The Wilson Journal of Ornithology 119(4):558–569, 2007

PREY USE AND PROVISIONING RATES OF BREEDING FERRUGINOUS AND SWAINSON'S HAWKS ON THE SOUTHERN GREAT PLAINS, USA

MATTHEW D. GIOVANNI,[1,4,5] CLINT W. BOAL,[1,2] AND HEATHER A. WHITLAW[3]

ABSTRACT.—We collected diet data at 12 Ferruginous Hawk (*Buteo regalis*) and 14 Swainson's Hawk (*B. swainsoni*) nests in a short-grass prairie and agricultural community in the panhandle area of northwest Texas and southwest Oklahoma, and in northeastern New Mexico during the 2003–2004 breeding seasons. We documented 959 Ferruginous Hawk and 1,058 Swainson's Hawk prey deliveries during ~5,618 hrs of video monitoring. Ferruginous Hawks delivered 10.0 ± 0.7 ($\bar{x}$ ± SE) prey species per nest and typically larger prey. Swainson's Hawks delivered 13.4 ± 1.1 prey species per nest and typically smaller prey. There was a dietary overlap (Simplified Morisita Index [C_H]) of 0.31 in prey species delivery frequency and 0.56 in prey species' biomass. Ferruginous Hawks made 4.6 deliveries/day at 480 g/delivery whereas Swainson's Hawks delivered smaller prey items (147 g/delivery) but more frequently (7.0 deliveries/day). Deliveries/day and mass/day increased with increasing brood sizes of both species, but deliveries/day/nestling and mass/day/nestling decreased. Provisioning rates did not vary significantly over the nestling period. These data represent the most accurate diet quantification to date for Ferruginous and Swainson's hawks. Ferruginous Hawks used a larger array of prey types than shown in other studies based on indirect diet analysis methods. The low interspecific diet overlap suggests that prey is partitioned, which may facilitate the well-documented sympatric distribution of the two species. *Received 31 August 2006. Accepted 23 December 2006.*

Food and feeding habits are among the most fundamental components of animal ecology (Errington 1935). Initial studies of raptor diets were directed at assessing impacts of depredation on game species and livestock (Errington 1930). More recent studies provide information on raptor niches in relation to community structure, and on the availability and distribution of prey species (Johnson 1981, Marti 1987). Prey availability and composition can affect all aspects of raptor species ecology including population trends (Newton 1979, Woffinden and Murphy 1989, Cully 1991, Olsen 1995). Thus, quantifying and understanding diets is an essential component for successful management and conservation of raptor species.

Ferruginous Hawks (*Buteo regalis*) and Swainson's Hawks (*B. swainsoni*) are often sympatric in grasslands, shrub-steppe, and deserts (Bechard and Schmutz 1995, England et al. 1997). Both species have experienced population declines, primarily due to habitat conversion and degradation, but also from persecution and secondary pesticide poisoning (Schmutz and Fyfe 1987, Houston and Schmutz 1995, England et al. 1997). Research on sympatric Ferruginous and Swainson's hawk populations has been limited to the northern and western regions of their breeding distribution. Most studies have focused on interspecific comparisons of nest site selection, distribution, productivity, and success but also on diet composition and responses to prey fluctuations, and effects of anthropogenic activities (Thurow and White 1983, Steenhof and Kochert 1985, Schmutz and Hungle 1989, Cully 1991, Restani 1991).

Diets of Ferruginous Hawks are monotypic compared to the more generalist diet of Swainson's Hawks (Bechard and Schmutz 1995, England et al. 1997). Jackrabbits (*Lepus* spp.) tend to be the dominant prey of Ferruginous Hawks west of the Continental Divide whereas ground squirrels (*Spermophilus* spp.) and prairie dogs (*Cynomys* spp.) are dominant

[1] Department of Range, Wildlife, and Fisheries Management, Texas Tech University, Lubbock, TX 79409, USA.

[2] Texas Cooperative Fish and Wildlife Research Unit, Department of Range, Wildlife, and Fisheries Management, Texas Tech University, Lubbock, TX 79409, USA.

[3] Texas Parks and Wildlife Department, Texas Tech University, Lubbock, TX 79409, USA.

[4] Current address: School of Natural Resources, University of Nebraska, Lincoln, NE 68583, USA.

[5] Corresponding author;
e-mail: mgiovan1@bigred.unl.edu

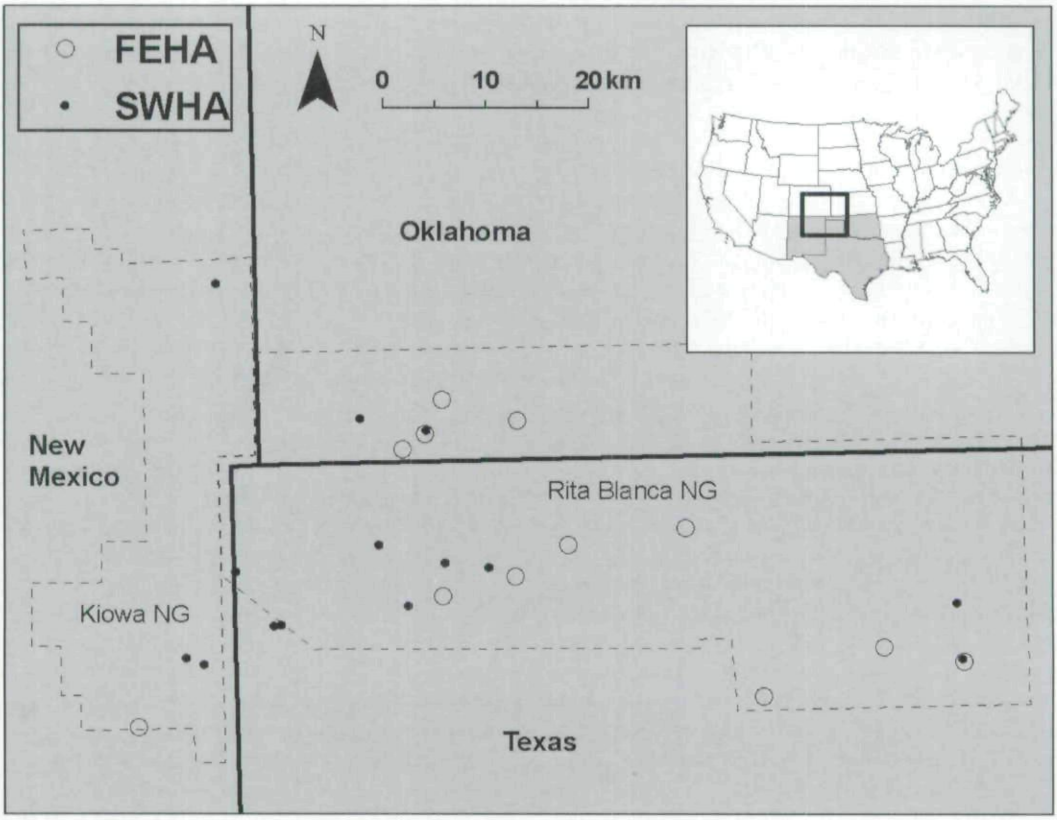

FIG. 1. Study area and distribution of 12 Ferruginous Hawk nests (FEHA) and 14 Swainson's Hawk nests (SWHA).

prey to the east (Bechard and Schmutz 1995). Prairie dogs are an important, if not critical, prey item for migrating and wintering Ferruginous Hawks in Texas and adjacent states (Schmutz and Fyfe 1987, Cully 1991, Allison et al. 1995, Plumpton and Andersen 1997). The availability of prairie dogs appears to have induced Ferruginous Hawks to forage and over-winter in heavily cultivated areas of Texas (Schmutz and Fyfe 1987) and fragmented suburban areas of eastern Colorado (Plumpton and Andersen 1998).

The importance of prairie dogs as prey for breeding Ferruginous and Swainson's hawks has not been well investigated. Furthermore, breeding season diets of Ferruginous Hawks in the southern extent of their range are mostly unknown. The potential use of black-tailed prairie dogs (*Cynomys ludovicianus*) or species associated with prairie dog colonies (Kotliar et al. 1999) by Swainson's Hawks has also not been investigated. An understanding of the potential relationships between black-tailed prairie dogs and these two raptor species is important because prairie dogs have been and continue to be subject to extensive eradication efforts throughout their range, and have experienced an estimated 98% population decline (Kotliar et al. 1999).

The overall objective of this study was to quantify the breeding season diets of coexisting Ferruginous and Swainson's hawk populations. Our specific objectives were to: (1) identify the prey species of both hawk species in terms of delivery frequency and biomass, (2) examine dietary breadth and overlap, (3) compare daily provisioning rates, and (4) evaluate the effects of brood size and nestling age on prey provisioning.

METHODS

Study Area.—The study area (Fig. 1) encompassed the U.S. Forest Service Rita Blanca National Grasslands in Dallam County, Texas and southern Cimarron County, Oklahoma, and the eastern section of the Kiowa National Grasslands in Union County, New Mexico and adjacent private property where access was permitted (36° 20′ N, 102° 40′ W). This tri-state area is within the Southern Great Plains Region with elevations ranging from 1,144 to 1,558 m. The historical plant community type is short-grass prairie, the driest of the mid-continental grasslands (Brown 1985), and sporadic droughts are common in the region (Samson et al. 2004). Warm, dry summers and cold, dry winters are typical of the study area with Dallam County, Texas, receiving an average of 18.6 cm of precipitation annually, most of it from April to August (National Weather Service 2004).

The national grasslands included in this study encompassed ~81,000 ha of various sized tracts of short-grass and mixed-grass prairie interspersed among private property holdings. They supported cattle grazing, outdoor recreation, and wildlife management (U.S. Department of Agriculture 2004). The adjacent private property supported agricultural crops such as corn, sorghum, and wheat, cattle ranching, and a variety of range management and conservation programs.

Common vegetation included warm- and cool-season grasses such as *Bouteloua* and *Elymus* spp., buffalo grass (*Buchloe dactyloides*), silver bluestem (*Bothriocloa laguroides*), and other species including sagebrush (*Artemisia* spp.), plains yucca (*Yucca angustifolia*), buffalo gourd (*Cucurbita foetidissima*), and plains sunflower (*Helianthus petiolaris*). Trees and woody shrubs were sparse and consisted primarily of crop, road, and residence shelterbelts. Tree species included Siberian elm (*Ulmus pumila*) and plains cottonwood (*Populus deltoids occidentalis*). Less common species included Russian olive (*Elaeagnus angustifolia*), eastern red cedar (*Juniperus virginiana*), and black locust (*Robinia psuedoacacia*).

Nest Selection and Video-monitoring.—We located breeding Ferruginous Hawk and Swainson's Hawk pairs by visiting known nest sites (unpubl. data), and conducting road surveys during courtship and incubation periods beginning in March for Ferruginous Hawks and April for Swainson's Hawks. We assessed the status of nests from a distance with optics and an extendable mirror-pole at the nest site. We considered an area occupied by a breeding pair of hawks if an adult pair was present at the nest site and nest-building, or if eggs or nestlings were present.

We used video-recording systems (Giovanni 2005) to document prey deliveries at a different sample of Ferruginous Hawk and Swainson's Hawk nests each year. We randomly selected nests for video-monitoring but logistical restraints (i.e., private property access and unsafe nest substrates) prevented us from using some of the initially selected nests. We installed video systems during the nestling period and moved video systems to a new nest site after failure or fledging of young at the initial nest. We programmed the systems to record from 0630 to 2130 hrs CDT at 72-hr (1.3 frames/sec) and 48-hr (0.8 frames/sec) speeds (Smithers et al. 2005). This allowed recording 3–4 days of 15-hr daylight intervals on a single 2-hr tape. We changed videotapes and batteries twice each week to insure continuous video coverage.

We attempted to identify prey items to the lowest taxonomic level possible. We categorized delivered prey as unknown when no image of the item was visible but a delivery was evident based on behavior of the hawks. We grouped eastern (*Sylvilagus floridanus*) and desert (*S. audubonii*) cottontails, and yellow-faced (*Cratogeomys castanops*) and plains (*Geomys bursarius*) pocket gophers into single, generic prey types (i.e., "cottontails" and "pocket gophers"). We assumed all grasshopper deliveries to be plains lubber grasshoppers (*Brachystola magna*) (Pfadt 1994).

Age and Mass Estimates.—We estimated age and biomass of mammalian prey based on relative size. For instance, juvenile black-tailed prairie dogs and black-tailed jackrabbits (*Lepus californicus*) were visibly smaller than their adult counterparts. We assumed prey to be adult age when it was not clearly juvenile. We also assumed avian prey to be of adult status unless juvenile plumage was detectable.

We used the mean mass of males and females for non-sexually dimorphic prey species. We used the mean of mass estimates for eastern and desert cottontails, and also for yellow-faced and plains pocket gophers. We obtained other mammal mass estimates from Davis and Schmidly (1994), Best (1996), and Hoogland (1996). We obtained mass estimates for bird prey from Dunning (1984), plains lubber grasshoppers from Schell et al. (1994), snake species from measurements taken at fortuitous encounters within the study area (Giovanni 2005) and museum specimens, Texas horned lizards (*Phrynosoma cornutum*) and Great Plains skinks (*Eumeces obsoletus*) from unpublished data, and birds, frogs and toads, rodents, lizards, and snakes not identified to species from Steenhof (1983).

Some prey deliveries were unidentifiable due to immediate ingestion or obstructed viewing during feeding. We estimated biomass for unidentifiable prey (to calculate prey provisioning rates) by calculating a mean mass of the less conspicuous but frequently delivered prey species (e.g., grasshoppers for Swainson's Hawks).

We assumed that adult males fed away from the nest, as suggested by their frequent delivery of partial prey items and minimal time at the nest. Ascertaining if the adult female was feeding in concert with nestlings was difficult due to the time-lapsed recording and resolution of the video footage. We were also restricted from identifying if digestive tracts were ingested because of limited video resolution. We made no assumptions addressing the ingestion of foods in digestive tracts of prey and considered delivered prey an index of ingested food.

Delivery Rate Analyses.—We calculated prey delivery frequency and provisioning as deliveries/day and deliveries/nestling/day. We estimated g/delivery, g/day, and g/nestling/day for biomass delivery analysis. We also examined patterns of delivery rates among nests with different brood sizes and temporal patterns in prey delivery rates across the nestling growth period. We estimated hatching dates by backdating from nestling age estimates (Moritsch 1983, 1985) of the oldest nestling (Warnke et al. 2002), and used delivery rate data up to fledging ages of 50 days for Ferruginous Hawks (Bechard and Schmutz 1995) and 45 days for Swainson's Hawks (England et al. 1997). We used 5-day nestling age intervals to standardize prey provisioning rates across the nestling period. We calculated g/hr and g/nestling/hr by summing delivered prey biomass within the 5-day age intervals, and then dividing by the total hours of video footage for the intervals and nestling number.

Statistical Analyses.—We used Statistica 6.1 (StatSoft, Inc. 2003) for data analyses and all tests were conducted at an *alpha* level of 0.05. We attempted to correct data having non-normal experimental error distributions with appropriate transformations (Zar 1999). We tested for homogeneous variances among treatments with Levene's test when normality was satisfied (Zar 1999). We then tested for interspecific differences with a t-test for independent samples by group (i.e., group 1 being Ferruginous Hawks and group 2 being Swainson's Hawks) or with a one-way ANOVA (Zar 1999). We used the nonparametric equivalents when transformations failed to normalize data (Zar 1999).

We made interspecific comparisons of percent delivery frequency and biomass of black-tailed prairie dogs, mammals, mammals weighing $>$200 g, birds, reptiles and amphibians, grasshoppers, diet richness, and diet breadth. We also examined interspecific provisioning rates on the basis of deliveries/day and g/day. We examined deliveries/nestling/day and g/nestling/day to examine possible influences of brood size on provisioning rates. We used repeated-measures ANOVA (Zar 1999) to compare nestling provisioning rates across time by measuring deliveries/hr and deliveries/nestling/hr, and g/hr and g/nestling/hr with pooled diet data from 5-day intervals based on nestling age. We used Smith's Measure of Niche Breadth (*FT*) (Smith 1982) to calculate dietary breadth, and the Simplified Morisita Index (C_H) (Krebs 1999) to calculate interspecific prey species' delivery frequency and biomass overlap. We reported comparative data as means and standard errors.

RESULTS

Ferruginous Hawk Food Habits.—We video-monitored six Ferruginous Hawk nests in 2003 and six different nests in 2004, and assumed all nesting pairs (12) to be different and independent between years. We recorded 3,231 daylight hrs ($\bar{x}$ = 269 ± 44 hrs/nest) of video footage, and identified 740 of 937 (79%) prey items to species, genus, or family.

Rodents and rabbits dominated Ferruginous Hawk diets, comprising 73.2% of the prey and 81.7% of the prey biomass delivered to nests.

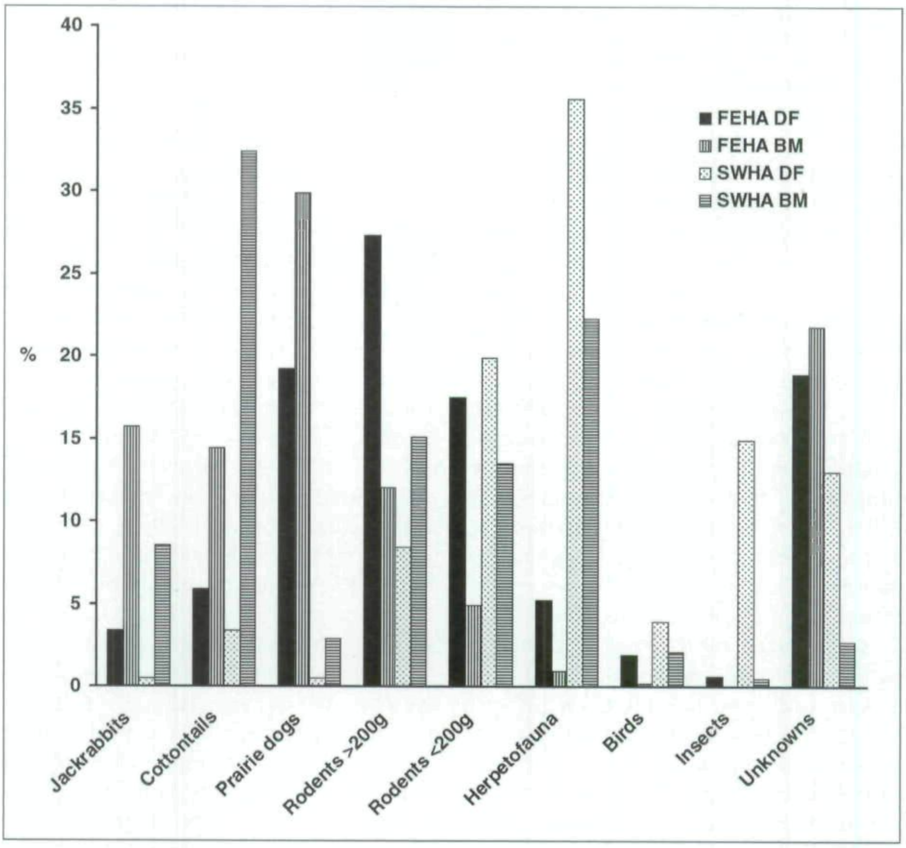

FIG. 2. Prey type delivery frequency (DF) and biomass (BM) for Ferruginous Hawk (FEHA) (n = 12) and Swainson's Hawk (SWHA) nests (n = 14) during the 2003–2004 breeding seasons.

Frequently delivered prey types included pocket gophers (25.2%), black-tailed prairie dogs (19.2%), thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*; 10.3%), and cottontails (5.9%) (Fig. 2, Appendix). Black-tailed prairie dogs (29.9%), black-tailed jackrabbits (15.8%), cottontails (14.4%), and pocket gophers (10.9%) accounted for most of the prey biomass (71%) (Fig. 2, Appendix).

Swainson's Hawk Food Habits.—We video-monitored 6 Swainson's Hawks nests in 2003 and 8 different nests in 2004, and assumed all nesting pairs to be different and independent between years. We recorded 2,387 daylight hrs ($\bar{x}$ = 171 ± 25 hrs/nest) of video footage, and identified 831 of the 1,057 (79%) prey deliveries to species, genus, or family.

Frequently delivered prey types included grasshoppers (14.9%), Texas horned lizards (13.4%), Great Plains skinks (11.8%), and pocket gophers (5.9%) (Fig. 2, Appendix). Reptiles, amphibians, and insects accounted for 51% of the prey delivered by Swainson's Hawks, but small mammals accounted for 72% of the prey biomass. Important prey types in terms of biomass included cottontails (32.4%), pocket gophers (9.8%), black-tailed jackrabbits (8.5%), and bullsnakes (*Pituophis catenifer sayi*; 8.2%) (Fig. 2, Appendix).

Comparative Food Habits.—Ferruginous Hawks delivered black-tailed prairie dogs ($\bar{x}$ = 18.9 ± 5.2% per nest) more frequently than Swainson's Hawks ($\bar{x}$ = 0.5 ± 0.2% per nest; U = 236, P < 0.001). Ferruginous Hawks used mammalian prey of >200 g ($\bar{x}$ = 55.6 ± 3.5% per nest) more than Swainson's Hawks ($\bar{x}$ = 13.4 ± 2.7% per nest; t_{24} = 9.72, P < 0.001). Swainson's Hawks delivered more grasshoppers ($\bar{x}$ = 12.7 ± 4.3% per nest vs. $\bar{x}$ = 0.4 ± 0.3% per nest; U = 24, P < 0.001), and reptiles and amphibians ($\bar{x}$ = 38.0 ± 5.6%

TABLE 1. Mean (± SE) deliveries/nestling/day (d/n/d) and g/nestling/day (g/n/d) for Ferruginous Hawk nests with two nestlings (n = 1), three nestlings (n = 6), and four nestlings (n = 5), and Swainson's Hawk nests with one nestling (n = 2), two nestlings[a] (n = 6), and three nestlings[b] (n = 6).

	Ferruginous Hawk		Swainson's Hawk	
Brood size	d/n/d	g/n/d	d/n/d	g/n/d
1			5.1 ± 1.7	483 ± 133
2	1.9	750	3.1 ± 0.6	466 ± 57
3	1.7 ± 0.2	694 ± 83	2.8 ± 0.2	347 ± 54
4	1.1 ± 0.1	626 ± 56		

[a] One of the six nests with two nestlings experienced a single nestling mortality; this nest was subsequently analyzed as a nest with one nestling.
[b] One of the nests with three nestlings experienced a single nestling mortality; this nest was subsequently analyzed as a nest with two nestlings.

per nest vs. $\bar{x}$ = 4.7 ± 1.2% per nest; t_{24} = 5.3, $P < 0.001$) than Ferruginous Hawks.

Most of the biomass consumed per nest by both hawk species consisted of mammals (t_{24} = 1.46, P = 0.16). Swainson's Hawks delivered more mass than Ferruginous Hawks in reptile and amphibian prey ($\bar{x}$ = 23.5 ± 4.0% per nest vs. $\bar{x}$ = 0.8 ± 0.2% per nest; U = 19, $P < 0.001$), birds ($\bar{x}$ = 2.3 ± 0.8% per nest vs. $\bar{x}$ = 0.3 ± 0.1% per nest; U = 45.0, P = 0.040), and grasshoppers ($\bar{x}$ = 0.7 ± 0.4% per nest vs. $\bar{x}$ = 0% per nest; U = 25, P = 0.008).

Ferruginous Hawks had a lower measure of diet richness per nest (10.0 ± 0.7) than Swainson's Hawks (13.4 ± 1.1; t_{24} = 2.4, P = 0.024), but diet breadth did not differ between Ferruginous (FT = 0.86) and Swainson's hawks (FT = 0.88; t_{24} = 0.88, P = 0.39). Prey overlap, on a scale of 0 to 1 with 0 indicating no dietary overlap and 1 indicating complete dietary overlap, was low in terms of prey species used (C_H = 0.31), but higher in terms of prey species' biomass contribution (C_H = 0.56).

Swainson's Hawks made more prey deliveries/day (7.0 ± 0.7 per nest) than Ferruginous Hawks (4.6 ± 0.3 per nest; U = 33.0, P = 0.008), but delivered smaller prey (147 ± 23 g/delivery) than Ferruginous Hawks (480 ± 32 g/delivery; t_{24} = 8.7, $P < 0.001$). This resulted in fewer total grams delivered/day (1,029 ± 104) at Swainson's Hawk nests compared to Ferruginous Hawk nests (2,209 ± 171; t_{24} = 6.8, $P < 0.001$). Swainson's Hawks made more prey deliveries/nestling/day (3.4 ± 0.5) than Ferruginous Hawks (1.4 ± 0.1; U = 8.0, $P < 0.001$), but delivered fewer g/nestling/day (401 ± 38) than Ferruginous Hawks (670 ± 46; t_{24} = 4.5, $P < 0.001$).

Deliveries/day did not differ among Ferruginous Hawk nests with broods of 2, 3, and 4 nestlings (H = 2.5, P = 0.28) but deliveries/nestling/day decreased with broods of 2, 3, and 4 nestlings ($F_{2,9}$ = 5.67, P = 0.025) (Table 1). Adults delivered ~500 g of additional food/day with each additional nestling, but this trend was not significant ($F_{2,9}$ = 1.7, P = 0.24) (Table 1). The provisioned g/nestling/day did not decrease with increasing brood size ($F_{2,9}$ = 0.32, P = 0.73) (Table 1), but the apparent decrease may be biologically relevant; our sample size was insufficient to reveal statistical significance.

We observed similar effects of brood size on delivery rates with Swainson's Hawks. Prey deliveries/day among Swainson's Hawk nests tended to increase with increasing brood sizes but differences were not significant ($F_{2,13}$ = 2.4, P = 0.13). An apparent decrease in deliveries/nestling/day with increasing brood size was not significant (H = 3.99, P = 0.14) (Table 1). There appeared to be an increase in delivered g/day as brood size increased, but differences were not significant ($F_{2,9}$ = 1.7, P = 0.24). Ultimately, provisioned g/nestling/day did not differ among brood sizes ($F_{2,13}$ = 0.62, P = 0.55) (Table 1).

Provisioning rates of Ferruginous Hawks did not vary with 5-day nestling growth intervals in terms of delivered g/hr ($F_{8,49}$ = 0.58, P = 0.79) or g/nestling/hr ($F_{8,49}$ = 0.78, P = 0.62) (Table 2). Similarly, Swainson's Hawk prey provisioning rates did not vary with 5-day nestling growth intervals in terms of delivered g/hr ($F_{7,40}$ = 1.58, P = 0.17) or g/nestling/hr ($F_{7,40}$ = 0.59, P = 0.76) (Table 2).

DISCUSSION

Different life history traits (e.g., migratory behavior, morphology, and clutch size) may

TABLE 2. Prey deliveries/hr (d/hr), deliveries/nestling/hr (d/n/hr), g/hr, and g/nestling/hr (g/n/hr) ($\bar{x}$ ± SE) for Ferruginous Hawk (FEHA) (n = 12) and Swainson's Hawk (SWHA) nests (n = 14) during 5-day age intervals of the nestling development period.

	Age (days)								
	6–10	11–15	16–20	21–25	26–30	31–35	36–40	41–45	46–50
Prey deliveries/hr									
FEHA	0.26 ± 0.04	0.29 ± 0.04	0.38 ± 0.06	0.36 ± 0.03	0.34 ± 0.04	0.29 ± 0.02	0.32 ± 0.03	0.26 ± 0.01	0.22 ± 0.02
SWHA	0.35	0.36 ± 0.04	0.46 ± 0.17	0.45 ± 0.07	0.57 ± 0.07	0.48 ± 0.07	0.40 ± 0.04	0.44 ± 0.06	—
Deliveries/nestling/hr									
FEHA	0.08 ± 0.01	0.10 ± 0.01	0.13 ± 0.02	0.12 ± 0.01	0.10 ± 0.01	0.09 ± 0.01	0.10 ± 0.01	0.08 ± 0.01	0.07 ± 0.01
SWHA	0.35	0.31 ± 0.08	0.40 ± 0.19	0.26 ± 0.05	0.30 ± 0.05	0.22 ± 0.03	0.24 ± 0.05	0.24 ± 0.05	—
Grams/hr									
FEHA	129 ± 25	137 ± 8	168 ± 36	176 ± 27	173 ± 21	138 ± 14	172 ± 31	144 ± 10	144 ± 35
SWHA	25	27 ± 5	31 ± 10	36 ± 7	61 ± 11	66 ± 12	76 ± 14	52 ± 14	—
Grams/nestling/hr									
FEHA	39 ± 7	46 ± 3	56 ± 12	57 ± 9	53 ± 8	43 ± 4	52 ± 7	42 ± 3	48 ± 12
SWHA	25	21 ± 2	26 ± 11	22 ± 7	33 ± 7	31 ± 5	45 ± 14	25 ± 6	—

have varying effects on prey use and potential resource partitioning between Ferruginous and Swainson's hawks. Earlier diet studies of sympatric Ferruginous and Swainson's hawks indicated high diet overlap (82–98%) despite behavioral and morphological differences (Schmutz et al. 1980, Restani 1991). Ferruginous and Swainson's hawks in our study displayed low prey use overlap (31%) which may be geographically and/or temporally unique. It is also possible that lower diet overlap is more common in other sympatric populations, but only detectable with more accurate data obtained by nest video monitoring rather than analysis of pellet and prey remains (Simmons et al. 1991, Lewis 2001). Low interspecific dietary overlap and high dietary breadth could indicate high prey availability and low interspecific dietary competition. However, confirmation requires estimates of prey densities across breeding seasons (Schmutz and Hungle 1989, Woffinden and Murphy 1989).

A few relatively larger mammalian prey species dominated prey delivery frequency and percentage biomass delivered by Ferruginous Hawks in our study population. Breeding Ferruginous Hawks preyed primarily upon black-tailed jackrabbits in Utah (Woffinden and Murphy 1977), northern pocket gophers (*Thomomys talpoides*) and ground squirrels in Idaho (Wakeley 1978, Steenhof and Kochert 1985), Richardson's ground squirrels (*Spermophilus richardsoni*) in North Dakota (Gilmer and Stewart 1983), Wyoming (MacLaren et al. 1988), and Alberta (Schmutz et al. 1980), and *Spermophilus* ground squirrels in Montana (Restani 1991). Prairie dog species are the main prey resource for wintering Ferruginous Hawks (Schmutz and Fyfe 1987, Cully 1991, Plumpton and Andersen 1997). Gunnison's prairie dog (*Cynomys gunnisoni*) was reported as a primary breeding season prey resource in New Mexico (Cartron et al. 2004), but the diet percentage was derived from pellet and prey remains. Indirect methods of diet analysis (i.e., analysis of pellets and remains) are known to bias results toward species whose remains are more detectable (e.g., large bones, thick skin, bright feathers) (Collopy 1983, Simmons et al. 1991, Bielefeldt et al. 1992), but Cartron et al.'s (2004) data still indicate the regular use of prairie dogs by breeding Ferruginous Hawks. The finer resolution of our data indicate black-tailed prairie dogs were the second most frequently delivered prey item to Ferruginous Hawk nests and contributed the most biomass. Thus, we believe that black-tailed prairie dogs are a substantial, if not critical, prey resource for breeding Ferruginous Hawks in the Southern Great Plains.

Previous diet assessments for breeding Swainson's Hawks vary widely across their range but were dominated by *Spermophilus* ground squirrels, small rodents, and birds in Alberta (95.3%; Schmutz et al. 1980), California (82.6%; Woodbridge 1987), North Dakota (100%; Gilmer and Stewart 1984), Saskatchewan (95.6%; England et al. 1997), and Washington (50%; Fitzner 1980). In Washington, however, reptiles (32%) and insects (12%) were also important prey resources (Fitzner 1980). Swainson's Hawks in Utah preyed primarily upon *Lepus* and *Sylvilagus* rabbits (56.1%) but also insects (19.5%), small rodents (12.2%), and birds (9.7%) (Smith and Murphy 1973). Reptiles (42.2%) dominated the Swainson's Hawk diet in Arizona (Porton 1977), and insects (54.9%) dominated in New Mexico (Bednarz 1988). The breeding Swainson's Hawks we monitored delivered primarily reptiles and amphibians (35.6%), rodents (28.7%), and grasshoppers (14.9%). This large variability among diets confirms the opportunistic ability of Swainson's Hawks to use a diversity of prey types across their range.

Breeding adults apparently compensate for the extra caloric demand of larger broods by foraging more often and/or further from the nest, and selecting different types and sizes of prey (Wright et al. 1998). Peregrine Falcons (*Falco peregrinus*) in Alaska (Palmer et al. 2004) and Northern Goshawks (*Accipiter gentilis*) in Minnesota (Smithers et al. 2005) increased prey delivery rates and prey size with larger broods, but deliveries/nestling still decreased. Similarly, Masman et al. (1988) showed that Eurasian Kestrels (*Falco tinnunculus*) responded to experimentally increased brood sizes by increasing foraging efforts and food delivery rates, and changing food type and size.

Prey size, deliveries/day, g/day, and deliveries and g/nestling/day did not vary significantly for Ferruginous Hawk nests with different brood sizes in our study area. However, sample sizes for both hawk species may have been too low to detect statistical relationships between prey delivery rates and brood sizes at an *alpha* level of 0.05. Ferruginous Hawks delivered ~500 g of additional food/day with each additional nestling increase in brood size, and this trend is probably biologically significant. Nestling provisioning rates in g/nestling/day, however, decreased with increasing brood size. Thus, Ferruginous Hawks delivered more g/day with increasing brood size but did not maintain a constant nestling provisioning rate.

Our results are similar to those of Palmer et al. (2004) and Smithers et al. (2005) in that Ferruginous and Swainson's hawks increased prey deliveries and mass/day, but did not compensate sufficiently with increased delivery frequency or larger prey items to maintain consistent g/nestling/day with increasing brood sizes. This suggests that single nestlings may receive an abundance of food while nestlings in larger broods may receive the necessary caloric requirements but experience comparatively slower growth rates and poorer physiological condition at fledging (Olendorff 1974, Wakeley 1978).

Prey delivery and nestling provisioning rates, and caloric requirements also can vary across the nestling growth period. Olendorff (1974) found that food consumption of captive Ferruginous Hawk nestlings peaked at post-hatch week 4 (days 22–28) and food consumption of Swainson's Hawk nestlings peaked at post-hatch week 5 (days 29–35). Our results approximate these findings as Ferruginous Hawks delivered the most g/nestling/hr during post-hatch days 21–25, and Swainson's Hawks delivered the most g/nestling/hr during post-hatch days 36–40.

Prey use overlap was low between breeding Ferruginous and Swainson's hawks, but overlap in terms of prey contributing the most biomass was higher. This may be explained by Swainson's Hawks taking fewer of the large prey types used frequently by Ferruginous Hawks, and those prey contributing disproportionately more biomass to the diet. We suspect consistent deliveries of small prey, compared to irregular or occasional deliveries of large prey, is of equal or more importance for breeding Swainson's Hawks (e.g., consistent provisioning of metabolic water; Kirkley and Gessaman 1990).

Ferruginous Hawks preyed primarily upon prairie dogs and pocket gophers. These species should be considered when making management decisions for breeding and non-breeding Ferruginous Hawks on the Southern Great Plains. Numerous studies have shown that Ferruginous Hawks tend to have lower reproductive success and emigrate following primary prey population declines (Smith et al. 1981, Schmutz and Hungle 1989, Woffinden and Murphy 1989, Cully 1991). These trends may be particularly important where prairie dogs are a primary breeding or non-breeding season prey species, as they are still subject to unregulated eradication and control efforts throughout most of their range (Kotliar et al. 1999).

ACKNOWLEDGMENTS

We thank Chris Taylor for dedicated field work, and all the cooperative and enthusiastic residents that provided property access. We thank the Texas Parks and Wildlife Department, U.S. Geological Survey, Texas Cooperative Fish and Wildlife Research Unit, and Dan Garcia and the U.S. Forest Service, Kiowa and Rita Blanca National Grasslands, for financial and logistical support. We are grateful to E. A. Horne, T. J. LaDuc, and Donald Ruthven for contributing unpublished mass data for the Great Plains skink, various snake species, and the Texas horned lizard, respectively. This manuscript benefited from comments by C. E. Braun, Marco Restani, J. K. Schmutz, B. L. Smithers, and an anonymous reviewer.

LITERATURE CITED

ALLISON, P. S., A. W. LEARY, AND M. J. BECHARD. 1995. Observations of wintering Ferruginous Hawks (*Buteo regalis*) feeding on prairie dogs (*Cynomys ludovicianus*) in the Texas panhandle. Texas Journal of Science 47:235–236.

BECHARD, M. J. AND J. K. SCHMUTZ. 1995. Ferruginous Hawk (*Buteo regalis*). The birds of North America. Number 172.

BEDNARZ, J. C. 1988. A comparative study of the breeding ecology of Harris' and Swainson's hawks in southeastern New Mexico. Condor 90: 311–323.

BEST, T. 1996. *Lepus californicus*. Mammalian Species Accounts (V. Hayssen, Editor). Number 530. American Society of Mammalogists. www.science.smith.edu/departments/Biology/VHAYSSEN/msi/msiaccounts.html (accessed October 2006).

BIELEFELDT, J., R. N. ROSENFIELD, AND J. M. PAPP. 1992. Unfounded assumptions about diet of the Cooper's Hawk. Condor 94:427–436.

BROWN, L. 1985. Grasslands. Audubon Society nature guides, Alfred A Knopf, Inc., New York, USA.

CARTRON, J. E., P. J. POLECHLA JR., AND R. R. COOK. 2004. Prey of nesting Ferruginous Hawks in New Mexico. Southwestern Naturalist 49:270–276.

COLLOPY, M. W. 1983. A comparison of direct observations and collections of prey remains in determining the diet of Golden Eagles. Journal of Wildlife Management 47:360–368.

CULLY JR., J. F. 1991. Response of raptors to reduction of a Gunnison's prairie dog population by plague. American Midland Naturalist 125:140–149.

DAVIS, W. B. AND D. J. SCHMIDLY. 1994. The mammals of Texas. Texas Parks and Wildlife Press, Austin, USA.

DUNNING JR., J. B. 1984. Body weights of 686 species of North American birds. Western Bird Banding Association Monograph 1.

ENGLAND, A. S., M. J. BECHARD, AND C. S. HOUSTON. 1997. Swainson's Hawk (*Buteo swainsoni*). The birds of North America. Number 265.

ERRINGTON, P. L. 1930. The pellet analysis method of raptor food habits study. Condor 32:292–296.

ERRINGTON, P. L. 1935. The significance of food habits research in wild life management. Science 81: 378–379.

FITZNER, R. E. 1980. Behavioral ecology of the Swainson's Hawk (*Buteo swainsoni*) in Washington. PLN-2754. Pacific Northwest Laboratory, Richland, Washington, USA.

GILMER, D. S. AND R. E. STEWART. 1983. Ferruginous Hawk populations and habitat use in North Dakota. Journal of Wildlife Management 47:146–157.

GILMER, D. S. AND R. E. STEWART. 1984. Swainson's Hawk nesting ecology in North Dakota. Condor 86:12–18.

GIOVANNI, M. D. 2005. Prey partitioning between sympatric grassland raptors. Thesis. Texas Tech University, Lubbock, USA.

HOUSTON, C. S. AND J. K. SCHMUTZ. 1995. Declining reproduction among Swainson's Hawks in prairie Canada. Journal of Raptor Research 29:198–201.

HOOGLAND, J. L. 1996. *Cynomys ludovicianus*. Mammalian Species Accounts (V. Hayssen, Editor). Number 535. American Society of Mammalogists. www.science.smith.edu/departments/Biology/VHAYSSEN/msi/msiaccounts.html (accessed October 2006).

JOHNSON, D. R. 1981. The study of raptor populations. University of Idaho Press, Moscow, USA.

KIRKLEY, J. S. AND J. A. GESSAMAN. 1990. Water economy of nestling Swainson's Hawks. Condor 92: 29–44.

KOTLIAR, N. B., B. W. BAKER, A. D. WHICKER, AND G. PLUMB. 1999. A critical review of assumptions about the prairie dog as a keystone species. Environmental Management 24:177–192.

KREBS, C. J. 1999. Ecological methodology. Second

Edition. Addison-Welsey Educational Publishers, Inc., Menlo Park, California, USA.

LEWIS, S. B. 2001. Breeding season diet of Northern Goshawks in southeast Alaska with a comparison of techniques used to examine raptor diet. Thesis. Boise State University, Boise, Idaho, USA.

MACLAREN, P. A., S. H. ANDERSON, AND D. E. RUNDE. 1988. Food habits and nest characteristics of breeding raptors in southwestern Wyoming. Great Basin Naturalist 48:548–553.

MARTI, C. D. 1987. Raptor food habits studies. Pages 67–80 *in* Raptor management techniques manual (B. A. Giron Pendelton, B. A. Millsap, K. W. Cline, and D. M. Bird, Editors). National Wildlife Federation, Washington, D.C., USA.

MASMAN, D., S. DAAN, AND C. DIJKSTRA. 1988. Time allocations in the kestrel (*Falco tinnunculus*), and the principle of energy minimization. Journal of Animal Ecology 57:411–432.

MORITSCH, M. Q. 1983. Photographic guide for aging nestling Red-tailed Hawks. Snake River Birds of Prey Project, USDI, Bureau of Land Management, Boise, Idaho, USA.

MORITSCH, M. Q. 1985. Photographic guide for aging nestling Ferruginous Hawks. Snake River Birds of Prey Project, USDI, Bureau of Land Management, Boise, Idaho, USA.

NATIONAL WEATHER SERVICE FORECAST OFFICE. 2004. Amarillo, Texas. www.srh.weather.gov/ama/html/climo.htm (accessed November 2004).

NEWTON, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, South Dakota, USA.

OLENDORFF, R. R. 1974. Some quantitative aspects of growth in three species of *Buteo*. Condor 76:466–468.

OLSEN, P. 1995. Australian birds of prey. Johns Hopkins University Press, Baltimore, Maryland, USA.

PALMER, A. G., D. L. NORDMEYER, AND D. D. ROBY. 2004. Nestling provisioning rates of Peregrine Falcons in interior Alaska. Journal of Raptor Research 38:9–18.

PFADT, R. E. 1994. Field guide to common western grasshoppers. University of Wyoming Agricultural Experiment Station, Laramie, USA. http://www.uwyo.edu/CES/PUBS/Weeds_Insects/Weed_Insect_Pubs_Main.html (accessed October 2006).

PLUMPTON, D. L. AND D. E. ANDERSEN. 1997. Habitat use and time budgeting by wintering Ferruginous Hawks. Condor 99:888–893.

PLUMPTON, D. L. AND D. E. ANDERSEN. 1998. Anthropogenic effects on winter behavior of Ferruginous Hawks. Journal of Wildlife Management 62:340–346.

PORTON, I. J. 1977. Some aspects of the breeding behavior of Swainson's Hawks. Thesis. University of Arizona, Tucson, USA.

RESTANI, M. 1991. Resource partitioning among three *Buteo* species in the Centennial Valley, Montana. Condor 93:1007–1010.

SAMSON, F. B., F. L. KNOPF, AND W. R. OSTLIE. 2004. Great Plains ecosystems: past, present, and future. Wildlife Society Bulletin 32:6–15.

SCHELL, S., J. LOCKWOOD, S. SCHELL, AND K. ZIMMERMAN. 1994. Field guide to common western grasshoppers. University of Wyoming Agricultural Experiment Station, Laramie, USA.

SCHMUTZ, J. K. AND R. W. FYFE. 1987. Migration and mortality of Alberta Ferruginous Hawks. Condor 89:169–174.

SCHMUTZ, J. K. AND D. J. HUNGLE. 1989. Populations of Ferruginous and Swainson's hawks increase in synchrony with ground squirrels. Canadian Journal of Zoology 67:2596–2601.

SCHMUTZ, J. K., S. M. SCHMUTZ, AND D. A. BOAG. 1980. Coexistence of three species of hawks (*Buteo* spp.) in the prairie-parkland ecotone. Canadian Journal of Zoology 58:1075–1089.

SIMMONS, R. E., D. M. AVERY, AND G. AVERY. 1991. Biases in diets determined from pellets and remains: correction factors for a mammal and bird-eating raptor. Journal of Raptor Research 25:63–67.

SMITH, D. G. AND J. R. MURPHY. 1973. Breeding ecology of raptors in the eastern Great Basin of Utah. Brigham Young University Science Bulletin, Biological Services 18(3):1–76.

SMITH, D. G., J. R. MURPHY, AND N. D. WOFFINDEN. 1981. Relationships between jackrabbit abundance and Ferruginous Hawk reproduction. Condor 83:52–56.

SMITH, E. P. 1982. Niche breadth, resource availability, and inference. Ecology 63:1675–1681.

SMITHERS, B. L., C. W. BOAL, AND D. E. ANDERSEN. 2005. Northern Goshawk food habits in Minnesota: an analysis using time-lapse video recording systems. Journal of Raptor Research 39:264–273.

STATSOFT, INC. 2003. Statistica. Version 6.1. Tulsa, Oklahoma, USA.

STEENHOF, K. 1983. Prey weights for computing percent biomass in raptor diets. Journal of Raptor Research 17:15–27.

STEENHOF, K. AND M. N. KOCHERT. 1985. Dietary shifts of sympatric buteos during a prey decline. Oecologia 66:6–16.

THUROW, T. L. AND C. M. WHITE. 1983. Nest site relationship between the Ferruginous Hawk and Swainson's Hawk. Journal of Field Ornithology 54:401–406.

U.S. DEPARTMENT OF AGRICULTURE. 2004. Cibola National Forest: Kiowa and Rita Blanca National Grasslands. www.fs.fed.us/r3/cibola/districts/kiowa.shtml (accessed October 2006).

WAKELEY, J. S. 1978. Activity budgets, energy expenditures, and energy intakes of nesting Ferruginous Hawks. Auk 95:667–676.

WARNKE, D. K., D. E. ANDERSEN, C. R. DYKSTRA, M. W. MEYER, AND W. H. KARASOV. 2002. Provisioning rates and time budgets of adult and nestling Bald Eagles at inland Wisconsin nests. Journal of Raptor Research 46:121–127.

WOFFINDEN, N. D. AND J. R. MURPHY. 1977. Population dynamics of the Ferruginous Hawk during a prey decline. Great Basin Naturalist 37:411–425.

WOFFINDEN, N. D. AND J. R. MURPHY. 1989. Decline of a Ferruginous Hawk population: a 20-year summary. Journal of Wildlife Management 53:1127–1132.

WOODBRIDGE, B. 1987. Biology and management of Swainson's Hawks in the Butte Valley, California. USDA, Forest Service, Klamath National Forest, Goosenest Ranger District, Mt. Hebron, California, USA.

WRIGHT, J., C. BOTH, P. A. COTTON, AND D. BRYANT. 1998. Quality vs. quantity: energetic and nutritional trade-offs in parental provisioning strategies. Journal of Animal Ecology 67:620–634.

ZAR, J. H. 1999. Biostatistical analysis. Fourth Edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

APPENDIX. Prey delivery frequency (DF) and biomass (BM) at Ferruginous Hawk (n = 12) and Swainson's Hawk nests (n = 14) during the 2003–2004 breeding seasons.

	Ferruginous Hawk			Swainson's Hawk		
Prey type	*n*	% DF	% BM	*n*	% DF	% BM
Rodentia						
Pocket gopher spp. (*Geomys bursarius*) (*Cratogeomys castanops*)	236	25.2	10.9	62	5.9	9.8
Black-tailed prairie dog (*Cynomys ludovicianus*)	180	19.2	29.9	5	0.5	2.9
Thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*)	96	10.3	3.8	35	3.3	4.8
Southern plains woodrat (*Neotoma micropus*)	20	2.1	1.1	26	2.5	4.9
Spotted ground squirrel (*Spermophilus spilosoma*)	20	2.1	0.5	10	0.9	0.8
Ord's kangaroo rat (*Dipodomys ordii*)	19	2.0	0.3	35	3.3	1.9
Northern grasshopper mouse (*Onychomys leucogaster*)	6	0.6	<0.1	21	2.0	0.6
Deer mouse (*Peromyscus maniculatus*)	6	0.6	<0.1	43	4.1	0.8
Hispid cotton rat (*Sigmodon hispidus*)	1	0.1	<0.1	28	2.6	3.8
Hispid pocket mouse (*Chaetodipus hispidus*)	0	0.0	0.0	14	1.3	0.4
Plains pocket/harvest mouse (*Perognathus flavescens*) (*Reithrodontomys montanus*)	0	0.0	0.0	10	0.9	0.1
House mouse (*Mus musculus*)	0	0.0	0.0	4	0.4	0.1
Norway rat (*Rattus norvegicus*)	0	0.0	0.0	1	0.9	0.4
Unknown rodent spp.	16	1.7	0.2	10	0.1	0.3
Totals	600	63.9	47.0	304	28.7	31.6
Lagomorpha						
Cottontail spp. (*Sylvilagus floridanus*) (*S. audubonii*)	55	5.9	14.4	36	3.4	32.4
Black-tailed jackrabbit (*Lepus californicus*)	32	3.4	15.7	5	0.5	8.5
Totals	87	9.3	30.1	41	3.9	40.9
Reptilia and Amphibia						
Texas horned lizard (*Phrynosoma cornutum*)	23	2.5	0.2	131	12.4	3.0
Eastern yellow-bellied racer (*Coluber constrictor flaviventris*)	4	0.4	0.1	30	2.8	2.5
Bullsnake (*Pituophis catenifer sayi*)	3	0.3	0.3	28	2.6	8.2
Great Plains skink (*Eumeces obsoletus*)	2	0.2	<0.1	125	11.8	2.4
Western coachwhip (*Masticophus flagellum testaceus*)	1	0.1	0.1	12	1.1	3.6
Western Plains garter snake (*Thomnophis radix haydeni*)	1	0.1	<0.1	0	0.0	0.0
Plains hognose (*Heterodon nasicus nasicus*)	0	0.0	0.0	6	0.6	0.7
Central Plains milk snake (*Lampropeltis triangulum gentiles*)	0	0.0	0.0	2	0.2	0.1
Ground snake (*Sonora semiannulata*)	0	0.0	0.0	1	0.1	<0.1
Unknown frog/toad spp.	9	1.0	<0.1	13	1.2	0.2
Unknown snake spp.	6	0.6	0.2	10	0.9	1.4
Unknown lizard spp.	0	0.0	0.0	20	1.9	0.2
Totals	49	5.2	0.9	378	35.6	22.3

APPENDIX. Continued.

Prey type	Ferruginous Hawk *n*	Ferruginous Hawk % DF	Ferruginous Hawk % BM	Swainson's Hawk *n*	Swainson's Hawk % DF	Swainson's Hawk % BM
Aves						
Burrowing Owl (*Athene cunicularia*)	3	0.3	0.1	0	0.0	0.0
Western Meadowlark (*Sturnella neglecta*)	2	0.2	<0.1	6	0.6	0.4
Common Nighthawk (*Chordeiles minor*)	1	0.1	<0.1	0	0.0	0.0
Lark Bunting (*Calamospiza melanocorys*)	1	0.1	0.0[a]	1	0.1	<0.1
Scaled Quail (*Callipepla squamata*)	0	0.0	0.0	3	0.3	0.4
European Starling (*Sturnus vulgaris*)	0	0.0	0.0	1	0.1	0.1
Killdeer (*Charadrius vociferous*)	0	0.0	0.0	1	0.1	0.1
Loggerhead Shrike (*Lanius ludovicianus*)	0	0.0	0.0	1	0.1	<0.1
Unknown bird	11	1.2	0.1	27	2.6	1.1
Totals	18	1.9	0.2	40	3.9	2.1
Insecta						
Grasshopper spp. (*Brachystola magna*)	6	0.6	<0.1	157	14.9	0.5
Unknown	177	18.9	21.8	137	13.0	2.7
Totals	937			1057		

[a] Prey item flew away after delivery.