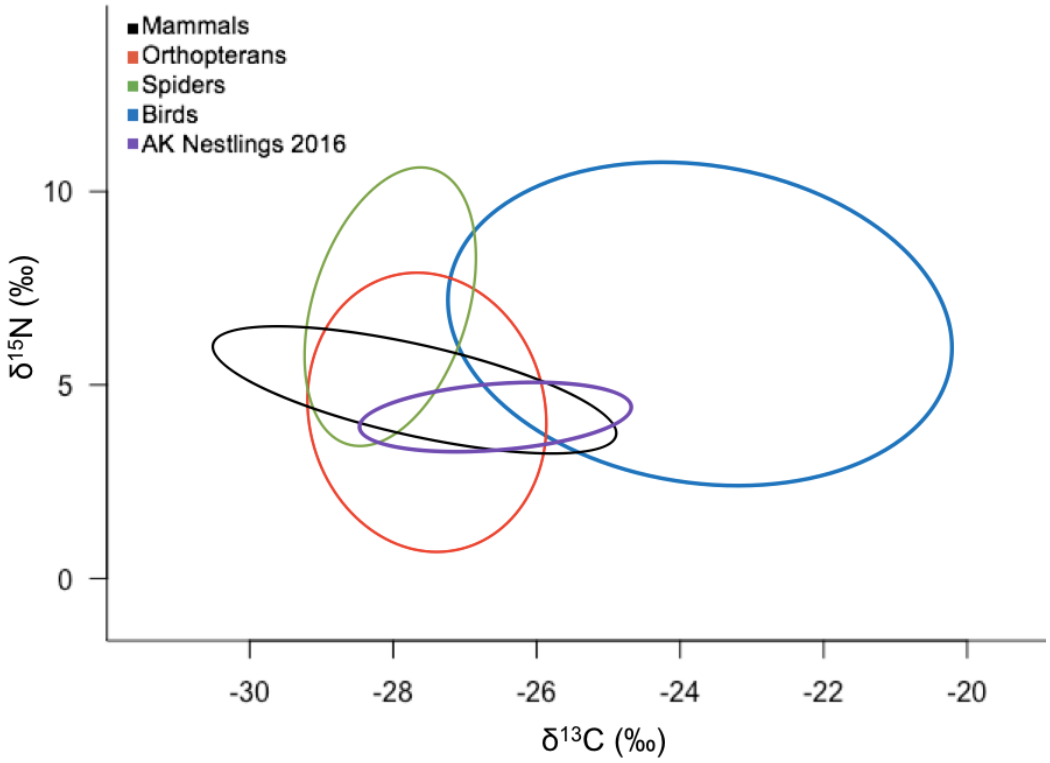

Figure 3.9. Bayesian standard ellipses area (SEA_B) of prey items collected in 2015 with diet corrected nestlings from 2016. Diet corrections for $\delta^{13}C$ was 1.25‰ and was 2.5‰ for $\delta^{15}N$. The greatest SEA was in avian prey species ($SEA_B = 7.73$), followed by orthopterans ($SEA_B = 3.02$). American Kestrel nestlings in 2016 had the lowest SEA_B of all groups.

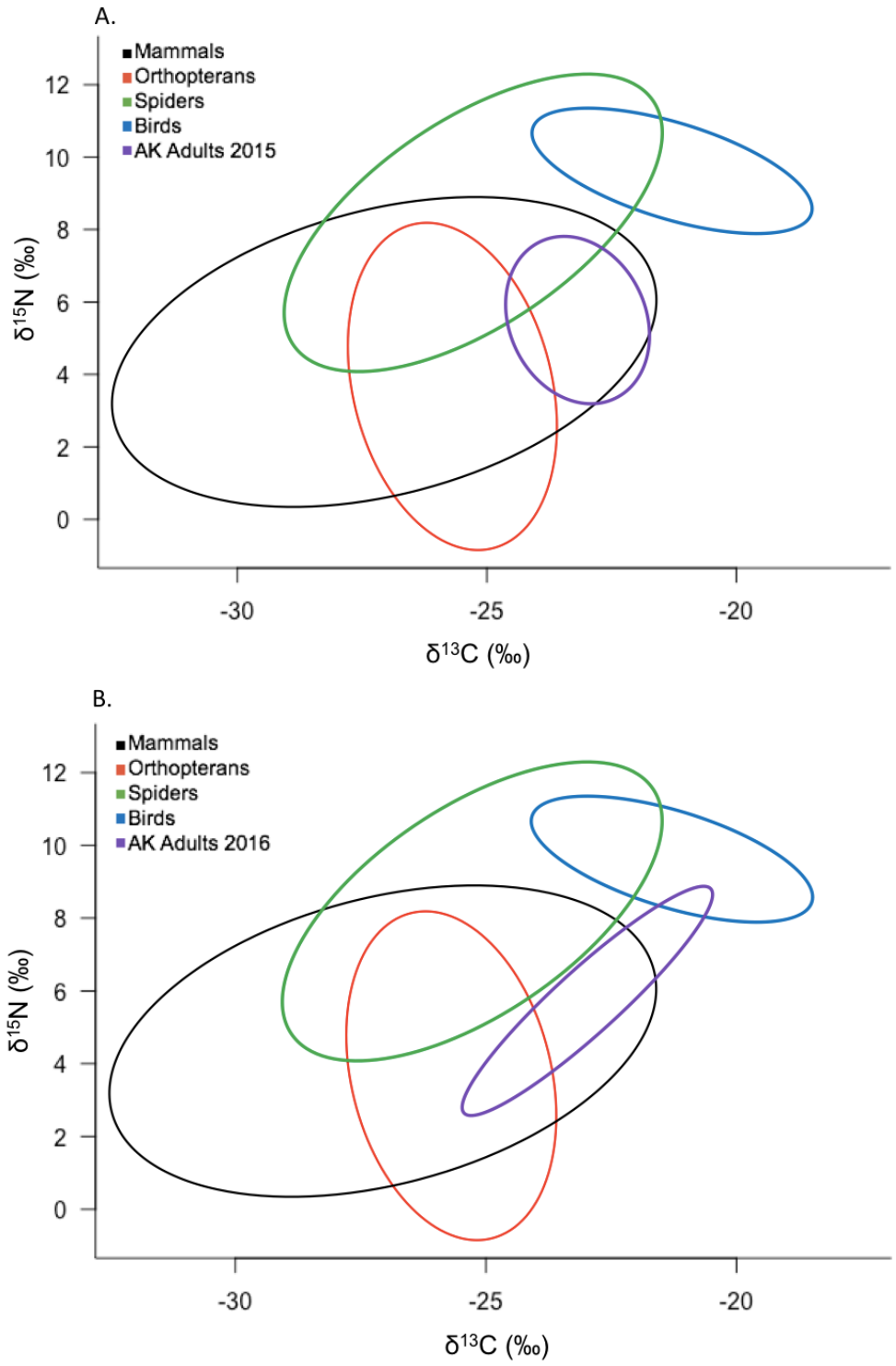

Figure 3.10. Bayesian standard ellipses area (SEA_B) of prey items collected in 2015 compared to diet corrected adults from 2015 (A) and 2016 (B). A) Adult feathers from 2015 had a SEA_B of 1.81 B) SEA_B of 2016 adult feathers was 1.41.

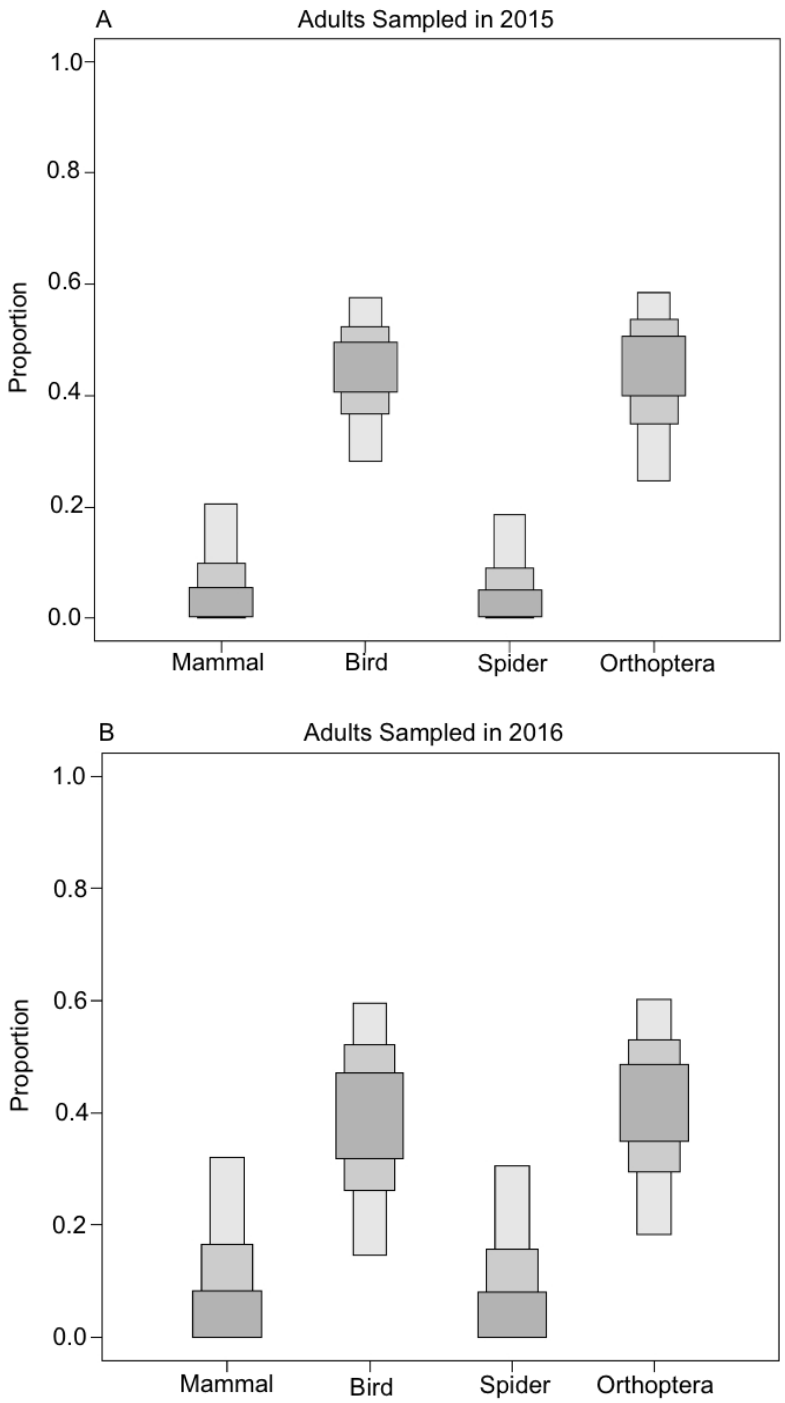

Figure 3.11. SIAR mixing model results for adults sampled in 2015 and in 2016. The variation in grey represents the confidence intervals of 95% (light grey), 75%, and 25%. (A) The adults sampled in 2015 had high proportions of birds and orthopterans with very few mammals and spider proportions. (B) The adults sampled in 2016 contained proportions of birds and orthopterans.

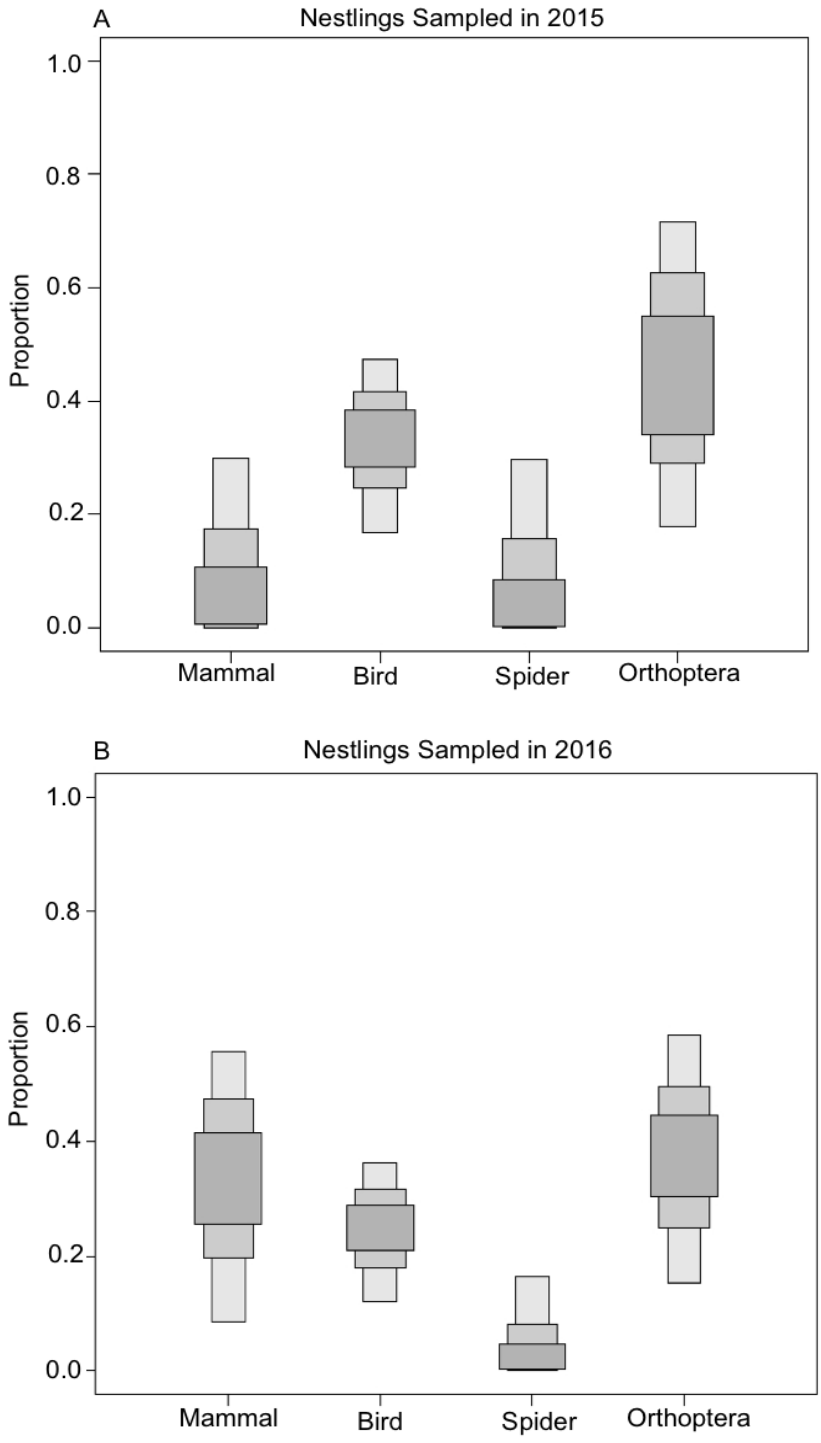

Figure 3.12. SIAR mixing model results for nestlings sampled in 2015 and in 2016. The variation in grey represents the confidence intervals of 95% (light grey), 75%, and 25%. (A) The nestlings revealed high proportions of orthopterans and birds similar to adults sampled in 2015 and 2016. (B) The nestlings sampled in 2016 also had high proportions of orthopteran species and the major vertebrate prey was mammals as well as birds.

CHAPTER 4: CONCLUSIONS

Several aspects of American Kestrel breeding productivity were studied using nest boxes placed on the Merced Vernal Pools Grassland Reserve (MVPGR). Additionally, I completed the analyses of two years of the kestrel's dietary resources and determined the importance of diet items during the kestrel breeding season. In chapter two, the breeding productivity of American Kestrels occupying nest boxes on the MVPGR was determined for three years: 2014, 2015, and 2016. Additionally, the number of banded and recaptured adult and nestling kestrels over the three-year period was documented. My objectives were to quantify the breeding productivity from three years of data to compare results at the MVPGR to other kestrel nest box monitoring programs. Breeding productivity was determined using occupancy rates, clutch size, hatching success, fledging success, and nesting success. The research conducted in this study demonstrated the potential success of nest box programs for kestrel survival in an arid environment. The monitoring process over a multi-year period illuminated areas of improvement needed in terms of both research and conservation efforts.

The MVPGR kestrel nest box program successfully banded 30 adults, 97 nestlings, and recaptured 16 adults over a three-year period. Within the first year and continuing to the second year, kestrels rapidly adopted the nest boxes on the MVPGR. Kestrels' breeding productivity fluctuated yearly, with nest box occupancy increasing from 2014 to 2016. Hatching and fledging successes declined dramatically in 2016 owing to predation, nest abandonment, and nests that never hatched. Unhatched clutches were the principal contributor to low hatching success. Nest abandonment and unhatched clutches were greatest in 2016, a year that had increased spring precipitation. Additionally, five nestlings were lost to cannibalism, which only occurred in 2016. The findings of this study in regards to nest box occupancy, hatching success, and fledging success were similar to those found in other nest box programs in North America. The clutch size average, however, was lower than averages found in other monitoring programs.

Central California American Kestrel populations have received little research attention despite the knowledge of population losses. A severe drought continues to affect Central California, and little research has endeavored to determine the manner in which drought affects regional wildlife, including kestrels. Examination of nest box productivity during extreme environmental conditions, such as a prolonged drought, is needed to assess the impact of climate dynamics on an already declining kestrel population. Fertility issues in breeding pairs, for example, potentially reflect a biological response to extreme environmental conditions. Further knowledge of ways in which the effects of drastic environmental conditions and climate change impact fertility, is needed to identify the exact causes of population declines and to determine subsequent mitigation strategies.

Erecting nest boxes for kestrels can be important in ensuring the conservation of local American Kestrels, as nest boxes are rapidly adopted by kestrels in need of a nesting

area. Longer term studies will better identify population trends and changes in breeding productivity and should be continued at the MVPGR. Examining predation rates proved useful in identifying areas to improve fledging success for the MVPGR nest box program. Reduction of predation rates will undoubtedly increase fledging populations. Predation of young in nest boxes by raccoons and gopher snakes could be specific to the MVPGR, but predation rates should be evaluated at other nest box monitoring programs to determine the influence of predators on breeding productivity. For conservation purposes, nest box programs in regions that may no longer have suitable nesting habitats for kestrels should consider erecting nest boxes in areas that are ideal for foraging, such as a grassland. In this study, the addition of nest boxes to an open grassland habitat, that otherwise may not have natural nesting sites for American Kestrels, has proven to be successful. Furthermore, the continued use of banding and recapturing adults and young in a location can provide insight on dispersal and return rates of a breeding population. Banding will assist in tracking emigration into the local population and the breeding success of an individual overtime.

Chapter three addressed American Kestrel diet breadth, composition, and intraspecific diet variation using pellets, prey remain analysis, and stable isotope analysis. Using a dual technique approach to determine diet, I addressed questions related to population diet breadth, individual specialization, differences between age classes, and yearly variation in prey composition. The first objective was to determine diet composition and breadth of kestrels during the breeding season in 2015 and 2016 using pellet and prey remain analysis. The second objective was to examine dietary niche variation between occupied nest boxes by using pellets, prey remains, and stable isotope compositions. Lastly, using stable isotope analysis I determined diet variation between adults and nestlings. I used stable isotope mixing models and Bayesian ellipses to reconstruct diet and measure isotopic niche width of kestrels.

The composition of prey was similar in both years, yet 2016 contained more prey items in nest boxes despite having the same number of nest boxes and a smaller number of nestlings. Key prey resources were identified as orthopterans (grasshoppers, katydids, and crickets), spiders, and small avian species. Mammals, beetles, and lizards were identified in diets as well. American Kestrel diet breadth did not appear to be influenced by environmental conditions, as there were no notable differences in diet breadth between 2015, a dry year, and 2016, a wetter year. I hypothesized that diet breadth would be dependent upon environmental conditions (Figure 4.1). The timing and quantity of rainfall may need to be more extreme (e.g. increased drought or rainfall) to make an impact on diet breadth. This increase in rainfall in 2016 may not have been enough to influence the diet breadth of kestrels. The unchanged diet breadth between years highlights the opportunistic nature of kestrels despite the change in environmental conditions. The increased number of prey items in 2016 could indicate a bottom-up effect due to precipitation. In bottom-up systems, increases in vegetation from precipitation result in an increase in the abundance of herbivores. In response to a surplus of prey, predator populations increase. For the kestrels in my study, the increase in the amount of

prey consumed did not result in a greater productivity for kestrels. Fledging success was greater in 2015 when the abundance of prey found in nest boxes was lower.

Dietary differences between occupied nest boxes were measured from pellets and prey analyses in both 2015 and 2016. In 2016, niche overlap analyses revealed that there was more variation between nest boxes compared to 2015. Seasonal trends in prey proportions were documented in 2016 with spiders being found more in higher proportions in nests initiated earlier in the breeding season, while grasshoppers were more frequent in nests initiated later in the season. The hypothesis that diet overlap within the population would be smaller in 2016 compared to 2015 was loosely supported by niche overlap analyses (Figure 4.2, Figure 4.3). However, the changes in the diet variability from 2015 and 2016 may not necessarily be due to the changes in environmental conditions. The increased variability and reduction in overlap from 2015 to 2016 may reflect natural year to year variation in kestrel diet.

Stable isotope analysis of American Kestrels and associated prey revealed trophic changes, intraspecific diet variation, changes in baseline vegetation, and potential physiological differences in individuals. The MVPGR is a C_3 plant based ecosystem, therefore all of the $\delta^{13}C$ values of prey and kestrels were between -21.8‰ to -28.0‰. Nitrogen isotopes in prey were varied, because of the diverse trophic levels. The majority of prey had $\delta^{2}H$ values that were consistent except for mammals. Mammals had a striking range in $\delta^{2}H$ values over two years (Range = -42‰ to -117‰). Kestrel feather $\delta^{13}C$ and $\delta^{2}H$ values were significantly different between age groups and between years. Stable isotopes of $\delta^{15}N$, $\delta^{13}C$, and $\delta^{2}H$ revealed that there are individuals in the kestrel population feeding at a higher trophic level than others. Stable isotope mixing models indicated that adult diets in 2015 and 2016 were composed principally of orthopterans (2015 = 25-59%, 2016 = 18-60%) and birds (2015 = 28-58%, 2016 = 15-60%). In 2015 nestling diets were similar to adult diet with slightly different proportions of orthopterans (18-72%) and birds (17-47%). In 2016, diets were comprised of orthopterans (15-58%) and mammals (9-56%).

Stable isotope analysis of $\delta^{15}N$, $\delta^{13}C$, and $\delta^{2}H$ indicated that adult kestrels were feeding at a higher trophic level compared to nestlings. Additionally, the high level of variation in $\delta^{13}C$ over the course of 2015 and 2016 demonstrates how precipitation can influence isotopic composition at higher trophic levels due to changes in the baseline vegetation. This study also illustrates how $\delta^{2}H$ values within a population can range within one location depending on tissue growth, diet, and trophic position. I found that it is important to examine stable isotope composition over multiple years to determine the extent of variation within a population. Large amount of variation in $\delta^{2}H$ may have implications for those using $\delta^{2}H$ for migratory studies. Migratory studies attempting to locate breeding grounds of migratory birds may falsely assign individuals to breeding locations if variation in $\delta^{2}H$ due to diet, trophic level, and isotopic routing is not considered.

Kestrels at my study site consumed a large number of spiders during the start of the breeding season. Stable isotope mixing model results did not show the incorporation of spiders into kestrel tissue possibly because spiders have low protein content or because feather were grown at a different time. In hindsight, it would have been best to couple the isotopic composition of kestrel blood sampled periodically with that of kestrel feathers. Stable isotopes of invertebrates and their incorporation rates into avian predator's diet have yet to be examined, and serve as an opportunity to further assess the nutritional value of arachnids in avian diets.

Breeding productivity and nest box monitoring should continue on the MVPGR to contribute to the understanding of long-term kestrel population trends. Food resources important for growth, survival, and reproduction are key for conservation and management of the American Kestrel. My study identified orthopterans, mostly grasshoppers and katydids, as key prey resources late in the breeding season when nestlings are close to fledging, especially for late nest initiations. Orthopteran prey could also be an important resource for migrating individuals to increase fat stores before moving to wintering grounds. Small avian prey, specifically horned larks, are also important contributors to kestrel diet as they make up a large portion of the biomass consumed.

American Kestrel populations have declined since the 1960s and the cause has yet to be identified. Exploration of kestrel biology, such as diet and reproduction, is necessary to determine the root causes of kestrel population loss. My research demonstrated the effect of environmental conditions on breeding productivity, diet, and stable isotope compositions, demonstrating that the American Kestrel is an adaptive bird that can quickly move into new territory and take advantage of abundant prey.

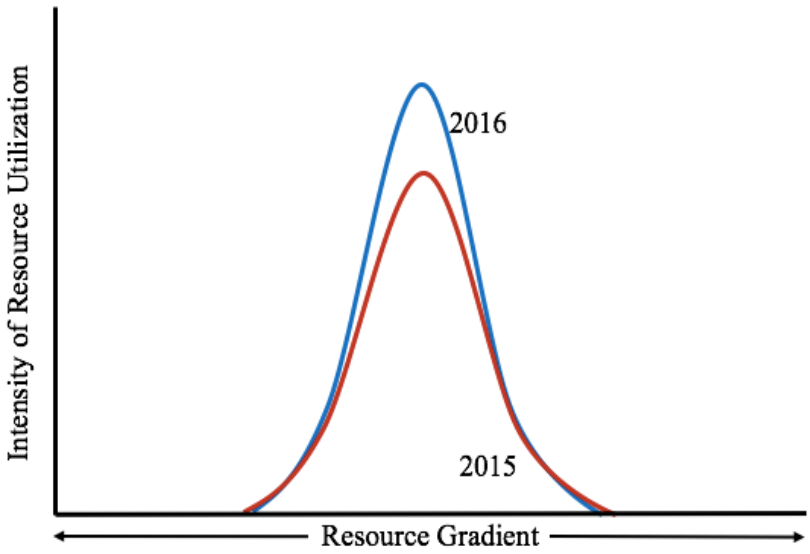

Figure 4.1. Diet breadth in 2015 and 2016 was similar. The intensity of the resource use was greater in 2016 despite having a lower number of nestlings and the same number of nest boxes sampled from.

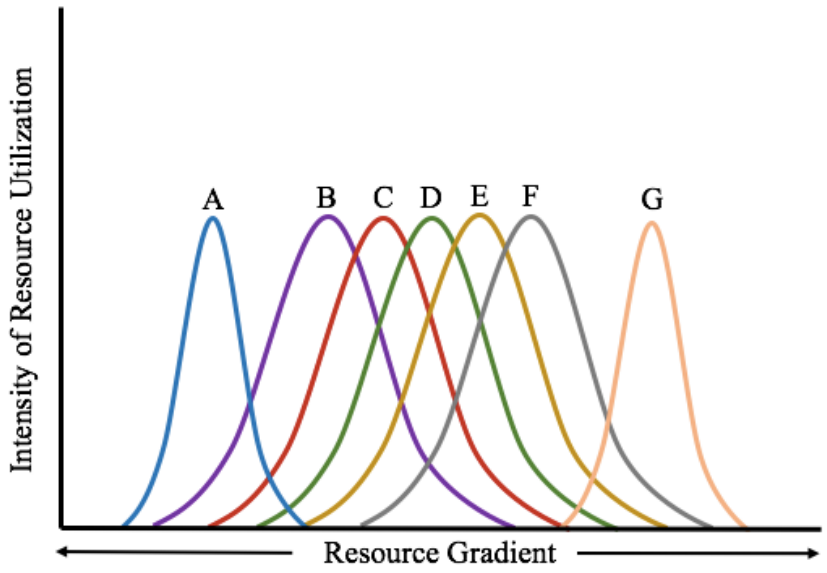

Figure 4.2. Representation of measured individual niche breadth and variation between nest boxes in 2015. Pairwise overlap was high between most individuals except for a few outliers. Diet breadth was similar between nest boxes.

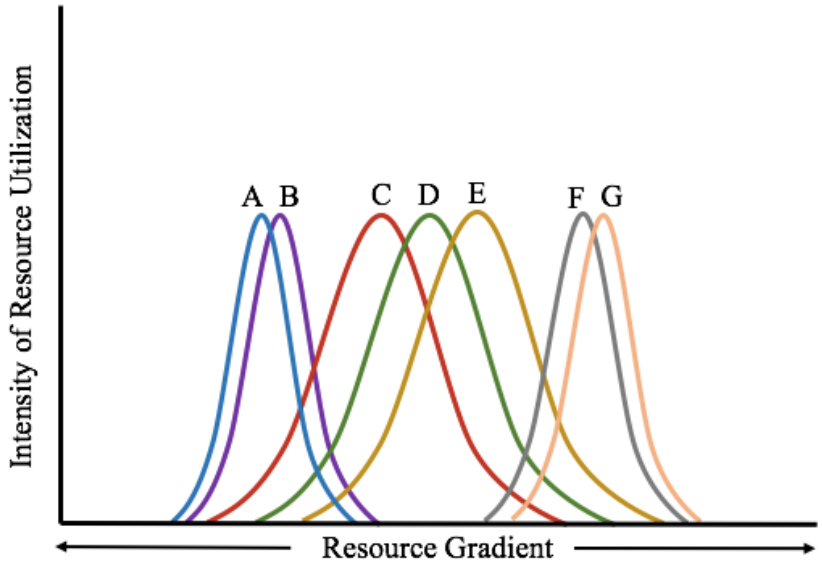

Figure 4.3. Representation of measured individual niche breadth and variation between nest boxes in 2016.

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APPENDIX A: RAW DATA

Table A.1. Stable isotope averages and standard deviations per individual nestling from 2016.

Box	Band Number	Sex	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{2}H$ (‰)	± SD ($\delta^{15}N$)	± SD ($\delta^{13}C$)	± SD ($\delta^{2}H$)
3	1783-96412	M	6.8	-26.3	-61.3	0.2	0.1	4.1
3	1783-96414	F	7.4	-25.7	-62.4	0.6	0.5	8.3
28	1783-96431	M	7.4	-24.7	-56.4	0.6	1.3	17.4
28	1783-96432	F	7.8	-24.4	-53.2	0.5	1.0	10.9
6	1783-96419	M	6.6	-25.4	-55.0	0.0	0.1	5.0
6	1783-96420	F	7.0	-25.7	-66.2	0.1	0.3	11.7
14	1783-96427	F	6.8	-25.4	-66.7	0.1	0.2	6.0
14	1783-96428	M	7.1	-25.3	-63.2	0.3	0.2	3.9
14	1783-96429	F	7.6	-24.4	-50.5	-	-	-
6	N/A	M	8.2	-24.5	-47.8	0.2	0.1	5.4
5	1783-96422	M	7.2	-25.6	-59.3	0.2	0.1	5.1
5	1783-96424	F	6.8	-26.1	-70.7	0.1	0.1	5.2
2	1783-96434	M	7.5	-25.6	-75.3	0.6	0.5	13.4
2	1783-96435	F	8.0	-25.1	-68.8	0.4	0.3	5.7
24	1783_96436	M	7.7	-24.1	-56.5	0.1	0.1	3.7
24	1783_96439	F	8.2	-23.3	-45.6	0.0	0.3	12.2
26	1783-96444	F	7.0	-24.0	-67.9	0.2	0.3	5.7
26	1783-96445	M	7.1	-23.8	-63.4	0.3	0.5	8.5
12	1783-96446	F	6.9	-24.0	-67.1	0.3	0.5	20.2
12	1783-96447	M	6.6	-25.0	-78.8	0.24	0.32	5.7

Table A.2. Nest box pellet and prey proportions per box.

Box #	Year	Mammals	Birds	Lizard	Coleoptera	Orthoptera	Araneae
2	2015	0.023	0.047	0.000	0.047	0.140	0.744
4	2015	0.008	0.008	0.000	0.397	0.444	0.143
7	2015	0.016	0.016	0.000	0.048	0.571	0.349
10	2015	0.065	0.129	0.000	0.032	0.548	0.226
12	2015	0.000	0.018	0.000	0.018	0.509	0.455
15	2015	0.003	0.003	0.000	0.003	0.386	0.604
16	2015	0.000	0.048	0.000	0.000	0.238	0.714
20	2015	0.000	0.000	0.000	0.025	0.850	0.125
21	2015	0.011	0.011	0.000	0.011	0.511	0.457
24	2015	0.000	0.125	0.000	0.188	0.469	0.219
25	2015	0.000	0.011	0.063	0.042	0.358	0.526
2	2016	0.007	0.014	0.000	0.072	0.424	0.482
3	2016	0.000	0.007	0.000	0.014	0.043	0.935
5	2016	0.004	0.023	0.004	0.012	0.394	0.564
6	2016	0.004	0.023	0.000	0.012	0.086	0.875
7	2016	0.000	0.006	0.000	0.006	0.959	0.030
12	2016	0.005	0.005	0.027	0.075	0.812	0.075
14	2016	0.007	0.010	0.003	0.007	0.066	0.907
24	2016	0.014	0.070	0.000	0.014	0.606	0.296
26	2016	0.023	0.023	0.023	0.163	0.488	0.279
28	2016	0.000	0.125	0.000	0.000	0.500	0.375
29	2016	0.000	0.020	0.020	0.000	0.900	0.060

Table A.3. All vertebrate values collected in 2015 from American Kestrel nest boxes.

Order	Year	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{2}H$ (‰)
Bird	2015	8.4	-21.1	-105
Bird	2015	10.0	-22.7	-99
Bird	2015	10.1	-22.4	-96
Bird	2015	8.8	-19.9	-88
Bird	2015	10.2	-22.5	-82
Bird	2015	9.0	-19.9	-82
Bird	2015	9.4	-19.5	-79
Bird	2015	10.8	-21.5	-76
Bird	2015	10.3	-22.3	-71
Bird	2015	9.0	-20.0	-51
Bird	2015	9.2	-21.9	-110
Bird	2015	9.3	-21.9	-95
Bird	2015	9.1	-21.9	-94
Mammal	2015	7.3	-22.6	-41.7
Mammal	2015	5.2	-21.0	-39.5
Mammal	2015	2.5	-24.6	-85.8
Mammal	2015	3.9	-23.9	-83.3
Mammal	2015	4.4	-27.2	-106.3
Lizard	2015	5.8	-23.8	-74
Lizard	2015	5.3	-24.5	-77
Lizard	2015	5.6	-24.4	-84
Lizard	2015	5.9	-24.2	-84
Lizard	2015	7.0	-24.2	-99

Table A.4. All invertebrate values collected in 2015 from American Kestrel nest boxes.

Order	Year	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{2}H$ (‰)
Spider	2015	9.2	-22.7	-89
Spider	2015	10.1	-23.1	-54
Spider	2015	7.1	-26.7	-85
Spider	2015	10.7	-25.70	-72
Spider	2015	8.1	-26.3	-85
Spider	2015	7.3	-26.3	-77
Spider	2015	5.6	-26.1	-62
Spider	2015	7.1	-25.6	-76
Beetle	2015	4.8	-25.9	-70
Beetle	2015	2.1	-26.7	-46
Beetle	2015	5.9	-27.1	-67
Orthoptera	2015	2.0	-24.8	-74
Orthoptera	2015	3.7	-25.6	-65
Orthoptera	2015	8.9	-26.4	-77
Orthoptera	2015	3.1	-26.0	-78
Orthoptera	2015	3.2	-25.3	-66
Orthoptera	2015	5.9	-27.0	-77
Orthoptera	2015	6.7	-25.6	-67
Orthoptera	2015	2.8	-25.4	-69
Orthoptera	2015	1.6	-24.9	-72
Orthoptera	2015	2.7	-26.0	-64
Orthoptera	2015	2.5	-27.9	-62
Orthoptera	2015	3.9	-25.1	-71
Orthoptera	2015	4.4	-25.6	-66
Orthoptera	2015	4.1	-25.0	-61
Orthoptera	2015	2.8	-25.8	-69
Orthoptera	2015	4.3	-25.2	-44
Orthoptera	2015	1.2	-26.3	-70
Orthoptera	2015	3.2	-24.8	-79

Table A.5. All vertebrate values collected in 2016 from American Kestrel nest boxes.

Order	Year	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{2}H$ (‰)
Mammal	2016	6.0	-25.2	-116.8
Mammal	2016	4.3	-23.7	-79.1
Mammal	2016	4.6	-24.0	-87.5
Mammal	2016	4.6	-24.3	-86.3
Mammal	2016	5.2	-26.5	-88.3
Bird	2016	6.8	-25.0	-71
Bird	2016	6.9	-25.0	-73
Bird	2016	4.8	-25.3	-82
Bird	2016	4.9	-21.6	-87
Bird	2016	5.3	-21.8	-94
Bird	2016	5.6	-21.9	-90
Bird	2016	6.8	-24.7	-72
Bird	2016	6.9	-24.5	-68
Bird	2016	6.9	-24.3	-64
Bird	2016	7.3	-24.3	-73
Bird	2016	7.5	-24.3	-75
Bird	2016	5.3	-22.1	-85
Bird	2016	5.4	-21.3	-91
Bird	2016	5.4	-21.9	-85
Bird	2016	5.7	-25.3	-68
Bird	2016	6.3	-25.2	-73
Bird	2016	6.8	-25.1	-69
Bird	2016	5.8	-23.8	-85
Bird	2016	6.1	-23.0	-91
Bird	2016	5.4	-22.7	-84
Bird	2016	5.8	-22.0	-81
Bird	2016	5.0	-23.0	-83
Bird	2016	10.2	-24.4	-87
Bird	2016	9.8	-24.9	-93
Bird	2016	12.2	-21.4	-55
Bird	2016	5.5	-25.1	-67
Bird	2016	5.2	-25.4	-71
Lizard	2016	6.8	-20.7	-82
Lizard	2016	6.9	-21.0	-64
Lizard	2016	6.9	-21.1	-87
Lizard	2016	7.0	-22.3	-72
Lizard	2016	8.6	-24.3	-80
Lizard	2016	7.4	-22.2	-75
Lizard	2016	7.9	-22.9	-86
Lizard	2016	6.2	-25.0	-81

Table A.6. All invertebrate values collected in 2015 from American Kestrel nest boxes.

Order	Year	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{2}H$ (‰)
Spider	2016	6.2	-28.6	-85
Spider	2016	6.7	-28.9	-70
Spider	2016	5.6	-28.0	-68
Spider	2016	6.8	-27.4	-77
Spider	2016	11.6	-27.7	-110
Spider	2016	7.7	-27.0	-97
Spider	2016	7.6	-28.5	-103
Spider	2016	7.2	-28.0	-83
Spider	2016	8.7	-27.6	-78
Spider	2016	5.7	-28.2	-74
Spider	2016	6.1	-27.8	-87
Spider	2016	7.6	-27.4	-80
Spider	2016	7.1	-27.8	-93
Spider	2016	4.9	-28.3	-91
Spider	2016	5.8	-28.8	-84
Spider	2016	6.4	-28.7	-84
Spider	2016	7.8	-27.8	-79
Spider	2016	8.4	-28.0	-81
Spider	2016	5.0	-27.8	-65
Spider	2016	6.0	-28.0	-79
Spider	2016	6.9	-27.9	-76
Orthoptera	2016	4.2	-27.7	-65
Orthoptera	2016	4.0	-27.2	-68
Orthoptera	2016	2.1	-26.9	-63
Orthoptera	2016	3.1	-26.7	-70
Orthoptera	2016	3.8	-27.1	-58
Orthoptera	2016	3.8	-27.4	-74
Orthoptera	2016	3.4	-27.1	-76
Orthoptera	2016	4.3	-27.4	-72
Orthoptera	2016	4.7	-27.2	-67
Orthoptera	2016	4.7	-27.5	-87
Orthoptera	2016	2.9	-28.0	-83
Orthoptera	2016	3.7	-26.5	-71
Orthoptera	2016	2.7	-27.0	-71
Orthoptera	2016	5.4	-27.5	-67
Orthoptera	2016	5.3	-27.9	-69
Orthoptera	2016	3.5	-28.0	-75
Orthoptera	2016	5.4	-28.3	-74

Table A.6. Continued.

Order	Year	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{2}H$ (‰)
Orthoptera	2016	3.4	-28.1	-83
Orthoptera	2016	1.8	-27.3	-71
Orthoptera	2016	5.0	-29.0	-77
Orthoptera	2016	1.0	-28.0	-59
Orthoptera	2016	3.2	-27.9	-76
Orthoptera	2016	6.3	-28.5	-68
Orthoptera	2016	3.7	-27.4	-62
Orthoptera	2016	4.9	-26.2	-78
Orthoptera	2016	6.4	-27.5	-63
Orthoptera	2016	3.3	-27.1	-91
Orthoptera	2016	5.4	-28.1	-65
Orthoptera	2016	3.9	-27.6	-76
Orthoptera	2016	4.4	-27.8	-98
Orthoptera	2016	4.6	-28.3	-85
Orthoptera	2016	6.0	-28.4	-74
Orthoptera	2016	5.8	-27.0	-71
Orthoptera	2016	8.9	-26.3	-75
Orthoptera	2016	3.4	-26.6	-77
Orthoptera	2016	6.0	-28.7	-87
Orthoptera	2016	4.3	-28.0	-92
Beetle	2016	6.4	-27.5	-88
Beetle	2016	7.3	-27.6	-83
Beetle	2016	6.7	-29.0	-77
Beetle	2016	2.3	-28.8	-87
Beetle	2016	2.4	-27.9	-87
Beetle	2016	3.8	-26.2	-66
Beetle	2016	7.3	-28.2	-64
Beetle	2016	7.5	-28.6	-78
Beetle	2016	8.2	-28.0	-83
Beetle	2016	10.7	-27.7	-77
Beetle	2016	9.7	-24.9	-56
Beetle	2016	9.2	-27.9	-64

Table A.7. All stable isotope data for 2015 American Kestrel adults and nestlings.

Year	Age	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{2}H$ (‰)
2015	Nestling	7.8	-22.3	-41
2015	Nestling	8	-22.1	-25
2015	Nestling	8	-21.9	-22
2015	Nestling	8.3	-23.2	-70
2015	Nestling	5.5	-23.1	-52
2015	Nestling	8.5	-22.3	-48
2015	Nestling	6.3	-22.6	-53
2015	Nestling	5.5	-23.9	-51
2015	Nestling	5.9	-23	-55
2015	Adult	7.5	-21.8	-11
2015	Adult	9.4	-20.7	4
2015	Adult	8	-21.6	0
2015	Adult	7.9	-22	-22
2015	Adult	7.5	-21.3	6
2015	Adult	9.1	-21.4	11
2015	Adult	10	-22.4	1
2015	Adult	9.9	-22.7	14
2015	Adult	7.4	-22.3	-13
2015	Adult	7.8	-21.6	2
2015	Adult	8.3	-22.4	2

Table A.8. All stable isotope data for 2016 American Kestrel adults and nestlings.

Year	Age	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{2}H$ (‰)
2016	Nestling	6.8	-26.3	-61
2016	Nestling	7.4	-25.7	-62
2016	Nestling	6.6	-25.4	-55
2016	Nestling	7	-25.7	-66
2016	Nestling	7.2	-25.6	-59
2016	Nestling	6.8	-26.1	-71
2016	Nestling	6.8	-25.4	-67
2016	Nestling	7.1	-25.3	-63
2016	Nestling	7.4	-24.7	-56
2016	Nestling	7.8	-24.4	-53
2016	Nestling	7.7	-24.1	-57
2016	Nestling	7	-24	-68
2016	Nestling	7.1	-23.8	-63
2016	Nestling	6.9	-24	-67
2016	Nestling	6.6	-25	-79
2016	Adult	8.5	-21.5	-45
2016	Adult	8.4	-21.6	-40
2016	Adult	7.4	-22.2	-19
2016	Adult	9.1	-21.4	-33
2016	Adult	8.3	-22.3	-37
2016	Adult	12	-18.8	-62
2016	Adult	8.9	-22.1	-20
2016	Adult	7.7	-22.4	-29
2016	Adult	7.9	-21.8	-25
2016	Adult	8.4	-21.8	-18