DIET AND BEHAVIOR OF FERRUGINOUS HAWKS NESTING IN TWO GRASSLANDS IN NEW MEXICO WITH DIFFERING ANTHROPOGENIC ALTERATION

By

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The following individuals have read and discussed the thesis submitted by William Hanlon Keeley, and they also evaluated his presentation and response to questions during the final oral examination. They found that the student passed the final oral examination, and that the thesis was satisfactory for a master's degree in Raptor Biology.

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CHAPTER ONE

FOOD HABITS OF BREEDING FERRUGINOUS HAWKS IN TWO GRASSLANDS IN NEW MEXICO WITH DIFFERING ANTHROPOGENIC ALTERATION

Abstract

I analyzed regurgitated pellets, prey remains, and video recordings to describe Ferruginous Hawk (*Buteo regalis*) diet in two grasslands in New Mexico, USA, the Estancia Valley and the Plains of San Agustin, that differed in anthropogenic alteration. Video monitoring revealed Ferruginous Hawks provisioned nestlings with more biomass than pellet analysis estimates from the same nests. Three mammalian prey species, Botta's pocket gopher (*Thomomys bottae)*, Gunnison's prairie dog (*Cynomys gunnisoni)*, and desert cottontail (*Sylvilagus audubonii)*, contributed similar proportions to Ferruginous Hawk diet in percent biomass while Botta's pocket gopher dominated diet in percent frequency. Ferruginous Hawks breeding in the anthropogenically-altered Estancia Valley consumed more Gunnison's prairie dogs than Ferruginous Hawks in the rural Plains of San Agustin, regardless of calculative method, while Ferruginous Hawks in the Plains of San Agustin consumed more desert cottontails. From 1998-2005, Ferruginous Hawks in the Estancia Valley produced significantly more fledglings per nesting attempt than Ferruginous Hawks in the Plains of San Agustin. This indicated that the persistence of colonial mammals like Gunnison's prairie dogs, which offer minimal predatory search time, may have increased Ferruginous Hawk reproductive output and helped to offset the effects of moderate levels of human development. Intact Gunnison's prairie dog colonies should be conserved in the Estancia Valley to enable maintenance of current Ferruginous Hawk productivity levels in the midst of increased human development, a threat that is becoming more pronounced. Further documentation of behavior and food requirements of Ferruginous Hawks in anthropogenically-altered landscapes is necessary to conserve this grassland obligate whose habitat is rapidly diminishing.

Introduction

Ferruginous Hawk (*Buteo regalis*) populations are declining throughout the species' range (Olendorff 1993, Bechard and Schmutz 1995, Collins and Reynolds 2005). Cumulative encroachments into Ferruginous Hawk breeding habitat include energy development (oil and gas: Ingelfinger and Anderson 2004; wind: Kuvelsky et al. 2007), and human population growth (Theobald et al. 1997). Anthropogenic habitat loss has wide ranging effects on many natural wildlife populations (McDonnell and Pickett 1990), especially in the western United States (Germaine et al. 1998, Odell and Knight 2001, Lenth et al. 2006) where the human population is growing 2-3 times faster than any other part of the country (Baron et al. 2000). Greater than 60% of counties in the West are experiencing "rural sprawl", where rural areas (outside city and town limits) are growing at a faster rate than urban areas (Theobald 2001). Increased human development negatively affects species that are more abundant in large habitat patches (i.e., "area-sensitive", Robbins et al. 1989) like Ferruginous Hawks (Bechard et al. 1990, Berry et al.

1998), an ecological specialist (Plumpton and Andersen 1998) and grassland obligate species, which have historically inhabited grasslands with low levels of human alteration (Knopf 1994).

Temperate grasslands are considered the most imperiled biome on earth (Hoekstra et al. 2005) and have decreased in area by more than 50% in the United States. From 1950-2000, the area modified by human activity grew nearly tenfold in counties adjacent to metropolitan counties, with the largest growth in the West (Brown et al. 2005). Indeed, as the human ecological footprint expands, large open tracts of natural grasslands are becoming less abundant. This is a definitive problem for wide-ranging predators like Ferruginous Hawks that will abandon sites if disturbed during the nesting season (White and Thurow 1985, Bechard and Schmutz 1995, Ward 2001).

Exurban development, a semi-rural land-use characterized by low housing density (~2 ha per unit or more) and large-lot development (Daniels 1999), is increasing at a rate of 10-15% per year and is now the fastest growing form of land use in the United States (Theobald 2001, Brown et al. 2005). Exurban development increases fragmentation, contributes to habitat loss (Theobald et al. 1997), and affects abundance of native species and community composition in birds, mammals, and herpetofauna (e.g., Hansen et al. 2005).

Knowledge of a species' diet is essential to understanding its ecology, life history, and conservation needs. The diet of the Ferruginous Hawk has been documented throughout its range, but thorough research on diet composition on the southern edge of the species' breeding distribution is limited (Olendorff 1993, Bechard and Schmutz 1995).

Diet and other dynamics of peripheral populations are important to monitor because they may represent persistence in less suitable habitat (Brown 1984, Lawton 1993) and develop unique behavioral traits that allow adaptation to marginal environments (Lesica and Allendorf 1995). Recent studies have found high survival in peripheral populations following range contractions in core areas of many species (Lomolino and Channell 1995). This finding supports their high conservation value. Alternatively, some authors suggest that peripheral populations are important to conserve because of their inherent susceptibility to extirpation (Lesica and Allendorf 1995), their divergent genetic composition (Mayr 1963), and their initial responses to climate change (Hampe and Petit 2005).

In this chapter, I describe Ferruginous Hawk diet in two grasslands in New Mexico, the Estancia Valley and the Plains of San Agustin, that differed in anthropogenic alteration. The Estancia Valley is an exurban environment that is increasingly pressured from neighboring Albuquerque while the Plains of San Agustin has retained a rural human population for generations. Plumpton and Andersen (1998) postulated that wintering Ferruginous Hawks would become behaviorally plastic and more tolerant of human disturbance when black-tailed prairie dogs (*Cynomys ludovicianus*) were abundant.

As Gunnison's prairie dogs are currently under consideration by the US Fish and Wildlife Service to be listed under the Endangered Species Act (US Fish and Wildlife Service 2008), and because descriptions of Ferruginous Hawks breeding in anthropogenically-altered landscapes are lacking, my research objectives were as follows:

1.) describe dietary differences between study areas by testing the hypothesis: Gunnison's prairie dogs constitute a larger portion of Ferruginous Hawk diet in the Estancia Valley than in the Plains of San Agustin.
2.) test the efficacy of using remote video monitoring to describe Ferruginous Hawk diet
3.) explore the possibility that Ferruginous Hawks can exhibit behavioral flexibility and become more tolerant of human disturbance during the breeding season if Gunnison's prairie dogs are available.

Methods

Study Areas

I studied breeding Ferruginous Hawks on private and public lands in the Estancia Valley and Plains of San Agustin, two grasslands located approximately 350 km apart in New Mexico (Figures 1.1, 1.2). There were four nests outside of the study areas that I also sampled during my research. To provide a more complete description of breeding Ferruginous Hawk food habits in New Mexico, I incorporated data gathered from those nests into my “overall” descriptions of diet composition but excluded them from discussions focused on study area variation.

Environmental Variation

The Estancia Valley spans approximately 300,000 ha in Torrance and Santa Fe counties, New Mexico (Figure 1.1). The Sandia and Manzano Mountains separates the Estancia Valley from Albuquerque (Pop.: 448,607), which is 30 km west. My study area represents 158,000 ha in the western half of the Estancia Valley and is loosely bordered by State Highway 41 to the east, the Manzano Mountains to the west, State Highway 60 to the south, and Interstate 40 to the north (Figure 1.1).

Dominant vegetation in the Estancia Valley is similar to vegetation present in the Plains of San Agustin. Large expanses of blue grama (*Bouteloua gracilis)* and buffalograss (*Buchloe dachtyloides*) meet widely scattered juniper *(Juniperus* spp.*)* trees. However, unlike the Plains of San Agustin, non-native trees like Chinese elm (*Ulmus parvifolia*), mainly associated with occupied dwellings and abandoned homesteads, are present and provide nesting substrates. Ferruginous Hawk nests in the Estancia Valley average 1947 m in elevation (n = 36, range: 1865-2054 m, this study). The town of Estancia, located in the center of the study area, averages 32.5 cm of precipitation while temperatures ranged from -9.2 to 31.4 °C (Western Regional Climate Center 2007b).

The Plains of San Agustin is located approximately 70 km west of Socorro (population in the year 2000 [hereafter “Pop.”]: 8,877). The Plains of San Agustin spans approximately 238,000 ha between Magdalena and Datil in Socorro and Catron counties, New Mexico. Geologically, the southwest-northeast oriented basin is constricted by the San Mateo Mountains to the east, the Gallinas Mountains to the northeast, the Datil and Mangas Mountains to the northwest, Tularosa Mountains to the west and Luera Mountains to the south (Figure 1.2).

The flat bottom of the Plains of San Agustin is an artifact of a Pleistocene-era lake and is characterized by species diagnostic to the desert short-grass prairie (Dick-Peddie 1993). Blue grama and buffalo grass co-dominate the open country while scattered, isolated junipers provide the majority of nesting sites for Ferruginous Hawks and other birds. Elevated from the basin floor, sagebrush (*Artemisia* spp.) and pinyon (*Pinus* *edulis*)-juniper woodlands dominate higher elevations (Dick-Peddie 1993) and meet mountainous areas like the continental divide to the west and the headwaters of the Gila River to the south. Ferruginous Hawk nests in the Plains of San Agustin average 2170 m above sea level (n = 41, range: 2025-2338 m, this study). The area receives 28.7 cm of annual precipitation while the average temperatures range from -10.3 to 29.3 °C (Western Regional Climate Center 2007a).

Anthropogenic Variation

To describe anthropogenic differences between the Estancia Valley and Plains of San Agustin, I used a geographic information system (ArcGIS 9.2, ESRI, Redlands, California) to analyze data obtained from federal and state government websites. Jane Farmer (BLM Socorro Field Office, Socorro, New Mexico) digitized the Plains of San Agustin boundary and I digitized the Estancia Valley boundary. I obtained 2006 land ownership data from the New Mexico Bureau of Land Management (BLM 2007) and used "X-Tools", an ArcGIS extension, to calculate area totals for surface ownership of both study areas. I obtained all other data including New Mexico counties and cities, from the New Mexico Resource Geographic Information System (University of New Mexico 2006).

I analyzed the most current anthropogenic data available that covered my study areas uniformly. For example, United States Census Bureau (USCB) Summary File 1 from 2000 (U.S. Census Bureau 2006) provided the most uniform coverage of occupied housing units and human population (via US Census Blocks) while USCB 2006 TIGER boundary files provided the most uniform road coverage in the Estancia Valley and the Plains of San Agustin. To facilitate my analysis, I used TGR2SHP v7.01 (Ralston 2008) to convert UCSB TIGER boundary files into a road layer. I used the digitized study area boundaries as a template to clip census block and road layers and used X-Tools to calculate total length of roads within each study area. I summed road lengths (km) across all Census Feature Classification Codes (CFCC), which categorize roads based on their use and structure (U.S. Census Bureau 2007). I then used these data in a GIS to determine the road density within each study area and the distance between a successful Ferruginous Hawk nest (≥ 1 young fledged) and the nearest road.

Gunnison's Prairie Dogs

In 2004, in both study areas, I visited Gunnison's prairie dog colonies that were initially located during aerial and ground surveys conducted in 1999 (Cook et al. 2003, G. Garber Hawks Aloft, Inc. unpublished data) to document colony movement and occupancy at these sites. To determine occupancy, I used binoculars to survey each colony for 10 min from my vehicle for two consecutive days in fair weather. In 2005, in the Plains of San Agustin, a minimum of two observers accompanied the pilot in a Cessna 205 fixed wing aircraft to find new Gunnison's prairie dog colonies. Air speed during surveys averaged 160 kilometers per hour and altitude ranged from 90-240 m above ground. Aerial line transects were spaced 500 m apart and were either 11 or 18 km long, depending on public property boundaries.

Ferruginous Hawk Nesting Productivity

In April of each year, aerial surveys were conducted to determine occupancy (i.e., nestlings or eggs observed on the nest or adult in incubating posture) at known nest sites. New nests were marked using a Garmin 92 Global Positioning System (Garmin International Inc., Olathe, KS, USA) designed for use in aircraft. A minimum of two observers accompanied the pilot in a Cessna 205 fixed wing aircraft. Air speed during surveys averaged 160 kilometers per hour and altitude ranged from 90-240 m above ground. Following aerial surveys, each occupied nest was visited a minimum of two times to determine breeding productivity. I considered nestlings to be fledged when they reached 80% of their fledging age, or 32 days.

Diet

I analyzed prey remains, regurgitated pellets, and time-lapse video to compare the diet composition of breeding Ferruginous Hawks in two grasslands in New Mexico during 2004 and 2005. For all techniques, I described diet composition in percent frequency and percent biomass. I defined percent frequency as the number of individuals of one species divided by number of all prey items delivered to a nest and percent biomass as one species' contribution to total prey biomass delivered to a nest. To compute prey biomass, I obtained weights from published sources (Smith and Murphy 1973, Steenhof 1983) or calculated a mean weight obtained from a minimum of 20 individuals per species from the Denver Museum of Nature and Science in Denver, Colorado, USA, or the Museum of Southwestern Biology at the University of New Mexico, Albuquerque, New Mexico, USA. I combined results from two sampling techniques, prey remains and regurgitated pellets, to create one metric to facilitate comparison of food habits between study areas. I summed these data conservatively to avoid potentially counting the same individual twice (Marti et al. 2007), but I also included data derived from each technique separately for future reference.

Pellet Collection and Analysis

I collected regurgitated pellets below each occupied Ferruginous Hawk nest tree and adjacent perch trees every 6-8 days from hatching to post-fledging or at least three times during the breeding season. To ensure an accurate representation of diet, I cleared all pellets near the nest tree prior to the 2004 breeding season and discarded all weathered pellets that were presumed to be from previous years.

I analyzed each day's collection separately using standard methods (Marti et al. 2007). I dissected each pellet by hand and identified mammalian prey using dentition patterns to species whenever possible. Most pellets I dissected contained a mandible and/or a maxilla, which proved to be the most reliable in quantifying diet. I used the ulna, radius, and femur as supplemental tools to identify prey. For some ground squirrel species, like spotted (*Spermophilus spilosoma*) and thirteen-lined (*S. tridecemlineatus*) ground squirrels, dentition patterns were very similar and species level identification was not possible, so I classified both as *Spermophilus* spp. and used the mean of their combined published weights to calculate biomass (Appendix A).

I enumerated mammalian prey by grouping similar structures from one pellet and recorded the minimum number of individuals represented by its identifying structures (Mollhagen et al. 1972). For example, if one pellet produced three left mandibles, two right mandibles and two right ulna of the same species, I recorded three individuals consumed. These methods likely provided a conservative estimate of enumerated prey because I identified and counted individuals using only the most frequently encountered structure. I identified avian prey to species whenever possible by feather pattern and color and assumed that detection of feathers in one pellet was equal to one individual consumed. I identified insects to family or order by distinguishable body segments and enumerated them in methods similar to mammalian prey.

I identified mammalian prey by matching dentition patterns from a complete (i.e., skulls and skins) reference collection obtained from the Denver Museum of Nature and Science and published resources (Glass 1974, Findley et al. 1975, Hall 1981, Schwartz and Schwartz 1981, Dalquest and Horner 1984). I identified avian prey by matching feather patterns from the Vertebrate Museum, Department of Biology, Boise State University, Boise, Idaho, USA. After analyzing each collection, I placed all bones into a labeled glass jar to use for future reference.

Prey Remains

I collected prey remains using methods similar to pellet collection. I did not remove prey below the nest as this could have altered fledgling fitness. If I found whole or partially consumed prey, I noted the species and left the body intact. If I could not identify the species in the field, I clipped a body part (i.e., mammal's foot) to aid in later identification. I followed procedures similar to those described above for identifying and enumerating prey remains.

Video Monitoring

I installed "Basic Sentinel I All Weather Video Surveillance Systems" from Sandpiper Technologies, Inc. (Manteca, CA, USA) to monitor prey deliveries. I set the time-lapse system to record 20 frames per sec (one third real-time) which fit approximately 24.5 hrs of nest activity onto one T-160 videotape. I used TDK High Quality videotapes as media and powered the systems with a Sears 12 volt 91.6 ampere deep-cycle marine battery. I divided each video-recorded day into three approximately 5 hr time blocks: time block “A” (0520-1030 H), time block “B” (1030-1540 H), and time block “C” (1540-2050 H) and randomly selected two blocks to record per day. This enabled me to return to the nest every other day to refresh tapes and batteries. As some nests were 350 km apart, this sampling regime was the most effective option logistically to sample bird activity at the nest.

Because cattle grazed land surrounding Ferruginous Hawk nests, I buried the 50-75 m co-axial cable that connected the VCR to the camera (dimensions: 6 x 4 x 4 cm) ≥ 10 cm underground. I also cached the VCR and battery in a camouflage tent and built a fence around the structure using t-posts and chicken wire as a safety precaution to mitigate potential damage to the video system.

I attached the camera to a 3.8 cm diameter wooden dowel using automobile radiator hose clamps and secured this apparatus to a tree branch using U-shaped pole fasteners. The distance between the camera and nest varied among sites because of incongruities in nest tree structure (range: 0.7 – 1.7 m), but I set it at approximately 1 m whenever possible (Booms and Fuller 2003).

Following each field season, I used the time-lapse VCR to playback each videotape on a Sony television with a 68 cm screen. This setup enabled frame-by-frame analysis in high quality resolution. For every delivery, I noted prey type to species whenever possible. To determine species of prey delivered, I used several physical attributes such as pelage pattern, shape of eyes and head, length of tail, and size of body and feet, and referenced the skins collection from the Denver Museum of Nature and Science. Furthermore, because there was a large weight discrepancy between young and adult Gunnison’s prairie dogs, I categorized them separately whenever possible and used appropriate weights for biomass calculations (Appendix A). Prey that I determined to be re-delivered were noted and only counted once during videotape analysis.

In some instances when analyzing video, I was not able to identify the prey item to species. In these cases, I categorized the prey item into general taxa (i.e., bird, mammal, etc.) and for mammalian prey, further classified them based on body size. For unidentified small birds, I used the average of three passerine weights as the biomass for "unidentified bird" (Appendix A). For unidentified small mammals (i.e., mouse size), I used the mean biomass of three mouse-sized species that Ferruginous Hawks took as prey as the weight for "unknown mammal 1". For larger unidentified mammals, I used averaged weights from five larger-sized mammalian prey items to provide a surrogate biomass measure ("unknown mammal 2"). This technique improved precision of estimates of delivered biomass for video-monitored nests.

Food-niche Breadth

I estimated Ferruginous Hawk food niche breadth with Levins' (1968) modification of Simpson's index (D) (food-niche breadth = $1/D = 1/\sum p_i^2$, where p_i represents the frequency of each species of prey in the diet). According to Marti et al. (2007), this number better represents diet diversity than Shannon's diversity index and is more widely used (Steenhof and Kochert 1985, MacLaren 1986, Marti et al. 1993, Moulton et al. 2005) and thus was comparable with other studies. I used this index to compare Ferruginous Hawk diet breadth between study areas and with other estimates from the western United States.

Statistical Analysis

I used JMP 5.0 statistical software (SAS Institute, Inc., Cary, NC, USA) to test for differences in sampling technique, occupied housing units and population per US Census Block, and components of diet composition between the Estancia Valley and Plains of San Agustin. I tested for differences between sampling techniques using a paired t-test. When data met statistical assumptions, I reported *t*-statistics with associated probability value; when they did not, I reported Wilcoxon rank sum Z scores and associated p-values for non-parametric data (Zar 1999).

When making multiple comparisons from the same dataset, some researchers employ a Bonferroni adjustment to control Type I error (Rice 1989). However, other researchers, especially in the field of ecology, contend that by adjusting the alpha level, sound inference is compromised (Moran 2003, Nakagawa 2004). I did not use a Bonferroni adjustment but made *a priori* rules governing what I would judge scientifically significant. For *a priori* hypotheses on differences in diet composition between study areas, I did not change alpha from 0.05. For all other diet composition comparisons, I required alpha ≤ 0.05 in both analytical methods (percent frequency and percent biomass) to assign statistical significance for that particular comparison, thereby reducing the chance of Type I error, but concurrently maintaining the ecological significance of the findings. For comparisons unrelated to diet composition, I considered probability values significant if they were less than or equal to 0.05 and report means and standard errors throughout.

Results

Study Areas

Anthropogenic Variation

In 2000, private, state, and public land accounted for 53, 35, and 12% of surface ownership in the Plains of San Agustin and 96, 4, and 0% in the Estancia Valley, respectively. The Estancia Valley is close to heavily urbanized Albuquerque, and the towns of Moriarty (Pop.: 1765), Estancia (Pop.: 1584), and Mountainair (Pop.: 1116) are in the Estancia Valley (Figure 1.1). Alternatively, no established towns exist in the Plains of San Agustin; the closest town, Magdalena (Pop.: 913), is 20 km away.

In 2000, 16,338 people lived in 6,094 housing units in the Estancia Valley while 61 people in 20 houses dotted the landscape in the Plains of San Agustin (Table 1.1). Consequently, USCB census blocks in the Estancia Valley had more people (Wilcoxon Rank Sum: $Z = 13.37$; $p < 0.00001$) and more occupied houses ($Z = 13.54$; $p < 0.00001$) than census blocks in the Plains of San Agustin.

In 2006, overall road density in the Estancia Valley was almost twice that found in the Plains of San Agustin (Table 1.1). Specifically, roads characterized by the USCB as unpaved roads that link small towns (“A41”, Appendix B), were twice as dense in the Estancia Valley while roads characterized as service roads for ranches and oil rigs (“A74”), or roads requiring 4-wheel drive (“A51”) were 33% more dense in Plains of San Agustin. Nests with successful Ferruginous Hawk breeding attempts (≥ 1 fledgling, $n = 31$) were 531 ± 67 m from the nearest road. Successful nests in the Estancia Valley ($n = 18$) were 403 ± 82 m to the nearest road while successful nests in the Plains of San Agustin were 708 ± 97 m from the nearest road, a difference which was statistically significant ($t_{29} = -2.40$, $p = 0.02$, Table 1.1). Ferruginous Hawks produced more fledglings per nesting attempt in the Estancia Valley (n = 35, 2.43 ± 0.194) than in the Plains of San Agustin (n = 25, 1.48 ± 0.231) during my study ($t_{58} = 3.15$, $p = 0.003$).

Gunnison's Prairie Dog Colonies

Of the 47 occupied Gunnison's prairie dog colonies documented in 1999 in the Estancia Valley, 57% (n = 27) remained occupied in 2004, and 12 new colonies were found. In 2004, in the Plains of San Agustin, Gunnison's prairie dogs still occupied all colonies located in 1999 (n = 5), but aerial surveys did not locate new colonies in the area.

Diet

Regurgitated Pellets

I identified 985 prey items representing at least 27 species from 844 pellets collected near 49 successful Ferruginous Hawk nests in New Mexico (Appendix A). Mammals represented 89% of all prey items (i.e., frequency) and 98% of all biomass. Botta’s pocket gophers (*Thomomys bottae*) made up one-third of biomass and almost 40% of diet by frequency. Gunnison’s prairie dogs and desert cottontail rabbits (*Sylvilagus audubonii*) also substantially contributed (i.e. ≥ 10%, Marti et al. 1993) to biomass while *Spermpohilus* spp. made up one quarter by frequency (Appendix C).

I collected 669 pellets, yielding 729 prey items, from 29 successful nests in the Estancia Valley (2004:10 nests, 2005: 19 nests) and 144 pellets, yielding 207 prey items, from 16 successful nests in the Plains of San Agustin (2004: 3 nests, 2005: 13 nests). Although I identified more than three times as many prey items in the Estancia Valley, many similarities existed in Ferruginous Hawk diet between my two study areas.

Mammals constituted similar portions of diet in both study areas for frequency (88%) and biomass (98%). Botta's pocket gopher was the most common prey for Ferruginous Hawks in the Estancia Valley and Plains of San Agustin in terms of biomass (~34%) and frequency (~39%). *Spermophilus* spp. also composed a substantial part of Ferruginous Hawk diet in the Estancia Valley and Plains of San Agustin in terms of biomass (14% and 12%, respectively) and frequency (~25%).

Prey Remains

In 2004-05, I found 45 prey remains at 16 nests in the Estancia Valley and 14 remains at five nests in the Plains of San Agustin. When combined, these 59 prey remains represented 14 different species (Appendix D). Notable additions to Ferruginous Hawk diet composition detected only from this technique included rock squirrel (*Spermophilus variegatus*), Common Raven (*Corvus corax*), Chihuahuan Raven (*C. cryptoleucus*), and long-tailed weasel (*Mustela frenata*).

Overall, mammals constituted 89% and 94% by frequency and biomass, respectively, of prey remains collected from all nests sampled (Appendix C). Desert cottontail contributed the highest dietary proportion for frequency (22%) and biomass (29%), but Gunnison's prairie dog and Botta's pocket gopher also represented at least 10% to diet in both analytical methods.

Pellets and Prey Remains

Overall.

I detected at least 1035 prey items from 49 successful nests in New Mexico, when pellets and prey remains were combined. Prey species richness increased from 20 (using pellets alone) to 27, a 35% increase following data integration.

In total, Ferruginous Hawks consumed at least 16 different mammalian species, 7 birds, 2 reptiles, and 2 insect orders (Appendix D).

I recorded at least 5,061 ± 572 g (range: 434 - 17,178 g) of prey in each nest (n = 49), and 2,097 ± 233 g per nestling (Table 1.2). Among major prey types, I detected Botta's pocket gophers most frequently at nests (n = 47 nests, 96%), followed closely by *Spermophilus* spp. (n = 44 nests, 88%). I detected Gunnison's prairie dogs and desert cottontails at similar, moderate proportions. Of non mammalian prey, I found birds and insects at approximately 40% and 33% of sampled nests, respectively (Table 1.2).

Mammals accounted for 90% of Ferruginous Hawk diet by frequency and 98% by biomass (Table 1.3). Botta’s pocket gopher constituted significant portions of diet in both analytical techniques (frequency: 37%; biomass: 29%). Desert cottontail composed only 9% of Ferruginous Hawk diet by frequency but constituted three times that for biomass. Similarly, Gunnison's prairie dog represented 11% of Ferruginous Hawk diet by frequency but double that amount in biomass. Alternatively, *Spermophilus* spp. occurred frequently (24%) in diet but was 10% of biomass. Black-tailed jackrabbits (*Lepus californicus*) were much less commonly detected (frequency: 1.5%) but did constitute 6% of biomass consumed by Ferruginous Hawks. Similarly, rock squirrels represented 4% of diet by frequency and 7% by biomass.

Birds and insects each represented 5% of Ferruginous Hawk diet by frequency but considerably smaller portions of total biomass. I identified Western Meadowlark (*Sturnella neglecta*) as the most common avian prey item while insect families were composed of Acrididae (grasshoppers) and Scarabidae (scarab beetles) (Table 1.3).

Study Area Variation. Numerically, Ferruginous Hawks in the Estancia Valley provisioned nestlings with 79% more biomass than hawks in the Plains of San Agustin (Table 1.2). When controlling for number of young, Ferruginous Hawks did not deliver significantly more biomass or prey items to nests in the Estancia Valley than to nests in the Plains of San Agustin.

I found mammals in all nests sampled (n = 45) but other taxa were not as common. I identified avian remains in 59% (n = 17) of Estancia Valley nests but only 19% (n = 3) of Plains of San Agustin nests (Table 1.2). While I detected insects at similar, moderate rates in nests of both study areas, I found reptiles in a higher percent of occupied nests in the Estancia Valley than in the Plains of San Agustin. Among mammals, I detected Botta's pocket gopher most frequently in all nests, regardless of study area. Only one nest in each study area did not contain evidence of Botta's pocket gopher. I found remnants of Gunnison's prairie dog in 72% (n = 21) of nests in the Estancia Valley but in only 38% (n = 6) of Plains of San Agustin nests. Among leporids, I identified desert cottontail in a larger proportion of nests in the Plains of San Agustin than in the Estancia Valley and black-tailed jackrabbits at equally lower numbers of nests in both study areas (~12%). I observed *Spermophilus* spp. at equally high levels (89%), and insects at similar, moderate levels (~36%) between study areas.

Mammals dominated Ferruginous Hawk diet in both study areas across both analytical methods as this prey group nearly supplied 100% of the biomass to young in the Estancia Valley (Table 1.4). Among other prey classes, I detected more avian prey in the diet of Estancia Valley hawks than in the diet of Plains of San Agustin hawks. Specifically, I found three times more avian prey items in the diet of Estancia Valley hawks, which translated to six times more biomass, than in the diet of Plains of San Agustin hawks. Alternatively, I identified twice as many insects in pellets collected from Plains of San Agustin nests than from Estancia Valley nests.

In both study areas, Ferruginous Hawks showed similar use of a few mammalian species. Specifically, Botta's pocket gopher constituted equally large portions of Ferruginous Hawk diet by frequency (37%) and biomass (30%) while *Spermophilus* spp. contributed substantially to frequency (25%) and to biomass (13%) (Table 1.3).

However, some clear differences existed between the diets of Ferruginous Hawks in the two study areas. Across both analytical methods, Estancia Valley adults consumed significantly more Gunnison’s prairie dogs while Plains of San Agustin adults consumed significantly more desert cottontails (Table 1.4). Desert cottontails provided the largest portion of biomass (35%) and were frequently delivered (20%) to Plains of San Agustin nests, nearly doubling Estancia Valley measures. Alternatively, Ferruginous Hawks in the Estancia Valley consumed three times more Gunnison's prairie dogs than hawks in the Plains of San Agustin. As a corollary, Gunnison's prairie dogs contributed one quarter of all biomass consumed by Estancia Valley hawks but only represented 6% of biomass consumed by Plains of San Agustin hawks. Ferruginous Hawks did not take black-tailed jackrabbits very frequently (Estancia Valley: < 1%; Plains of San Agustin: 3%), but the leporid provided a substantial amount of biomass to nests in the Plains of San Agustin.

Food Niche Breadth and Diet Diversity. In all nests sampled in New Mexico (n = 49), Ferruginous Hawks delivered 5.00 ± 0.29 (range: 2-10) different prey species and registered a food-niche breadth (Levins 1968) of 4.14. There was no difference in food-niche breadth or prey species richness between study areas (Table 1.2).

Video

I completed all installation operations between 0700-0830 H and stayed no longer than 56 min at any site to limit nestling exposure to me. In order to avoid nest desertion by adults (Olendorff 1973, White and Thurow 1985, Ward 2001), I established all video systems after young had attained 7 days of age (mean age: 12.7 ± days (n = 15), range: 8-18). I recorded 1,373 hr of nest activity from six video-monitored nests in New Mexico from which I identified 612 prey deliveries to video-monitored nests. Of these prey deliveries, 2.6% (n = 16) were items that were delivered once, taken away from the nest, and subsequently redelivered. On 10 occasions, adults delivered live prey to the nest, all of which were spotted ground squirrels.

I categorized 11.75% of prey items to order, 4.6% to family, 3.6% to genus, and 78.85% to species across both study areas. I placed all but 1.2% of prey items delivered into prey categories (Appendix C).

Ferruginous Hawks delivered 20,928 ± 5082 g of prey to video-monitored nests (n = 6). Mammals represented 96% of Ferruginous Hawk diet by frequency and 99% by biomass (Appendix C). Ferruginous Hawks delivered spotted ground squirrels most frequently (28%), but Gunnison’s prairie dogs contributed the most biomass (30%). Other important mammalian prey included Botta’s pocket gopher (frequency: 25%) and desert cottontail rabbits (biomass: 14%). At video-monitored nests, avian consumption by Ferruginous Hawks was confined to passerines and was low, registering only 2% of overall diet by frequency. Reptiles were even less frequently consumed as they provided fewer than 1% of prey items.

I recorded 577.5 hr of activity from three nests in the Plains of San Agustin and 796.25 hr of activity from three nests in the Estancia Valley. I documented 310 prey deliveries to Plains of San Agustin nests and 302 prey deliveries to Estancia Valley nests. Of these, 2.9% (n = 9) and 2.2% (n = 7) were prey items redelivered to nests in the Plains of San Agustin and Estancia Valley, respectively, and were not included in diet analyses. Video-monitored Ferruginous Hawks delivered on average 7.3 different prey species in the Estancia Valley (range: 6-9) and 8.3 different species in the Plains of San Agustin (range: 7-9). Levins' (1968) food niche breadth index for video-monitored nests was similar between study areas, each registering approximately 3.5.

The camera systems recorded 99.9% and 96.1% of prey deliveries to nests in the Plains of San Agustin and Estancia Valley, respectively. That is, in some instances, prey items were already on the nest when video recording began. Gunnison's prairie dogs composed the majority of Ferruginous Hawk diet in the Estancia Valley in frequency (36%) and biomass (57%), but the rodent represented < 7% of diet composition in the Plains of San Agustin (Table 1.5). Alternatively, Botta's pocket gophers represented 35% of diet by frequency and 33% by biomass for Ferruginous Hawks in the Plains of San Agustin, but this prey item constituted less than half those proportions in the diet of Estancia Valley hawks. In a similar trend, desert cottontail rabbits contributed substantially to biomass consumed by Ferruginous Hawks in the Plains of San Agustin, but represented < 5% of total biomass consumed by Estancia Valley adults. Spotted ground squirrels were a major contributor to the diet of Ferruginous Hawks in both study areas. This sciurid represented 23% and 8% in the Estancia Valley and 34% and 16% in the Plains of San Agustin by frequency and biomass, respectively.

Comparison of Techniques

I identified 597 prey items using time-lapse video at six Ferruginous Hawk nests but only identified 59 prey items when pellets and prey remains were combined from the same nests (Table 1.6). Video monitoring revealed Ferruginous Hawks delivering significantly more biomass to each nest than that estimated using pellets and prey remains for the same nests (comparative: 20,928 ± 3,569 vs. 2,908 ± 3,569 g; paired t-test: $t_5 = 3.81$, $p = 0.01$), and more biomass when compared to all nests sampled (comparative: 20,928 ± 3,569 vs. 5,061 ± 771 g; df = 53, $Z = 3.60$, $p = 0.0003$). Video documented deer mice (*Peromyscus* spp.), kangaroo rats (*Dipodomys* spp.), and reptiles as Ferruginous Hawk prey, but these items were not detected in pellets or prey remains collected from the same nests. Alternatively, I identified seven rock squirrels from pellets and prey remains but none from video monitoring of the same nests.

Video monitoring and pellet and prey remains produced similar estimates of avian prey and Botta's pocket gopher but provided opposing accounts of two important prey items – Gunnison's prairie dogs and desert cottontails. Video delegated Gunnison's prairie dog a larger portion and desert cottontail a smaller portion of total biomass delivered than did pellets and prey remains combined (Table 1.6).

Pellet and prey remain analysis revealed an association between Gunnison's prairie dogs and nesting Ferruginous Hawks, but video monitoring documented a stronger relationship between predator and prey (Figure 1.3). Gunnison's prairie dogs at one video monitored nest constituted 87% of biomass, a number 22% greater than the next largest.

Both techniques provided similarly low estimates of food niche breadth for nests which received both sampling regimes (video: 3.61; pellet/prey remains: 3.30) but video monitoring produced a higher count of prey species than the other techniques (same nests (n = 6): 7.83 ± 0.54 vs. 3.83 ± 0.54, paired t-test: $t_5 = 4.47$, p = 0.007; video (n = 6) versus all nests (n = 49): 7.83 ± 0.81 vs. 5.12 ± 0.28, $t_{53} = 4.39$, p = 0.0027) (Table 1.6, 1.2).

Discussion

This study represents the most extensive description of Ferruginous Hawk diet composition to date. I documented 1640 prey items using three sources – regurgitated pellets, prey remains, and time-lapse video monitoring. My results suggest Ferruginous Hawks breeding in New Mexico fed heavily on mammals, particularly Botta’s Pocket Gopher and sciurid rodents. Spotted ground squirrel, thirteen-lined ground squirrel, rock squirrel, Gunnison’s prairie dog, and Botta's pocket gopher together represented more than three quarters of all prey and 65% of all biomass.

Mine is the first study to identify ravens as a food item for Ferruginous Hawks. Stalmaster (1988) and Fitzner et al. (1977) documented one member of the family corvidae, the Black-billed Magpie (*Pica pica*), as Ferruginous Hawk prey but I found remnants of one Common Raven and one Chihuahuan Raven within and below two nests in New Mexico.

Comparison of Techniques

In a comparison of techniques in assessing the diet of Northern Goshawks (*Accipiter gentilis*), Lewis et al. (2004) underscored Craighead and Craighead’s (1956) posit that assessing raptorial diet using only regurgitated pellets tends to underestimate the abundance of small prey items. My results were similar to Lewis et al. (2004) and Collopy (1983) in that I detected larger prey items more consistently in pellets and prey remains, smaller prey using direct observations (i.e., video), and significantly more prey items delivered using direct observations than using only pellets and prey remains. Video monitoring revealed 10 times more prey were delivered than pellet and prey remains analysis estimated from the same nests. Video also recorded the delivery of six times more biomass and twice as many species. Video monitoring provided unique insight into descriptions of diet that could not be accomplished by analyzing pellets and prey remains. Video surveillance facilitated delineation between young and adult Gunnison's prairie dogs, a task not easily accomplished using regurgitated bones, and allowed recognition of partial carcass deliveries, which occurred occasionally with larger mammals like Gunnison's prairie dogs and desert cottontail rabbits. Taken together, these opportunities suggest an advantage to video monitoring to comprehensively describe raptorial diets.

However, the time and logistics involved in the installation and maintenance of these cameras as well as refreshing tapes and batteries, especially in multi-use environments of the high desert, is not without problems. On several occasions, the video system failed from heat exposure or disturbance from cattle, causing minor loss of recorded nest activity at some sites. Furthermore, on four occasions at two different nests, mammalian tracks near the nest tree revealed that a porcupine (*Erethizon dorsatum*), had chewed through the cable, apparently while ascending the nest tree. Thus, there are merits and problems associated with the techniques used to study food habits, but it is clear that video monitoring is important if improving the accuracy of diet composition is a goal.

Comparison to Other Studies Throughout Breeding Range

Although some consider Ferruginous Hawks to be predatory specialists with strong dependence on a single prey item (Schmutz et al. 1980), their diet varies geographically and changes in response to prey abundance (Steenhof and Kochert 1988). Ferruginous Hawks feed extensively on mammals, but research shows the dietary contributions of sundry mammals are not equal throughout this raptor's breeding range.

During a comprehensive five-year study on 75 nesting pairs in Utah's sagebrush-steppe, Smith and Murphy (1978) estimated that black-tailed jackrabbits made up over 90% of total biomass consumed by Ferruginous Hawks. Schmutz et al. (1980), who recorded more prey items than any other description of Ferruginous Hawk diet prior to this study (Table 1.7), noted that Ferruginous Hawks relied heavily on Richardson's ground squirrel (*Spermophilus richardsonii*) in Alberta grasslands (biomass: 89%, frequency: 87%). In North Dakota, Gilmer and Stewart (1983) and Lokemoen and Duebbert (1976) found similar proportions of Richardson's ground squirrel in the diet of Ferruginous Hawks in their respective study areas, but to a much lesser degree than Schmutz et al. (1980) documented.

In Idaho, Howard and Wolfe (1976) documented flexible Ferruginous Hawk food habits in relation to various habitat types. Northern pocket gophers (*Thomomys talpoides*) made up 57% and black-tailed jackrabbits represented 3% of all prey delivered in grassland areas while in desert-shrub habitat, jackrabbits constituted 67% of diet by frequency and no northern pocket gophers were detected. Black-tailed jackrabbits constituted about 85% of biomass delivered to the seven nests they studied in sagebrush habitats. This further suggests that leporids provide the majority of nourishment in sagebrush-steppe environments.

My finding that mammals constituted 90% of Ferruginous Hawk diet by frequency was comparable (i.e., ± 5%) to some food habits studies conducted throughout this species' breeding range (Smith and Murphy 1978, Schmutz et al. 1980, Gilmer and Stewart 1983) but different than others. Olendorff (1973), Lokemoen and Duebbert (1976), Fitzner et al. (1977), Blair and Schitowsky (1982), Ensign (1983), and Steenhof and Kockert (1985) found mammals to be taken at lower frequencies while MacLaren (1986) and Stalmaster (1988) found that mammals completely dominated Ferruginous Hawk diet (Table 1.7).

In the grasslands of eastern Colorado, Olendorff (1973) recorded a fairly even Ferruginous Hawk diet, with thirteen-lined ground squirrels constituting 41% of diet by frequency. He attributed this dietary evenness to the substantial contribution of avian prey. Specifically, he noted recently fledged grassland passerines represented a quarter of all Ferruginous Hawk prey in his study.

Other research has documented major avian contributions to Ferruginous Hawk diet. Fitzner et al. (1977) estimated that avian prey contributed nearly 20% to overall diet by frequency (although their sample size was limited to two breeding pairs), while Blair and Schitowsky (1982) reported 27% of all prey items were birds. Furthermore, Ensign (1983) found avian prey in Montana contributed over 40% to Ferruginous Hawk diet by frequency, a proportion not matched in any other study to date (Table 1.7). He attributed this abundance of avian prey in the diet to depauperate mammalian prey availability that caused a predatory shift to more available prey. In my study, birds represented 5% of Ferruginous Hawk diet by frequency, a percentage comparable to the majority of other studies.

Some descriptions of Ferruginous Hawk food habits solely report diet composition in terms of frequency of occurrence, rather than providing contributional estimates of biomass for various taxa. When avian prey constitute a major prey source by frequency but do not represent a significant energy source for nestlings, a frequency measure alone can overestimate the importance of such prey. Accounts that attribute importance to birds as Ferruginous Hawk prey underscore the importance of using biomass as a measure to further describe raptor diet composition. This issue is especially evident in the case of grassland songbirds which weigh relatively little but sometimes represent a large percentage of total prey delivered (Olendorff 1973, Ensign 1983). For instance, Stalmaster (1988) estimated avian prey to represent 13% of diet composition by frequency but only 3% by biomass in his description of Ferruginous Hawks in Colorado and Utah. In my study, estimates of avian prey contributions for percent frequency and percent biomass were somewhat similar, likely due to the presence of larger birds such as corvids in the diet.

Of notable interest in my study was the discovery of two ravens, the Common Raven and Chihuahuan Raven, under two nests in the Estancia Valley. Common Ravens were nesting approximately 125 m away from an occupied Ferruginous Hawk nest, and I observed the adults of both species interact in the air on two occasions. In July 2005, four Common Raven wing remnants of adult plumage and size were found underneath the Ferruginous Hawk nest. The wing chord size fell within the published size range of

Common Raven (Pyle 1997). Another July collection at a separate occupied Ferruginous Hawk nest resulted in two much smaller wing remnants. This length measurement was less than the range for Common Raven, but larger than American Crow (*Corvus brachyrhynchos)*, and was within the size range of Chihuahuan Raven (Pyle 1997). Chihuahuan Raven is considered an uncommon breeder in the Estancia Valley as the northern edge of the species' breeding range coincides with the southern edge of the Valley (Bednarz and Raitt 2002, W. H. Keeley, personal observation). Because ravens attain adult plumage and size when fledged, and because they breed in the Estancia Valley, I concluded that the wing remnants were of a Chihuahuan Raven.

Some researchers have identified the importance of reptiles and insects in the diet of nesting Ferruginous Hawks. Fitzner et al. (1977) reported a relatively even distribution of prey classes in Ferruginous Hawk diet, with reptiles and insects representing 35% of diet by frequency. However, this may be an artifact of a low sample size (Table 1.7). Lokemoen and Duebbert (1976) noted that insects constituted 22% of all prey items documented. However, even with a relatively large delivery frequency, insects and reptiles are similar to birds in that these taxa cannot be considered major contributors (i.e. ≥ 10%) to total biomass. Importantly, for all studies that used biomass to describe diet composition, mammals dominated Ferruginous Hawk diet as that prey represented between 93 and 99% of total biomass.

Some authors have documented Ferruginous Hawks' strict use of a single mammalian prey species and the consequent relation between prey abundance and the hawks' breeding productivity. During one year of their study, Smith and Murphy (1978) estimated black-tailed jackrabbits made up 95% of total biomass delivered to nests and documented breeding adults delivering 14,163 grams of biomass per nest (n = 77), a figure that is less than my estimate using time-lapse video but which nearly triples my estimate using methods similar to theirs, and is 10 times the amount Lokemoen and Duebbert (1976) recorded in their description of diet composition at 27 Ferruginous Hawk nests. Smith and Murphy (1978) correlated prey abundance, biomass delivery, and the nesting success of Ferruginous Hawks in Utah. When prey abundance was high, the birds were more successful nesting then in low prey years. Woffinden and Murphy (1989) attributed this, in part, to the negative relationship between prey abundance and predatory search time. When prey was limited, the pairs' reproductive output was affected as the female hawk was forced to leave the nest to forage and thus spent less time caring for eggs and young. From 1967-1989, Woffinden and Murphy (1989) observed a reduction and eventual extirpation of a Ferruginous Hawk population following a population crash of jackrabbits in central Utah.

In contrast, my study indicated a more evenly distributed diet for Ferruginous Hawks breeding in New Mexico. Botta's pocket gopher, desert cottontail, and Gunnison's prairie dog each contributed over 20% of diet by biomass with only 8% separating their respective contributions. An evenly distributed diet suggests a level of predatory flexibility that could benefit the persistence of a species in times of low prey or an otherwise changing environment. Most research on breeding Ferruginous Hawk diet composition has identified ground squirrels (*Spermophilus* spp.) as the primary prey source (Table 1.7), but my data demonstrate that multiple prey species supported Ferruginous Hawks nesting in New Mexico.

Additionally, my study suggests that lagomorphs constituted a major prey item for Ferruginous Hawks in terms of frequency (10%) and biomass (30%) mostly from desert cottontails (frequency: 9%, biomass: 24%). Adult hawks delivered rabbits seven times as frequently and the species provided four times more biomass than jackrabbits. Comparatively, the degree to which Ferruginous Hawks in New Mexico relied on lagomorphs is similar to that described in other studies, save the strict prey use documented for Ferruginous Hawks in Utah.

Authors have noted the importance of prairie dogs to wintering Ferruginous Hawks (Cully 1991, Plumpton and Andersen 1998, Bak et al. 2001), but the role of these species during the nesting season is less understood. Blair and Schitowsky (1982) estimated black-tailed prairie dogs contributed 1% to overall frequency while Ensign (1983) estimated this number to be less than 1%. Alternatively, Stalmaster (1988) and MacLaren (1986) listed black-tailed prairie dogs as an important Ferruginous Hawk food source because the mammal represented 49% and 22% of total biomass in their studies in Colorado and Wyoming, respectively. My data suggest Gunnison's prairie dogs are an important food source for Ferruginous Hawks nesting in New Mexico. I found Gunnison's prairie dog remains in 63% of nests sampled, and it represented substantial portions of Ferruginous Hawk diet composition in terms of percent frequency and biomass. Further, video-monitoring revealed that Gunnison's prairie dogs dominated the diet of some Ferruginous Hawks in my study at a level comparable to the use of Richardon's ground squirrels by hawks in Alberta (Schmutz and Hungle 1989).

Ferruginous Hawks preyed on two mammals of note in my study, kangaroo rats (*Dipodomys* spp.) and the long-tailed weasel (*Mustela frenata*). Contrary to other accounts (Cartron et al. 2004), the long-tailed weasel is documented fairly frequently as Ferruginous Hawk prey, but it has never represented more than 1% of diet by frequency in any study (Weston 1969, Olendorff 1973, Howard and Wolfe 1976, Smith and Murphy 1978, MacLaren 1986, Cartron et al. 2004, this study). The continued appearance of this species in the diet of Ferruginous Hawks across multiple regions suggests that these predators may use similar prey.

Recently, Boal and Giovanni (2007) argued that kangaroo rats are not strictly nocturnal as previously thought (Daly et al. 2000) because of their prevalence in the diet of buteos. I identified 16 individual remains of Ord's kangaroo rat (*Dipodomys ordii*) from pellets and prey remains from 22% of nests sampled. Also, my video systems recorded the delivery of 12 individuals of Ord's kangaroo rat and five banner-tailed kangaroo rats (*Dipodomys spectabilis*) throughout the day, but the species represented only 1.5% of total Ferruginous Hawk diet by frequency. Therefore, although it is apparent that Ord's kangaroo rat did not represent a major portion of Ferruginous Hawk diet in New Mexico as compared to data collated by Olendorff (1993), who reported kangaroo rats constituting 6.6% of Ferruginous Hawk prey by frequency, video evidence from this study supported the assertion that kangaroo rats were not strictly nocturnal in New Mexico.

Food-niche Breadth and Species Richness

Steenhof and Kochert (1985) reported a food niche breadth of 4.24 for 11 breeding pairs of Ferruginous Hawks in Idaho, although Marti et al. (1993) calculated a breadth of 6.1 from a larger sample size from the same study area. MacLaren (1986) measured a food niche breadth of 4.7 for Ferruginous Hawks in Wyoming. At 4.14, my estimate of food-niche breadth for Ferruginous Hawks was comparable to that of MacLaren (1986) and Steenhof and Kochert (1985) but lower than Marti et al. (1993). Among North American raptors of similar size, some species fed on a broader suite of prey, including Red-tailed Hawks (*Buteo jamaicensis*: 7.80) and Great Horned Owls (*Bubo virginianus*: 7.55, Marti et al. 1993), while others shared breadths similar to Ferruginous Hawks like Golden Eagles (*Aquila chrysaetos*, 4.07) and Burrowing Owls (*Athene cunicularia*, 4.22, Moulton et al. 2005). Falcons had somewhat narrower breadths than Ferruginous Hawks, such as Prairie Falcons (*Falco mexicanus*, 3.62) and American Kestrels (*Falco sparverius*, 3.43) (Marti et al. 1993).

When compared to measures published for Red-tailed Hawks and Great Horned Owls, which are widely considered predatory generalists, Ferruginous Hawks in my study consumed a relatively narrow range of prey. However, my study documented at least 27 different prey species from pellets and prey remains - 16 mammals, 7 birds, 2 reptiles, and 2 insect orders. Similarly, Smith and Murphy (1978) reported 25 species in Ferruginous Hawk diet during their 5 year study in Utah, 14 mammals, 7 birds, and 4 reptiles. It is important to note that Ferruginous Hawks in Utah predominantly consumed one species, whereas hawks in my study areas consumed a relatively even diet. My data are in contrast to Ensign (1983) who found half as many (n = 8) mammalian prey species but 57% (n = 11) more avian prey species in the diet of Ferruginous Hawks breeding in Montana, and Cartron et al. (2004) who reported 18 vertebrate species, 13 mammals, 3 birds, 2 reptiles, and 2 arthropod orders for a similar Ferruginous Hawk community in New Mexico. Therefore, while the food niche breadth of Ferruginous Hawks in New Mexico was narrower than that documented for generalist raptors, it is much broader, intra-specifically, for hawks studied by Schmutz et al. (1980) and Smith and Murphy (1978). Thus, while Ferruginous Hawks may be considered predatory specialists when compared to Red-tailed Hawks and Great Horned Owls, Ferruginous Hawks in my study exhibited a relatively enhanced level of intra-specific predatory generalism.

Comparison to Cartron et al. (2004)

Cartron et al. (2004) analyzed regurgitated pellets and prey remains collected at least once from 26 occupied Ferruginous Hawk nests throughout New Mexico to assess diet composition. My study is different from theirs in three regards. First, although they sampled nests in the Estancia Valley and Plains of San Agustin, their sampling regime was cursory and thus their sample size was not sufficient enough to statistically test for dietary differences between study areas (Cartron et al. 2004). Second, their description of diet composition did not include a biomass measurement so comparison between my study and theirs is limited to a discussion of diet by frequency. Finally, I used video monitoring to develop a more accurate account of Ferruginous Hawk diet in New Mexico, whereas they only analyzed pellets and prey remains.

Interestingly, even though I identified 5 times more prey items and doubled the sampling effort of Cartron et al. (2004), some similarities existed between our studies. For example, although my data suggest Ferruginous Hawks consumed more mammals (90 vs. 80% by frequency), my estimate of avian contribution to diet is similar (~5%) to theirs (Table 1.7). Both studies also estimated similar contributions of three key mammalian prey species, Gunnison's prairie dog, desert cottontail, and Botta's pocket gopher, to overall Ferruginous Hawk diet composition.

In contrast, a comparison of diet composition between study areas revealed several key differences between my study and Cartron et al. (2004). Cartron et al. (2004) recorded a higher prevalence of Botta's pocket gophers in the diet of Ferruginous Hawks in the Plains of San Agustin (59 vs. 37%) and more Gunnison's prairie dogs in the diet of Estancia Valley hawks (17 vs. 12%) than I did. My study also differs from Catron et al. (2004) by delegating importance to the use of desert cottontails by hawks in the Plains of San Agustin. Desert cottontails represented 13% of diet by frequency in the Plains of San Agustin in my study, but the leporid contributed only 5% of diet composition in theirs. Although, Cartron et al. (2004) did not estimate food-niche breadth, my results reflect a more even use of prey by Ferruginous Hawks nesting in the Plains of San Agustin because the hawks I studied there consumed more desert cottontail rabbits and less Botta's pocket gophers than the hawks they studied. Finally, because video monitoring revealed adults provisioning nestlings with 10 times more biomass and significantly more prey species than pellets and prey remains estimated, my study depicted a more accurate account of Ferruginous Hawk prey use in New Mexico than previously known.

Study Area Variation

My data suggested Ferruginous Hawks in the Estancia Valley and Plains of San Agustin consumed significantly different proportions of two major prey items in terms of biomass and frequency. Regardless of calculative method, Ferruginous Hawks in the Estancia Valley (exurban environment) consumed more Gunnison's prairie dogs, and hawks in the Plains of San Agustin (rural environment) consumed more desert cottontails.

Steenhof and Kochert (1985) found that the abundance of a prey species in a raptor’s diet was proportional to its local abundance. My results supported this finding in that Gunnison's prairie dog colonies were more numerous in the Estancia Valley than in the Plains of San Agustin, and the rodent was more prevalent in the diet of Ferruginous Hawks in the Estancia Valley. Because of declining numbers of extant prairie dog colonies in the Plains of San Agustin, Ferruginous Hawks breeding in that area may have been forced to shift their prey use to leporids.

Why would Gunnison's prairie dogs be more widespread in a landscape with significant amounts of human pressure than a rural environment? Several sources have documented a history of declining Gunnison's prairie dog numbers in Catron and Socorro counties, the two counties which comprise the Plains of San Agustin, and have further contended that historical government-sponsored poisoning campaigns are the cause. Oakes (2000) estimated the Gunnison's prairie dog population in these counties to be 2,458,650 in 1916. Luce (2005) then estimated the population to be approximately 12,000 in 1984; but by 2000, that estimate had fallen to 6,000 animals. My study reinforced this trend as no new colonies were located in the Plains of San Agustin during extensive aerial searches conducted in 2005.

Gunnison's prairie dogs are located in dense colonies, which theoretically offer a lower search time for predators and consequently creates a positive predatory association (Krebs and Davies 1993). From this predator/prey relationship, a reasonable hypothesis may be deduced: Ferruginous Hawks in the Estancia Valley possess a narrower food niche-breadth than Ferruginous Hawks in the Plains of San Agustin. Because Gunnison's prairie dog colonies are more numerous in the Estancia Valley, hawks there would consume more of the prey and thus food-niche breadth would be lower. Although Ferruginous Hawks consumed different prey in each study area, they shared similarly moderate food-niche breadths when compared to other intra-specific diet diversity measurements found in the literature. This suggested that either prey availability was equally low in both study areas (MacArthur and Pianka 1966) or Ferruginous Hawks in my study were a moderately specialized predator, independent of their primary prey source.

Indeed, I detected Gunnison's prairie dogs at twice the proportion of Estancia Valley nests than Plains of San Agustin nests, but I also detected the majority of other major prey species more frequently in Estancia Valley nests than Plains of San Agustin nests (except desert cottontails). This trend may be another indicator that Ferruginous Hawks in the Estancia Valley fed on a broader suite of mammals when compared to hawks in the Plains of San Agustin even though Levins (1968) index was equal between study areas. Related, one drawback to Levins measure of food niche breadth, along with all other indices that estimate diet diversity, is the assumption that all food resources are equally available (Marti et al. 2007). Based on the number of prairie dog colonies I located in the Estancia Valley versus the Plains of San Agustin, this assumption may have been violated in my study.

Gunnison’s prairie dogs represented between one quarter and one half of all biomass consumed by Ferruginous Hawks in the Estancia Valley, depending on whether pellets and prey remains or video monitoring was used to assess diet. Undoubtedly, Gunnison's prairie dog form an essential part of Ferruginous Hawk diet in the Estancia Valley. The presence of a consistent food source that confers minimal predatory search time has been associated with increased organismal fitness (Krebs and Davies 1993) and reproductive output (Smith and Murphy 1978). My data support this theory because Ferruginous Hawks nesting in the Estancia Valley have experienced significantly higher productivity than those nesting in the Plains of San Agustin during my study and an extended period from 1998-2005 (Keeley 2004, this study).

In February 2008, the US Fish and Wildlife Service (USFWS) published a 12 month finding to list Gunnison's prairie dog as threatened under the Endangered Species Act in some parts of its range (USFWS 2008). The interim decision which followed listed the Gunnison's prairie dog as endangered in montane areas but not in grasslands. Among recognized threats, USFWS acknowledged the species' susceptibility to bubonic plague and increased habitat loss that led to reduced connectivity of historical habitat.

Gunnison's prairie dogs are believed to be more susceptible to plague than other members of the genus *Cynomys* because of their less exclusive territorial behavior and higher densities, both of which contribute to increased communicability of plague. Furthermore, plague is only present throughout approximately 66% of black-tailed prairie dog's range (US Fish and Wildlife Service 2006) in comparison to 100% of Gunnison's prairie dog's range (Cully 1989, Girard et al. 2004). Finally, once a plague epizootic is established, mortality rates of Gunnison's prairie dogs typically reach 99 to 100% (Rosamarino 2004).

Historical poisoning campaigns supported by the federal government at the turn of the century also affected population status of Gunnison's prairie dogs. Oakes (2000) postulated that following poisoning campaigns in the early 1900s, Gunnison's prairie dog habitat in New Mexico decreased by 1 million ha to 3.6 million ha in 1921. From 1916 to

1961, Gunnison's prairie dog habitat decreased by approximately 97% in New Mexico and 95% range-wide. Further, Seglund et al. (2005) reported that prairie dogs occupied 144,000 ha in New Mexico in 1961 but they inhabited only 4,000 ha in 2004. While the decrease from 1916 to 1961 was attributed to a combination of factors (i.e., poisoning, habitat conversion, plague epizootics), the decrease from 1961 to 2004 was primarily attributed to habitat loss (Seglund et al. 2005).

Although I did not witness a population reduction of Gunnison's prairie dogs from plague during my study, habitat conversion was an obvious cause of prairie dog range reduction in the Estancia Valley. Of the 20 prairie dog colonies that were occupied in 1999 but not in 2004, seven had been consumed by development and one was purposely exterminated by the land owner.

Natural habitat alteration in the Estancia Valley continues to increase primarily because of its proximity to a metropolitan area. From 1980 to 2000, land use considered “exurban development” (i.e., 0.7 - 17 ha per housing unit [HU]) doubled in area in counties comprising the Estancia Valley while urban development (i.e., less than 0.7 ha per HU) tripled (Theobald 2005). This type of growth has significant implications for native species, especially in grasslands, which are considered the earth’s most imperiled biome (Hoekstra et al. 2005).

In the nesting season, Ferruginous Hawks avoid humans and are sensitive to disturbance (Olendorff 1973, White and Thurow 1985, Stalmaster 1988, Roth and Marzluff 1986, Ward 2001). In winter, Plumpton and Andersen (1998) contended that Ferruginous Hawks in a suburban habitat were behaviorally plastic and more tolerant of human disturbance when black-tailed prairie dogs were abundant. However, seasonal differences exist in behavior and energetic requirements as Ferruginous Hawks become territorial and focused on raising young in the breeding season (Newton 1979), but gather gregariously around prairie dog colonies during winter (Bechard and Schmutz 1995). If prairie dogs are abundant during the nesting season, can breeding Ferruginous Hawks show similar tolerance to disturbance as described by Plumpton and Andersen (1998)? The positive outcome to this question remains largely unsupported in the literature but authors have documented the opposite scenario. That is, pairs attempting to breed in times of low prey abundance are more intolerant of human disturbance (Smith and Murphy 1979, White and Thurow 1985).

My study suggests that Ferruginous Hawks in the Estancia Valley may be able to maintain stable reproductive output in a relatively altered environment because Gunnison's prairie dogs constitute substantial portions of the hawks' diet. This underscores the importance of conserving and managing for the expansion of extant prairie dog colonies. Gunnison's prairie dogs represented between one quarter and one half of all biomass consumed by Ferruginous Hawks in the Estancia Valley and therefore play an important role in maintaining Ferruginous Hawk fitness in that grassland.

However, a potential lag time may exist in response to human encroachment, especially in areas like the Estancia Valley where growth is relatively recent (~10 years). Research suggests that urbanization operates at time scales too fast for evolutionary adjustment (DeLeo and Levin 1997) and that negative responses to urbanization may continue to intensify for several decades after development (Donnelly 2002, Ianni 2004). Therefore, it is possible that the effects of recent habitat modifications on the presence and the landscape surrounding Gunnison's prairie dog colonies in the Estancia Valley may not be immediate but cumulative in nature and thus may begin to erode Ferruginous Hawk reproductive output in the near future.

Is the Estancia Valley approaching the threshold at which the landscape becomes too modified for use by breeding Ferruginous Hawks? Berry et al. (1998) found Ferruginous Hawks avoided areas with >5% urban development along the Front Range of Colorado and Bechard et al. (1990) noted Ferruginous Hawks nested more than twice as far from humans than other buteos. Indeed, some portions of the Estancia Valley have been directly affected as development encroaches on raptor nesting sites and envelops Gunnison’s prairie dog colonies, but indirect effects are also apparent as current human development continues to alter the distribution of Gunnison's prairie dogs and fragment previously intact grasslands into spatially disjoint landscape units. Theobald (2005) estimated that the area consumed by exurban and urban development in counties comprising the Estancia Valley will double from 2000 to 2020. Concurrent with this growth, habitat fragmentation associated with roads and other human infrastructure can alter predator-prey associations and ecosystem functions by rendering some areas unusable (Berry et al. 1998, Marzluff 2001, Marzluff and Ewing 2001, Hansen et al. 2005), especially for raptors that are commonly associated with prairie dog colonies, such as Ferruginous Hawks. During my study, anecdotal observations supported this assertion as I rarely saw Ferruginous Hawks foraging in Gunnison's prairie dog colonies close to roads.

Anthropogenic influence was very different in my study areas. Roads were twice as dense, and population and housing density were significantly greater in the Estancia Valley than in the Plains of San Agustin. Although road density is a good predictor of wildlife abundance and richness (Germaine et al. 1998), it may not have the same effect on nesting birds as they can choose sites that maximize their distance from roads. Overall, occupied Ferruginous Hawk nests were farther from roads than the estimate MacLaren (1986) provided (440 m) but much closer than the estimate Ensign (1983) provided (~4000 m). Unfortunately, these studies report no information as to which type of road was closest to occupied nests, which is important because the effect of roads on animals is not equal across all road types (Forman 2000, Theobald 2003). In the Estancia Valley, 76% of occupied nests were closest to roads characterized by the US Census Bureau as ones which connect cities and towns, while 38% of occupied nests in the Plains of San Agustin were closest to service roads primarily found in very rural areas and accessible by four wheel drive vehicles only. Although use of both road types could disturb nesting Ferruginous Hawks, a higher density of connector roads implies an increased level of habitat fragmentation and corresponding disturbance.

My data suggested Ferruginous Hawks nesting in these two grasslands consume different diets and demonstrated the importance of extant prairie dog colonies to nesting Ferruginous Hawks. Hawks in the Plains of San Agustin consumed leporids and ground squirrels and thus their food habits closely resemble diet hawk diet in the intermountain western United States and northern great plains (Table 1.7), while hawks in the Estancia Valley consumed more prairie dogs, a diet which closely resembled that in published accounts from the desert southwest.

Because peripheral populations occur in less suitable habitats, some authors consider these populations as sources for the development of distinct traits that allow adaptation during environmental change (Lesica and Allendorf 1995). My study suggested that hawks in the Plains of San Agustin may have been able to adapt to an altered trophic structure following massive prairie dog eradication by consuming leporids and hawks in the Estancia Valley may have been able to tolerate an altered environment because of Gunnison's prairie dogs. However, the continued persistence of Ferruginous Hawks in these grasslands cannot be assumed. Woffinden and Murphy (1989) estimated that each Ferruginous Hawk pair attempting to breed needed to produce 1.5 fledglings to maintain a stable population, assuming 66% first year mortality and 25% adult mortality. If I applied Woffinden and Murphy’s assumptions to hawks in my study, hawks in the Estancia Valley are maintaining a stable population but those in the Plains of San Agustin are not.

To my knowledge, mine is the first study to document a higher productivity rate for Ferruginous Hawks nesting in a human-altered environment compared to a rural setting. However, as Gunnison's prairie dog colonies continue to become subsumed by development in the Estancia Valley, I predict that predatory search time will increase and adults will spend more time foraging and less time caring for eggs and young. This could directly affect Ferruginous Hawk fitness and thus maintenance of a stable breeding population. Therefore, my study underscores the importance of conserving intact, extant Gunnison's prairie dog colonies in the Estancia Valley and increasing the number of colonies in the Plains of San Agustin in order to stabilize these Ferruginous Hawk peripheral populations.

The continued study of breeding Ferruginous Hawks in disturbed and natural environments is needed to expand the knowledge of this species’ behavioral thresholds, especially in grasslands where conservation of a colonial prey source is a viable management tool.

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Table 1.1. Anthropogenic measures (comparative: mean ± SE) for the Plains of San Agustin and the Estancia Valley, New Mexico, USA. Data derived from US Census Bureau Summary File 1 (2000).

	Estancia Valley	Plains of San Agustin	Z^a	df	p
Area (ha)	158,773	238,781			
Total number of US census blocks	1,247	167			
Total number of occupied houses	6,094	20			
Total population	16,338	61			
Houses/census block	4.89 ± 0.276	0.12 ± 0.73	13.54	1,412	0.00001
People/census block	13.1 ± 0.753	0.37 ± 2.1	13.38	1,412	0.00001
Road density (km/ha)	0.0130	0.0072			
Distance from occupied nest to nearest road (m)	403 ± 82	708 ± 97	2.40	29	0.02

[a] Data were compared using Wilcoxon rank sums test

Table 1.2. Pellets and prey remains combined to calculate frequency of occurrence for major Ferruginous Hawk food types (%), mean (± SE) biomass and prey items delivered per nestling, mean (± SE) prey species richness, and mean (± SE) food niche breadth (1/d), per nest sampled in Estancia Valley (n = 29), Plains of San Agustin (n = 16), and overall (n = 49) in New Mexico, 2004-2005. Noted in parenthesis is the number of nests where the species was detected.

	Estancia Valley	Plains of San Agustin	Overall	Z (t)[a]	df	p
Total prey items	765	221	1,035			
Thomomys bottae	97% (28)	94% (15)	96% (47)			
Cynomys gunnisoni	72% (21)	38% (6)	63% (31)			
Sylvilagus audubonii	66% (19)	81% (13)	69% (34)			
Lepus californicus	10% (3)	31% (5)	10% (8)			
Birds	59% (17)	19% (3)	41% (23)			
Insects	35% (10)	38% (6)	33% (19)			
Reptiles	21% (6)	6% (1)	14% (7)			
Biomass (g) delivered	6,086 ± 869	3,394 ± 1965	5,061 ± 572	1.79	43	0.07
Biomass (g) delivered per nestling	2,410 ± 308	1,695 ± 415	2,097 ± 233	0.89	43	0.37
Prey items delivered	23.1 ± 4.1	9.0 ± 1.53	20.1 ± 2.8	1.68	43	0.09
Prey items delivered per nestling	10.4 ± 1.54	6.57 ± 2.1	8.63 ± 1.17	1.02	43	0.31
Food niche breadth (1/d)	4.05	4.05	4.14			
Food niche breadth (1/d) per nest	3.40 ± 0.22	3.24 ± 0.30	3.35 ± 0.17	(0.42)	43	0.68
Prey species richness	5.58 ± 0.41	4.43 ± 0.45	5.12 ± 0.29	1.64	43	0.10

[a] Parametric data were compared using t-test (parametric test statistics are shown in parenthesis); non-parametric data were compared using Wilcoxon rank sums test

Table 1.3. Ferruginous Hawk pellets and prey remains combined to calculate mean (± SE) percent frequency and percent biomass per nest in the Estancia Valley (n = 29), Plains of San Agustin (n = 16) and overall (n = 49) in New Mexico, 2004-2005. Prey categories in bold type represent group totals.

	Percent Frequency			Percent Biomass		
Prey	EV	PSA	Overall	EV	PSA	Overall
Mammals	88.4 ± 2.5	89.3 ± 3.3	89.6 ± 1.9	96.7 ± 1.0	99.3 ± 1.3	97.8 ± 0.7
Thomomys bottae	37.0 ± 3.8	3.0 ± 5.1	36.9 ± 2.8	30.5 ± 4.0	28.5 ± 5.4	28.8 ± 3.0
Spermophilus* spp.	24.6 ± 3.6	25.8 ± 4.8	24.4 ± 2.6	11.2 ± 2.2	10.8 ± 2.9	10.5 ± 1.6
S. variegatus	3.7 ± 1.4	3.2 ± 1.9	3.6 ± 1.0	7.6 ± 2.4	5.1 ± 3.3	7.0 ± 1.8
Cynomys gunnisoni	12.5 ± 2.0	3.7 ± 2.6	11.3 ± 1.9	24.3 ± 3.3	6.0 ± 4.4	20.7 ± 3.1
Lepus californicus	0.5 ± 0.9	3.4 ± 1.1	1.4 ± 0.7	2.2 ± 2.8	13.0 ± 3.7	5.5 ± 2.2
Geomys bursarius	0.8 ± 0.6	-	0.7 ± 0.5	0.4 ± 0.3	-	0.4 ± 0.3
Sylvilagus audubonii	6.9 ± 1.7	12.7 ± 2.3	8.7 ± 1.3	19.6 ± 4.2	35.1 ± 5.7	24.1 ± 3.3
Neotoma spp.	0.8 ± 0.4	0.2 ± 0.5	0.5 ± 0.3	0.4 ± 0.2	0.1 ± 0.3	0.3 ± 0.2
Peromyscus spp.	0.3 ± 0.4	-	0.5 ± 0.3	0.9 ± 0.6	-	tr.**
Dipodomys ordii	1.0 ± 0.7	2.5 ± 0.9	1.5 ± 0.5	0.3 ± 0.2	0.5 ± 0.2	0.4 ± 0.1
Birds	6.5 ± 1.5	2.0 ± 2.0	4.5 ± 1.1	3.2 ± 1.0	0.6 ± 1.3	2.1 ± 0.8
Sturnella neglecta	2.8 ± 1.1	0.4 ± 0.3	1.8 ± 0.7	1.1 ± 0.5	0.3 ± 0.2	0.8 ± 0.3
Eremophila alpestris	0.4 ± 0.3	-	0.2 ± 0.2	tr.	tr.	tr.
Corvidae	0.3 ± 0.3	-	0.2 ± 0.2	0.6 ± 0.6	-	tr.
Buteo spp.	0.3 ± 0.3	-	0.2 ± 0.2	0.9 ± 0.9	-	tr.
Unknown passerine	2.7 ± 0.9	1.6 ± 1.0	2.1 ± 0.6	0.5 ± 0.2	0.3 ± 0.2	0.4 ± 0.1
Insects	3.8 ± 1.8	7.7 ± 2.5	4.8 ± 1.4	tr.	tr.	tr.
Acrididae	1.5 ± 0.6	7.5 ± 3.1	3.3 ± 1.1	tr.	tr.	tr.
Scarabidae	2.3 ± 1.3	0.2 ± 0.2	1.4 ± 0.8	tr.	tr.	tr.
Reptiles	1.3 ± 0.8	1.0 ± 1.1	1.1 ± 0.6	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1

* Identified as *Spermophilus spilosoma* or *S. tridecemlineatus*

**tr. = trace amount detected ≤ 0.05

Table 1.4. Pellets and prey remains combined to calculate mean (± SE) percent frequency and percent biomass per nest for breeding Ferruginous Hawks in the Estancia Valley (n = 29) and Plains of San Agustin (n = 16) New Mexico, 2004-2005.

PERCENT FREQUENCY

	Study Area			
Prey Group	Estancia Valley	Plains of San Agustin	Z^a	p
Mammals	88.4 ± 2.5	89.3 ± 3.3	0.62	0.54
Thomomys bottae	37.0 ± 3.8	37.0 ± 5.1	0.012	0.99
Spermophilus spp.	24.6 ± 3.6	25.8 ± 4.8	-0.095	0.92
Cynomys gunnisoni	12.5 ± 1.9	3.7 ± 2.6	-2.70	0.0069*
Sylvilagus audubonii	6.9 ± 1.7	12.7 ± 2.3	1.98	0.047*
Lepus californicus	0.48 ± 0.85	3.4 ± 1.1	1.83	0.067
Birds	6.5 ± 1.5	2.0 ± 2.0	-2.31	0.02*
Reptiles	1.3 ± 0.8	1.0 ± 1.1	-1.17	0.24
Insects	3.8 ± 1.8	7.7 ± 2.5	0.57	0.59

PERCENT BIOMASS

	Study Area			
Prey Group	Estancia Valley	Plains of San Agustin	Z^a	p
Mammals	96.6 ± 0.99	99.3 ± 1.3	1.86	0.06
Thomomys bottae	30.5 ± 4.0	28.5 ± 5.4	0.38	0.70
Spermophilus spp.	11.2 ± 2.2	10.8 ± 2.9	0.12	0.91
Cynomys gunnisoni	24.2 ± 6.0	6.0 ± 4.4	-3.07	0.002*
Sylvilagus audubonii	19.6 ± 4.2	35.1 ± 5.7	1.93	0.05*
Lepus californicus	2.2 ± 2.8	13.0 ± 3.7	1.87	0.06
Birds	3.2 ± 0.99	0.58 ± 1.3	-2.33	0.02*
Reptiles	0.13 ± 0.08	0.08 ± 0.11	-1.17	0.24
Insects	0.01 ± 0.01	0.04 ± 0.01	0.51	0.61

*Only differences with alpha $\leqslant$ 0.05 in both analytical techniques were considered significant

[a] Data were analyzed using Wilcoxon rank sums test

Table 1.5. Mean (± SE) percent frequency and percent biomass per nest of prey items detected using time-lapse video at Ferruginous Hawk nests in the Estancia Valley (EV, n = 3) and Plains of San Agustin (PSA, n = 3), New Mexico, 2004-2005. Numbers in parenthesis represent group totals.

Prey	Percent Frequency		Percent Biomass	
	EV	PSA	EV	PSA
Mammals	(95.9 ± 3.3)	(96.4 ± 7.3)	(99.0 ± 0.4)	(99.4 ± 0.1)
Thomomys bottae	16.2 ± 7.9	34.9 ± 12.4	12.6 ± 6.5	33.1 ± 16.8
Spermophilus spp.*	(23.2 ± 7.9)	(34.5 ± 12.1)	(8.3 ± 2.9)	(15.8 ± 4.4)
Spermophilus tridecemlineatus	0.6 ± 0.36	0.7 ± 0.30	0.3 ± 0.2	0.3 ± 0.2
S. spilosoma	22.7 ± 4.2	33.8 ± 9.2	8.0 ± 3.9	15.5 ± 4.2
S. variegatus	-	-	-	-
Cynomys gunnisoni	12.5 ± 2.0	3.7 ± 2.6	57.2 ± 11.0	6.7 ± 1.5
C. gunnisoni (young)	5.1 ± 1.5	-	2.9 ± 0.6	-
Lepus californicus	-	-	-	-
Family Scuiridae	7.8 ± 2.0	1.2 ± 0.4	4.1 ± 1.0	1.0 ± 0.4
Unk. mammal 1	6.9 ± 1.5	7.5 ± 1.5	0.7 ± 0.2	1.2 ± 0.2
Unk. mammal 2	0.8 ± 0.6	2.9 ± 0.7	0.3 ± 0.2	1.9 ± 0.5
Sylvilagus audubonii	1.4 ± 3.7	5.4 ± 3.6	3.9 ± 9.9	24.5 ± 14.3
Neotoma spp.	0.3 ± 0.2	0.6 ± 0.8	0.2 ± 0.7	0.4 ± 0.5
Dipodomys spp.	1.4 ± 1.1	3.3 ± 1.2	0.4 ± 0.3	1.4 ± 0.5
Peromyscus spp.	1.4 ± 0.5	4.9 ± 1.3	0.1 ± 0.004	0.5 ± 0.1
Birds	2.8 ± 3.9	2.0 ± 0.4	0.6 ± 0.4	0.6 ± 0.09
Insects	-	-	-	-
Reptiles	0.6 ± 0.4	-	tr.**	-
Not Identified	0.8 ± 0.3	1.6 ± 0.7	-	-

* Identified as either *Spermophilus spilosoma* or *S. tridecemlineatus*

**tr. = trace amount detected ≤ 0.05

Table 1.6. Mean (± SE) percent frequency and percent biomass per nest from video monitored Ferruginous Hawk nests and pellets and prey remains collected at the same nests (n = 6) in New Mexico, 2004-2005. Numbers in parenthesis represent group totals.

Prey	Percent Frequency		Percent Biomass	
	Video	Pellets/Prey	Video	Pellets/Prey
Number of prey items identified	596	59	-	-
Prey species richness**	7.83 ± 0.54	3.83 ± 0.54	-	-
Mammals	(96.1 ± 0.32)	(88.2 ± 5.9)	(98.9 ± 0.2)	(99.7 ± 0.29)
Sciuridae	(52.2 ± 10.3)	(45.5 ± 13.0)	(51.9 ± 13.3)	(40.8 ± 15.2)
Thomomys bottae	25.5 ± 7.7	28.3 ± 10.1	26.1 ± 8.6	24.5 ± 13.1
Spermophilus spp.*	(28.9 ± 7.2)	(25.4 ± 8.3)	(14.5 ± 4.5)	(9.3 ± 3.2)
S. tridecemlineatus	-	-	-	-
S. spilosoma	-	-	-	-
S. variegatus	-	7.9 ± 5.1	-	13.9 ± 8.9
Cynomys gunnisoni	(18.8 ± 9.9)	(12.2 ± 6.1)	(34.6 ± 14.7)	(17.5 ± 8.3)
C. gunnisoni (young)	2.6 ± 1.6	-	1.6 ± 0.84	-
Unknown Sciuridae	4.6 ± 2.1	-	2.9 ± 1.1	-
Lepus californicus	-	-	-	-
Sylvilagus audubonii	3.4 ± 1.0	12.8 ± 5.1	16.8 ± 5.9	33.9 ± 12.9
Neotoma spp.	0.35 ± 0.21	1.7 ± 1.7	0.35 ± 0.17	0.52 ± 0.52
Dipodomys spp.	2.3 ± 0.97	-	1.0 ± 0.46	-
Peromyscus spp.	3.2 ± 1.2	-	0.32 ± 0.14	-
Unk. mammal 1	7.2 ± 1.4	-	1.1 ± 0.42	-
Unk. mammal 2	1.9 ± 0.74	-	1.3 ± 0.57	-
Birds	(2.4 ± 0.31)	(3.0 ± 3.0)	(0.70 ± 0.11)	(0.29 ± 0.29)
Insects	-	8.7 ± 6.0	-	0.05 ± 0.04
Reptiles	(0.28 ± 0.28)	-	0.21±0.21	-
Not Identified	1.2 ± 0.52	2.5 ± 0.9	0.3 ± 0.2	0.5 ± 0.2

* Identified as either *Spermophilus spilosoma* or *S. tridecemlineatus*

** paired t-test: $t_5 = 4.47$, $p = 0.007$

Table 1.7. A compilation of publications on Ferruginous Hawk diet noting percent frequency (F) and percent biomass (B) of selected prey taxa, including contribution of primary prey sources (Townsends' Pocket Gopher (*Thomomys townsendii*, TPG), northern pocket gopher (*Thomomys talpoides*, NPG), thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*, ST), black-tailed jackrabbit (*Lepus californicus*, BTJR), white-tailed jackrabbit (*Lepus townsendii*, WTJR), Richardson's ground squirrel (*Spermophilus richardsonii*, RGS), spotted ground squirrel (*Spermophilus spilosoma*, SS), Botta's pocket gopher (*Thomomys bottae*, BPG), and Gunnison's prairie dog (*Cynomys gunnisoni*, GPD). Also noted is whether the authors documented prairie dogs as prey.

Authors (Yr.)	Years	Location	# nesting pairs	# prey items	Mammals		Birds		Reptiles		Insects		Important prey source (%)	Prairie dogs?
					B	F	B	F	B	F	B	F		
Steenhof and Kochert (1985)	4	ID	11	220	-	80	-	6	-	11	-	3	TPG (35%)	N
Fitzner et al. (1977)	1	WA	2	161	-	48	-	19	-	24	-	11	NPG (25%)	N
Blair and Schitowsky (1982)	2	SD	35	690	-	70	-	27	-	2	-	-	ST (44%)	Y
Smith and Murphy (1978)	5	UT	75	957	99	90	0.3	7	0.6	2	-	-	BTJR (F:42%, B:90%)	N
Ensign (1983)	2	MT	14	504	-	58	-	42	-	-	-	-	WTJR (F:24%)	Y
Schmutz et al. (1980)	2	Alberta	50	1225	96	94	4	6	-	-	-	-	RGS (F:87%, B:89%)	N
Gilmer and Stewart (1983)	3	ND	239	449	93	94	7	6	-	-	-	-	RGS (F:60%, B:66%)	N
Lokemoen and Duebbert (1976)	2	ND	27	130	93	72	7	6	-	-	-	22	RGS (F:58%, B:68%)	N

Howard and Wolfe (1976)	2	ID	7	133	-	85	-	10	-	5	-	-	NPG in grass (F:58%); BTJR in sage-steppe (F:67%)	N
Cartron et al. (2004)	1	NM	25	260	-	80	-	5	-	2	-	13	BPG (F:41%)	Y
Stalmaster (1988)	7	UT/CO	107	476	97	87	3	13	-	-	-	-	GPD (F:42%, B:49%)	Y
MacLaren (1986)	2	WY	23	237	98	89	2	11	-	-	-	-	WGS (F:35%); Leporids (B:48%)	Y
Roth and Marzluff (1984)	5	KS	27	72	-	86	-	13	-	1	-	-	ST (F:42%)	Y
Olendorff (1973)	3	CO	16	131	-	76	-	24	-	-	-	-	ST (F:41%)	N
This Study (pellets/prey remains)	2	NM	49	1035	98	90	2	5	0.1	1.1	0.02	5	BPG (F:37%, B:29%)	Y
This Study (video)	2	NM	6	596	99	96	0.7	2	0.2	0.3	-	-	SS (F:28%); GPD (B:34%)	Y

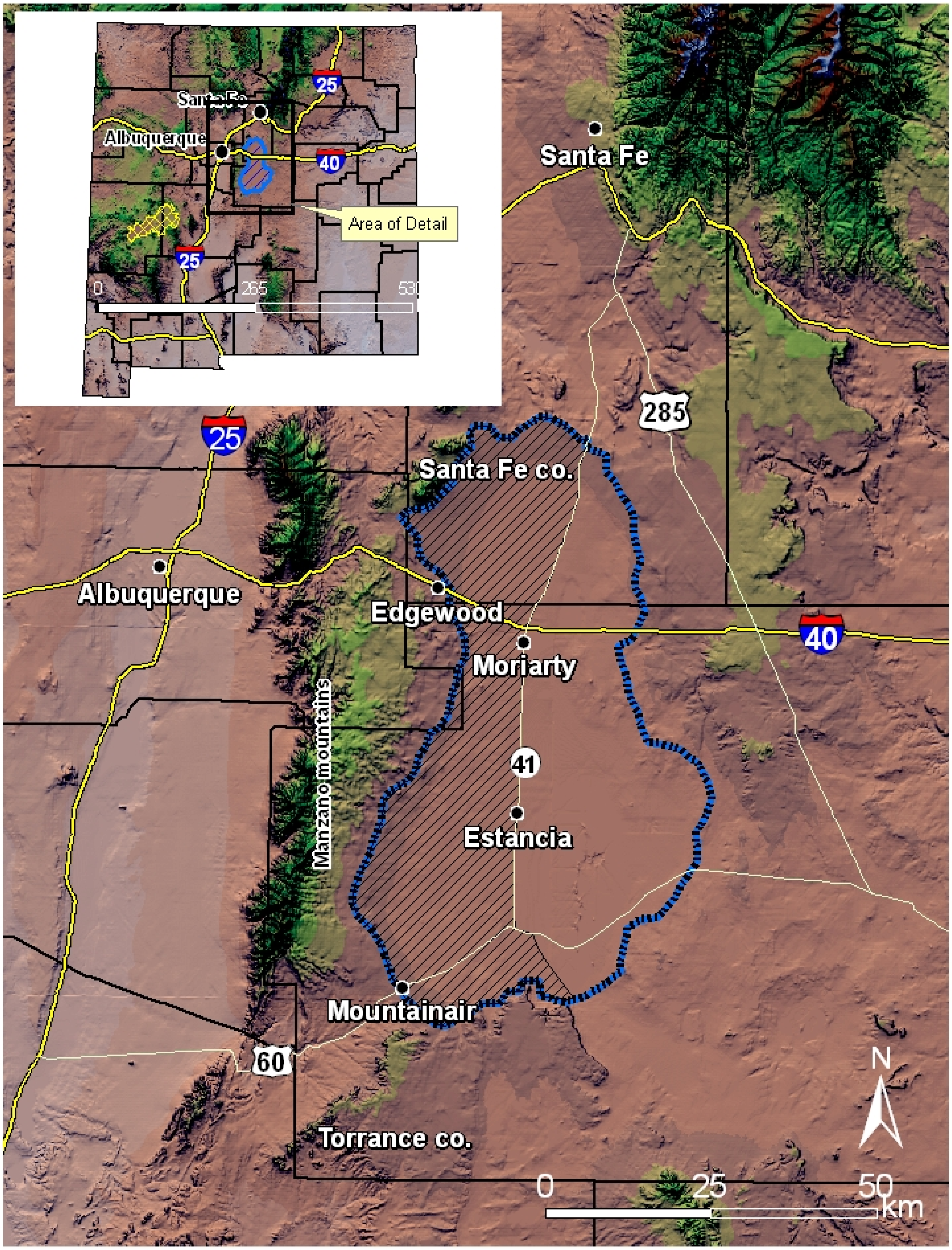

Figure 1.1. Map of the Estancia Valley, New Mexico, USA (simple hatch) with inset of New Mexico showing location of the Estancia Valley (dark outline, simple hatch) in relation to the Plains of San Agustin (light outline, cross hatch).

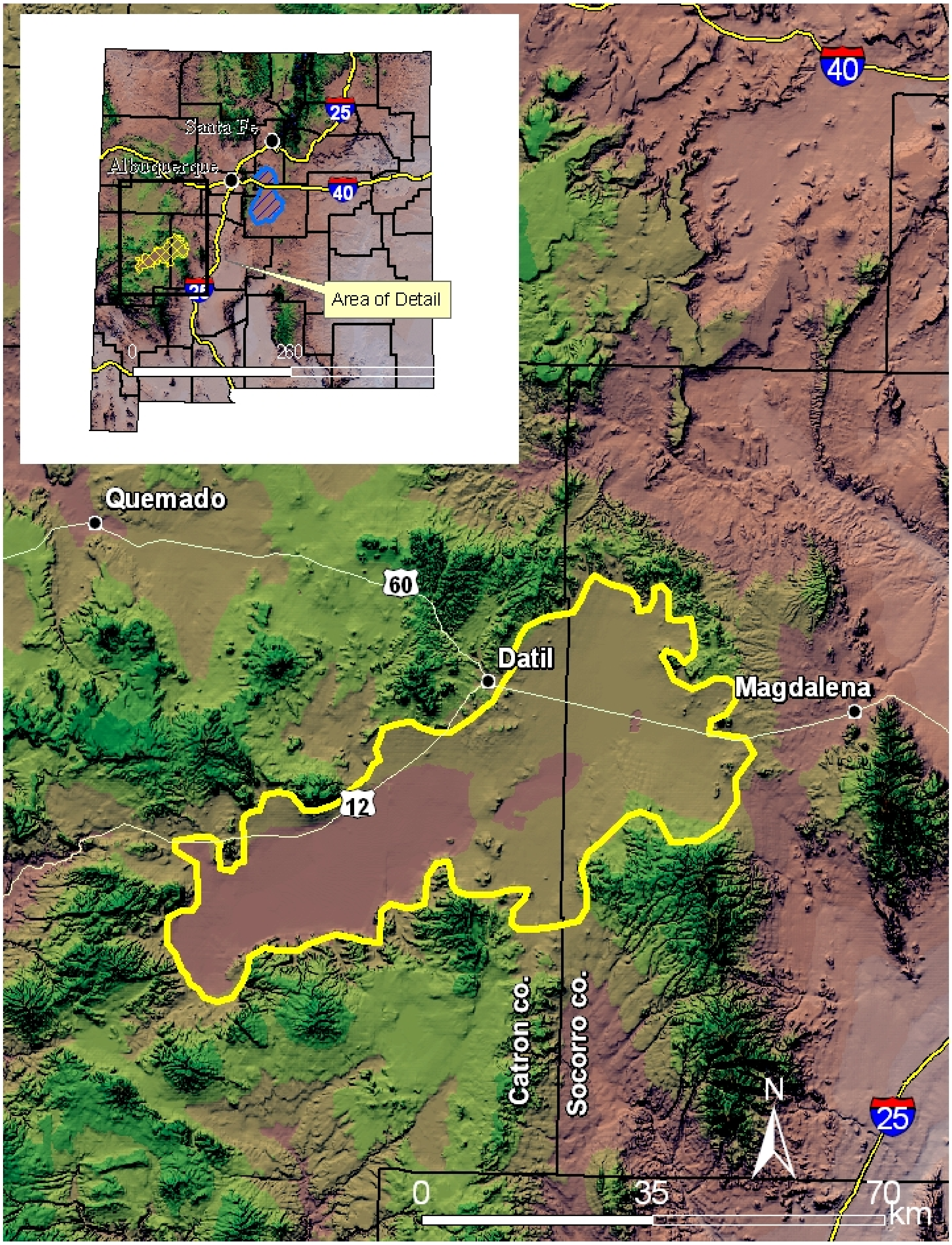

Figure 1.2. Map of the Plains of San Agustin, New Mexico, USA with inset showing location of the Estancia Valley in relation to the Plains of San Agustin.

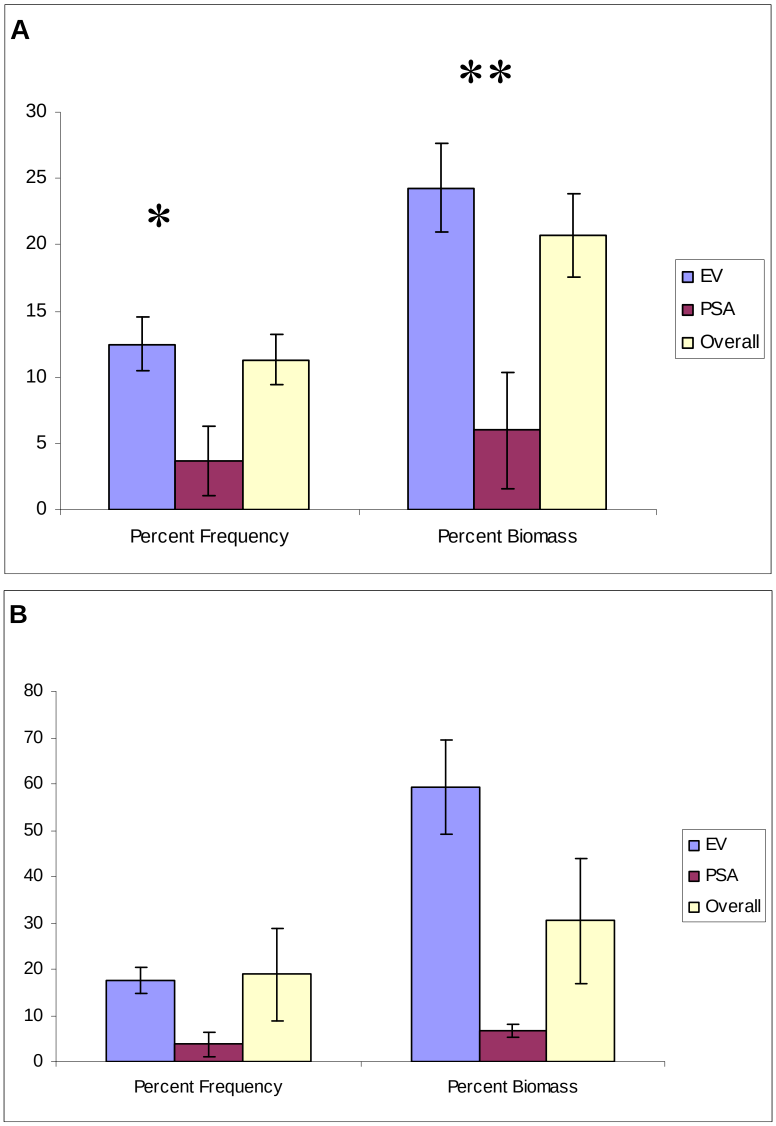

Figure 1.3. Mean (± SE) percent frequency and percent biomass per nest of Gunnison's prairie dogs detected in pellets and prey remains (A) from occupied Ferruginous Hawk nests in the Estancia Valley (EV: n = 29), Plains of San Agustin (PSA: n = 16), all nests sampled in New Mexico (n = 49), and nests monitored by time-lapse video (EV: n = 3, PSA: n = 3) (B), 2004-2005. Using pellets and prey remains, a study area effect was significant for percent frequency (*Wilcoxon rank sum: Z = 2.70, p = 0.0069) and percent biomass (**Wilcoxon rank sum: Z = 3.07, p = 0.002).

CHAPTER TWO

NESTING BEHAVIOR, PROVISIONING RATES, AND PARENTAL ROLES OF FERRUGINOUS HAWKS IN TWO GRASSLANDS IN NEW MEXICO WITH DIFFERING ANTHROPOGENIC ALTERATION

Abstract

Descriptions of Ferruginous Hawk (*Buteo regalis*) parental roles and feeding ecology are limited to anecdotal accounts using out-dated methods. In 2004-2005, I collected and analyzed 1,373 hr of video from six time-lapse video-monitored nests in two New Mexico grasslands with different levels of anthropogenic alteration to establish baseline data on key components of the nesting behavior of a grassland raptor. Ferruginous Hawks delivered 93.3 grams of biomass per hour to each nest (g/hr), 42 g/nestling/hr, and 208 g/prey delivery, with the majority of provisioning occurring in the morning and afternoon hours. Males delivered most prey items (72%) and provisioned nestlings at a higher prey-delivery rate but females delivered more mass per delivery. Females delivered most desert cottontails (*Sylvilagus audubonii*), but there was no clear delineation of differential prey use between sexes. Females spent more time at the nest than males during the nestling stage, more time at the nest on days when males delivered more mass to the nest and less time at the nest as nestlings grew older. Ferruginous Hawks in the human-altered Estancia Valley delivered more prey items in the morning while hawks in the rural Plains of San Agustin delivered more items during mid-day.

Mass-provisioning rate was greater in the Estancia Valley throughout the day. Numerically, hawks in the Estancia Valley supplied nests with 87% more mass per delivery (271 vs. 145 g/delivery) and 60% more mass per nestling per hour (52 vs. 32 g/nestling/hr) but 25% fewer prey items per hour (0.51 vs. 0.41 items/hr) than adults in the Plains of San Agustin. These measures suggest that video-monitored hawks in the Plains of San Agustin spent more time foraging but delivered smaller prey than hawks in the Estancia Valley. Further, hawks in the Plains of San Agustin foraged more during mid-day hours, potentially because sufficient food resources could not be obtained in the morning. On average, females in the Plains of San Agustin spent twice as much time away from nests than females in the Estancia Valley following a disturbance that caused them to flee. The presence of a colonial food source, such as Gunnison's prairie dogs (*Cynomys gunnisoni*), may help decrease variables associated with optimal foraging theory, such as predator search time and prey handling, thereby increasing provisioning efficiency and reproductive output.

Introduction

Although food habits of Ferruginous Hawks (*Buteo regalis*) have been documented over much of their breeding range, relatively little is known about the species' nesting behavior, feeding ecology, and parental roles. All available data on these key reproductive components can be considered anecdotal and antiquated as they emanate from direct observational accounts of one or two nests from at least 30 years ago when human land-use patterns were different (Bailey 1928, Ligon 1961, Angell 1969, Wakeley 1978).

Temple (1972) found time-lapse video recording to be an effective tool to examine brooding behavior and nest attentiveness but noted it could not capture behavior that required faster exposure rates. Video monitoring has recently been shown to be an effective medium to document avian nesting behavior and parental care (Cutler and Swann 1999, Booms and Fuller 2003, Sabine et al. 2005, Reif and Tornberg 2006) because technological advances have improved the cost effectiveness and logistics of operation.

Ferruginous Hawks are considered a sensitive species by the Bureau of Land Management and United States Forest Service (Bechard and Schmutz 1995, Collins and Reynolds 2005). Thus, their behavior and population status may be adversely affected by human encroachment onto grasslands, a nationally imperiled biome (Hoekstra et al. 2005). These grasslands are facing increasing pressure from exurban and rural residential development in many portions of the United States (Theobald 2001).

Human encroachment into raptor nesting habitat may alter the birds' nesting behavior by modifying multiple ecological factors related to breeding success, including predator and prey abundance, proximity to disturbance, and prey composition and availability (Newton 1979). Changes associated with abundance or composition of primary prey resources, regardless of the cause, may especially alter the role of female raptors, forcing them to hunt when the male is not provisioning the nest at a sufficient rate. Consequently, low prey availability may cause female nest attentiveness to decrease which can affect reproductive output as nestlings become more susceptible to predation and heat stress. This may be especially evident for Ferruginous Hawks, which have shown affinities to unshaded nesting sites (Howard and Hilliard 1980) and sensitivity to heat stress (Tomback and Murphy 1981).

I previously documented different Ferruginous Hawk diet compositions between two grassland sites in New Mexico (Chapter One). Specifically, I found that Ferruginous Hawks in the Estancia Valley consumed significantly more Gunnison's prairie dogs (*Cynomys gunnisoni*) than hawks in the Plains of San Agustin. Colonial prey located in dense patches, like Gunnison's prairie dogs, may help to improve the provisioning effectiveness of males (Krebs and Davies 1993, Korpimäki et al. 1994), thereby allowing the female to be more attentive to the brood during crucial times of the nesting cycle.

In this chapter, I compare Ferruginous Hawk nesting behavior and parental roles at time-lapse video-monitored nests to expand existing information on Ferruginous Hawk parental roles and nesting behavior, and to explore potential relationships between prey use and hawk behavior. Specifically, I identified several research questions: 1) is there evidence of prey partitioning between sexes?; 2) do adults provision nestlings equally throughout the day and throughout the nesting cycle? ; 3) how often do adults eviscerate prey prior to delivery?; 4) is female nest attendance affected by male provisioning rate?

To maintain stable populations of Ferruginous Hawks in natural areas that are realizing increased human pressure, studies must provide empirical data on nesting behavior and parental roles as well as the relationship among these variables and diet composition.

Methods

Study Areas

Environmental Variation

I studied breeding Ferruginous Hawks on private and public lands in the Estancia Valley and Plains of San Agustin, two grasslands located approximately 350 km apart in New Mexico (Figures 1.1, 1.2). The Estancia Valley spans approximately 300,000 ha in Torrance and Santa Fe counties, New Mexico (Figure 1.1). The Sandia and Manzano Mountains separates the Estancia Valley from Albuquerque (Pop.: 448,607), which is 30 km west. My study area represents 158,000 ha in the western half of the Estancia Valley and is loosely bordered by State Highway 41 to the east, the Manzano Mountains to the west, State Highway 60 to the south, and Interstate 40 to the north (Figure 1.1).

Dominant vegetation in the Estancia Valley is similar to that found in the Plains of San Agustin. Large expanses of blue grama (*Bouteloua gracilis)* and buffalograss (*Buchloe dachtyloides*) meet widely scattered juniper *(Juniperus* spp.*)* trees. However, unlike the Plains of San Agustin, non-native trees like Chinese elm (*Ulmus parvifolia*), mainly associated with occupied dwellings and abandoned homesteads, are present and provide nesting substrates. Ferruginous Hawk nests in the Estancia Valley average 1947 m in elevation (n = 36, range: 1865-2054 m, this study). The town of Estancia, located in the center of the study area, averages 32.5 cm of precipitation while temperatures ranged from -9.2 to 31.4 °C (Western Regional Climate Center 2007b).

The Plains of San Agustin is located approximately 70 km west of Socorro (population in the year 2000 [hereafter "Pop."]: 8,877). The Plains of San Agustin spans approximately 238,000 ha between Magdalena and Datil in Socorro and Catron counties, New Mexico. Geologically, the southwest-northeast oriented basin is constricted by the San Mateo Mountains to the east, the Gallinas Mountains to the northeast, the Datil and Mangas Mountains to the northwest, Tularosa Mountains to the west and Luera Mountains to the south (Figure 1.2).

The flat bottom of the Plains of San Agustin is an artifact of a Pleistocene-era lake and is characterized by species diagnostic to the desert short-grass prairie (Dick-Peddie 1993). Blue grama and buffalo grass co-dominate the open country while scattered, isolated junipers provide the majority of nesting sites for Ferruginous Hawks and other birds. Elevated from the basin floor, sagebrush (*Artemisia* spp.) and pinyon (*Pinus edulis*)-juniper woodlands dominate higher elevations (Dick-Peddie 1993) and meet mountainous areas like the continental divide to the west and the headwaters of the Gila River to the south. Ferruginous Hawk nests in the Plains of San Agustin average 2170 m above sea level (n = 41, range: 2025-2338 m, this study). The area receives 28.7 cm of annual precipitation while the average temperatures range from -10.3 to 29.3 °C (Western Regional Climate Center 2007a).

Anthropogenic Variation

To describe anthropogenic differences between the Estancia Valley and Plains of San Agustin, I used a geographic information system (ArcGIS 9.2, ESRI, Redlands, California) to analyze data obtained from federal and state government websites. Jane Farmer (BLM Socorro Field Office, Socorro, New Mexico) digitized the Plains of San Agustin boundary and I digitized the Estancia Valley boundary. I obtained 2006 land ownership data from the New Mexico Bureau of Land Management (BLM 2007) and used “X-Tools”, an ArcGIS extension, to calculate area totals for surface ownership of both study areas. I obtained all other data including New Mexico counties and cities, from the New Mexico Resource Geographic Information System (University of New Mexico 2006).

I analyzed the most current anthropogenic data available that covered my study areas uniformly. United States Census Bureau (UCSB) 2006 TIGER boundary files provided the most uniform road coverage in the Estancia Valley and the Plains of San Agustin (U.S. Census Bureau 2006). To facilitate my analysis, I used TGR2SHP v7.01 (Ralston 2008) to convert UCSB TIGER boundary files into a road layer. I used these data in a Geographic Information System to determine the road density within each study area and the distance between successful Ferruginous Hawk nests (≥ 1 young fledged) and the nearest road.

Ferruginous Hawk Nesting Productivity

In April of each year, aerial surveys were conducted to determine occupancy (i.e., nestlings or eggs observed on the nest or adult in incubating posture) at known nest sites. New nests were marked using a Garmin 92 Global Positioning System (Garmin International Inc., Olathe, KS, USA) designed for use in aircraft. A minimum of two observers accompanied the pilot in a Cessna 205 fixed wing aircraft. Air speed during surveys averaged 160 kilometers per hour and altitude ranged from 90-240 m above ground. Following aerial surveys, each occupied nest was visited a minimum of two times to determine breeding productivity. I considered nestlings to be fledged when they reached 80% of their fledging age, or 32 days.

Video Monitoring

I installed "Basic Sentinel I All Weather Video Surveillance Systems" from Sandpiper Technologies, Inc. (Manteca, CA, USA) to describe nesting behavior. I set the time-lapse system to record 20 frames per sec (one third real-time) which fit approximately 24.5 hrs of nest activity onto one T-160 videotape. I used TDK High Quality videotapes as media and powered the systems with a Sears 12 volt 91.6 ampere deep-cycle marine battery. I divided each video-recorded day into three 5-hr time blocks: time block “A” (0520-1020 H), time block “B” (1020-1520 H), and time block “C” (1520-2020 H) and randomly selected two blocks to record per day. This enabled me to return to the nest every other day to refresh tapes and batteries.

Because cattle grazed land surrounding Ferruginous Hawk nests, I buried the 50-75 m co-axial cable that connected the VCR to the camera (dimensions: 6 x 4 x 4 cm) ≥ 10 cm underground. I also cached the VCR and battery in a camouflage tent and built a fence around the structure using t-posts and chicken wire as a safety precaution to mitigate potential damage to the video system.

I attached the camera to a 3.8 cm-diameter wooden dowel using automobile radiator hose clamps and secured this apparatus to a tree branch using U-shaped pole fasteners. The distance between the camera and nest varied among sites because of nest tree structure (range: 0.7 – 1.7 m), but I set it at approximately 1 m whenever possible (Booms and Fuller 2003).

I used the time-lapse VCR to playback each videotape on a Sony television with a 68 cm screen. This setup facilitated frame-by-frame analysis in high quality resolution. For every delivery, I noted prey type to species whenever possible. To distinguish prey species, I used pelage pattern, shape of eyes and head, length of tail, and size of body and feet. As there was a large weight discrepancy between young prairie dogs and adults, I categorized them separately whenever possible and used appropriate weights for biomass calculations (Appendix A). Prey items that I determined to be re-delivered (i.e., looked like an item recently removed from the nest) were only counted once during videotape analysis.

In some instances when analyzing video, I was not able to identify the prey item to species. In these cases, I categorized the prey item into general taxa (bird, mammal, etc.) and for mammalian prey, further classified them based on body size. For unidentified small birds, I used the average of three passerine weights as the biomass for "unidentified bird" (Appendix A). For unidentified small mammals (i.e., mouse size), I used the mean biomass of three mouse-sized species that Ferruginous Hawks took as prey as the weight for "unknown mammal 1". For larger unidentified mammals, I used averaged weights from five larger-sized mammalian prey items to provide a surrogate biomass measure ("unknown mammal 2"). This technique improved precision of estimates of delivered biomass for video-monitored nests.

Nesting Behavior

I distinguished between male and female Ferruginous Hawks at video-monitored nests using a variety of indicators including reversed sexual size dimorphism, unique feather patterns, and general behavior (sex by inference). I used these characterizations to describe female and male Ferruginous Hawk nesting behavior and provisioning rates.

I calculated the percentage of time female and male adult Ferruginous Hawks spent at the nest each day per nest using video footage. If the adult was not on the nest but was in the nest tree and within the view of the camera, I considered this at the nest. To determine evisceration status, I examined the video frame-by-frame: eviscerated prey were noticeably limp with excess skin or a visceral gash whereas intact prey were plump with a tighter pelage. To investigate human-related disturbance effects on the birds, I used a combination of video footage and field observation to measure the duration of female absence following my approach to the nesting site to refresh tapes and batteries (after subtracting the time I spent near the nesting site). Only instances where the female was at the nest prior to my approach and the video system recorded the female's return to the nest qualified for this analysis. I used the age of the oldest nestling (Moritsch 1985) to describe relationships between female nest attendance and brood age.

Statistical Analysis

I performed all analyses with JMP 5.0 statistical software (SAS Institute, Inc., Cary, NC). I used paired t-tests when testing for inter-sexual differences in provisioning rates of adults from the same nest and two sample t-tests to test for differences between independent groups. I used a one-way ANOVA to test for differences in daily time recorded among time blocks and two-way ANOVAs to test for differences in: 1) provisioning rate of both sexes combined (mass-delivery rate and prey-delivery rate) between one spatial scale (study area, two levels) and one temporal scale (daily time block, three levels); 2) female nest attendance (time at nest) by disturbance level (two levels, video system serviced?: yes or no) and study area. When a significant interaction existed, I used student's t-test for post-hoc means comparisons.

When data met homogeneity of variance assumptions for between group comparisons, I reported *t*-statistics with associated probability values; when they did not, I reported Wilcoxon rank sum Z scores and associated probability values for non-parametric data. I used Spearman's rank correlation to assess the relationship between continuous variables associated with nesting behavior when normality assumptions were not met (Zar 1999). I performed three correlation analyses: 1) adult provisioning rate (g/day) by nestling age; 2) female nest attendance (percent of daily time spent at the nest) by nestling age; 3) and female nest attendance by male biomass delivered (g/day).

I present descriptive statistics to compare Ferruginous Hawk behavior between study areas and sexes because limited sample size restricted my ability to make meaningful statistical inferences for those comparisons. To expand comparison among previous studies, I provide results of provisioning rates for the entire brood (i.e., g/day and deliveries/day) as well as for each nestling within east nest (g/nestling/day and deliveries/nestling/day). I report significant probability values as those with an alpha level less than or equal to 0.05 and report means and standard errors throughout.

Results

Study Area Variation

Nests with successful Ferruginous Hawk breeding attempts (n = 31) were 531 ± 67 m from the nearest road. Successful nests in the Estancia Valley (n = 18) were 403 ± 82 m to the nearest road while successful nests in the Plains of San Agustin were 708 ± 97 m from the nearest road. This spatial difference was statistically significant ($t_{29} = -2.40$, p = 0.02, Table 1.1). Video-monitored nests in my study (n = 6) were 731 ± 219 m from the nearest road. Video-monitored nests in the Estancia Valley (n = 3) and Plains of San Agustin (n = 3) were situated 535 ± 262 m and 927 ± 365 m from the nearest road, respectively. Ferruginous Hawks at two nests and one nest in each study area produced two and three fledglings, respectively. Ferruginous Hawks in the Estancia Valley produced more fledglings per nesting attempt (n = 35, 2.43 ± 0.194) than in the Plains of San Agustin (n = 25, 1.48 ± 0.231) during my study ($t_{58} = 3.15$, $p = 0.003$).

Camera Installation and Performance

I recorded 1,373 total hours (mean: 229.0 ± 29.2 hr) of activity from three nests in the Estancia Valley and three nests in the Plains of San Agustin (Table 2.1). I installed all cameras between 0700-0830 H and stayed no longer than 56 min at any site to limit nestling exposure. To avoid nest desertion by adults (Olendorff 1973, White and Thurow 1985, Ward 2001), I established all video systems after nestlings (n = 15) had attained 7 days of age (mean nestling age: 12.7 ± 0.8 days, range: 8-18) and removed the survellience systems after the young had fledged. At two nest sites, the video image was compromised by wind or other interference that caused approximately 90 hr of nest activity to be excluded from further analyses.

Provisioning Rate: Prey Deliveries

The video systems recorded 597 prey deliveries or almost one prey delivery for every two hours that the nests were video-monitored (0.46 ± 0.035 prey deliveries/hr). Males and females delivered 72.5% (n = 433) and 23.6% (n = 141) of all prey items, respectively. I was unable to identify the adult’s sex in 3.9% (n = 23) of prey deliveries. Males provisioned broods, and each nestling within the brood, at a significantly greater rate than females (males: 0.33 ± 0.05 vs. females: 0.12 ± 0.02 deliveries/hr, paired t-test: t5 = 3.45, p = 0.018; males: 0.14 ± 0.018 vs. females 0.06 ± 0.012 deliveries/nestling/hr, t5 = 3.57, p = 0.016).

I sampled each time block for similar numbers of hours ($F_{2,\ 264} = 0.897$, $p = 0.41$). Numerically, video-monitored Ferruginous Hawks ($n = 6$) delivered the most prey per hour in time block B (0.53 ± 0.079 prey items/hr), recorded a moderate delivery rate in time block A (0.46 ± 0.072 prey items/hr), and delivered the fewest prey items per hour in time block C (0.32 ± 0.045 prey items/hr). Ferruginous Hawks in the Estancia Valley ($n = 3$) delivered 0.41 ± 0.019 prey deliveries/hr while hawks in the Plains of San Agustin ($n = 3$) delivered 0.51 ± 0.055 prey deliveries/hr.

Between study areas, differences in the Ferruginous Hawk prey-delivery rate depended on time block (interaction term: $F_{2,\ 12} = 4.36$, $p = 0.0377$, Figure 2.1). Ferruginous Hawks in the Estancia Valley provisioned their broods at the greatest rate in time block A (0.55 ± 0.127 deliveries/hr) while adults in the Plains of San Agustin provisioned their broods at the greatest rate in time block B (0.65 ± 0.097 deliveries/hr).

Provisioning Rate: Biomass

Ferruginous Hawks delivered over 127 kg of prey to six video-monitored nests (21.2 ± 5.0 kg/nest), 93.3 ± 14.8 g/hr to each brood, and 42 ± 8.4 g/hr to each nestling in each nest (Table 2.1). As nestlings grew older, adults did not deliver more biomass to the brood ($n = 125$ days; Spearman rank correlation: $r_s = 0.114$, $p = 0.19$).

Between study areas, differences in Ferruginous Hawk mass-delivery rates were independent of time block. There was no interaction between study area and time block (2 way ANOVA: $F_{2,12} = 1.68$, $p = 0.22$), nor did time block affect mass-delivery rate ($F_{2,12} = 1.28$, $p = 0.31$). However, there was a significant effect of study area on Ferruginous Hawk mass-delivery rate ($F_{1,12} = 5.51$, $p = 0.037$). Ferruginous Hawks in the

Estancia Valley delivered 110.4 ± 13.0 g/hr while hawks in the Plains of San Agustin supplied delivered 50% less biomass (67.0 ± 13.0 g/hr, Table 2.1).

Among time blocks, Ferruginous Hawks delivered 99.8 ± 21.3 g/hr to video-monitored nests (n = 6) in time block A and 98.6 ± 16.3 g/hr in time block B, but the provisioning rate fell to 67.9 ± 18.6 g/hr in time block C. Ferruginous Hawks in the Estancia Valley delivered 143.9 ± 16.4, 102.0 ± 31.7, and 85.3 ± 36.5 g/hr in time blocks A, B, and C, respectively, while hawks in the Plains of San Agustin delivered 55.6 ± 7.5, 95.1 ± 17.6, 50.5 ± 9.9 g/hr in time blocks A, B, and C, respectively.

When compared to females, males did not deliver more biomass per hour to broods or to each nestling within each brood (61.9 ± 16.5 vs. 28.4 ± 5.0 g/hr.; paired t-test: $t_5 = 1.76$, $p = 0.14$; 27.4 ± 8.4 vs. 13.3 ± 2.9 g/nestling/hr; paired t-test: $t_5 = 1.557$, $p = 0.18$). Further, males did not deliver broods a significantly larger portion of total biomass (males: 62.3 ± 7.3%, females: 34.1 ± 7.4%; paired t-test: $t_5 = 1.97$, $p = 0.11$). I could not distinguish the adult's sex for 4% of the biomass delivered.

Males in the Plains of San Agustin (n = 3) and Estancia Valley (n = 3) supplied broods with 63.2 ± 11.2% and 61.4 ± 11.7% of all biomass, respectively. Females in the Plains of San Agustin (n = 3) and Estancia Valley (n = 3) delivered 38.6 ± 11.7% and 29.6 ± 10.6% of total biomass, respectively (student's t-test: $t_4 = 0.568$, $p = 0.60$).

Males in the Estancia Valley delivered 75.6 ± 30.4 g/hr (35.2 ± 16.6 g/nestling/hr) and males in the Plains of San Agustin delivered 48.2 ± 15.6 g/hr (19.7 ± 3.6 g/nestling/hr). Females in the Estancia Valley delivered 30.4 ± 9.1 g/hr (14.2 ± 5.3 g/nestling/hr) and females in the Plains of San Agustin delivered 26.5 ± 10.5 g/hr (12.4 ± 3.8 g/nestling/hr, Table 2.1).

Biomass per Delivery

Ferruginous Hawks supplied broods with 208.1 ± 37.0 g/prey delivery (n = 597). Females delivered significantly more biomass per prey delivery than males (255.7 ± 44.9 vs. 190.2 ± 29.4 g/delivery, paired t-test: $t_5 = 2.73$, $p = 0.041$). Estancia Valley hawks delivered 271 ± 37.9 g/delivery while hawks in the Plains of San Agustin delivered 145 ± 37.9 g/delivery (student's t-test: $t_4 = 5.56$, $p = 0.077$). In the Estancia Valley, females and males delivered 319 g/delivery and 259 g/delivery, respectively, while females and males in the Plains of San Agustin delivered with 192 g/delivery and 121 g/delivery, respectively.

Adult Prey Use

Females delivered spotted ground squirrels (*Spermophilus spilosoma*) to the nest most often (30% of all individuals delivered), while males most commonly delivered Botta's pocket gopher (*Thomomys bottae*) to nests (27%). Adults delivered Gunnison's prairie dogs in similar proportions between sexes (17-19%), even though males delivered three times as many individuals (Table 2.2).

Gunnison's prairie dogs represented 39% of all biomass that females delivered and 49% of all biomass delivered by the male (Table 2.2). Desert cottontails (*Sylvilagus audubonii*) were a major prey source for female Ferruginous Hawks as the leporid represented 27% of all biomass that females delivered (rank #2). Rabbits only registered 7% (rank #4) of total male biomass.

Evisceration Rate

The hawks eviscerated prey prior to 30% (n = 182) of all deliveries, and males and females did so at equal rates. I considered this a conservative estimate of evisceration rate because I was unable to determine evisceration status of almost half of all prey items delivered. Of the 108 prey items transported intact, 12% (n = 13) were alive. All prey items delivered alive were spotted ground squirrels.

Prior to delivery, adults eviscerated three of the four most commonly delivered species ≥ 70% of the time. Desert cottontails registered the highest evisceration rate with 93% (n = 14) of individuals gutted, followed by Gunnison's prairie dogs (n = 44, 75%) and Botta's pocket gophers (n = 69, 70%). Of the most commonly delivered species, only spotted ground squirrels were delivered whole more than gutted (n = 36, 39% gutted).

Female Nest Sanitation

Of 714 female nest departures recorded by video, 11% (n = 80) were positive departures, that is, one in which the female removed an item from the nest (i.e., remnant prey or regurgitated pellet). Of those occasions, 60% (n = 55) of the time the female removed a carcass, while 28% (n = 25) of the time the female removed a nestling's regurgitated pellet. Adults removed a prey item from the nest but re-delivered it after 2% (n = 14) of departures.

Of 718 female nest arrivals captured on video, 59% (n = 423) were positive because the female either delivered prey or nesting material to the nest (stick, grass bunch, cow dung, or leaves of the Yucca plant). Of those arrivals, females delivered prey 33% (n = 141) and nesting material 67% (n = 282) of the time.

Females in the Estancia Valley and in the Plains of San Agustin registered similar counts of positive departures (Estancia Valley: 45, Plains of San Agustin: 43). Among these instances, females in the Plains of San Agustin removed pellets twice as many times as females in the Estancia Valley. However, even though females in the Estancia

Valley registered almost twice as many positive arrivals as females in the Plains of San Agustin (288 vs. 149 arrivals with prey or nesting item), the latter delivered eight more prey items than the former.

Parental Behavior

Females spent a significantly greater portion of each day at the nest than males (females: 33.9 ± 8.01%, males: 0.26 ± 0.11%; paired t-test: $t_5 = 4.184$, $p = 0.009$). Following prey deliveries, males ($n = 6$) spent an average of 30 ± 6.9 sec at the nest. In total, males fed nestlings on three occasions, delivered nesting material once, and exhibited brooding behavior once during surveillance. Males in the Plains of San Agustin spent 23.1 ± 3.9 sec (mean range per nest: 7.6-28.9 sec) at the nest after a prey delivery while males in the Estancia Valley averaged 39.8 ± 14.0 sec (mean range: 6.3-71.3 sec) at the nest post prey delivery. The mean time at nest for males in the Estancia Valley included a case where the male delivered prey and remained on the nest in the female's absence approximately 47 min to shade and feed the nestlings. This example represented a 410% increase from the closest record from other video-monitored nests in this study (next closest: 11 min). If this observation is removed as an anomaly, combined male time at nest dropped to 24.5 ± 2.5 sec and male time at nest in the Estancia Valley decreased to 26.1 ± 3.2 sec.

Overall, females at each nest spent 33.2 ± 7.3% of recorded time at the nest per day, including 3.4 ± 0.47% of each day feeding nestlings. Nestlings ($n = 14$) began to feed themselves at 23.7 ± 1.3 days of age (range: 19-27). At video-monitored nests in the Estancia Valley, females spent 40.5 ± 16.3% (mean range: 17-72%) of total time recorded at the nest and females in the Plains of San Agustin spent 27.2 ± 3.4% (mean range: 26-34%) at the nest (Table 2.3). Females in the Estancia Valley and females in the Plains of San Agustin spent 3.9 ± 0.86% and 3.0 ± 0.44% of total time recorded feeding young, respectively. Female time at nest (%/day) was correlated with grams of biomass delivered by the male (g/hr) ($n = 125$ days; $r_s = 0.242$, $p = 0.006$), and female nest attendance per day was negatively associated with age of the oldest nestling ($n = 125$ days; $r_s = -0.560$, $p < 0.0001$).

Disturbance

Female time at nest was not affected by servicing the video system ($F_{1,8} = 0.103$, $p = 0.75$), nor were there effects of study area ($F_{1,8} = 1.03$, $p = 0.35$) on female time at nest. Females spent 31.7 ± 8.0% of daily time at the nest on days when I serviced the video-system and 34.7 ± 8.3% on days when I did not service the video system. Females in the Plains of San Agustin spent similarly low proportions of time at the nest regardless of this disturbance, whereas Estancia Valley females exhibited more variation in nest attendance (Table 2.3).

In 25 instances, females were recorded by video or otherwise observed flushing from the nest as I approached to service the video recording system and were subsequently captured on video returning to the nest. Females ($n = 6$) spent 131 ± 41.3 min away from the nest after I left the area. Females in the Plains of San Agustin and Estancia Valley spent 183 ± 76.3 and 80 ± 10.2 min away from the nest, respectively.

Discussion

To my knowledge, mine is the first study that used time-lapse video to describe inter- and intra-sexual differences in Ferruginous Hawk parental care and provisioning rates. Giovanni et al. (2007) described Ferruginous Hawk provisioning rates but did not delineate between sexes. Wakeley (1978) and Angell (1969) described some aspects of parental care and nesting behavior but they were limited to descriptions resulting from direct observations of two pairs and one pair of breeding Ferruginous Hawks, respectively.

Ferruginous Hawks in my study provisioned broods with more prey deliveries, 0.46 per hour, than the 0.38 prey deliveries documented in Giovanni et al. (2007). Similar results were observed when controlling for number of nestlings per nest as Ferruginous Hawks in my study provisioned individual nestlings with 50% more deliveries than the peak of provisioning Giovanni et al. (2007) documented (0.20 vs. 0.13 deliveries/nestling/hr). Importantly, male prey-delivery rates in my study were similar to the combined effort by adults in their study, and adults in the Plains of San Agustin in my study provisioned nests at a higher prey-delivery rate than the Ferruginous Hawks they studied. In contrast, Ferruginous Hawks in my study supplied nests with 25% less biomass than adults did in the least-provisioned nestling stage in their study (93 vs. 129 g/hr) and 50% fewer g/hr in the nestling stage with their highest provisioning rate (176 g/hr) . When controlling for brood size, mass-delivery rates by Ferruginous Hawks in my study matched those reported in just three of nine nestling stages in Giovanni et al. (2007).

Ferruginous Hawks in my study consistently delivered more prey items per hour but less biomass per hour when compared with Ferruginous Hawks in Giovanni et al. (2007). A couple potential explanations follow. First, Ferruginous Hawks in their study frequently preyed upon black-tailed prairie dogs (*Cynomys ludovicianus*) and plains pocket gophers (*Geomys bursarius*), both of which weigh more than Gunnison's prairie dogs and Botta's pocket gophers, the comparable prey species in my study. Next, one of my study areas, the Plains of San Agustin, may have been prey-limited, thus decreasing my overall estimate of mass-provisioning rate. Comparative evidence from pellets and prey remains analysis supports this distinction as hawks in the Estancia Valley consumed 79% more biomass per nest than hawks in the Plains of San Agustin (Table 1.2).

Although Ferruginous Hawks in the Estancia Valley provisioned young with 62% more g/hr and 87% more g/delivery than adults in the Plains of San Agustin, the latter delivered 25% more prey items per hour. This suggests that video-monitored adults in the Plains of San Agustin most likely foraged more often for smaller prey items. Behavioral evidence from video footage supports these findings. Nestlings in the Plains of San Agustin commonly mantled prey immediately following delivery, regardless of whether they were able to feed themselves. This led to many occasions when the nestlings would fight one another for prey, which sometimes forced the adult that was attempting to feed the young to leave the nest. Further, males in the Plains of San Agustin frequently delivered prey to the nest only to have it consumed whole by the adult female immediately upon delivery. I did not often observe these behaviors at video-monitored nests in the Estancia Valley, but rather frequently noted prey accumulating on the side of the nest while satiated nestlings slept.

Mass-delivery and prey-delivery rates from Ferruginous Hawks in the Estancia Valley were comparable to those documented by Giovanni et al. (2007). This further suggests that adults in the Plains of San Agustin may have been attempting to breed in comparatively low prey availability conditions.

Activity Periods: Prey-Delivery

Ferruginous Hawks supplied broods at similar prey- and mass-delivery rates in the morning and afternoon, with a noticeable decrease in the early evening hours. My results contrast those reported by Wakeley (1974) and Smith and Murphy (1973) for Ferruginous Hawk activity periods, both of which recorded adults delivering prey most often during crepuscular hours. This difference may be related to diet composition of Ferruginous Hawks because studies that observed dusk foraging also documented a strict dietary reliance on leporids, which are highly crepuscular, whereas hawks in my study consumed more diurnally-active sciurid rodents.

Ferruginous Hawks in the Estancia Valley provisioned broods at the greatest rate in the morning, while adults in the Plains of San Agustin provisioned broods at the greatest rate mid-day. Interestingly, leporids represented a substantial portion of the diet in the Plains of San Agustin while Gunnison's prairie dogs represented an equally substantial portion of diet composition in the Estancia Valley (Table 1.5). Adults in the Plains of San Agustin delivered at least 70% more biomass per hour and 80% more prey items per hour during mid-day than in the morning. Alternatively, Estancia Valley adults delivered the majority of their biomass to nestlings in the morning and supplied broods with more biomass per hour than adults in the Plains of San Agustin throughout the day. Taken together, this suggests that adults in the Plains of San Agustin foraged more during mid-day hours, possibly because sufficient food resources could not be obtained in the morning.

Parental Roles

Overall, male Ferruginous Hawks supplied broods with three-fourths of all prey items but spent less than 1% of recorded time at the nest. Clearly, the role of males during brood rearing was to provide food and not to tend to the nestlings, but the female's role was less one-dimensional. Females in my study provided a little over one-third of all biomass to nests but were also present at the nest one third of recorded time. This daily attentiveness is more than the 25% daily nest attendance documented by Collopy (1984) for female Golden Eagles (*Aquila chrysaetos*). Mine is the first study, to my knowledge, to simultaneously quantify provisioning rates and nest attendance in female Ferruginous Hawks. Wakeley (1978) found that only males foraged at the two nests he observed. He subsequently noted that females and offspring only consumed what the male delivered until the first female foraging bout occurred during the fifth week post-hatching. Angell (1969) reported some female foraging in his observations of one nest and Smith and Murphy (1978) refer to some occasions of females and males hunting together in 40 hr of nest observation.

Among other large raptors, Booms and Fuller (2003) found that female Gyrfalcons (*Falco rusticolus*) delivered half of all prey items to each nest and Collopy (1984) noted that female Golden Eagles supplied a substantial portion of biomass to nests, primarily after the first two weeks of brood rearing. However, direct comparisons between those studies and mine are impossible because neither study simultaneously quantified both components.

One limitation of my study was that the video systems only captured nest activity and therefore could not assess the prevalence of prey exchange behavior. Although it is possible that some prey items were killed by males and delivered by females, no accounts of prey exchange behavior by Ferruginous Hawks exist in the literature. However, extensive direct observations of Ferruginous Hawk prey deliveries to nests in the Estancia Valley in 2003 indicated that prey exchange behavior was low (< 1% of all deliveries; G. Garber, Hawks Aloft, Inc., unpublished data), and that males supplied broods with the majority of biomass early in the morning. The latter observation is one that my findings support.

If males deliver large amounts of biomass, females may be able to spend more time at nests caring for young. My data support this as a positive relationship existed between biomass delivered per day by the male and female nest attendance. This demonstrates that the role of the female in providing parental care depended, in part, on the ability of the male to supply nestlings with sufficient food. When males cannot meet the energetic requirements of the brood, the female may be forced to shift from nestling care to hunting, as suggested in the provisioning rates and nest attendance measures for females in the Plains of San Agustin. Pearse et al. (2004) found that additional food provided to females increased average length of incubation bouts and nest attentiveness in sympatric wren species. In raptors, Dewey and Kennedy (2001) experimentally determined that supplemental feeding of breeding Northern Goshawks (*Accipiter gentilis*) increased the time the female spent at or near the nest.

Of notable exception in my study was one female nesting on an artificial structure in the Estancia Valley which remained at the nest 71% of each day. Interestingly, a Gunnison's prairie dog colony was near this nest and could have been exploited sufficiently enough by the male to allay female foraging, but adults here provisioned nestlings at the lowest rate among all video-monitored nests (26.1 g/nestling/hr).

My data reinforce the hypothesis that female birds that receive a sufficient amount of biomass can apportion more time to nestling care. In my study, males in the Estancia Valley provisioned broods with 58% more biomass per hour but 28% fewer prey items per hour than males in the Plains of San Agustin while females in the Plains of San Agustin contributed almost half of all biomass delivered to nestlings in the morning (26 of 56 g/hr). This suggests that males in the Plains of San Agustin likely foraged more often but provisioned young at a lower rate than males in the Estancia Valley. Meanwhile, females in the Plains of San Agustin may have been required to forage to meet the brood's energetic requirements.

Previous studies have related low food supplies to low female nest attendance, low tolerance to disturbance, or reduced reproductive output in passerines (Pearse et al. 2004), accipiters (Ward and Kennedy 1994, Doyle and Smith 1994, Salafsky et al. 2007) and buteos (Smith et al. 1981, Smith and Murphy 1979, White and Thurow 1985). In my study, Ferruginous Hawks in the Estancia Valley produced significantly more fledglings per nesting attempt than adults in the Plains of San Agustin. Therefore, my data also support assertions that male provisioning rate can affect reproductive output. This effect may be direct as low provisioning rates leads to nestling starvation or indirect as low male provisioning rates forces the female to leave the nestlings unattended and susceptible to predation.

However, females may naturally spend less time at the nest independent of male provisioning rates. My data support this as female time at nest was negatively correlated to age of the oldest nestling. After a certain period, potentially when nestlings are able to thermoregulate and feed themselves, females spend less time at the nest. This trend was also documented in breeding Golden Eagles in Idaho (Collopy 1984). Ferruginous Hawk nestlings in my study began to feed themselves later than the estimate of 16-18 days provided by Bechard and Schumtz (1995). Once nestlings were able to perform this task, females would be less prone to injury from aggressive hunger-motivated advances by the nestlings if they left the nest after food deliveries.

Prey Evisceration

Ferruginous Hawks eviscerated approximately one-third of all prey items prior to delivery, which was similar to prey delivered by Gyrfalcons (Booms and Fuller 2003), but lower than the 43% evisceration rate of Richardson’s ground squirrels (*Spermophilus richardsonii*) delivered by Ferruginous Hawks in Alberta (Bechard and Schmutz 1995). Evisceration of prey prior to delivery may slow bacterial degradation of the carcass (Bechard and Schmutz 1995), maximize prey palatability (Schmutz et al. 1989), or it may be a tool to decrease prey mass to minimize energetic expenditure of delivering prey to the nest (i.e., load-size effect; Pennycuick et al. 1989, Korpimaki et al. 1994). In support of the latter hypothesis, Sodhi (1992) found male merlins (*Falco columbarius*) more likely to prepare prey before transportation at greater distances from their nests.

My data suggest all these factors may play a role in causing Ferruginous Hawks in New Mexico to eviscerate prey. Of the hundreds of feeding events recorded by video, even those where prey were delivered intact, I rarely observed viscera being consumed directly. Rather, adults would consistently remove meat and skin from prey and feed it to nestlings. It was also evident that Gunnison's prairie dogs were consumed immediately and were the preferred food item in contrast to Botta's pocket gophers which were routinely passed over when other carcasses were available. Further, it was evident that remnant carcasses in the nest would quickly attract insects and that fresh prey remains underneath nests became bloated and sordid in the New Mexico heat. To abate this, females kept nests clear of carcasses. I also observed females at all video-monitored nests consuming the regurgitated pellets of nestlings on many occasions, presumably to enable its deposition away from the nest site. This behavior implied that regurgitated pellets can also attract nest parasites or predators. Interestingly, females in the Plains of San Agustin removed pellets twice as frequently as did females in the Estancia Valley, which may partly explain the discrepancy in the number of prey items identified from pellet analysis that was part of my study.

My data also support the load-size effect hypothesis because the heaviest prey items (desert cottontails) were eviscerated most often while one of the lightest (spotted ground squirrel) were delivered whole most frequently. In fact, the latter species was delivered alive on occasion and was the only species I observed delivered in this condition. To my knowledge, this behavior has not been documented in Ferruginous Hawks prior to my study. Because delivering live ground squirrels was equally divided among all video-monitored nests, its role may be interpreted as behavior limited to one pair but rather it may aid in the development of nestlings' predatory cues. Often the female would be on the nest watching the nestlings pick at the live ground squirrel, which implied that the female may have fostered this behavior. On a few occasions, the ground squirrel escaped from the nestlings' grasp and jumped from the nest, but the female usually re-delivered it and continued to allow the nestlings to grasp and pick at it until their interest waned. With an estimated weight of 88 grams and body length of 16.5 cm (Fitzgerald et al. 1994), the spotted ground squirrel may be an optimal specimen to enable rapacious skill development in Ferruginous Hawk nestlings.

Food-niche Hypothesis

Ferruginous Hawks exhibit pronounced reversed size dimorphism, a trait unique to raptors and skuas (*Stercorarius* spp.), where the female is larger than the male (Snyder and Wiley 1976, Bechard and Schmutz 1995). One explanation offered to account for this characteristic is the food-niche hypothesis that argues this trait evolved to expand the food-niche of a breeding pair, thereby decreasing inter-sexual competition for food and maximizing foraging efficiency (Storer 1966, Earhart and Johnson 1970, Newton 1979). In support of this, females in my study delivered significantly heavier prey items than males even though the females showed some propensity to deliver spotted ground squirrels, one of the smaller sciurids in the study areas.

Delineating specific differential prey use between male and female Ferruginous Hawks was less clear. Females delivered the majority of desert cottontails, which represented over one quarter of all biomass delivered by that sex but only constituted 7% of all biomass delivered by the male, whereas Botta's pocket gophers represented a substantial portion of biomass delivered by the male. Gunnison's prairie dogs were equally important to both sexes, underscoring the importance of Gunnison's prairie dogs as prey for both sexes.

Disturbance

Overall, I documented a pronounced response to researcher disturbance relative to other studies on Ferruginous Hawk behavior. Video-monitored females in my study spent more time away from the nest than documented by Holmes (1994) following a similar disturbance. She noted a return time for female Ferruginous Hawks of 35 min during incubation and 13 min during the nestling stage. In the Estancia Valley, an area with increased human pressure, adults returned six times more slowly than recorded by Holmes (1994). This indicated that video-monitored Ferruginous Hawks in my study areas may have been sensitive to human approach. Unfortunately, Holmes (1994) did not provide any data regarding diet composition or prey availability, and thus any correlation between prey and human tolerance can not be inferred from her study. However, she estimated nests to be 516 m from permanent sources of human development (i.e. road, occupied house, oil well) while video-monitored nests in my study were 731 m away from the nearest road. Further, Holmes (1994) visited each nest four consecutive times in the same day in her study area that was located in rural Weld county, Colorado. This disturbance regime in a relatively unpopulated area may have familiarized the birds to her presence and ultimately modified nest defense behavior (Holmes 1994).

Proximity to human development may influence Ferruginous Hawk behavioral thresholds. In support of this, females in the anthropogenically-altered Estancia Valley returned to the nest following a disturbance in less time, on average, and with less variation than females in the Plains of San Agustin. The latter group took more than twice as long on average and up to 6.5 hr to return to the nest following a disturbance that caused them to flee. Females in the Estancia Valley spent 25% more time on the nest on days when I serviced the video system than females in the Plains of San Agustin spent on the nest during service-free days. This further suggests that females in the Plains of San Agustin were not spending optimal amounts of time at the nest.

Because of my limited sample size, data obtained from video-monitoring nests in this study should be viewed critically, especially when used to compare Ferruginous Hawk behavior between study areas. However, these data expose behavioral trends that support several hypotheses regarding raptor parental roles and feeding ecology. My study underscores the interdependence of parental roles. Males delivered the majority of biomass but females delivered heavier prey items and cared for the nestlings. I previously found that hawks in the Estancia Valley supplied nestlings with more Gunnison's prairie dogs than hawks in the Plains of San Agustin (Chapter One). It is possible that the type of prey used may not only affect Ferruginous Hawk reproductive output but also account for some of the behavioral incongruities among hawks in both study areas. Further study of Ferruginous Hawk nesting behavior using time-lapse video is needed to develop a more complete account of the effects of anthropogenic pressure and variation in primary prey resources on provisioning rates, parental care, and feeding ecology of this species.

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Table 2.1. Operational information and provisioning rate data for nests monitored by time-lapse video in the Estancia Valley (EV) and Plains of San Agustin (PSA), New Mexico, 2004-2005. Female time at nest is mean (± SE) percent of time spent at the nest per day per nest throughout the nesting cycle.

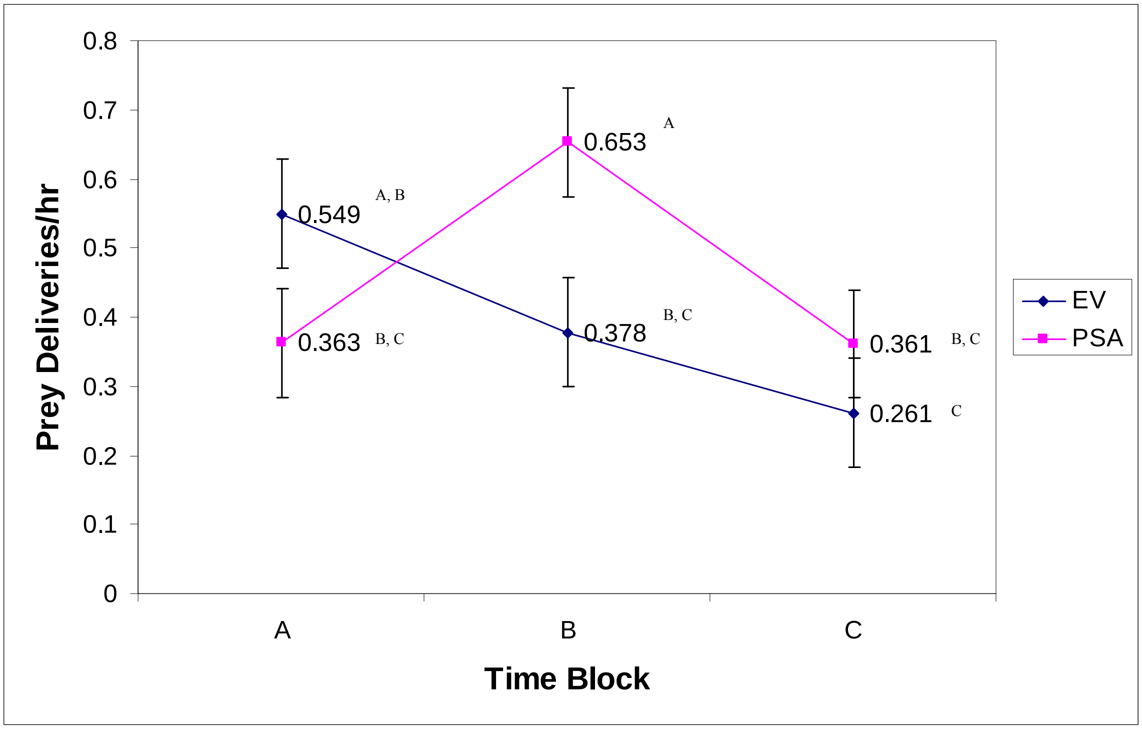
Nest number	Study Area	Number of hours recorded	Number of nestlings	Total biomass delivered (g)	Biomass delivered /hr	Male biomass delivered /hr	Female biomass delivered /hr	Total prey deliveries /hr	Female deliveries/hr	Male deliveries /hr	prey items
MN02	EV	273.1	2	44146.6	161.65	136.33	25.32	0.436	0.054	0.381	125
MS10	EV	263.2	3	20626.3	78.37	46.26	17.79	0.418	0.076	0.258	116
SD01	EV	168.7	2	16109.7	95.49	44.08	48.11	0.373	0.184	0.184	60
AH05	PSA	180.1	2	12141	67.41	35	32.41	0.478	0.133	0.344	88
OP01	PSA	152.3	2	9490.9	62.32	29.65	32.67	0.440	0.164	0.276	68
AH06	PSA	244.4	3	23055.6	94.34	79.97	14.36	0.622	0.106	0.516	151
	EV	235 ± 33.3	2.3 ± 0.33	26960 ± 8691	111.8 ± 25.4	75.6 ± 30.4	30.4 ± 9.1	0.41 ± 0.02	0.10 ± 0.03	0.27 ± 0.06	
	PSA	194 ± 27.3	2.3 ± 0.33	14895 ± 4150	74.7 ± 9.9	48.2 ± 15.9	26.5 ± 6.1	0.51 ± 0.06	0.13 ± 0.02	0.38 ± 0.07	
	ALL	213 ± 21.5	2.3±0.21	20928 ± 5082	93.3 ± 14.8	61.9 ± 16.5	28.4 ± 5.0	0.46 ± 0.04	0.120 ± 0.02	0.326 ± 0.05	

Table 2.2. The top five prey species in terms of total biomass delivered to video-monitored nests (n = 6) by male and female Ferruginous Hawks nesting in New Mexico, during 2004-2005, with numbers of individual prey items and percent frequency noted for each sex.

Common Name	Total Count	Female count	Frequency of Female delivery (%)	Male count	Frequency of Male delivery (%)	Female biomass (g)	Female Rank by biomass	Female biomass (%)	Male biomass (g)	Male Rank by biomass	Male biomass (%)	Total Biomass (g)	Total biomass (%)
Gunnison's prairie dog	107	24	17.0	83	19.1	13,389	1	39.3	41,842	1	49.0	56,512	49.2
Desert cottontail	18	11	7.8	7	1.6	9,220	2	27.1	5,867	4	6.7	15,087	12.4
Botta's pocket gopher	170	29	20.6	141	32.6	4,930	3	14.5	23,970	2	27.2	28,900	23.7
Spotted ground squirrel	139	42	29.8	97	22.4	3,691	4	10.9	8,526	3	9.7	12,218	10.0
family: sciuridae	28	10	7.1	18	4.16	1,496	5	4.4	2,692	5	3.1	4,188	3.4
Other	112	25	17.7	87	20.1	1,310		3.9	3,948		4.5	5,258	4.3
Total	574	141		433		34,037			88,127			122,164	

Table 2.3. Mean (± SE) female time spent away from the nest (minutes) following an approach by the researcher to service the video-monitoring system. Also included is the proportion of each day the female spent on the nest: a) on all days combined; b) on days when the video system was serviced; c) on days when it was not serviced. Number of instances when disturbance response was recorded is noted in parenthesis.

Nest	Study Area	Female time away from nest following disturbance (n)	Overall female time at nest (% / day)	Female time at nest (% / day) on days with no disturbance	Female time at nest (% / day) on days with disturbance
MN02	EV	61.9 ± 19.1 (6)	32.9 ± 4.3	39.1 ± 6.2	25.8 ± 6.0
MS10	EV	96.8 ± 37.4 (5)	71.6 ± 5.8	73.3 ± 7.8	66.4 ± 9.2
SD01	EV	83.2 ± 21.8 (6)	16.9 ± 5.3	16.0 ± 7.8	15.7 ± 8.0
AH05	PSA	331.0 ± 64.0 (2)	21.7 ± 5.5	27.0 ± 7.5	12.1 ± 8.5
OP01	PSA	77.0 ± 26.5 (3)	26.3 ± 5.8	22.8 ± 7.5	32.5 ± 9.2
AH06	PSA	140.3 ± 94.4 (3)	33.6 ± 4.6	30.1 ± 6.6	38.0 ± 6.8
	PSA	182.8 ± 76.3 (8)	40.5 ± 16.3	26.6 ± 2.1	27.6 ± 7.9
	EV	80.6 ± 10.2 (17)	27.2 ± 3.4	42.8 ± 16.6	35.9 ± 15.5
	All	131.6 ± 41.3 (25)	33.2 ± 7.3	34.7 ± 8.3	31.7 ± 8.0



	Time Block A	Time Block B	Time Block C
Estancia Valley	0.549 ± 0.079 ^{A,B}	0.378 ± 0.079 ^{B,C}	0.261 ± 0.079 ^{C}
Plains of San Agustin	0.363 ± 0.079 ^{B,C}	0.653 ± 0.079 ^{A}	0.361 ± 0.079 ^{B,C}

Figure 2.1. Results of a two-way ANOVA with time block (3 levels) and study area (2 levels) as independent variables and the number of prey deliveries per hour as the response variable. Data were derived from observation of recorded nest activity at three video-monitored nests in the Estancia Valley and three in the Plains of San Agustin, New Mexico, USA, during 2004-05. Noted below are least square means taken from a post-hoc means comparison (LS means student t test). Levels not connected by the same letter are significantly different.

CHAPTER THREE

COWARDLY OR COURAGEOUS: FERRUGINOUS HAWK FLUSHING DISTANCE AND NEST DEFENSE BEHAVIOR AS RELATED TO INCREASED ANTHROPOGENIC INFLUENCE IN NEW MEXICO

Abstract

As natural habitat is increasingly modified, land managers must devise plans that include restricted zones around sensitive sites to minimize deleterious effects caused by human disturbance. Here I provide empirical data on the nest defense response of Ferruginous Hawks (*Buteo regalis*) to a human intruder as related to anthropogenic influence, parental investment, and repeated intrusions. A distance of 610 m prevented 95% of nest-attending Ferruginous Hawks from flushing in response to a human intruder. I recorded a 20% increase in average flushing distance on consecutive visits. This suggests that hawks may become more sensitive with intrusions. Female hawks defended nests with significantly more aggression than males by diving and calling more while I was near the nest tree, and calling more during my approach. Hawks nesting in a human-altered environment defended nests with similar intensity to hawks in a rural setting, but the former allowed an intruder to approach an average of 120 m closer to the nest before flushing. This suggests some response mediation may have occurred among hawks that nested close to humans. There was no relationship between Ferruginous Hawk nest

defense response and nestling age, but overall response levels were comparable to those documented for sympatric buteos in other studies. Establishing disturbance free zones surrounding nesting sites and conserving extant prairie dog (*Cynomys* spp.) colonies should be objectives of any management plan focused on the long-term maintenance of Ferruginous Hawk populations.

Introduction

As demand for multi-use land escalates, providing adequate habitat for wildlife is becoming increasingly difficult. In the western United States, the human population is growing 2-3 times faster than any other part of the country (Baron et al. 2000) and the demand for energy extraction — Bureaun of Land Management (BLM) leases ca. 15 million ha of land for energy production (BLM 2005) — continues to affect endemic species (Walker et al. 2008). Federal law prohibits the taking of birds, their young, or their nests and in the case of eagles, further prevents interference with normal nesting behavior (USFWS 2007). Thus, land managers may be required to establish human-restricted zones near breeding sites of sensitive raptors to minimize human-related disturbances.

Ferruginous Hawks (*Buteo regalis*) are considered a “sensitive species” by BLM and United States Forest Service (Bechard and Schmutz 1995, Collins and Reynolds 2005). Human disturbance near Ferruginous Hawk nesting sites has caused decreases in nesting success and productivity (White and Thurow 1985), the abandonment of previously occupied territories (Ward 2001), and ultimate contraction of the species’ breeding range via habitat loss (Hoekstra et al. 2005). Unfortunately, to abate this threat, little empirical data exist on Ferruginous Hawks' tolerance thresholds for these disturbances, especially in human-altered habitats (Richardson and Miller 1997).

One measure used to establish human-restricted zones surrounding raptor nests is flushing distance. Flushing occurs when an animal flees in response to a disturbance or threat, whereas flushing distance is the distance between the disturbance and the animal when flushed (Altmann 1958, Suter and Joness 1981, Holmes et al. 1993). Flushing is an adaptive reaction that is energetically costly. Therefore, perhaps a safety threshold must be violated before animals flush. In Ferruginous Hawks, this threshold may be affected by multiple factors that may not be mutually exclusive, including: time of year, nesting substrate, nest position and height, type of disturbance, prey abundance, and tolerance level, among other things. Thus, studies that provide insight on the relationship between these factors and the response of Ferruginous Hawks are valuable in establishing human-restricted protection zones.

Defending a nest is also risky and energetically costly for adults as they may be killed or injured by the intruder (Curio 1987, Wallin 1987). Various models have been offered to account for observed patterns in avian nest defense behavior. Some models predict that birds nesting in open landscapes should avoid aggressive nest behavior to minimize the conspicuousness of the nestlings to predators (Harvey and Greenwood 1978, Greig-Smith 1980, Bures and Pavel 2003), while others predict that nests easily accessed by predators (i.e., those positioned low to the ground) may cause adults to engage in a more robust nest defense response (Morrison et al. 2006). Parental investment models contend that nest defense intensity should increase as the energy invested by the parent increases, expressed either by age of young (i.e., age-investment hypothesis, Andersson et al. 1980) or brood size (Trivers 1972, Barash 1975, Redondo 1989), while other models suggest increases in nest defense intensity are associated with problems related to repeated human intrusion without persecution (Knight and Temple 1986).

Human disturbance may also negatively influence avian behavior. However, some birds can habituate to consistent, similar stimuli and may subsequently maintain reproductive fitness (Miller et al. 1998, Lord et al. 2001, Walker et al. 2006). Plumpton and Andersen (1998) postulated that Ferruginous Hawks over-wintering in Colorado became "behaviorally plastic" and tolerant of human disturbance and alteration of landscapes, provided that adequate supplies of black-tailed prairie dogs (*Cynomys ludovicianus*) were available. During the nesting season, however, research has suggested that Ferruginous Hawks are particularly vulnerable to human activity during the nesting season (Olendorff and Stoddard 1974, Fyfe and Olendorff 1976, Woffinden and Murphy 1977, Roth and Marzluff 1986, Bechard et al. 1990) and are prone to desert their nests if disturbed during incubation (White and Thurow 1985, Ward 2001).

In this chapter, my research objectives were to: 1) document Ferruginous Hawk nest defense behavior and describe parental roles; 2) use flushing distance to expand empirical knowledge of Ferruginous Hawk spatial buffer zones during the nesting season, with the specific goal of comparing flushing distance in two grasslands which differed in anthropogenic alteration; 3) test existing hypotheses that offer explanations for observed patterns in nest defense behavior; 4) explore the potential for mediation in nest defense behavior as related to anthropogenic influence of the surrounding landscape.

I predicted that Ferruginous Hawks in the human-altered Estancia Valley (“exurban hawks”) would be familiar with human stimuli and thus would exhibit less intense or similar nest defense behavior than birds in the rural Plains of San Agustin (“rural hawks”). Alternatively, previous exposure to humans may have sensitized exurban hawks. This experience could enhance their nest defense response either during initial or subsequent visits to the nest. By comparing the hawks’ response to human intrusion in the Estancia Valley to that in the Plains of San Agustin, I simultaneously tested Knight and Temple’s (1986) revisitation hypothesis and investigated the effects of habitat alteration on nest defense behavior. Following parental investment theory, I predicted nest defense intensity would be related to brood age and/or brood size. I also predicted that females would defend the nest more aggressively than males because females were the primary nest defender in other studies on raptor nest defense (Andersen 1990, Sergio and Bogliani 2001).

Methods

Study Areas

I studied breeding Ferruginous Hawks on private and public lands in the Estancia Valley and Plains of San Agustin, two grasslands located approximately 350 km apart in New Mexico (Figures 1.1, 1.2). There were four nests outside of the study areas that I also sampled during my research. To provide a more complete description of nest defense response by breeding Ferruginous Hawks in New Mexico, I incorporated data gathered from those nests into my “overall” descriptions of nest defense behavior but excluded them from discussions focused on study area variation.

Environmental Variation

The Estancia Valley spans approximately 300,000 ha in Torrance and Santa Fe counties, New Mexico (Figure 1.1). The Sandia and Manzano Mountains separates the Estancia Valley from Albuquerque (Pop.: 448,607), which is 30 km west. My study area represents 158,000 ha in the western half of the Estancia Valley and is loosely bordered by State Highway 41 to the east, the Manzano Mountains to the west, State Highway 60 to the south, and Interstate 40 to the north (Figure 1.1).

Dominant vegetation in the Estancia Valley is similar to that found in the Plains of San Agustin. Large expanses of blue grama (*Bouteloua gracilis)* and buffalograss (*Buchloe dachtyloides*) meet widely scattered juniper *(Juniperus* spp.*)* trees. However, unlike the Plains of San Agustin, non-native trees like Chinese elm (*Ulmus parvifolia*), mainly associated with occupied dwellings and abandoned homesteads, are present and provide nesting substrates. Ferruginous Hawk nests in the Estancia Valley average 1947 m in elevation (n = 36, range: 1865-2054 m, this study). The town of Estancia, located in the center of the study area, averages 32.5 cm of precipitation while temperatures range from -9.2 to 31.4 °C (Western Regional Climate Center 2007b).

The Plains of San Agustin is located approximately 70 km west of Socorro (population in the year 2000 [hereafter "Pop."]: 8,877). The Plains of San Agustin spans approximately 238,000 ha between Magdalena and Datil in Socorro and Catron counties, New Mexico. Geologically, the southwest-northeast oriented basin is constricted by the San Mateo Mountains to the east, the Gallinas Mountains to the northeast, the Datil and Mangas Mountains to the northwest, Tularosa Mountains to the west and Luera Mountains to the south (Figure 1.2).

The flat bottom of the Plains of San Agustin is an artifact of a Pleistocene-era lake and is characterized by species diagnostic to the desert short-grass prairie (Dick-Peddie 1993). Blue grama and buffalo grass co-dominate the open country while scattered, isolated junipers provide the majority of nesting sites for Ferruginous Hawks and other birds. Elevated from the basin floor, sagebrush (*Artemisia* spp.) and pinyon (*Pinus edulis*)-juniper woodlands dominate higher elevations (Dick-Peddie 1993) and meet mountainous areas like the continental divide to the west and the headwaters of the Gila River to the south. Ferruginous Hawk nests in the Plains of San Agustin average 2170 m above sea level (n = 41, range: 2025-2338 m, this study). The area receives 28.7 cm of annual precipitation while the average temperatures range from -10.3 to 29.3 °C (Western Regional Climate Center 2007a).

Anthropogenic Variation

To describe anthropogenic differences between the Estancia Valley and Plains of San Agustin, I used a geographic information system (ArcGIS 9.2, ESRI, Redlands, California) to analyze data obtained from federal and state government websites. Jane Farmer (BLM Socorro Field Office, Socorro, New Mexico) digitized the Plains of San Agustin boundary and I digitized the Estancia Valley boundary. I obtained 2006 land ownership data from the New Mexico Bureau of Land Management (Bureau of Land Management 2007) and used "X-Tools", an ArcGIS extension, to calculate area totals for surface ownership of both study areas. I obtained all other data including New Mexico counties and cities, from the New Mexico Resource Geographic Information System (University of New Mexico 2006).

I analyzed the most current anthropogenic data available that covered my study areas uniformly. For example, United States Census Bureau (USCB) Summary File 1 from 2000 (United States Census Bureau 2006) provided the most uniform coverage of occupied housing units and human population (via US Census Blocks) while USCB 2006 TIGER boundary files provided the most uniform road coverage in the Estancia Valley and the Plains of San Agustin. To facilitate my analysis, I used TGR2SHP v7.01 (Ralston 2008) to convert UCSB TIGER boundary files into a road layer. I used the digitized study area boundaries as a template to clip census block and road layers and used X-Tools to calculate total length of roads within each study area. I summed road lengths (km) across all Census Feature Classification Codes (CFCC), which categorize roads based on their use and structure (US Census Bureau 2007). I then used these data in a GIS to determine the road density within each study area and the distance between a successful Ferruginous Hawk nest (≥ 1 young fledged) and the nearest road.

Ferruginous Hawk Nesting Productivity

In April of each year, aerial surveys were conducted to determine occupancy (i.e., nestlings or eggs observed on the nest or adult in incubating posture) at known nest sites. New nests were marked using a Garmin 92 Global Positioning System (Garmin International Inc., Olathe, KS, USA) designed for use in aircraft. A minimum of two observers accompanied the pilot in a Cessna 205 fixed wing aircraft. Air speed during surveys averaged 160 kph and altitude ranged from 90-240 m above ground. Following aerial surveys, each occupied nest was visited a minimum of two times to determine productivity. I considered nestlings to be fledged when they reached 80% of their fledging age, or 32 days.

Nest Defense Behavior

I recorded nest defense behavior of Ferruginous Hawks at a subset of the nests from which I also used to describe diet composition (see Chapter One). I did not perform nest defense trials until the nestlings were at least one week old to avoid nest desertion (Busch et al. 1978, White and Thurow 1985, Ward 2001) and ceased trials after the nestlings had grown large enough to fledge. I visited nests early in the morning or evening, on days free of rain and when wind speeds were less than 25 km/hr.

To initiate nest defense, I walked directly toward nests at a constant speed while observing the nest tree. I approached the nest from ≥ 600 m from a direction where the nest was within view for the entire approach. I marked my position with surveying flags when the adult flushed from the nest and when an adult uttered its first alarm call, and then continued my approach to the nest tree. I stopped when I arrived to approximately 3 m from the tree and recorded the following information using a hand-held tape-recorder: 1) the number of nestlings and age (Mortitsch 1985); 2) the sex of the responding adult(s); 3) the number of alarm calls emitted by the responding adult(s); 4) the number of dives executed by the adult(s); 5) distance (visually estimated) that the nearest adult approached. I recorded this information for 5 min during each visit to each nest.

I defined a dive as any downward break from horizontal or ascending flights made by a defending adult (Knight et al. 1989). The precision of the estimated distance from me to the hawk during its closest dive followed Andersen (1990): to the nearest meter from one to five meters, to the nearest 5 m from 5 to 50 m, to the nearest 10 m from 50 to 100 m, and to the nearest 25 m at distances greater than 100 m. Following the 5 min sampling period, I estimated the distance from the survey flags to the nest tree using a Bushnell Yardage Pro Rangefinder (Bushnell Corporation, Overland Park, KS, USA) with 500 m range. If any flag-to-tree distance was greater than 500 m, I used a Garmin XLII GPS unit with 6 m accuracy to mark my location and that of the nest tree and used a geographic information system to measure the distance between the two points.

Statistical Analysis

To describe inter-sexual differences in nest defense behavior, I only included cases where both adults responded to the intruder in the beginning of the trial (Andersen 1990, Sergio and Bogliani 2001). I used reversed sexual size dimorphism (Snyder and Wiley 1976, Olendorff 1973) and differences in alarm-call tone (Bechard and Schmutz 1995) to help distinguish between male and female Ferruginous Hawks. I focused on the behavior of the primary nest defender in these analyses to control for situations where one partner arrived late in the trial. I defined the primary nest defender as the sex that responded to the intruder more aggressively by calling more, and diving towards the intruder more often and to closer distances.

I included only the first visit to each nest in statistical analyses of nest defense intensity between sexes and between study areas (Andersen 1990). However, I recorded nest-defense behavior at a subset of nests twice during the same nesting season to test the explanation of Knight and Temple (1986) for observed behavioral patterns following repeated human intrusions. I only included positive occurrences (i.e., instances where an adult was visually located) for all analyses except those comparing nest defense responses between consecutive researcher intrusions. For these analyses, I recorded a zero value for response variables such as the number of calls uttered and dives performed if I did not observe either adult during the approach and the subsequent 5 min sampling period. Statistical relationships did not change if these cases were excluded from the analyses and I deemed an adult's lack of nest defense to be biologically relevant.

I performed all analyses with JMP 5.0 statistical software (SAS Institute, Inc., Cary, NC). I used paired t-tests to analyze inter-sexual differences in nest defense intensity, and to compare intensity during consecutive visits to the same nest. I conducted multiple regression analyses with nestling age (average age of the brood), number of nestlings in the nest, and distance from the nest to the nearest road as independent variables and the primary nest defender's number of calls, number of dives, and closest dive, as dependent variables in separate regression analyses (Zar 1999). I used a two-factor factorial with repeated measures on one factor to analyze nest defense behavior between study areas and visit number. For this analysis, I assigned study area as a between groups factor and visit number as the within subjects factor. When data met statistical assumptions, I present *t*-statistics with associated probability value; when they did not, I present Wilcoxon rank sum Z scores and associated p-values for non-parametric data (Zar 1999). I considered probability values significant if they were less than or equal to 0.05 and report means and standard errors throughout.

Results

I conducted nest defense trials at 12 nests in the Plains of San Agustin (2004: 4 nests; 2005: 8), 23 nests in the Estancia Valley (2004: 9; 2005: 14), and 5 nests in the Western study area (2004: 2; 2005: 3). There were no inter-year differences among nest defense variables (e.g., number of calls, number of dives, etc.) so I pooled data between years. I recorded nest defense behavior at 53% (n = 21) of nests twice.

At least one adult responded in 80% (n = 49) of nest defense trials. Neither adult responded in 20% of the first (n = 8) and second (n = 4) trials. Both adults defended the nest in 39% (n = 24) of all trials, including 38% (n = 15) and 43% (n = 9) of the first and second trials, respectively. Males defended the nest in 44% (n = 27) of all trials, including 38% (n = 15) of the first trial and 57% (n = 12) of the second trial while females defended the nest in 75% (n = 46) of all trials, including 78% (n = 31) and 71% (n = 15) of the first and second trials, respectively.

While I was 3 m from the nest tree, females called significantly more times than males (17.6 ± 3.54 vs. 7.93 ± 2.16, paired $t_{14} = 2.376$; $p = 0.0323$) and numerically performed more dives (4.86 ± 1.33 vs. 2.0 ± 0.49, paired $t_{14} = 2.02$, $p = 0.063$. Females also called significantly more as I approached the nest (8.06 ± 2.11 vs. 1.13 ± 0.69, paired $t_{14} = 3.44$, $p = 0.002$). Therefore, it was evident that females were the primary nest defender even when both sexes defended the nest. I identified the female and male as the primary nest defender at 71% (n = 43) and 8% (n = 5) of all trials, respectively.

Study Areas

Anthropogenic Variation

In 2000, private, state, and public land accounted for 53, 35, and 12% of surface ownership in the Plains of San Agustin and 96, 4, and 0% in the Estancia Valley, respectively. The Estancia Valley is close to heavily urbanized Albuquerque, and the towns of Moriarty (Pop.: 1765), Estancia (Pop.: 1584), and Mountainair (Pop.: 1116) are in the Estancia Valley (Figure 1.1). Alternatively, no established towns exist in the Plains of San Agustin; the closest town, Magdalena (Pop.: 913), is 20 km away. In 2000, 16,338 people lived in 6,094 housing units in the Estancia Valley while 61 people in 20 houses dotted the landscape in the Plains of San Agustin (Table 1.1). Consequently, USCB census blocks in the Estancia Valley had more people (Wilcoxon Rank Sum: $Z = 13.37$; $p < 0.00001$) and more occupied houses ($Z = 13.54$; $p < 0.00001$) than census blocks in the Plains of San Agustin.

In 2006, overall road density in the Estancia Valley was almost twice that found in the Plains of San Agustin (Table 1.1). Nests with successful Ferruginous Hawk breeding attempts (≥ 1 fledgling, $n = 31$) were 531 ± 67 m from the nearest road. Successful nests in the Estancia Valley ($n = 18$) were 403 ± 82 m to the nearest road while successful nests in the Plains of San Agustin were 708 ± 97 m from the nearest road, a difference which was statistically significant ($t_{29} = -2.40$, $p = 0.02$, Table 1.1)

I sampled 23 nests in the Estancia Valley and 12 nests in the Plains of San Agustin. During the first visit, both adults defended the nest in 48% ($n = 11$) of trials in the Estancia Valley and 25% ($n = 3$) of all trials in the Plains of San Agustin. Neither adult responded in 13% ($n = 3$) and 25% ($n = 3$) of all initial trials in the Estancia Valley and Plains of San Agustin, respectively. Ferruginous Hawks in the Estancia Valley produced more fledglings (2.43 ± 0.194) per nesting attempt ($n = 35$) than in the Plains of San Agustin ($n = 25$, 1.48 ± 0.231) during my study ($t_{58} = 3.15$, $p = 0.003$).

While I was 3 m from the nest tree, the primary nest defender in the Estancia Valley did not call more than the primary nest defender in the Plains of San Agustin (NS, Estancia Valley: 15.3 ± 2.40 ($n = 20$), Plains of San Agustin: 21.4 ± 3.97 ($n = 9$), $Z =$

1.23, p = 0.22). The primary nest defender at nests in each study area also performed similar numbers of dives (Estancia Valley: 4.80 ± 0.94 (n = 20); Plains of San Agustin: 4.56 ± 1.40 (n = 9), Wilcoxon rank sums: Z = 0.12, p = 0.91).

Numerically, Ferruginous Hawks in the Plains of San Agustin (n = 6) flushed from the nest at a distance 38% greater those in the Estancia Valley (n = 8), although the difference was not statistically significant (454 ± 45.2 vs. 330 ± 41.2 m; $t_{12} = 2.017$, p = 0.064). There was no difference in the closest dive distance that the primary nest defender at nests in both study area (Estancia Valley: 27.7 ± 6.15 m (n = 17), Plains of San Agustin: 43.9 ± 15.6 m (n = 9), Wilcoxon rank sums: Z = 1.11, p = 0.27). There was no difference between study areas in the distance at which the defending adult emitted its first alarm call during my approach (Estancia Valley: 213 ± 35.2 m (n = 13), Plains of San Agustin: 231 ± 44.8 m (n = 8); t = -0.32; p = 0.75).

Initial Nest Defense Trial

Nestling age ranged from 9-38 days when I conducted my initial nest defense trials (n = 40), and there was no difference in the age of the nestlings between study areas at the time of trial ($t_{19} = 1.42$, p = 0.17). During those visits, the adult was present on the nest 35% (n = 14) of the time and flushed when I reached 383.6 ± 33.9 m from the nest tree. Human-restricted spatial buffer zones were calculated as the radius of restricted activity around a nest which would prevent flushing by approximately 95% of the individuals (Altmann 1958, White and Thurow 1985, Holmes 1994). In my study, a distance of 610 m would achieve this goal (Table 3.1). Ferruginous Hawks uttered an alarm call before I reached the nest at 53% (n = 21) of the trials. In those instances, first-call distances averaged 212.2 ± 26.9 m.

When at least one adult responded to the first trial, the primary nest defender conducted the following responses while I was at the base of the nest tree: dove 4.31 ± 0.075 times (n = 32 trials, range: 0-15 dives), emitted 16.0 ± 2.01 calls (n = 32 trials), and approached me to an average distance of 32.4 ± 6.53 m (n = 27 trials). In cases where the primary nest defender did not dive (n = 5), it approached to a distance of 250 ± 28.1 m from me.

Revisitation Hypothesis

Of the 21 nests at which I was able to record nest defense behavior during consecutive visits, 81% (n = 17) were located in the Estancia Valley. Adults did not respond in 19% (n = 8) of all trials testing the revisitation hypothesis. There were no cases where an adult did not respond during the first and second trials at the same nest, and zero values for response variables were equally divided between the first and second visits (n = 4 for each visit). I did not observe any nest defender during 17% (n = 6) in the Estancia Valley and 25% (n = 2) of trials in the Plains of San Agustin.

While I was at the base of the nest tree, the primary nest defender called 12.71 ± 2.66 times during the first visit and 20.3 ± 4.15 during the second, a difference which was 59% greater numerically, but was not statistically significant (paired $t_{20} = 1.987$, $p = 0.0607$). There was no difference in number of dives performed by the primary nest defender during consecutive visits (visit 1: 3.47 ± 0.940, visit 2: 6.04 ± 1.830 dives, non-parametric paired $t_{20} = 1.552$, $p = 0.188$) or in the closest distance that the nest defender approached (visit 1: 71.8 ± 21.6, visit 2: 85.3 ± 32.0, paired $t_{13} = -0.58$, $p = 0.56$). Flushing distance was obtained at four nests during consecutive visits. Numerically, flushing distance during consecutive visits to the same nest were 20% greater during the second visit (visit 1: 347 ± 71.5 m, visit 2: 419 ± 76.9 m), but the difference was not statistically significant (paired $t_3 = 2.67$; $p = 0.0755$).

Number of calls, number of dives, and closest dive performed by the primary nest defender, were not related to the distance to the nearest road, the average age of the nestlings, or the number of nestlings in the nest. These regression analyses explained less than 2% of the observed variation in the dependent variable.

No significant interactions existed between study area and visit number, using number of calls uttered and dives performed by the primary nest defender (while I was at the base of the tree) as dependent variables. Numerically, dives and calls increased with visit number in both study areas and nest defense responses in the Estancia Valley were greater than in the Plains of San Agustin. However, these differences were not statistically significant. During the initial visit, Ferruginous Hawks in the Estancia Valley (n = 17) and Plains of San Agustin (n = 4) performed 3.9 ± 1.1 and 1.5 ± 1.0 dives and 13.9 ± 3.1 and 7.5 ± 3.5 calls, respectively. During the subsequent visit, Ferruginous Hawks in the Estancia Valley (n = 17) and Plains of San Agustin (n = 4) performed 6.6 ± 2.2 and 3.5 ± 2.9 dives and 21.8 ± 4.8 and 12.3 ± 9.2 calls, respectively.

Discussion

The importance of statistical versus biological significance in ecological research has been debated by multiple authors (Cherry 1998, Johnson 1999). Because my sample size was limited, I discuss the importance of statistical significance as well as biological significance for nest defense responses that required energy expenditure and incurred risk to the nest defender. These include the number of dives the defending adult performed, the closest approach to the intruder, and flushing distance. I will also discuss the biological significance of not responding to human intrusion as this was directly related to parental care. For these metrics and others, my data suggest behavioral trends existed. However, because the number of successful Ferruginous Hawk breeding attempts was limited, establishing statistical significance proved difficult, mainly because of high within-group variation.

Spatial Buffer Zone

In our study, distances of 610 m and 650 m were required to prevent 95% and 100% of the individuals from flushing, respectively. Importantly, when all visits were included in the analysis, the the flushing distance was 633 m (range: 617-648 m). This suggests that repeated intrusions within this range will still cause disturbance to nest-attending Ferruginous Hawks. As a sensitive species whose population status is tenuous (Olendorff 1993, Bechard and Schmutz 1995, Collins and Reynolds 2005), establishing a human-restricted buffer zone to prevent all nesting Ferruginous Hawks from flushing should be the goal of any land management agency responsible for maintaining or improving reproductive output.

Flushing from the nest in response to a disturbance or threat may increase the defending adult's energy expenditure, interrupt normal feeding behavior, and increase the chance of nestling predation and exposure to inclement weather. White and Thurow (1985) noted that undisturbed Ferruginous Hawks produced significantly more fledglings per nesting attempt than disturbed pairs. Importantly, 33% of the nests they disturbed were abandoned by the adults whereas none of the nests I approached were abandoned. My recommended human-restricted spatial buffer zone for nesting Ferruginous Hawks is substantially larger than the 250 m zone recommended by White and Thurow (1985) and larger than the buffer of 450 m suggested by Ensign (1983), but less than the 800 m (1/2 mile) restricted zone recommended by Suter and Joness (1981), the Colorado Division of Wildlife (CDOW 2008) and US Fish and Wildlife Service, Utah field office (Romin and Muck 2002). My recommendations are similar to Holmes (1994) who suggested a 640 m spatial buffer for Ferruginous Hawks during the nestling phase. Interestingly, my study and hers reported equal estimates of mean flushing distance for Ferruginous Hawks (380 vs. 383 m).

While this study suggests a smaller buffer zone than most government agencies, my trials were somewhat limited by topography and property boundaries. Rarely was I able to begin my approach without an obstructed view of an occupied nest from 800 m away because of land-ownership or landscape features. Thus, topography as well as type of disturbance should be considered in establishing restricted zones around raptor nests because behavioral responses by Ferruginous Hawks at the nest may depend on the type of proximate disturbance. Smith et al. (2007) found that Ferruginous Hawk nest use and activity was greater in areas with less oil and gas development within a 800 m radius. The authors subsequently recommended that the size of this buffer be maintained to manage for Ferruginous Hawks under increasing pressure from energy extraction. Because government agencies must manage for all types of disturbance, it is appropriate for them to establish protective buffer zones that protect Ferruginous Hawks under all circumstances.

Study Area Variation

Habituating to human activity may be adaptive by controlling an animal's stress response, increasing parental attentiveness to nestlings, or decreasing energy expenditure. In support of this, American Crows (*Corvus brachyrhynchos*) and Black-billed Magpies (*Pica pica*) in urban areas exhibited a lower response to human intrusion than did those in rural settings (Knight et al. 1987, Kenney and Knight 1992), and Miller et al. (2001) noted habituation to recreational trail use by some grassland bird species, Magellanic Penguins (*Spheniscus magellanicus*) decreased their stress response as measured by plasma corticosterone levels after increased human exposure (Walker et al. 2006), and New Zealand Dotterels (*Charadrius obscurus*) showed some level of habituation to humans at busy beaches (Lord et al. 2001).

In my study, there was a 38% increase in flushing distance for hawks nesting in a rural landscape as compared to those nesting in an exurban environment. Spatially, this was equivalent to exurban hawks allowing the intruder to approach an average of 120 m closer to the nest before flushing. This differs from White and Thurow (1985) who documented Ferruginous Hawks' sensitization to human intrusion and decreased reproductive output as exposure to disturbance increased, and Holmes (1994) who found that this species returned to the nest more quickly following disturbance if nests were farther from sources of permanent human activity.

Mine may be the first study to observe a less intense behvioral response from Ferruginous Hawks nesting near humans. In 2004-2005, exurban hawks produced significantly more fledglings per nesting attempt than rural hawks, even though exurban pairs nested closer to permanent human development. In contrast, Keough (2006) documented higher productivity levels at nests further from active oil and gas wells. Other ecological factors may have affected Ferruginous Hawk productivity in my study including prey use (see Chapter One) and its effect on parental care, but my data do not refute the possibility that familiarization to human stimuli positively affected reproductive output in the exurban environment. Although measures of nest defense response I recorded during my study such as the number of calls uttered, the number of dives performed, and the closest approach distance did not statistically support clear habituation (i.e., response level of exurban individuals significantly lower than the response level of rural individuals), there was no statistical evidence that exurban hawks were sensitized to human intrusion (i.e., response level of exurban individuals significantly higher than the response level of rural individuals). Further, all measures of nest defense were numerically lower on average in the exurban environment than in the rural setting. This suggests a behavioral trend may have been present, but variation was too high to assign statistical significance. Therefore my prediction that exurban hawks would be more tolerant of human influence when compared with rural hawks remains tenable, mainly because I observed similar nest defense responses regardless of the level of human landscape alteration. This conclusion is similar to Plumpton and Andersen (1998) who concluded Ferruginous Hawks were more tolerant to disturbance because they were using (i.e., hunting, perching) habitat closer to human habitation.

However, even though exurban hawks produced more fledglings than rural hawks, both populations were not as productive as other populations range-wide. Nesting productivity rates in both study areas (Plains of San Agustin: 1.48 vs. Estancia Valley: 2.43 fledglings/nesting attempt) were lower than those in White and Thurow (1985) for their disturbed (1.71) and undisturbed (3.68) nests, lower than the average of 2.71 reported by Schmutz et al. (2008), and lower than the 2.82 average reported by Houston and Zazelenchuk (2005). Because of this, factors such as human disturbance, habitat fragmentation, and/or prey abundance, may be ultimately limiting Ferruginous Hawk reproductive output in New Mexico.

Woffinden and Murphy (1989) estimated that each Ferruginous Hawk pair attempting to breed needed to produce 1.5 fledglings to maintain a stable population, assuming 66% first year mortality and 25% adult mortality. If I applied these assumptions, rural Ferruginous Hawks in my study barely fledged enough young to maintain a stable population during my study as well as in an extended period from 1998-2005 when hawks produced 1.53 fledglings from 95 nesting attempts (Keeley 2004; this study). Therefore, Ferruginous Hawks in the rural Plains of San Agustin may be in danger of local extirpation if management actions are not taken to ensure their survival. Such actions would include nest-tree protection, augmentation of nesting sites (i.e. artificial nesting platforms), conservation of extant prairie dog colonies as well as repopulation of historic colonies on public land via translocation. While the Ferruginous Hawk population in the Estancia Valley is currently meeting the standard recruitment rate, exurban development of the area is expected to double before 2020 (Theobald 2005). This predicted increase in human population is likely to further affect the birds' reproductive output.

The ability of birds to tolerate disturbance at the nest site and maintain reproductive output may be related to their physiological condition, a metric sometimes measured indirectly by the abundance or availability of food. Wallin (1987) found that the physical condition of female Tawny Owls (*Strix aluco*) influenced nest defense intensity. White and Thurow (1985) related Ferruginous Hawk physiological condition to disturbance sensitivity as they noted a 33% desertion rate following brief disturbances during years of low jackrabbit (*Lepus* spp.) density. Woffinden and Murphy (1977) attributed a 43% mortality rate of Ferruginous Hawk nestlings to lack of parental nest attentiveness caused by low prey abundance. Ensign (1983) also imputed low Ferruginous Hawk nesting productivity (0.56 fledglings/nesting attempt) to low primary prey availability.

Plumpton and Andersen (1998) noted that over-wintering Ferruginous Hawks became tolerant of human disturbance provided that a consistent food source was available. Although Plumpton and Andersen’s (1998) study was conducted in winter when raptors’ resource defense behavior is different than in the breeding season (Newton 1979), especially for Ferruginous Hawks which gather gregariously around prairie dog colonies during that season (Bechard and Schmutz 1995), it introduced the idea that if provided adequate food resources, breeding Ferruginous Hawks may be able to tolerate some level of human-caused habitat alteration.

In my study, video-monitored Ferruginous Hawks in an exurban environment provisioned nestlings with significantly more biomass than hawks in a rural setting (Chapter One), suggesting that the former group may have been in better physiological condition. Further, exurban hawks consumed significantly more Gunnison's prairie dogs than rural hawks (Chapter One). Abundant sources of colonial prey like prairie dogs could increase Ferruginous Hawk adult fitness because of the decreased search time required to forage in dense prey patches and the decreased travel time required to locate prey (Krebs and Davies 1993). These factors, which are part of optimal foraging theory (MacArthur and Pianka 1966), can affect physiological condition and alertness to intruders, which can subsequently alter reproductive output and nest defense behavior (Martindale 1982, Montgomerie and Weatherhead 1988). In support of this, I did not see or hear any adult in 90% more nest defense trials in the rural landscape, whereas both adults responded to 90% more trials in the exurban habitat. Further, video-monitored females in the rural setting delivered 10% more biomass than exurban females, on average. Because nest defense in my study was primarily a duty of the female, the difference in provisioning among females between study areas may account for the numeric differences I observed in nest defense response.

Although wildlife habituation to human activity may improve fitness, it can also be maladaptive if the species is persecuted. In particular, persecution should select against aggressive female raptors, since they spend the most time at the nest and hence are more likely to be injured or killed (Newton 1979, Collopy 1984, Knight et al. 1989). All raptor species exhibit reversed sexual size dimorphism (Snyder and Wiley 1976); thus, the female may be better suited to defend the nest from possible predators that are larger in size (Andersson and Norberg 1981). In my study, females defended the nest more often and with more intensity than males as measured by number of calls emitted and number of dives performed. This heightened exposure increases the possibility of female persecution by a threatening intruder. In 2004, I discovered a dead female Ferruginous Hawk that had been shot (necropsy by University of New Mexico, Albuquerque, NM) while incubating four eggs in a nest in the Plains of San Agustin. Although this bird was not defending its nest when it was shot, the example provides case history that persecution did occur in my study areas. In 2003, I found a dead female Ferruginous Hawk with both tarsi removed near a nest that contained three dead offspring. Because there were young in the nest and the female was found close to the nest, I determined that the female was defending the nest when it was killed. Finally, conversations with some ranchers in both study areas led me to believe that raptor persecution continues to persist in these grasslands. Therefore, female nest defense response may be muted in these grasslands as compared to other parts of the Ferruginous Hawk's range due to human persecution.

Theories on Nest Defense Intensity

Parental Investment

My results do not support the age-investment hypothesis (Andersson et al. 1980) for observed nest defense behavior because the nest defense response of Ferruginous Hawks did not increase as brood size or age increased. These results differ from those that documented increases in nest defense intensity as the nesting cycle progressed for Red-tailed Hawks (Andersen 1990), Eastern Screech-Owls (Sproat and Ritchison 1993), and Northern Hobbies (Sergio and Bogliani 2001). Some authors attributed an observed lack of increase in nest defense intensity in raptors to the heightened ability of nestlings to either defend themselves or flee. Wallin (1987) suggested this unique raptorial ability caused the nestlings' value to potential predators to decline.

Other hypotheses suggest that expected future reproduction may influence nest-defense behavior (Barash 1980, Montgomerie and Weatherhead 1988). Because adult survival and probability of nesting in subsequent years is higher in buteos than in other raptor families (Brown and Amadon 1968), some models predict these species will not defend their reproductive investment as vigorously as those species which do not live as long. Schmutz et al. (2008) estimated Ferruginous Hawk adult and first-year survival rates to be 75% and 54%, respectively, and Palmer (1988) noted that this species produces larger clutches and broods than any other North American buteo. These models suggest Ferruginous Hawk nest defense response will be low compared to other raptors. Indeed, early accounts of Ferruginous Hawk behavior labeled the species as “arrant cowards” (Dawson 1909) and speculated on how this ground-nesting species could escape coyote predation with such a lack of aggressive nest defense behavior (Taverner 1943). Angell (1969) also noted Ferruginous Hawks’ passive nest defense. Schmutz et al. (1980) found Swainson’s Hawks (*Buteo swainsonii*) to be more aggressive in nest defense than Ferruginous Hawks. Holmes (1994) stated that the latter species, unlike other buteos in her study, exhibited low levels of nest defense by calling and flushing away from observers instead of approaching them.

However, when comparing nest defense behavior of Ferruginous Hawks in my study to that described by Andersen (1990) for Red-tailed Hawks, a species whose nest defense response was described as “aggressive” by Andersen (1990) and Holmes (1994), Ferruginous Hawks defended their nests with similar intensity in terms of mean number of dives (2.9 vs. 4.3 dives) and mean distance of closest dive (31.7 vs. 32.4 m), but not mean number of calls (59.4 vs. 16.0). Interestingly, Ferruginous Hawks actually defended their nest with more intensity if one considers that Andersen’s sampling duration was twice as long as mine (i.e., 5 vs. 10 min.).

Red-tailed Hawks in Andersen (1990) nested higher in trees than Ferruginous Hawks in my study. This pattern was documented elsewhere (Bechard et al. 1990).

Therefore, it is possible that the comparable intensity of nest defense exhibited by these species may be a function of nest height. This explanation was offered by Morrison et al. (2006) to account for observed variation in nest defense response. It may also be possible that because Ferruginous Hawk nests were conspicuous, adults did not engage in nest defense until absolutely necessary to avoid attracting more predators (McLean et al. 1986). Similarly, Holmes (1994) found Ferruginous Hawk call rates to be higher during the more conspicuous nestling phase than the incubation stage.

Andersen (1990) noted that Red-tailed Hawks only called more (as opposed to dove more or approached closer) as nestling age increased. Calls involve relatively little cost to the defending adult as compared to dives, which can be risky behavior, especially when the defending adult either closely approaches or strikes the intruder (Greig-Smith 1980, Montgomerie and Weatherhead 1988). However, calls may also represent an initial, least-costly response to be followed by a more robust response (i.e., dives) if the action fails to drive away the intruder. Thus, my data show Ferruginous Hawk nest defense intensity to be similar to a sympatric buteo whose defense response has been historically characterized as more aggressive.

Revisitation Hypothesis

Knight and Temple (1986) suggested that observed increases in nest defense intensity during consecutive visits may be a result of methodological problems associated with repeatedly rewarding parent birds for successfully driving away the predator. Instead of responding to an increased level of parental investment, Knight and Temple (1986) hypothesized that nest defenders increased their response intensity with increasing numbers of nest visits because the birds experience positive reinforcement which causes a loss of fear. However, recent nest defense studies testing this theory in raptors did not support a revisitation effect (Andersen 1990, Sproat and Ritchison 1993, Sergio and Bogliani 2001).

Ferruginous Hawks in New Mexico did not increase their nest defense response as the nesting cycle progressed, but they did increase their response during consecutive visits. In my study, comparisons of nest defense response between visits suggest only marginal statistical support for the revisitation hypothesis ($p = 0.08$). However, the relationship between nest defense response and visit number may be of biological significance. For instance, mean numbers of calls and dives increased from 13 to 20 (59%) and from 3.5 to 6.0 (71%), respectively, from the first visit to the second visit while the mean flushing distance increased 20%, from 347 to 419 m. The amount of energy expended in increasing defense effort and flushing distance may be of physiological significance as nest defense behavior is energetically expensive (Montgomerie and Weatherhead 1988). Further, a sensitized disturbance response may affect reproductive output as parental attentiveness to the young decreases decreases while the adults repond to the disturbance. This can lead to nestling chilling or desiccation, or missed feedings (White and Thurow 1985). Because Ferruginous Hawks in my study did not increase their nest defense response as nestlings aged, but did increase the average number of dives and calls during consecutive nest visits, they may be responding to other factors besides an increased level of parental investment.

The majority of nests I used to test the effects of repeated intrusions were located in the exurban environment. As such, hawks may have been affected by anthropogenic influence at the landscape level or previous exposure to human-related disturbance.

However, there were no differences in nest defense response between study areas. This suggests that hawks in the Estancia Valley were not sensitized by previous exposure to humans. Holmes (1994) concluded that Ferruginous Hawks became less tolerant of disturbance (i.e., individuals became sensitized) because flushing distance increased with number of visits. However, she cautioned that her results could have been different if visits were not repeated during the same day. White and Thurow (1985) noted that flushing distance of Ferruginous Hawks increased over repeated visits during the incubation period and concluded that sensitization occurred as individuals gained more experience with the disturbance. My data conform with this trend and is consistent with the hypothesis that birds may respond to familiar stimuli differently than novel stimuli (Knight and Temple 1986).

In my study, adults did not respond in 19% (n = 8) of all trials testing the revisitation hypothesis. Since those instances were split evenly between first and second visits, there was no clear behavioral pattern to account for the absence of a nest defense response by Ferruginous Hawks. Statistical relationships did not change if these cases were excluded from the analyses and it seemed biologically relevant to include occasions where neither adult responded to a potential predator in close proximity to the nestlings. Unwatched nestlings are susceptible to predation and the instances of leaving nestlings unattended documented here may have contributed to the relatively low levels of reproductive output by hawks in both study areas.

Management Implications

To maintain stable Ferruginous Hawk reproductive output, it is imperative that land managers conserve existing Ferruginous Hawk food sources, mitigate habitat losses that affect prey availability, and establish buffer zones to protect nesting individuals from anthropogenic disturbance (i.e., human-restricted zones). I suggest establishing a spatial buffer zone with no human encroachment of at least 610 m around all occupied nests to help minimize human-caused, and thus avoidable, energy expenditure of the nest-attending adult. Repeated human intrusions within 650 m of a nest caused disturbance to some individuals in my study, and this should be considered when implementing protective closures. Although I specifically tested the effect of human approach on foot on Ferruginous Hawks, other research has correlated low Ferruginous Hawk nest use with high levels of oil and gas development. This suggests that individuals respond differently to various disturbances; hence, this should be taken into consideration when managing this species. Because female Ferruginous Hawks in this study were shown to exhibit a heightened nest defense response than previously documented and thus may expend more energy during these actions than previously thought, disturbances should be avoided to minimize reproductive failures. Ferruginous Hawk flushing distance was 20% lower in an exurban environment than a rural setting, a result which supports the possibility that some individuals may be able to tolerate human presence. However, it is probable that prey availability, among other variables, is a contributing factor in determining any level of tolerance to humans. Therefore, conserving areas with dense prey resources such as prairie dog colonies is critical to any management plan designed to maintain stable Ferruginous Hawk populations, especially in grasslands which are realizing greater anthropogenic pressure.

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Table 3.1. Quantiles and mean Ferruginous Hawk flush distance (m) during the first nest defense trial in the Estancia Valley (n = 8), Plains of San Agustin (n = 6), and both study areas combined, New Mexico, during 2004-2005.

	Estancia Valley	Plains of San Agustin	Combined
100%	483.0	648.0	648.0
90%	483.0	648.0	569.0
75%	455.0	529.5	471.8
50%	256.0	434.0	393.5
25%	221.0	373.3	248.3
10%	0.0	332.0	221.0
0%	0.0	332.0	219.0
mean	330.8 ± 41.2	454.2 ± 45.2	383.6 ± 33.9

APPENDIX A

Weights for All Prey Species and Prey Categories Consumed by Breeding Ferruginous Hawks in New Mexico, 2004-2005

Appendix A. Weights for all prey species and prey categories consumed by breeding Ferruginous Hawks in New Mexico, 2004-2005.

Prey Category	Common Name	Weight (g)	Source
MAMMALS			
Unknown Family Sciuridae	-	124	Mean of Unknown *Spermophilus spp*. and Cynomys Gunnisoni (young)
Unknown *Spermophilus spp*	-	88	Mean of thirteen-lined and spotted ground squirrel
S. tridecemlineatus	13 lined ground squirrel	88.2	Museum Southwestern Biology*
S. spilosoma	Spotted ground squirrel	87.9	Museum of Southwestern Biology
S. variegatus	Rock squirrel	741	Museum of Southwestern Biology
Cynomys gunnisoni	Gunnison's prairie dog	557.2	Museum of Southwestern Biology
C. gunnisoni (young)	-	160	Fitzgerald et al. (1994)
Thomomys bottae	Botta's pocket gopher	170	Smith and Murphy (1973)
Geomys bursarius	Plains pocket gopher	188.5	Museum of Southwestern Biology
Sylvilagus audobonii	Desert cottontail	838.2	Museum of Southwestern Biology
Lepus californicus	Black-tailed jackrabbit	1536	Steenhof (1983)
Peromyscus spp	-	17	Same as *P. maniculatus*
P. maniculatus	Deer mouse	17	Smith and Murphy (1973)
Dipodomys spectabilis	Banner-tailed kangaroo rat	115.5	Museum of Southwestern Biology
D. ordii	Ord's kangaroo rat	53	Steenhof (1983)
Microtus spp	-	38	Smith and Murphy (1973)
Neotoma spp	-	127.2	Average of *N. lepida* & *N. mexicana*
N. lepida	Desert woodrat	124	Steenhof (1983)
N. mexicana	Mexican woodrat	130.4	Museum of Southwestern Biology and Denver Museum of Nature and Science**
Onychomys leucogaster	Northern grasshopper mouse	38	Smith and Murphy (1973)
Mustela frenata	Long-tailed weasel	178	Smith and Murphy (1973)
Unknown mammal 1	-	28	Average of *O. leucogaster* & *P. maniculatus*
Unknown mammal 2	-	119.8	Average of *T. bottae*, *N. lepida*, *N. mexicana*, *S. spilosoma*, *S. tridecemlineatus*
BIRDS			
Sturnella neglecta	Western Meadowlark	40	Steenhof (1983)

Eremophila alpestris	Horned Lark	17	Steenhof (1983)
Lanius ludovicianus	Loggerhead Shrike	51	Steenhof (1983)
Zenaida macroura	Mourning Dove	134	Steenhof (1983)
Corvus corax	Common Raven	876	Steenhof (1983)
Corvus cryptoleucus	Chihuahuan Raven	556	Pyle (1997)
Buteo regalis	Ferruginous Hawk	977	Bechard and Schmutz (1995)
Unknown Passerine	-	36	Average of *S. neglecta*, *L. ludovicianus*, *E. alpestris*
REPTILES			
Unknown snake	-	190	Steenhof (1983)
Unknown lizard	-	17	Steenhof (1983)
Prairie lizard	*Sceloporus undulates*	17	Steenhof (1983)
INSECTS			
Grasshoppers	Orthoptera	0.62	Steenhof (1983)
Scarab beetle	Scarabaeidae	0.30	Steenhof (1983)

*Vertebrate Collection, Museum Southwestern Biology, University of New Mexico, Albuquerque, NM.

**Vertebrate Collection, Denver Museum of Nature and Science, Denver, CO.

APPENDIX B

Length (km), Type, and Density of Roads (km/ha) in Estancia Valley (EV) and Plains of San Agustin (PSA), New Mexico

Appendix B. Length (km), type, and density of roads (km/ha) in Estancia Valley (EV) and Plains of San Agustin (PSA), New Mexico. Data derived from United States Census Bureau TIGER files 2006.

Road Category	EV	Density	PSA	Density	Description
A11 A13 A15	8.15 0.229 11.5	0.0001 0.000001 0.0001	- - -	- - -	A1 – Primary Highway With Limited Access Interstate highways and some toll highways are in this category (A1) and are distinguished by the presence of interchanges. These highways are accessed by way of ramps and have multiple lanes of traffic. The opposing traffic lanes are divided by a median strip. The TIGER/Line files may depict these opposing traffic lanes as two distinct lines in which case, the road is called separated.
A21	34.17	0.0002	38.1	0.0002	A2 – Primary Road Without Limited Access This category (A2) includes nationally and regionally important highways that do not have limited access as required by category A1. It consists mainly of US highways, but may include some state highways and county highways that connect cities and larger towns. A road in this category must be hard-surface (concrete or asphalt). It has intersections with other roads, may be divided or undivided, and have multi-lane or single-lane characteristics
A31 A3	195.80 1795.8	0.0012 0.0113	81.25 1298.9	0.0003 0.0054	A3 - Secondary and Connecting Road This category (A3) includes mostly state highways, but may include some county highways that connect smaller towns, subdivisions, and neighborhoods. The roads in this category generally are smaller than roads in Category A2, must be hardsurface (concrete or asphalt), and are usually undivided with single-lane characteristics. These roads usually have a local name along with a route number and intersect with many other roads and driveways.
A41 A43	1600.0 0.46	0.0101 0.0000	1217.6 -	0.0051 -	A4 - Local, Neighborhood, and Rural Road A road in this category (A4) is used for local traffic and usually has a single lane of traffic in each direction. In an

					(A4 cont.) urban area, this feature is a neighborhood road and street that is not a thorough-fare belonging in categories A2 or A3. In a rural area, this is a short-distance road connecting the smallest towns; the road may or may not have a state or county route number. Scenic park roads, unimproved or unpaved roads, and industrial roads are included in this category. Most roads in the United States are classified as A4 roads
A51	64.1	0.0004	225.8	0.0009	A5 - Vehicular Trail. A road in this category (A5) is usable only by four-wheel drive vehicles, is usually a one-lane dirt trail, and is found almost exclusively in very rural areas. Sometimes the road is called a fire road or logging road and may include an abandoned railroad grade where the tracks have been removed. Minor, unpaved roads usable by ordinary cars and trucks belong in category A4, not A5.
A63	1.65	0.0000	-	-	A6 - Road with Special Characteristics. This category (A6) includes roads, portions of a road, intersections of a road, or the ends of a road that are parts of the vehicular highway system and have separately identifiable characteristics.
A73	0.13	0.0000	-	-	A73 - Alley, road for service vehicles, usually unnamed, located at the rear of buildings and property
A74	125.64	0.0008	161.18	0.0007	A74 – Private road or drive for service vehicles, usually privately owned and unnamed. Primary type of use is for access to oil rigs, farms, or ranches
P41	13.92	0.0001	-	-	Feature Class P, Provisional Features. Provisional features are those streets that were added from reference sources or other programs in preparation for Census 2000, but were not field verified by census staff during field operations or through the use of aerial photography or imagery. The numeric portion of the CFCC still classifies the street as if an "A" were preceding it.
Total road length (km)	2056.2		1724.3		
Total road density (km/ha)	0.0130		0.0072		

APPENDIX C

Mean (± SE) Percent Frequency and Percent Biomass Per Nest of Prey Items Detected Using Pellets (n = 49 Nests), Prey Remains (n = 49), and Time-Lapse Video (n = 6) to Describe Ferruginous Hawk Diet Composition in New Mexico, 2004-2005

Appendix C. Mean (± SE) percent frequency and percent biomass per nest of prey items detected using pellets (n = 49 nests), prey remains (n = 49), and time-lapse video (n = 6) to describe Ferruginous Hawk diet composition in New Mexico, 2004-2005. Numbers in parenthesis represent group totals.

Prey	Pellets		Prey Remains		Video Monitoring	
	Percent Frequency	Percent Biomass	Percent Frequency	Percent Biomass	Percent Frequency	Percent Biomass
TTL Mammals	(89.1 ± 2.1)	(98.1 ± 0.6)	(89.3 ± 5.5)	(93.8 ± 4.6)	(96.1 ± 0.3)	(99.2 ± 0.2)
Family: Sciuridae	-	-	-	-	4.6 ± 0.3	2.6 ± 1.0
Spermophilus spp*	(25.0 ± 2.8)	(12.2 ± 1.8)	(16.8 ± 6.0)	(8.8 ± 4.9)	(28.9 ± 2.1)	(12.1 ± 3.2)
S. tridecemlineatus	-	-	3.2 ± 2.5	0.4 ± 0.3	0.6 ± 0.3	0.3 ± 0.1
S. spilosoma	-	-	8.9 ± 5.0	5.3 ± 4.5	28.2 ± 7.0	11.8 ± 3.1
S. variegates	3.4 ± 1.0	6.7 ± 1.8	10.3 ± 5.9	10.0 ± 5.8	-	-
Cynomys gunnisoni	11.2 ± 2.0	21.5 ± 3.3	13.7 ± 5.7	16.9 ± 6.7	(18.8 ± 9.9)	(30.4 ± 13.5)
C. gunnisoni (young)	-	-	-	-	2.6 ± 1.6	1.4 ± 0.8
Thomomys bottae	39.0 ± 2.9	33.0 ± 3.0	14.3 ± 5.8	10.6 ± 5.0	25.5 ± 7.7	22.9 ± 7.9
Geomys bursarius	1.0 ± 0.8	0.9 ± 0.7	-	-	-	-
Sylvilagus audubonii	6.8 ± 1.2	20.2 ± 3.1	22.7 ± 6.3	29.1 ± 7.6	3.4 ± 1.0	14.2 ± 4.8
Mustela frenata	-	-	4.8 ± 4.8	0.8 ± 0.4	-	-
Lepus californicus	0.5 ± 0.3	2.8 ± 1.4	6.9 ± 3.9	13.6 ± 6.0	-	-
Neotoma spp	0.5 ± 0.3	0.3 ± 0.1	-	-	-	-
N. mexicana	0.2 ± 0.2	-	-	-	-	-
N. lepida	0.3 ± 0.2	-	-	-	-	-
Dipdomys spp	-	-	-	-	2.3 ± 1.0	0.9 ± 0.4
D. ordii	1.5 ± 0.5	0.4 ± 0.1	-	-	-	-
D. spectabilis	-	-	-	-	0.7 ± 0.3	0.4 ± 0.2
Onychomys leucogaster	0.1 ± 0.1	-	-	-	-	-

Peromyscus spp	0.2 ± 0.1	0.01 ± 0.01	4.8 ± 4.8	4.6 ± 4.5	3.2 ± 1.2	0.3 ± 0.1
Unk mammal 1**	-	-	-	-	7.2 ± 1.4	0.9 ± 0.2
Unk mammal 2***			-	-	1.9 ± 0.7	1.1 ± 0.5
TTL bird	(4.6 ± 1.3)	(1.8 ± 0.6)	(10.6 ± 5.5)	(6.2 ± 4.6)	(2.4 ± 0.3)	(0.6 ± 0.1)
Sturnella neglecta	2.0 ± 0.7	0.9 ± 0.3	1.0 ± 1.0	0.2 ± 0.2	-	-
Eremophila alpestris	0.2 ± 0.2	0.01 ± 0.01	2.4 ± 2.4	0.2 ± 0.2	-	-
Unk Passerine	2.5 ± 0.8	0.8 ± 0.4	-	-	-	-
TTL Insecta	(5.2 ± 1.5)	(0.02 ± 0.01)	-	-	-	-
Grasshopper	3.6 ± 1.2	0.02 ± 0.01	-	-	-	-
Scarab Beetle	1.5 ± 0.8	0.004 ± 0.003	-	-	-	-
TTL Reptile	(1.1 ± 0.6)	-	-	-	(0.3 ± 0.3)	(0.2 ± 0.2)
Snake spp	-	-	-	-	0.3 ± 0.3	-
Lizard spp	1.1 ± 0.6	0.1 ± 0.06	-	-	-	-
Unknown delivery	-	-	-	-	1.2 ± 0.5	-

*either *S. spilosoma* or *S. tridecemlineatus*

** size of mouse

***size of ground squirrel

APPENDIX D

Minimum Number Of Identified Prey for Each Analytical Method Used to Describe Ferruginous Hawk Diet Composition from Nests in the Estancia Valley (n = 29), Plains Of San Agustin (n = 16), and Western Study Area (n = 4), New Mexico, 2004-2005

Appendix D**.** Minimum numbers of identified prey for each analytical method used to describe Ferruginous Hawk diet composition from nests in the Estancia Valley (n = 29), Plains of San Agustin (n = 16), and the western study area (n = 4), New Mexico, 2004-2005.

Prey Category	Common Name	Estancia Valley			Plains of San Agustin			Western Study Area	Total
		pellets (n = 29)	prey remains (n = 16)	video (n = 3)	pellets (n = 16)	prey remains (n = 5)	video (n = 3)	pellets (n = 4)	
MAMMALS									
Family: Sciuridae		0	0	21	0	0	3	0	24
Unknown *Spermophilus* spp.*		144	0	0	50	4	0	8	206
Spermophilus tridecemlineatus	thirteen-lined ground squirrel	6	2	2	0	0	2	0	12
S. spilosoma	spotted ground squirrel	26	4	62	6	1	85	0	184
S. variegatus	rock squirrel	13	4	0	4	0	0	2	23
Cynomys gunnisoni	Gunnison's prairie dog	89	5	114	5	2	3	15	233
Thomomys bottae	Botta's pocket gopher	313	5	53	82	3	120	18	594
Geomys bursarius	plains pocket gopher	5	0	0	0	0	0	1	6
Sylvilagus audobonii	desert cottontail	25	14	3	20	1	16	4	83
Lepus. californicus	black-tailed jackrabbit	0	3	0	4	2	0	0	9
Peromyscus spp.		2	0	5	0	0	16	0	23
P. maniculatus	deer mouse	0	0	0	0	1	0	0	1
Dipodomys spectabilis	banner-tailed kangaroo rat	0	0	1	0	0	4	0	5

D. ordii	Ord's kangaroo rat	11	0	4	4	0	8	1	28
Neotoma spp.		0	0	1	0	0	2	0	3
N. lepida	desert woodrat	2	0	0	1	0	0	0	3
N. mexicana	Mexican woodrat	2	0	0	0	0	0	0	2
Onychomys leucogaster	northern grasshopper mouse	2	0	0	0	0	0	0	2
Mustela frenata	long-tailed weasel	0	1	0	0	0	0	0	1
Unk mammal 1		0	0	15	0	0	21	0	36
Unk mammal 2		0	0	2	0	0	10	0	12
BIRDS									
Sturnella neglecta	Western Meadowlark	24	1	0	2	0	0	0	27
Eremophila alpestris	Horned Lark	1	1	0	0	0	0	0	2
Lanius ludovicianus	Loggerhead Shrike	0	1	0	0	0	0	0	1
Zenaida macroura	Mourning Dove	0	1	0	0	0	0	0	1
Corvus corax	Common Raven	0	1	0	0	0	0	0	1
Corvus cryptoleucus	Chihuahuan Raven	0	1	0	0	0	0	0	1
Buteo spp.		0	1	0	0	0	0	0	1
Unknown Passerine		16	0	8	4	0	6	0	34
REPTILES									
Unknown snake		0	0	1	0	0	0	0	1
Unknown lizard		0	0	0	1	0	0	0	1
Sceloporus undulatus	Prairie lizard	10	0	0	0	0	0	0	10
INSECTS									
Family Acrididae	Grasshopper	15	0	0	23	0	0	0	38
Family Scarabidae	Beetle	23	0	0	1	0	0	0	24
Unknown		0	0	3	0	0	5	0	8
TOTAL		729	45	295	207	14	301	49	1640

*Idenitified as *Spermophilus spilosoma* or *S. tridecemlineatus*