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Source: Journal of Raptor Research, 51(4) : 397-408

Published By: Raptor Research Foundation

URL: <https://doi.org/10.3356/JRR-16-85.1>

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THE JOURNAL OF RAPTOR RESEARCH

A QUARTERLY PUBLICATION OF THE RAPTOR RESEARCH FOUNDATION, INC.

VOL. 51

DECEMBER 2017

No. 4

J. Raptor Res. 51(4):397–408

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NESTING BEHAVIOR, PROVISIONING RATES, AND PARENTAL ROLES OF FERRUGINOUS HAWKS IN NEW MEXICO

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ABSTRACT.—A better understanding of feeding ecology and parental roles is important for conservation of Ferruginous Hawks (*Buteo regalis*) and their habitat. In 2004–2005, we collected and analyzed 1373 hr of video from six time-lapse video-monitored nests in New Mexico, U.S.A., to address these behavioral data gaps. Ferruginous Hawks delivered 93 g of prey biomass per hr to each nest (g/hr), 42 g/nestling/hr, and 208 g/prey delivery. Males delivered most prey items (72%) and twice the overall prey biomass of females, but females delivered larger prey items in each delivery. As predicted by the food-niche hypothesis, males and females used prey differently, with females delivering a disproportionate number of desert cottontails (*Sylvilagus audubonii*) and males delivering Botta's pocket gopher (*Thomomys bottae*) most often. Desert cottontails, the heaviest prey item, were most often delivered eviscerated. Females spent 33% of recorded time at the nest, whereas males spent <1%. We found a positive relationship between female nest attendance and male provisioning rate, and a negative relationship between female nest attendance and nestling age; the role of the male was to deliver prey whereas the female's initial role was to feed and care for nestlings, then to find food as nestlings began feeding themselves and became homeothermic. Evidence of intersexual differences in prey use may provide managers justification to focus limited resources on actions that create habitat heterogeneity and, consequently, a more diverse prey base.

KEY WORDS: *Ferruginous Hawk*; *Buteo regalis*; *feeding ecology*; *nesting behavior*; *parental roles*; *provisioning rates*; *time-lapse video*.

COMPORTAMIENTO DE NIDIFICACIÓN, TASAS DE PROVISIÓN Y ROLES PARENTALES DE *BUTEO REGALIS* EN NUEVO MÉXICO

RESUMEN.—Para la conservación de *Buteo regalis* y su hábitat, es importante tener un mejor conocimiento de su ecología trófica y de los roles parentales. Para completar estos vacíos de información sobre su comportamiento, en 2004 y 2005 recolectamos y analizamos 1373 horas de video de seis nidos monitoreados por video a intervalos de tiempo en Nuevo México, EE.UU. *B. regalis* aportó 93 gramos de biomasa de presa por hora a cada nido (g/h), 42 g/polluelo/h y 208 g/provisión de presa. Los machos aportaron la mayor cantidad de presas (72%) y el doble de la biomasa total aportada por las hembras, pero las hembras aportaron presas de mayor tamaño en cada aporte. Tal y como predice la hipótesis del nicho alimenticio, los

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machos y las hembras utilizaron las presas de forma diferente, con las hembras aportando un número desproporcionado de individuos de *Sylvilagus audubonii* y los machos aportando con mayor frecuencia individuos de *Thomomys bottae*. *S. audubonii*, la presa más pesada, a menudo fue aportada eviscerada. Las hembras permanecieron en el nido el 33% del tiempo registrado, mientras que los machos permanecieron <1%. Encontramos una relación positiva entre la atención de la hembra al nido y la tasa de aporte del macho, y una relación negativa entre la atención de la hembra al nido y la edad del pollo. El rol del macho fue aportar las presas mientras que el rol inicial de la hembra fue alimentar y cuidar a los pollos, y posteriormente buscar alimento a medida que los polluelos comenzaron a alimentarse solos y pudieron controlar su temperatura. La evidencia de diferencias intersexuales en el uso de presas puede servir a los gestores como justificación para enfocar los recursos limitados en acciones que creen heterogeneidad de hábitat y consecuentemente una base de presas más diversa.

[Traducción del equipo editorial]

Ferruginous Hawk (*Buteo regalis*) populations are declining throughout their range for a variety of reasons, including habitat loss, human encroachment, and decline of prey populations (Collins and Reynolds 2005, Schmutz et al. 2008, Sauer et al. 2014). However, relatively little is known about behavioral components key to their conservation, such as the species' feeding ecology and parental roles. Existing studies that describe nesting behavior emanate from observational accounts of one or two nests, sometimes observed from a considerable distance (Bailey 1928, Ligon 1961, Angell 1969, Wakeley 1978).

Video monitoring may be an especially appropriate tool to better understand the nesting behavior of Ferruginous Hawks because the species may abandon nest sites if frequently disturbed by humans (White and Thurow 1985, Ward 2001) and is considered "sensitive" by the Bureau of Land Management and United States Forest Service (Bechard and Schmutz 1995, Collins and Reynolds 2005). Moreover, video recording of raptor nests has provided researchers an opportunity to more effectively study concepts related to raptor feeding ecology, including differential prey use between males and females (Newton 1979, Booms and Fuller 2003) and the energetic costs associated with delivering prey items to the nest (Pennycuik et al. 1988, 1989). Although video monitoring has been employed to document nesting behavior in falcons (Booms and Fuller 2003, Robinson et al. 2015) and accipiters (Reif and Tornberg 2006), video-generated information on behavioral patterns of buteos, particularly Ferruginous Hawks, is limited.

If conservation of Ferruginous Hawks is a management objective, then a better understanding of nesting behavior and parental roles is necessary, as these factors may affect nest productivity. For

example, the role of female raptors may shift from nest attentiveness and nestling care to hunting if the male is not provisioning the nest sufficiently. Decreased female nest attentiveness can reduce productivity, as nestlings become more susceptible to predation or heat stress (Lack 1968, Morris 1987). Colonial prey clustered in dense patches, such as Gunnison's prairie dogs (*Cynomys gunnisoni*), which have been identified as an important prey source for hawks nesting in our study area (Cartron et al. 2004, Keeley et al. 2016), may improve the provisioning effectiveness of males (Charnov 1976, Korpimäki et al. 1994), thereby allowing the female to be more attentive to the brood during crucial times of the nesting cycle. Finally, differential prey use by males and females may be advantageous to reduce competition for prey between the sexes and expand the nesting pair's food-niche, both of which may improve fitness (Newton 1979).

During 2004–2005, we used time-lapse video to describe provisioning rates, prey use, and behavior of Ferruginous Hawks nesting in New Mexico, U.S.A., at the southern periphery of the species' breeding range (Olendorff 1993), to provide empirical data that could aid in conserving this sensitive *Buteo*. Specifically, we assessed: (1) the parental roles of females and males during the nesting season; (2) whether there was differential prey use between males and females; (3) the relationship between provisioning rate and diurnal and seasonal cycles; and (4) female nest attendance as it relates to male provisioning rate.

METHODS

We used video recording to monitor Ferruginous Hawks nesting in two grassland sites in New Mexico, U.S.A.: the Plains of San Agustín (34°04.3'N, 107°39.17'W) and Estancia Valley (34°43.83'N, 106°09.02'W; Fig. 1). The Plains of San Agustín,

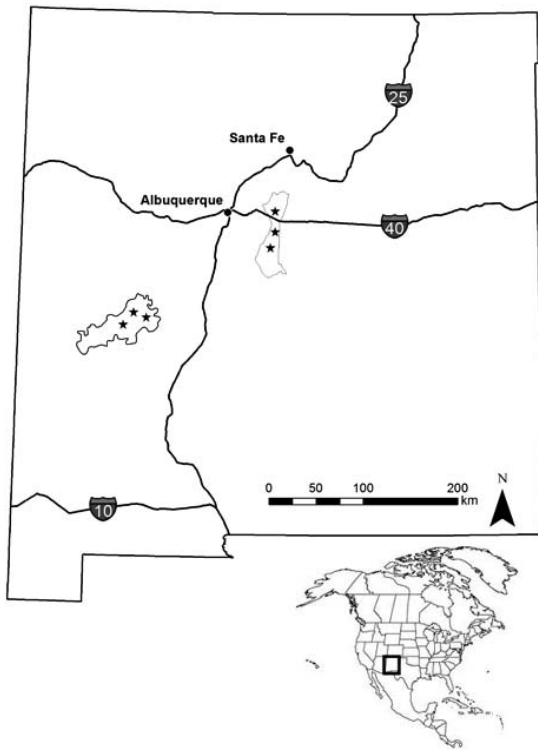


Figure 1. The Estancia Valley and Plains of San Agustin, in New Mexico, U.S.A., where we studied Ferruginous Hawk nesting behavior and feeding ecology, 2004–2005. Nest locations indicated by a star.

approximately 2000 masl and 238,000 ha in size, has an average maximum temperature of 18.6°C and receives 31.5 cm of precipitation (Western Regional Climate Center 2016a). Similarly, the Estancia Valley, at approximately 1860 masl, has an average maximum temperature of 20°C and receives 32.7 cm of precipitation annually (Western Regional Climate Center 2016b). The Plains of San Agustin and Estancia Valley share environments characteristic of the desert short-grass prairie (Dick-Peddie 1993): blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*) codominate the open country, and scattered, isolated junipers (*Juniperus monosperma*) provide the majority of nesting sites for Ferruginous Hawks. A more detailed habitat description is reported in Keeley (2009).

Video Monitoring. We installed “Basic Sentinel I All Weather Video Surveillance Systems” (Sandpiper Technologies, Inc., Manteca, CA U.S.A.) to monitor prey deliveries and behavior at Ferruginous Hawk

nests in 2004 and 2005. We chose nest sites based on permission from landowners, nest accessibility, nest tree structure, and probability of vandalism. We completed all installation operations between 0700–0830 H and stayed no longer than 56 min at any site to limit disturbance. We followed protocols provided by accepted ornithological societies (Fair et al. 1997). The distance between the camera (6 cm × 4 cm × 4 cm) and nest varied among sites, but we set it at approximately 1 m whenever possible (Booms and Fuller 2003). We used camouflage spray paint to conceal any metal parts used to attach the camera to the tree bole (Keeley 2009). To minimize risk to the nestlings, we established all video systems after the youngest nestling was at least 7 d old ($n = 15$ nestlings, \bar{x} : 12.7 ± 0.8 d, range: 8–18 d) and only removed the equipment after the young had fledged. Following installation, we vacated the territory quickly, but used the recording system to document an adult’s return to the nest. We set the time-lapse system to record 20 frames/sec (one third real-time), which fit approximately 24.5 hr of nest activity onto one videotape. To reduce disturbance to the nesting pair, we placed the video recorder and battery in a camouflaged tent 75 m from the nest tree, and connected them to the camera by coaxial cable. Nests were approached <75 m on three occasions during the nesting season to collect regurgitated pellets (Keeley et al. 2016). While we acknowledge that our presence in the area could affect the behavior of nesting hawks, we followed methods similar to those of other studies using video to monitor raptor nesting behavior (Booms and Fuller 2003, Giovanni et al. 2007). We divided each video-recorded day into three 5-hr time blocks: “morning” (0520–1020 H), “midday” (1020–1520 H), and “afternoon–evening” (1520–2020 H) and randomly selected two blocks to record per day. We subsequently combined data from these two blocks to assess relationships between biomass provisioning, nestling age, and parental roles (e.g., female nest attendance). This recording schedule allowed us to capture nesting activity when prey deliveries may be frequent (i.e., during sunrise and sunset) and allowed 2.5 d between visits to each video-monitored nest, which was necessary logistically due to the distance between study areas (350 km).

During analysis of video recordings, we identified the species of each prey delivery whenever possible using pelage and body characteristics and a reference collection of skins obtained from the Denver Museum of Nature and Science, Denver, Colorado,

U.S.A. To compute biomass delivery rate, we used masses from published sources (Smith and Murphy 1973, Steenhof 1983) or calculated the mean mass of a minimum of 20 individuals per prey species from the Museum of Southwestern Biology at the University of New Mexico, Albuquerque, New Mexico, U.S.A (Appendix). Because there was a large mass discrepancy between young and adult Gunnison's prairie dogs (*Cynomys gunnisoni*), we identified them separately whenever possible and used appropriate masses for biomass calculations (Keeley 2009). To determine prey delivery rates, we calculated two metrics (items/nestling/hr and g/nestling/hr) by computing this for each nest separately, then averaging across all nests. Prey that we determined to be redelivered (i.e., similar-looking prey item removed from the nest and delivered to the nest within 20 sec) were only counted once during videotape analysis of prey deliveries.

Nesting Behavior. We distinguished between male and female Ferruginous Hawks at video-monitored nests by size and unique feather patterns. We calculated the percentage of time female and male adult Ferruginous Hawks spent at the nest during each 10-hr recording session (hereafter "day") using video footage. If an adult was not on the nest, but was in the nest tree and within the view of the camera, we considered this at the nest. We used 22 d as an age threshold to define when nestlings began feeding themselves to investigate the relationship between female nest attendance and nestling "independence." To investigate the potential for adults to reduce the energetic cost of delivering heavy prey to the nest, we determined the prey evisceration status by examining the video frame-by-frame; intact prey were plump with a tight pelage, whereas eviscerated prey were noticeably limp with excess skin or a visceral gash. We used the age of the oldest nestling (Moritsch 1985) to describe relationships between brood age, female nest attendance, and biomass provisioning.

Statistical Analysis. We performed all analyses with JMP 11.0 statistical software (SAS Institute, Inc., Cary, NC U.S.A.). We used paired *t*-tests when assessing intersexual differences in adult provisioning rates and two-sample *t*-tests to test for differences between independent groups. We used one-way ANOVA to test for differences in provisioning rate by time block. When data met homogeneity of variance assumptions for between-group comparisons, we reported *t*-statistics with associated probability; when data did not meet these assumptions, we

used Wilcoxon rank sums and reported associated *Z*-scores. We used Spearman's rank correlation to assess the relationship between continuous variables associated with nesting behavior (e.g., biomass provisioning, nestling age, and female nest attendance) when normality assumptions were not met (Zar 1999). To assess behavioral patterns associated with seasonality, we used data from the 10-hr daily recording and considered this a "day." We used a chi-square test of association to assess differences in intersexual prey use for the five most frequently delivered prey types. We considered results statistically significant when *P*-values were ≤ 0.10 to reduce the chances of committing a type II error and provide flexibility in assessing raptor behavioral differences in natural systems (Cherry 1998, Zar 1999). We report metrics as mean \pm SE.

RESULTS

We recorded 1373 total hr of activity ($\bar{x} = 229.0 \pm 29.2$ hr per nest; range: 152–273 hr) from three nests in 2004 and three nests in 2005, all of which fledged young (a total of 14 offspring; range: 2–3 per nest). All young were present during installation and none perished during our study. Adults were away from the nest 220.3 ± 54.2 min following camera installation. We did not monitor the same nest twice during the study. The video systems recorded 597 prey deliveries, not including 16 instances of prey redelivered, or almost one prey delivery for every 2 hr of recorded time (0.46 ± 0.04 prey deliveries/hr). Adults delivered 0.20 ± 0.01 prey items/nestling/hr. Males delivered prey almost three times as often as females, a statistically significant difference (Table 1). Males delivered 73% ($n = 433$) of all prey items, whereas females delivered 24% ($n = 141$). We were unable to identify the adult's sex in 3% ($n = 23$) of prey deliveries. Ferruginous Hawks delivered prey items at similar rates in morning (0.46 ± 0.07 prey items/hr) and midday (0.52 ± 0.08 prey items/hr), but delivery rate tended to fall (0.31 ± 0.05 prey items/hr) in afternoon–evening, although the difference was not statistically significant ($F_{2,15} = 12.47$, $P = 0.12$).

Ferruginous Hawks delivered 125,570 g of prey ($\bar{x} = 20,928 \pm 5082$ g/nest) to six video-monitored nests, 93.3 ± 14.8 g/hr to each brood, 41.8 ± 8.4 g/hr/nestling, and 208.1 ± 37.0 g/delivery ($n = 597$; Table 1). Adults delivered more biomass as nestlings aged ($n = 125$ d; $\beta = 15.3$, $r_s = 0.1554$, $P = 0.08$; Fig. 2). Ferruginous Hawks delivered similar amounts of biomass among time periods (morning: 99.8 ± 21.3

Table 1. Provisioning rates and nest attendance by male and female Ferruginous Hawks nesting in New Mexico, U.S.A., from 2004–2005.

PREY DELIVERIES AND NEST ATTENDANCE	MALE	FEMALE	<i>t</i>	<i>P</i>
Deliveries (g/hr)	61.9 ± 16.5	28.4 ± 5.0	1.76 ^a	0.14
Deliveries (g/nestling/hr)	27.4 ± 8.4	13.3 ± 2.9	1.56 ^a	0.18
Deliveries (number/hr)	0.33 ± 0.05	0.12 ± 0.02	3.45 ^a	0.02
Deliveries (number/nestling/hr)	0.14 ± 0.02	0.06 ± 0.01	3.57 ^a	0.02
Mass per delivery (g)	190.2 ± 29.4	255.7 ± 44.9	2.73 ^a	0.04
Nest attendance (%/day)	0.26 ± 0.11	33.9 ± 8.0	4.18 ^a	0.0009

^a Paired *t*-test (*n* = 6).

g/hr, midday: 98.6 ± 16.3 g/hr, afternoon–evening: 67.9 ± 18.6 g/hr; $F_{2,15} = 0.92$; $P = 0.42$). Prey biomass delivered per hour did not differ between males and females, but females delivered 30% more biomass per prey delivery than males (Table 1).

The number of prey items delivered by males and females was not equally distributed among prey species ($df = 4$, $\chi^2 = 22.3$, $P = 0.002$, Fig. 3). Females delivered mainly spotted ground squirrels (*Xerospomophilus spilosoma*), while males delivered mostly Botta’s pocket gopher (*Thomomys bottae*, Fig. 3). Males delivered three times more Gunnison’s prairie

dogs than females, and females delivered a disproportionate number of desert cottontails (*Sylvilagus audubonii*).

Hawks eviscerated prey prior to ≥30% (*n* = 182) of deliveries, and males and females did so with similar frequency. We believe this is a conservative estimate of the evisceration rate because we were unable to determine evisceration status of 51% (*n* = 297) of all prey items delivered. Of the 108 prey items we determined were delivered intact, 12% (*n* = 13) were alive. All prey items delivered alive were spotted ground squirrels. Prior to delivery, adults eviscerated

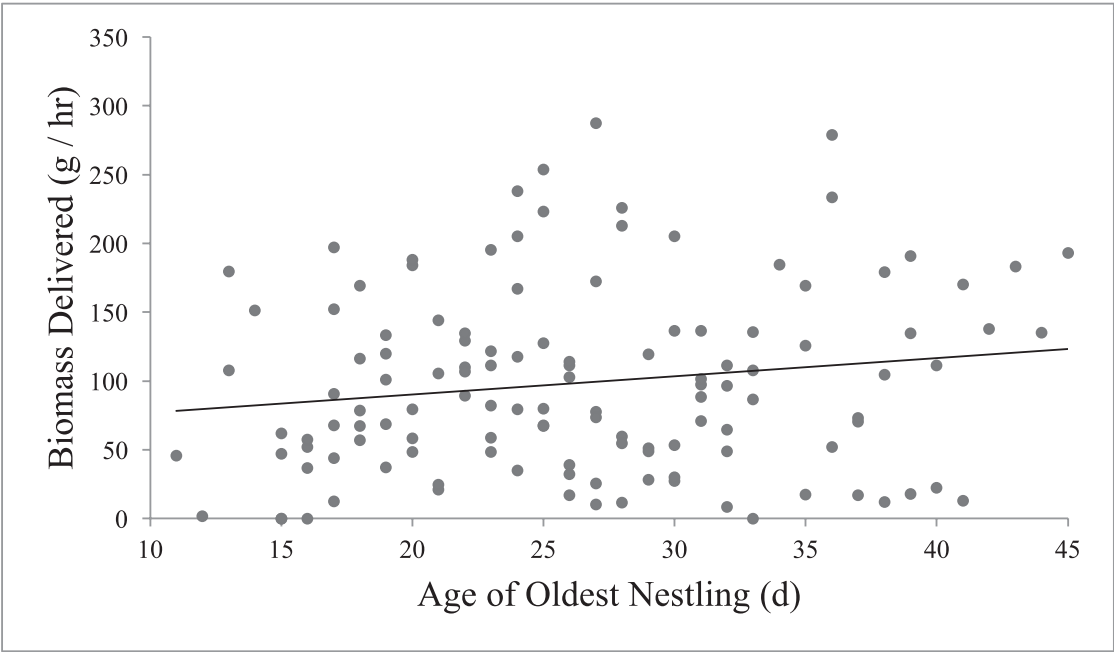


Figure 2. The relationship between provisioning rate (g/hr) by adult Ferruginous Hawks and nestling age (d) for each day of video-recorded nesting activity in New Mexico, U.S.A., 2004–2005. Data points are not independent of one another, as they were recorded at a total of six nests.

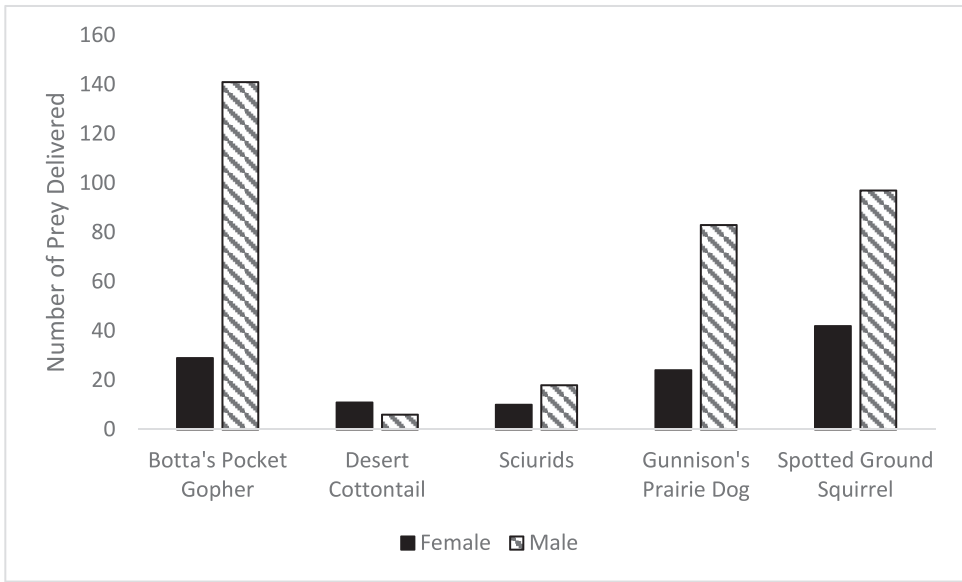


Figure 3. The number of the five most commonly delivered prey species by female (solid) and male (stripes) Ferruginous Hawks nesting in New Mexico, U.S.A., 2004–2005.

three of the four most commonly delivered species $\geq 70\%$ 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%).

Parental Behavior. Of the 718 arrivals of females to the nest captured on video, females delivered prey 20% ($n = 141$) and nesting material 39% ($n = 282$) of the time. Females spent 30% more time at the nest than males (Table 1). Following prey deliveries, males 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. Females spent $3.4 \pm 0.5\%$ of each day feeding nestlings, and nestlings ($n = 14$) began to feed themselves at 23.7 ± 1.3 d (range: 19–27 d). Female time at nest (%/d) was positively related to the biomass provision rate of the male ($n = 127$ d; $\beta = 0.37$, $r_s = 0.218$, $P = 0.01$, Fig. 4), negatively associated with age of the oldest nestling ($n = 127$ d; $\beta = -1.89$, $r_s = -0.512$, $P < 0.0001$, Fig. 5), and was greater prior to the earliest recording of self-feeding by nestlings ($Z_{126} = 4.31$, $P < 0.001$). Female hawks removed an item from the nest during 11% of the 714 instances where females were recorded leaving the nest. Of those occasions, the female removed a carcass in

60% ($n = 55$) of departures and removed a nestling’s regurgitated pellet in 28% ($n = 25$) of egresses. Adults removed a prey item from the nest but re-delivered it after 2% ($n = 16$) of departures.

DISCUSSION

This study represents the first to use time-lapse video to describe intersexual differences in Ferruginous Hawk prey use, parental care, and provisioning rates. Other studies have used video to describe Ferruginous Hawk provisioning rates without distinguishing between sexes (Giovanni et al. 2007), or used direct observation to describe parental care and nesting behavior from a few nests (Angell 1969, Wakeley 1974). Our goal for this study was to provide empirical data on little-understood aspects of Ferruginous Hawk behavior and feeding ecology to stimulate further research using time-lapse video to aid in conservation of Ferruginous Hawks and their grassland habitat. We found time-lapse video to be an effective tool to collect detailed behavioral observations of a species considered sensitive by most land managers. Although adults did not return to their nest for almost 4 hr following camera installation, they resumed prey delivery and other parental activities, and the six video-monitored nesting pairs successfully fledged all of their offspring. It is possible that our strategy of postpon-

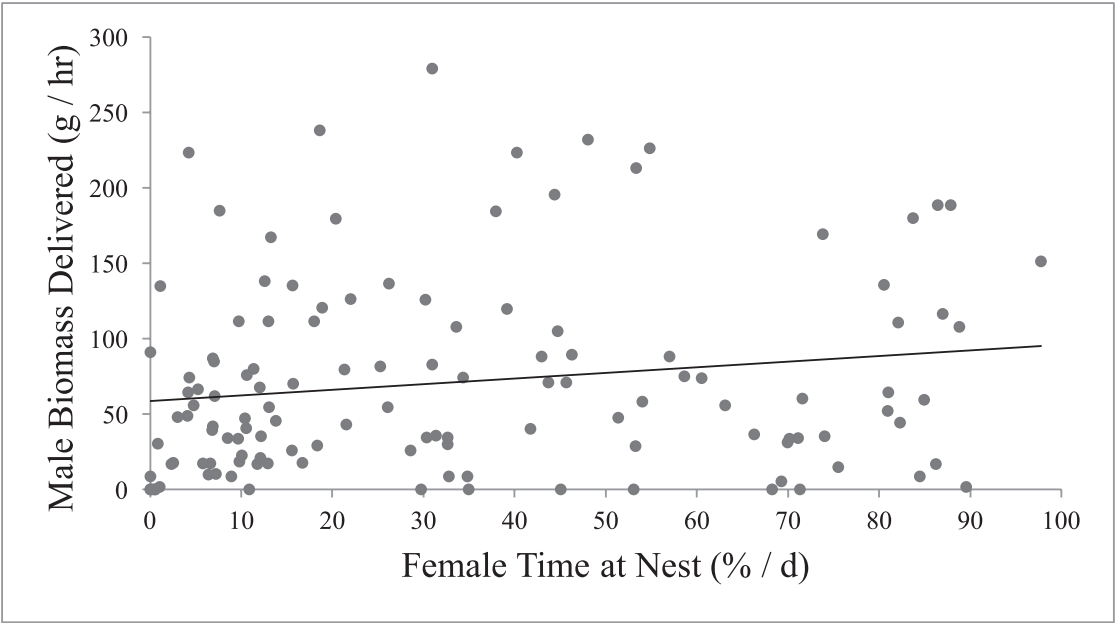


Figure 4. Relationship between male provisioning rate (g/hr) and female nest attendance (%/d) for Ferruginous Hawks nesting in New Mexico, U.S.A., 2004–2005. Data points are not independent of one another.



Figure 5. Relationship between female nest attendance (%/d) and nestling age (d) for Ferruginous Hawks nesting in New Mexico, U.S.A., 2004–2005. Data points are not independent of one another.

ing installation until nestlings were at least 7 d old translated to increased parental investment in their clutch and ultimately contributed to recommencement of parental duties. Our findings align with other studies on Ferruginous Hawk feeding ecology, and offer support for several hypotheses related to foraging theory, including the load-size effect, and the food-niche hypothesis. Taken together, our results can be used to create habitat management plans to benefit the persistence of a sensitive species in peripheral and core habitats.

Data on Ferruginous Hawk provisioning rates using video monitoring is scarce and limited to this study and one conducted by Giovanni et al. (2007), who monitored 12 nests in the southern Great Plains during the same time as our study. Although brood sizes in that study were larger (3.2 vs. 2.3), Ferruginous Hawks in our study provisioned broods with more prey deliveries per hour (0.46 vs. 0.38) and provisioned individual nestlings with 50% more deliveries (0.20 vs. 0.13 deliveries/nestling/hr). Delivery rates of prey items by males in our study were similar to the combined effort by adults in their study. In contrast, Ferruginous Hawks in our study delivered 25% less biomass per nest than did adults at the least-provisioned nestling stage in that study (93 g/hr vs. 129 g/hr) and 50% less biomass in the nestling stage with the highest provisioning rate (176 g/hr). However, when controlled for brood size, hawks in our study delivered only 10% less biomass per hour than documented in the Southern Great Plains study (42 vs. 46 g/nestling/hr). One cause of the difference in provisioning rates may be primary prey species; Ferruginous Hawks in the Southern Great Plains study frequently preyed upon black-tailed prairie dogs (*Cynomys ludovicianus*) and plains pocket gophers (*Geomys bursarius*), both of which have a greater mass than Gunnison's prairie dogs and Botta's pocket gophers, the comparable prey species in our study (Keeley et al. 2016). Indeed, Ferruginous Hawks in our study delivered 250 g less biomass per delivery than hawks did in their study, and 70 fewer g/delivery than Northern Goshawks (*Accipiter gentilis*) nesting in Minnesota (Smithers et al. 2005). However, Ferruginous Hawks in both studies delivered heavier prey, albeit less frequently, than recorded for Swainson's Hawks (*Buteo swainsoni*; Giovanni et al. 2007) or Gyrfalcons (*Falco rusticolus*) nesting in Greenland (Booms and Fuller 2003).

Females spent one-third of the recorded time at the nest, whereas males spent <1% of time at the

nest. As found in other studies on raptors (Wakeley 1974, Schmutz et al. 2014), the primary role of males was to deliver prey. Our results align with those reported for Gyrfalcons (Booms and Fuller 2003); video-monitored males rarely fed nestlings and did not remain at the nest following prey deliveries. Although we observed several instances of males feeding and shading nestlings in the absence of the female, and two instances of males at the nest for >10 min, males spent an average of only 30 sec at the nest following prey deliveries.

We found a strong positive relationship between female nest attendance and the amount of biomass delivered by the male. If males deliver sufficient prey, females may be able to spend more time at nests caring for young (Bukacinska et al. 1996, Wiehn and Korpimäki 1997). Alternatively, when males cannot meet the energetic requirements of the brood, the female may be forced to shift from nestling care to hunting, which may lead to nestling starvation or cause the female to leave the nestlings unattended and susceptible to predation (Newton 1979). This may be especially relevant for Ferruginous Hawks, a species whose nest inattentiveness has been associated with low nest success and productivity (Smith and Murphy 1979, Smith et al. 1981) and whose affinities for unshaded nesting sites (Howard and Hilliard 1980) make them more susceptible to heat stress (Tomback and Murphy 1981). Experimental studies of supplemental feeding support this concept, as female Northern Goshawks that received supplemental food spent more time at or near the nest and raised juveniles with greater nutritional condition and survival rates (Dewey and Kennedy 2001). Our findings also support other studies that indicate that females spend less time at the nest as nestlings age, and are able to thermoregulate and feed themselves independently (Collopy 1984), regardless of food availability or male provisioning rate (Dewey and Kennedy 2001). During the early part of the nestling period, the female may be entirely committed to brooding and may not be free to hunt, even if the male is not provisioning the nest sufficiently (Newton 1979).

We found that nestlings began feeding themselves later (16–18 d) than the age provided by Bechard and Schmutz (1995). This difference may be due to natural variation, weather conditions, or differences in prey use between our study and the studies they used to obtain their estimate, but once this “independence” occurred, females spent less time at the nest. Video from our study indicated that

Ferruginous Hawk nestlings commonly fought one another for prey following delivery, which sometimes caused the adult to stop feeding them and leave the nest. Spending less time at the nest may allow the female to forage, thereby increasing the amount of biomass delivered to the nest (Newton 1979). Our results align with those of Wakeley (1978), who observed female Ferruginous Hawks substantially reducing their time at the nest during the nestlings' third week of life.

Ferruginous Hawks supplied broods with prey at similar rates in the morning and midday, with a possible decrease in the afternoon–evening. Our results contrast those of Wakeley (1974) and Smith and Murphy (1973), who found that adults delivered most prey during crepuscular hours, with a noticeable lull in deliveries during midday. One limitation to this comparison is that we did not isolate provisioning data from the crepuscule; thus, some prey may have been delivered outside of this period, but still included in our “morning” and “afternoon–evening” bins. Nevertheless, this difference in foraging strategy may be related to Ferruginous Hawk prey use, because studies that observed dusk foraging also documented a strict dietary reliance on leporids, which are highly crepuscular, whereas hawks in our study consumed more diurnally active sciurid rodents (Keeley et al. 2016).

Ferruginous Hawks eviscerated approximately one-third of all prey items prior to delivery, which was similar to the rate reported for Gyrfalcons (Booms and Fuller 2003), but lower than the 43% evisceration rate of Richardson's ground squirrels (*Urocitellus 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, Booms and Fuller 2003), or it may be a method to decrease prey mass to minimize energetic expenditure of delivering heavy prey to the nest (i.e., load-size effect; Pennycuik et al. 1989, Korpimäki et al. 1994). Our data suggest all these factors may play a role in shaping Ferruginous Hawk behavior. Females kept nests clear of remnant carcasses and regurgitated pellets, which could attract parasites or predators. Also, desert cottontails and Gunnison's prairie dogs, the heaviest prey items, were eviscerated most often and spotted ground squirrels, one of the lightest, were delivered whole most frequently. In fact, the latter species was delivered alive several times at various nests and was

the only species we observed delivered in this condition. Often the female stood on the nest watching the nestlings pick at the live ground squirrel, which implied that the female may have fostered this behavior. The delivery of live prey to fledglings has also been observed for accipiters and falcons, and presumably helps fledglings develop foraging skills (Newton 1979). With an estimated weight of 88 grams and body length of 16.5 cm (Fitzgerald et al. 1994), the spotted ground squirrel may be optimally sized or docile, both of which may be ideal characteristics that allow nestlings to practice grabbing live prey, a necessary skill for *Buteos* as this is their primary method of dispatching prey (Sustaita and Hertel 2010).

Ferruginous Hawks exhibit pronounced reversed size dimorphism, a trait unique to raptors and skuas (*Stercorarius* spp.), where the female (mean mass: 1776 g) is larger than the male (mean mass: 1163 g; Bechard and Schmutz 1995). One partial explanation offered to account for this characteristic is the food-niche hypothesis, which posits this trait evolved to expand the food-niche of a breeding pair, thereby decreasing intersexual competition for food and maximizing foraging efficiency (Storer 1966, Earhart and Johnson 1970, Newton 1979). In support of this, and similar to patterns reported for Gyrfalcons (Booms and Fuller 2003), females in our study delivered heavier prey items than males and used prey differently. Females delivered the majority of desert cottontails, which represented over one quarter of all biomass delivered by the female but constituted only 7% of all biomass delivered by the male, whereas Botta's pocket gophers represented a substantial portion of biomass delivered by the male. Although males delivered three times more Gunnison's prairie dogs than females, the rodent represented approximately 22% of all prey deliveries for each sex, underscoring the importance of Gunnison's prairie dogs as prey for nesting Ferruginous Hawks (Keeley et al. 2016).

Although our findings emanate from six video-monitored nests, and thus should be interpreted cautiously, we report behaviors never before described for Ferruginous Hawks that support hypotheses on avian nesting strategies, raptor parental roles, and feeding ecology. Our study underscores the interdependence of parental roles: males delivered the majority of prey but females delivered heavier prey items and cared for the nestlings. Further study of Ferruginous Hawks

using video recording is warranted to develop a more complete account of this species' nesting behavior and feeding ecology, particularly in marginal habitat conditions common on the breeding range periphery. Peripheral populations are important to monitor because they may represent persistence in less suitable habitat (Brown 1984, Lawton 1993), may develop unique behavioral traits that allow adaptation to marginal environments (Lesica and Allendorf 1995), and may be the first to respond to climate change (Hampe and Petit 2005). Reports of high survival in peripheral populations following range contractions in core areas of many species (Lomolino and Channell 1995) underscore the high conservation value of peripheral populations. A better understanding of parental roles, feeding ecology, and nesting behavior may ultimately assist Ferruginous Hawk conservation in a changing environment. For instance, our finding of differential prey use between males and females provides empirical justification for managers to direct limited resources to projects that create habitat heterogeneity and, consequently, support a diverse and abundant mammal community.

ACKNOWLEDGMENTS

We thank G.L. Garber, S. Breslin, R.P. Kellermueller, and V.K. Keeley for their assistance and guidance on this project. We thank M.R. Fuller and J.R. Belthoff, and two anonymous reviewers for improving an earlier manuscript. We extend our gratitude to the private landowners in New Mexico who allowed us access to their property. We thank the Bureau of Land Management—Socorro Field Office, Sandpiper Technologies, Olendorf Memorial Library at Snake River Field Station, T. Rosenberry at the Global Raptor Information Network at The Peregrine Fund, Raptor Research Center at Boise State University, New Mexico Ornithological Society, Hawks Aloft, Denver Museum of Nature and Science, and the University of New Mexico Museum of Southwestern Biology for funding and other assistance.

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Received 7 October 2016; accepted 20 April 2017.

Appendix. Mass estimates of all mammal species and mammalian prey categories and the source of the estimates used to calculate prey biomass delivery for breeding Ferruginous Hawks in New Mexico, U.S.A., 2004–2005.

PREY CATEGORY	COMMON NAME	WEIGHT (g)	SOURCE
Unknown Family Sciuridae	-	124	Mean of unknown ground squirrel spp. and young Gunnison’s prairie dog
Unknown ground squirrel spp.	-	88	Mean of thirteen-lined and spotted ground squirrels
<i>Ictidomys tridecemlineatus</i>	Thirteen-lined ground squirrel	88.2	Museum Southwestern Biology (MSB) ^a
<i>Xerospermophilus spilosoma</i>	Spotted ground squirrel	87.9	MSB
<i>Otospermophilus variegatus</i>	Rock squirrel	423	MSB
<i>Cynomys gunnisoni</i>	Gunnison’s prairie dog	557.2	MSB
<i>C. gunnisoni</i> (young)	-	160	Fitzgerald et al. (1994)
<i>Thomomys bottae</i>	Botta’s pocket gopher	170	Smith and Murphy (1973)
<i>Geomys bursarius</i>	Plains pocket gopher	188.5	MSB
<i>Sylvilagus audubonii</i>	Desert cottontail	838.2	MSB
<i>Lepus californicus</i>	Black-tailed jackrabbit	1536	Steenhof (1983)
<i>Peromyscus</i> spp.	-	17	Same as deer mouse
<i>P. maniculatus</i>	Deer mouse	17	Smith and Murphy (1973)
<i>Dipodomys spectabilis</i>	Banner-tailed kangaroo rat	115.5	MSB
<i>D. ordii</i>	Ord’s kangaroo rat	53	Steenhof (1983)
<i>Microtus</i> spp.	-	38	Smith and Murphy (1973)
<i>Neotoma</i> spp.	-	127.2	Mean of desert woodrat and Mexican woodrat
<i>N. lepida</i>	Desert woodrat	124	Steenhof (1983)
<i>N. mexicana</i>	Mexican woodrat	130.4	MSB and DMNS ^b
<i>Onychomys leucogaster</i>	Northern grasshopper mouse	38	Smith and Murphy (1973)
<i>Mustela frenata</i>	Long-tailed weasel	178	Smith and Murphy (1973)
Unknown mammal 1	-	28	Mean of northern grasshopper mouse and deer mouse
Unknown mammal 2	-	119.8	Mean of Botta’s pocket gopher, desert woodrat, Mexican woodrat, spotted ground squirrel and thirteen-lined ground squirrel

^a Vertebrate collection, Museum of Southwestern Biology, University of New Mexico, Albuquerque, NM U.S.A.

^b Vertebrate collection, Denver Museum of Nature and Science, Denver, CO U.S.A.