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Sibling Aggression, Feeding Rates, and Hatch Rank of Nestling Red-shouldered Hawks (*Buteo lineatus*)

Sara J. Miller,[1][†] Cheryl R. Dykstra,[2][*][‡] Virginie Rolland,[3] Melinda M. Simon,[4] Jeffrey L. Hays,[4] and James C. Bednarz[5]

[1]*Arkansas State University, PO Box 599, State University, AR 72467 USA*

[2]*Raptor Environmental, West Chester, OH 45069 USA; ORCID: 0000-0002-9089-3847*

[3]*Department of Biological Sciences, Arkansas State University, Jonesboro, AR 72467 USA*

[4]*RAPTOR, Inc., Milford, OH 45150 USA*

[5]*Biological Sciences Department, University of North Texas, Denton, TX 76203 USA*

ABSTRACT.—In many raptor species, hatching asynchrony results in a size hierarchy among nestlings, which may facilitate brood reduction by means of sibling aggression-induced mortality, especially in times of low food resources. However, few researchers have investigated the relationships among hatching asynchrony, sibling aggression, and nestling feeding rates in raptors. We studied the influence of hatch rank, brood size, and brood age on aggression and feeding rates among Red-shouldered Hawk (*Buteo lineatus*) nestlings in suburban southwestern Ohio. Despite relatively modest hatching asynchrony, nestling hatch rank (along with brood size and brood age) was an important predictor of the amount of aggression exhibited by individual nestlings. The oldest nestlings exhibited more aggressive behavior than younger nestlings, although they did not consume significantly more food. Aggression rates were higher in broods of three than broods of two nestlings, and aggression decreased from week 2 to week 3, post-hatching. However, hatch rank was not an important determinant of nestling food consumption, and food consumption rates were unrelated to sibling aggression rates. Identifiable prey delivered to nestling Red-shouldered Hawks was diverse and consisted of 28.3% birds, 25.7% mammals, 23.4% amphibians, 16.4% reptiles, and 6.2% invertebrates (by biomass). The relatively high percentage of birds in the diet may reflect food availability in the suburban habitat surrounding the nests. Sibling aggression did not result in direct siblicide in our study, but four nestlings apparently starved. Overall, the oldest Red-shouldered Hawk nestlings in our study established their dominance early but this was not associated with a detectable advantage in terms of food consumption.

KEY WORDS: *behavior*; *brood size*; *diet*; *dominance*; *hatching asynchrony*; *nestling*; *urban*.

AGRESIÓN ENTRE HERMANOS, ÍNDICES DE ALIMENTACIÓN Y RANKING DE ECLOSIÓN DE POLLUELOS DE *BUTEO LINEATUS*

RESUMEN.—En muchas especies de aves rapaces, la asincronía en la eclosión da como resultado una jerarquía de tamaño entre los polluelos, lo que puede facilitar la reducción de la nidada por medio de la mortalidad inducida por la agresión entre hermanos, especialmente en épocas de bajos recursos alimenticios. Sin embargo, pocos investigadores han estudiado las relaciones entre la asincronía en la eclosión, la agresión entre hermanos y las tasas de alimentación de los polluelos en las aves rapaces.

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[*] Corresponding author: cheryldykstra@gmail.com

[†] Present address: RSPB UK Headquarters, The Lodge, Sandy, Bedfordshire, SG19 2DL, United Kingdom.

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Estudiamos la influencia del ranking de eclosión, el tamaño de la nidada y la edad de la nidada en la agresión y las tasas de alimentación entre polluelos de *Buteo lineatus* en los suburbios del suroeste de Ohio. A pesar de una asincronía en la eclosión relativamente moderada, el ranking de eclosión de los polluelos (junto con el tamaño y la edad de la nidada) fue un predictor importante de la cantidad de agresión exhibida por los polluelos individuales. Los polluelos mayores exhibieron un comportamiento más agresivo que los polluelos más jóvenes, aunque no recibieron una cantidad significativamente mayor de alimento. Las tasas de agresión fueron más altas en las nidadas de tres que en las nidadas de dos polluelos, y la agresión disminuyó de la semana dos a la semana tres después de la eclosión. Sin embargo, el ranking de eclosión no fue un determinante importante del consumo de alimentos de los polluelos, y las tasas de consumo de alimentos no estuvieron relacionadas con las tasas de agresión entre hermanos. Las presas identificables entregadas a los polluelos de *B. lineatus* fueron diversas y consistieron en 28.3% de aves, 25.7% de mamíferos, 23.4% de anfibios, 16.4% de reptiles y 6.2% de invertebrados (por biomasa). El porcentaje relativamente alto de aves en la dieta puede reflejar la disponibilidad de alimentos en el hábitat suburbano que rodea los nidos. La agresión entre hermanos no resultó en un fratricidio directo en nuestro estudio, pero aparentemente cuatro polluelos murieron de hambre. En general, los polluelos más viejos de *B. lineatus* en nuestro estudio establecieron su dominancia de forma temprana, pero esto no se asoció con una ventaja detectable en términos de consumo de alimentos.

[Traducción del equipo editorial]

INTRODUCTION

Raptors (Strigiformes, Falconiformes, and Accipitriformes) exhibit asynchronous hatching (Newton 1979), which typically results in a size hierarchy among nestlings associated with their hatch rank; the first-hatched nestling is often larger and behaviorally more advanced and the later-hatched siblings are progressively smaller. The larger, first-hatched nestling often establishes dominance at the beginning of the nestling period (Drummond et al. 1986) to gain an advantage over its siblings (Hahn 1981, Morandini and Ferrer 2015) and may compete with its siblings by acquiring more food from parents or by exhibiting aggression toward siblings (O'Connor 1978, Mock 1984). Nestling raptors of at least 11 species exhibit sibling aggression and competition (e.g., Byholm et al. 2011, Szojka et al. 2020, Walls and Kenward 2020, Mee et al. 2021, Soravia et al. 2021, and references therein). The severity of aggression seems to vary with species' size; large species often exhibit intense sibling aggression leading to obligate or facultative siblicide, medium-sized species occasionally show aggression and brood reduction, especially when food availability is low, and small species typically have no aggression-related brood reduction (Newton 1979). A meta-analysis of sibling aggression in 65 raptor species demonstrated that intensity of sibling aggression was greater in species with smaller clutch sizes and lower rates of food provisioning (Redondo et al. 2019).

Sibling aggression and competition can lead to brood reduction, either directly by siblicide or indirectly by starvation, as the aggressive nestlings may prevent smaller nestlings from accessing sufficient food (Stinson 1979, Morandini and Ferrer 2015). Brood reduction is related to feeding rates or food shortages among Swainson's Hawks (*Buteo swainsoni*; Bechard 1983), Madagascar Buzzards (*Buteo brachypterus*; Raveloson et al. 2021), Northern Goshawks (*Accipiter gentilis*; Estes et al. 1999, Lewis 2017), Ospreys (*Pandion haliaetus*; McLean and Byrd 1991, Steidl and Griffin 1991), and Tengmalm's/ Boreal Owls (*Aegolius funereus*; Valkama et al. 2002), and food supplementation can improve survival of last-hatched nestling raptors (Nägeli et al. 2022).

Sibling aggression does not always result in brood reduction, and instead may simply enable the dominant nestling(s) to acquire more food. The amount and intensity of such sibling aggression may vary with the amount of food available and may be influenced by a nestling's level of hunger (Morandini and Ferrer 2015). For example, experimental food deprivation triggered greater sibling aggression in nestling Ospreys (Machmer and Ydenberg 1998) and other species (Drummond 2001). Sibling aggression of broods of young nestling Black Kites (*Milvus migrans*) was inversely related to the amount of food biomass delivered to the nest (Viñuela 1999). Among Northern Goshawks, inexperienced females fed their young less often and the hungry nestlings exhibited more sibling aggression (Byholm et al. 2011).

In an experimental study of Red-shouldered Hawks (*Buteo lineatus*) in rural northeastern Arkansas, broods supplemented with food experienced decreased sibling aggression compared with control

broods (Townsend 2006), a response typical of many avian species (Morandini and Ferrer 2015). This suggests that if nestlings' appetites can be sufficiently satiated, there is less aggression and competition among siblings (Machmer and Ydenberg 1998, Morandini and Ferrer 2015), which may increase the nestling fledging success (González et al. 2006). Townsend (2006) also found that first-hatched nestlings were more aggressive and received more food than later-hatched siblings, but inferences from that study may be limited due to the lack of standardization for nestling age or brood size, and the small sample size.

In southwestern Ohio, we and others studied a suburban population of Red-shouldered Hawks from 1997 to 2019 (Dykstra et al. 2000, 2019, 2021a). Generally, Red-shouldered Hawks in this population engage in courtship behaviors and construct or refurbish nests from mid-February to mid-March, with egg laying beginning in mid- to late March (Dykstra et al. 2020, 2021b). Clutch size typically ranges from two to four eggs (Portnoy and Dodge 1979, Miller et al. 2020) and incubation lasts about 33 d per egg (Miller et al. 2020). Eggs hatch asynchronously (Miller et al. 2020), though nestling asynchrony is relatively modest compared to larger raptors (on average, 0.6 d between the first and second nestlings, and 1.2 d between the second and third nestling; Miller et al. 2020). Young fledge in approximately 6 wk (Wiley 1975, Portnoy and Dodge 1979). Within this population, adult Red-shouldered Hawks are resident year-round (Dykstra et al. 2001, 2019).

Our objectives were to understand the effects of hatch rank, brood age, and brood size on sibling behavioral interactions and feeding rates. We quantified prey delivery rates and types, nestling feeding rates, and aggressive sibling behaviors for two years (2011 and 2012). Because research on most other raptor species indicates that aggressive behavior tends to be most prevalent when nestlings are young (Meyburg 1974, Gargett 1978, Viñuela 1999, Soravia et al. 2021), we focused on the second and third week of the nestling phase. We expected that prey delivery rates and types would be similar to those previously reported for this population (Dykstra et al. 2003), but we expected greater accuracy in prey identification because our methods included video recordings at the nest. Based on previously published studies, we predicted that hatch rank would determine the dominance hierarchy among nestlings (Gonzalez-Voyer et al. 2007) and that the

first-hatched nestling would be more aggressive than younger siblings and consume the most food (Gerhardt et al. 1997, Morandini and Ferrer 2015). Finally, we predicted that overall (whole-brood) feeding rates would be inversely related to aggression rates among nestlings (as in Machmer and Ydenberg 1998, Viñuela 1999).

METHODS

Study Area. Our study area included suburban development surrounding the city of Cincinnati, Ohio, USA, in Hamilton, Clermont, and Warren Counties (elevation 140 to 270 masl). This part of the Interior Plateau ecoregion (Omernik 1987) is hilly and unglaciated and dissected by two large rivers, the Great Miami River and the Little Miami River, and numerous small streams in ravines and valleys. Second-growth oak-hickory (*Quercus* spp., *Carya* spp.) and beech-maple (*Fagus grandifolia*, *Acer saccharum*) associations characterize native upland forests. American sycamores (*Platanus occidentalis*) and beech dominate the bottomland riparian forests.

Suburban portions of the study area varied from densely populated (residential lots approximately 20 × 35 m) to sparsely populated (>2.5-ha residential lots, as well as undeveloped private land; Dykstra et al. 2000). Red-shouldered Hawk nests were typically located in private yards of residences surrounded by nonnative and planted native vegetation, but near native forest land in steep upland ravines or more level riparian or wet forest areas (Dykstra et al. 2003). Other non-residential portions of the study area include heavily used recreational lands (Dykstra et al. 2000).

Selection of Nests for Monitoring. We visited previously known Red-shouldered Hawk territories (Dykstra et al. 2000, 2009) from mid-February until the end of March to locate nests and determine occupancy. We considered a nest occupied if it had been improved with fresh sticks or green vegetation (Dykstra et al. 2000), and active if there was evidence that eggs had been laid, such as an incubating parent, small down feathers around the edge of the nest, or broken eggshells below the nest (Miller et al. 2015, 2020).

Video Monitoring. In 2011 and 2012, we installed video cameras at selected occupied nests either before eggs were laid or after eggs hatched in active nests (Miller et al. 2015, 2020). We selected the camera nests based on the suitability of the tree/nest for a camera placement that allowed a good view of

nest contents, safe access for climbers, and permission from landowners; these nests represented a small fraction of the known occupied nests in our study area (generally >100 per year; Dykstra et al. 2009, 2021a). All nests studied were in trees on private land. To avoid pseudoreplication, no nests were video-monitored in both years. We mounted cameras between 7 March and 10 May 2011, and 28 February and 9 May 2012. For nests with post-hatching installation, cameras were deployed when nestlings were estimated to be 4–10 d old, during mild to moderate weather conditions (e.g., no precipitation, low wind, or low sun exposure), with a minimum temperature of 15.5°C.

The digital video monitoring systems comprised a 24-hr time-lapse color/infrared video camera and a mini digital video recorder, powered by one deep-cycle 12-Volt marine battery. For more details of camera systems and installation, see Miller et al. (2020). SJM visited each camera nest every 3 d to exchange the memory card and battery. We removed cameras after nest failure or after nestlings fledged.

Measuring and Marking Nestlings. During the first week after hatching at nests where a camera was installed prior to egg laying, or during camera installation at post-hatching installation sites, we briefly removed the young from the nest for measurements and marking. We collected morphometric data including mass and wing chord, and if possible, tarsus length, seventh primary length, first and second secondary lengths, and toe pad length, depending on the development of the nestlings. Mass was measured with a Pesola spring scale (Schindellegi, Switzerland) to the nearest 5 g, and all other measurements were made with a ruler to the nearest 1 mm.

To differentiate nestlings in video recordings, we marked each on its head with a non-toxic Sprayolo liquid livestock dye (PBS Animal Health, Massillon, OH, USA), as in Townsend (2006). We assigned dye colors haphazardly and applied dye to the top of each nestling's head with a cloth or cotton balls. We returned nestlings to their nest within approximately 30 min. We monitored all nests post-marking/measuring and determined that nearly all parents resumed normal behavior within a short time (typically within 1 hr); adults at one nest where a camera was installed at 13 d post-hatching did not completely resume normal behavior until we removed the camera the next day (Miller et al. 2020). When nestlings were 2–4 wk old (but before the dye on their heads faded), we climbed to the nest again

and banded each nestling with an aluminum US Geological Survey (USGS) leg band on one leg and a unique, plastic, colored alpha-numeric band (Haggie Engraving Company, MD, USA) on the other. We also re-dyed the nestlings' heads and again collected morphometric data, including mass, wing chord, tarsus length, seventh primary length, first and second secondary lengths, and toe pad length. Nestlings were returned to their nest within 30 min.

We used the mean length of the first and second secondaries and the regression equation in Penak et al. (2013) to estimate the ages of nestlings in nests where the camera was installed post-hatching. For nests where cameras were installed prior to egg laying, hatch date of young was known within 0.25 d because of constant video-monitoring (Miller et al. 2020).

To rank nestlings by age, we compared the morphometrics of nestlings within each brood, using either mean secondary length (longer=older) for nestlings with measurable secondaries, or other measurements (e.g., wing chord) for nestlings with no measurable secondaries. In subsequent video analyses, we recorded feeding and aggressive behaviors of each nestling according to their rank: first-hatched nestling (rank "A"), second-hatched nestling (rank "B"), third-hatched nestling (rank "C"), fourth-hatched nestling (rank "D").

Video Data Sampling and Analysis. To subsample the large amount of video recorded during the nestling period, we selected nests that were recorded for the entirety of the second week (days 8–13) and/or third week (days 15–20) of the nestling period, and contained at least two nestlings during those periods. "Brood age" was assigned according to the age of the oldest nestling. Because most nestlings were dye marked during the first week after hatching, this week was excluded from analyses. If nestlings were not marked until the second week, we included only the third week in the analyses. If a nest was recorded during the second week, but failed before the third week ended, we included only the second week in the analyses.

In addition, we used a stratified random method to subsample each nest-week of video data. We divided each day into three 5-hr blocks between 0600 H and 2100 H (EST), based on the average length of day including civil twilight. To achieve a balanced sampling from all broods, we elected to extract data from an even number of days for each week of brood age; therefore, we sampled from 6 d of both the second and third week of brood age. We randomly

selected which time block to review for each of 6 d, during both the second and third nest-weeks, ensuring that each time block was reviewed in two different days in the 6-d week. This method created a 30-hr set of data equally distributed among the morning, midday, and evening time blocks, and spread over 6 d for each nest-week.

SJM reviewed the selected video recordings for each nest and recorded all feeding and aggression data. For prey delivery and feeding analyses, we identified which parent delivered prey and which fed the nestlings; individual identification was based on differences in the body size, plumage, or tail band patterns of each adult (Supplemental Material Fig. S1), with the female identified during egg laying (or early brooding for cameras installed post-hatching, assuming that the female parent does most of the brooding [Dykstra et al. 2020]). We identified each prey item to the lowest possible taxonomic level and classified the prey by approximate size (small, medium, large) relative to the adult hawk's bill size for prey classes with multiple sizes observed (i.e., passerines, frogs, snakes, and leeches; Table S1). We also recorded the number of "bites" each marked nestling consumed. We used previous calculations of prey mass (Dykstra et al. 2003) to estimate the mass of different prey types. To calculate an estimate of mass per bite for each prey type, we divided the estimated mass of a prey item by the number of bites required to consume one whole prey item of that type (Table S1). We used this mass/bite to calculate an estimate of the mass of food each nestling (rank A, B, C, or D) consumed during each feeding session, according to prey type. We totaled the mass of food consumed per nestling per 30-hr "week" for further comparisons. The 30-hr summation was selected (1) because the temporal stratification of 5-hr video blocks we analyzed (morning, midday, evening) would have required another random variable to account for any variance in food delivery rates throughout the day, (2) because the low number of aggressive acts per 5-hr block necessitated a weekly summation and we wanted to keep analyses consistent, and (3) because it allowed comparison with earlier studies (Snyder and Wiley 1976, Dykstra et al. 2003).

For nestling behavior analyses, we recorded incidences of sibling aggression, including identity of the aggressor and the receiver of aggressive acts (nestling rank A, B, C, or D), each nestling's age, whether the aggression occurred during a feeding, and the type of aggression. We classified type of aggression into five categories: head peck, body peck, beak bite, bite and twist, or tug-of-war (Poole 1979, Anderson et al. 1993, Boal and Bacorn 1994, Townsend 2006). We totaled the number of aggressive acts per nestling per 30-hr "week" for further comparisons.

Statistical Analyses. We examined two response variables—the amount of food consumed (total mass in g) and the number of aggressive acts—at both nestling and brood levels, in the computing software program R (R Core Team 2021). At the brood level, we summed the total amount of food consumed and the total number of aggressive acts displayed by all nestlings within each nest but separately for the second and third weeks of observation. At the nestling level, the measures of these two response variables were analyzed for each nestling. For both the nestling- and brood-levels, we analyzed the normally distributed "amount of food consumed" variable with linear mixed models using the function *lmer* in the R package *lme4* (Bates et al. 2015); for the overdispersed "number of aggressive acts" variable that had an excess of zeros, we used generalized linear mixed models (R package *glmmTMB* with the function *glmmTMB*; Brooks et al. 2017) with a zero-inflated negative binomial error distribution. For both response variables (food consumed and number of aggressive acts) at both nestling and brood levels, nest ID was a random effect to account for the variability among siblings (nestling level) and among nests that were associated with two separate weeks of data (nestling and brood levels).

Parent birds may be able to distinguish color on nestlings and may preferentially feed young with some color patterns (Dugas 2009). Similarly, nestlings might exhibit more aggressive behavior toward siblings with specific color patterns. Therefore, at the nestling level, we first tested for a fixed effect of the color of dye applied on both response variables. Additionally, because we collected data over two years, we also tested for a possible confounding year fixed effect. Once controlled for color and year (if needed), we compared models of both response variables at the nestling level with single, additive, and two-way interaction effects of hatch rank, brood size, and brood age (i.e., second or third week posthatching). However, the interaction between hatch rank and brood size was not possible without reducing the size of the data set, because third-ranked nestlings only belonged to broods of three. For the same reason, we tested whether brood size

was correlated with hatch rank or brood age by computing a squared generalized variance inflation factor (GVIF^2) for the food-consumed model with all additive predictors using function *vif* in package *car* (Fox and Weisberg 2019). A GVIF^2 < 2 indicates no multicollinearity (Hair et al. 2009).

In a second phase of analysis for the number of aggressive acts at the nestling level, we also considered amount of food consumed as a predictor as well as the additive or interaction effect of this variable with hatch rank or brood size depending on the best model for aggressive acts in the first phase. At the brood level, we used the same approach with brood size and brood age as fixed effects but dropped the nestling-level variable "hatch rank."

We compared single, additive, and interaction models for both response variables at both levels using the Akaike Information Criterion corrected for small sample size (AIC$_c$) using package *AICcmodavg* (Mazerolle 2020); the best model was that with the lowest AIC$_c$ (Anderson 2008). However, if two models were within a ΔAIC$_c \leq 2$, we applied the principle of parsimony (Burnham and Anderson 2002) and retained the model with fewer parameters. As a post-hoc test, we estimated the 95% confidence intervals for the difference of means (β) using the package *emmeans* (Lenth 2022) to determine which categories differed significantly when a predictor had more than two categories (e.g., hatch rank has three categories: first-, second-, and third-hatched); the effect was considered significant at $\alpha = 0.05$ if zero was not included in the confidence interval. Mean estimates of food consumed and aggressive acts are reported ± 1 SE.

RESULTS

In 2011 and 2012, we monitored 25 Red-shouldered Hawk nests with video cameras. In 2011, 11 nests received cameras: five prior to egg laying, and six after eggs hatched. In 2012, we installed cameras at 10 occupied nests prior to egg laying and at four nests after hatching. At all nests where cameras were installed during courtship, the birds laid eggs in their respective nest, suggesting that the installation caused little or no disturbance (Miller et al. 2020).

Of the 25 video-monitored nests, 20 had at least two nestlings that hatched, and we recorded 661 d of video at these nests. Of these 20 nests, three nests were excluded because they did not fit the review criteria described above (see Video Data Sampling and Analysis). Nine nests were reviewed for the second and third weeks, two nests were reviewed for

the second week only, and six nests were reviewed for the third week only (total 780 hr of video at 17 different nests, or 26 nest-weeks). For analyses of nestling feeding rates and aggression rates, we excluded the only nest with a brood of four nestlings, and thus included only broods of two or three in the analyses, for a total of 16 different nests, or 25 nest-weeks (750 hr) during weeks 2 and 3. However, the four-nestling brood was included in analyses of prey types and delivery rates.

Prey Types and Delivery Rates. At all nests, both the male and female parent delivered prey. Of the 457 prey deliveries for which the sex of the parent could be determined, male parents delivered 48.2% (range = 10.9–80.0%, *n* = 17 nests) and females delivered 51.8% (range = 20.0–89.1%, *n* = 17 nests). However, these results may not reflect which parent captured the prey, as males sometimes delivered prey to the female at an off-camera location, and the female then delivered it to the nest (C. Dykstra and S. Miller, unpubl. data). Of the 795 total prey items delivered by parents and consumed by nestlings, we identified 659 (82.8%) to taxonomic class, with a total biomass of 16,127 g (Table 1). We classified 95.6% of identified prey to a lower taxonomic level, ranging from order to species. Overall mean prey delivery rate was 1.02 ± 0.56 prey items/hr, or a biomass of 22.4 ± 6.0 g/hr, across nest-weeks 2 and 3. Segmented worms (class Clitellata), such as earthworms and leeches, made up the greatest proportion of prey items consumed (32.3%) but only 5.7% of the total biomass. Passerine birds, small mammals, and amphibians composed the greatest proportions of biomass consumed by nestlings (28.3%, 25.7%, 23.4%, respectively; Table 1). Invertebrates made up a greater proportion of the diet (by frequency) in week 3 than in week 2 (Table S2).

Feeding Rates. Females almost always fed the nestlings (97.0%; range = 56.8–100%, *n* = 17 nests); males rarely fed young (3.0%; range = 0–43.2%, *n* = 17 nests [total of 463 feeding events]) and usually only fed small prey items such as worms. The model that included dye color did not improve the null model (Table 2), indicating that the different dye colors applied to nestlings' heads did not influence the amount of food individual nestlings consumed. Similarly, the model with year did not perform better than the null model at the nestling or at the brood level (Table 2), suggesting no difference in amount of food consumed between years.

At the nestling level, the food-consumed model with all additive predictors (hatch rank, brood size,

Table 1. Identifiable prey fed to nestling Red-shouldered Hawks in Cincinnati, Ohio, documented by video monitoring in 2011 and 2012.

Prey Types	Biomass (g) Identified to Class or Subclass (%)	Number Identified to Class or Subclass (%)	Number Identified to Lower Taxonomic Level
Class Aves	4560.5 (28.3)	116 (17.6)	
Order Passeriformes			107
Family Turdidae			
Turdus migratorius (American Robin)			7
Family Paridae			
Poecile carolinensis (Carolina Chickadee)			1
Family Sittidae			
Sitta carolinensis (White-breasted Nuthatch)			1
Class Mammalia	4148.4 (25.7)	114 (17.3)	
Unidentified mammals			29
Order Insectivora			
Family Soricidae			36
Blarina brevicauda (shorttail shrew)			10
Family Talpidae			
Scalopus aquaticus (eastern mole)			5
Order Lagomorpha			
Family Leporidae			
Sylvilagus floridanus (eastern cottontail)			8
Order Rodentia			
Family Cricetidae			7
Microtus spp. (mice)			4
Family Sciuridae			
Tamias striatus (eastern chipmunk)			15
Class Amphibia	3768.6 (23.4)	121 (18.4)	
Order Anura			115
Family Ranidae			
Lithobates sp.			1
Lithobates catesbeianus (bullfrog)			5
Class Reptilia	2635.0 (16.4)	82 (12.4)	
Order Testudines			2
Order Squamata[a]			54
Family Colubridae			
Pantherophis spiloides (midland rat snake)			2
Family Natricidae			
Thamnophis spp. (garter or ribbon snakes)			24
Class Clitellata			
Subclass Oligochaeta (unidentified earthworms)	663.0 (4.1)	174 (26.4)	0
Subclass Hirudinea (unidentified leeches)	252.2 (1.6)	39 (5.9)	0
Class Crustacea	85.8 (0.5)	12 (1.8)	
Order Malacostraca (crayfish)			12
Class Actinopterygii (ray-finned fishes)	13.7 (<0.1)	1 (<0.1)	0
TOTAL	**16,127**	**659**	

[a] Prey consisted entirely of snakes.

and brood age) had $GVIF^2 = 1.00–1.02$, indicating no correlation among predictors. The best overall model incorporated all three predictors, with an interaction between brood size and age (Table 3).

However, this model was within $\Delta AIC_c \leq 2$ of the model without hatch rank (Table 3), suggesting that hatch rank did not influence the amount of food consumed. Overall, the mean amount of food

Table 2. Effect of year and color dye on amount of food consumed and number of aggressive acts at the nestling and brood levels in Red-shouldered Hawks ($n = 70$ nestlings from 16 nests) in Cincinnati, Ohio, in 2011–2012. Food models were linear mixed models, whereas aggression models were zero-inflated negative binomial mixed models, both with nest ID as a random effect. Italicized and bolded models are both the best (i.e., $\Delta AIC_c \leq 2$) and most parsimonious models.

			Nestling Level		Brood Level	
Confounding Predictor	Model	K^a	AIC_c^b	ΔAIC_c^c	AIC_c^b	ΔAIC_c^c
Amount of food consumed	*None (null model)*	*3*	***787.0***	***0.0***	***334.0***	***0.0***
	Year	4	789.1	2.1	336.7	2.7
	Color dye	9	796.1	9.1	NA	NA
Number of aggressive acts	*None (null model)*	*3*	***466.0***	***0.0***	***230.8***	***0.0***
	Year	4	466.5	0.5	233.0	2.2
	Color dye	9	474.7	8.7	NA	NA

[a] K is the number of parameters in the model.
[b] AIC_c is the Akaike Information Criterion corrected for small samples.
[c] $\Delta AIC_c = AIC_c - \min AIC_c$.

Table 3. Effect of brood age (second or third week post-hatching), brood size, and hatch rank on amount of food consumed and number of aggressive acts at the nestling and brood levels in Red-shouldered Hawks ($n = 70$ nestlings from 16 nests) in Cincinnati, Ohio, in 2011–2012. Food models were linear mixed models, whereas aggression models were zero-inflated negative binomial mixed models, both with nest ID as a random effect. Italicized and bolded models are both the best (i.e., $\Delta AIC_c \leq 2$) and most parsimonious models.

			Nestling Level		Brood Level	
Response Variable	Model	K^a	AIC_c^b	ΔAIC_c^c	AIC_c^b	ΔAIC_c^c
Amount of food consumed	Age*Size+Rank	8	781.75	0.00	NA	NA
	Age*Size	6	*782.29*	*0.54*	336.63	3.40
	Age+Rank	6	785.00	3.25	NA	NA
	Age	4	785.62	3.87	336.50	3.26
	Rank	5	786.27	4.52	NA	NA
	None (null model)	3	786.96	5.21	*333.96*	*0.73*
	Age+Size	5	786.99	5.24	335.50	2.27
	Age+Size+Rank	7	787.09	5.34	NA	NA
	Size	4	787.57	5.82	333.23	0.00
	Rank+Size	6	787.81	6.06	NA	NA
	Age*Rank	8	789.87	8.12	NA	NA
	Age*Rank+Size	9	792.12	10.37	NA	NA
Number of aggressive acts	Age+Size+Rank	7	*447.16*	*0.00*	NA	NA
	Age*Size+Rank	8	449.71	2.55	NA	NA
	Age*Rank+Size	9	450.52	3.36	NA	NA
	Age+Rank	6	452.36	5.20	NA	NA
	Age*Rank	8	455.04	7.88	NA	NA
	Age+Size	5	457.11	9.95	*228.30*	*0.00*
	Rank+Size	6	457.78	10.61	NA	NA
	Age*Size	6	459.49	12.32	231.75	3.44
	Rank	5	460.14	12.98	NA	NA
	Age	4	460.82	13.66	230.78	2.48
	Size	4	465.25	18.08	230.61	2.30
	None (null model)	3	466.00	18.83	230.82	2.52

[a] K is the number of parameters in the model.
[b] AIC_c is the Akaike Information Criterion corrected for small samples.
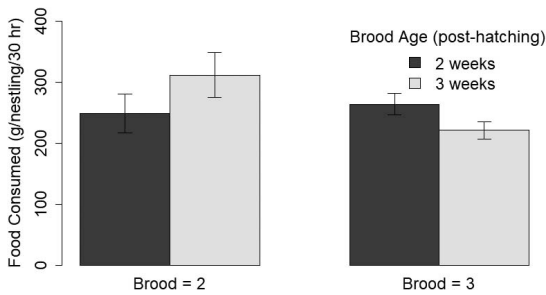[c] $\Delta AIC_c = AIC_c - \min AIC_c$.

Figure 1. Mean amount of food consumed by Red-shouldered Hawk nestlings ($n = 70$ nestlings from 16 nests) in Cincinnati, Ohio, in 2011–2012. Error bar represents 1 SE. Estimates were extracted from the most parsimonious nestling-level linear mixed model with an interaction of brood size (two or three nestlings) and brood age (weeks post-hatching) as fixed effects and nest ID as a random effect.

consumed by nestlings was 256 ± 16.6 g/nestling/30 hr. Food consumption by first-hatched nestlings (269 ± 18.1 g/nestling/30 hr dataset) was not significantly higher than for second-hatched nestlings (265 ± 18.1 g/nestling/30 hr) or third-hatched nestlings (235 ± 20.1 g/nestling/30 hr). Although the amount of food consumed did not differ between brood sizes ($\beta = 14.68$ [95% CI: −54.08 to 83.44] g/nestling/30 hr) or brood ages ($\beta = 62.52$ [95% CI: −7.04 to 132.07] g/nestling/30 hr), the negative interaction ($\beta = -105.61$ [95% CI: −181.45 to −29.78] g/nestling/30 hr) indicates that nestlings in broods of three consumed less food in week 3 than in week 2, whereas nestlings in broods of two

consumed more food in week 3 than in week 2; Fig. 1).

At the brood level, the food-consumed model with both predictors (brood age and size) had a $GVIF^2 = 1.04$, indicating that brood age and size were not correlated. The best overall model was the null model (Table 3); the summed amount of food consumed by all nestlings at each nest (669 ± 13.9 g/30 hr) was not associated with brood size or age.

Aggression Rates. The model that included dye color applied to nestlings did not improve the null model (Table 2), indicating that the different dye colors applied to nestlings' heads did not influence the number of aggressive acts exhibited by individual nestlings toward siblings. Similarly, the model with year did not outperform the null model at the nestling or brood level (Table 2), suggesting no difference in the number of aggressive acts between years. We did not document direct siblicide in our study; however, four nestlings apparently starved; two of these were last-hatched young that died in their first week of life (Barre and Whalen nests; Miller et al. 2015).

At the nestling level, the best overall model incorporated all three predictors in additive effects (Table 3). The first-hatched nestling committed 4.53 ± 1.85 aggressive acts/30 hr on average, but the number of aggressive acts was lower for second-hatched nestlings ($\beta = -0.94$ [95% CI: −1.55 to −0.292] acts) or third-hatched nestlings ($\beta = -1.55$ [95% CI: −2.310 to −0.805] acts) than for first-hatched nestlings, increased with brood size ($\beta = 1.81$ [95% CI: 0.54 to 3.08] acts), and decreased with brood age ($\beta = -0.94$ [95% CI: −1.45 to −0.43] acts;
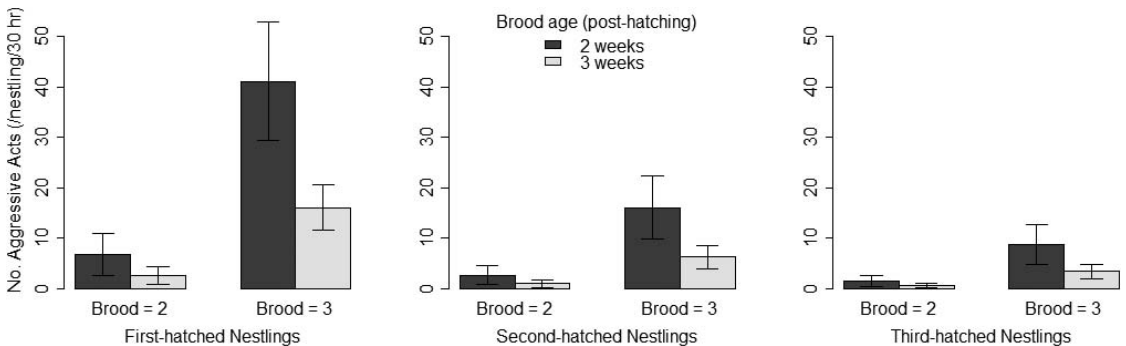

Figure 2. Mean number of aggressive acts displayed by Red-shouldered Hawk nestlings ($n = 70$ nestlings from 16 nests) in Cincinnati, Ohio, in 2011–2012. Error bar represents 1 SE. Estimates were extracted from the best nestling-level zero-inflated negative binomial linear mixed model with additive effects of hatch rank, brood size (two or three nestlings), and brood age (weeks post-hatching) as fixed effects and nest ID as a random effect.
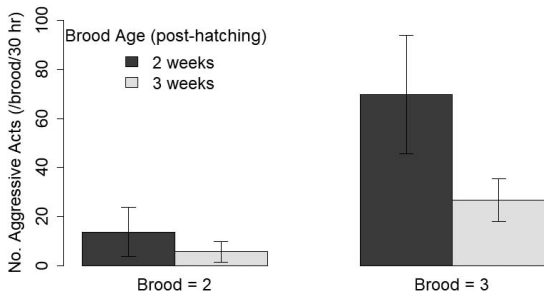
Figure 3. Mean number of aggressive acts displayed by Red-shouldered Hawk broods ($n = 16$ nests) in Cincinnati, Ohio, in 2011–2012. Error bar represents 1 SE. Estimates were extracted from the best brood-level zero-inflated negative binomial linear mixed model with additive effects of brood size two or three nestlings) and brood age (weeks post-hatching) as fixed effects and nest ID as a random effect.

Fig. 2). At the brood level, the best overall model included an additive effect of brood age and brood size (Table 3). Broods exhibited 19.1 ± 8.29 aggressive acts/30 hr on average, with fewer aggressive acts as the broods aged ($\beta = -0.89$ [95% CI: -1.62 to -0.15] acts/nest) but with more aggressive acts for broods of three ($\beta = 1.56$, 95% CI: 0.21 to 2.90 acts/nest) than for broods of two (Fig. 3).

Relationships between Feeding and Aggression Rates. Adding the amount of food consumed as a predictor to the best nestling-level aggression model did not improve its fit, suggesting that the individual number of aggressive acts was not influenced by the amount of food consumed (Table 4). Similarly, adding the summed total amount of food consumed per brood did not improve the fit of the best brood-level aggression model (Table 4), suggesting no

effect of total amount of food on total amount of aggression in each nest.

DISCUSSION

Sibling aggression in raptors has important implications for nestling survival and thus parent birds' reproductive rate (Lack 1947). Even nonlethal sibling aggression (Table S3) can influence the health and fitness of the youngest nestling (Wiebe and Bortolotti 1994, Bakaloudis et al. 2020). For species exhibiting facultative brood reduction, such as the Red-shouldered Hawk (Townsend 2006, Dykstra et al. 2020), the occurrence of siblicide is often thought to be related to food availability (Stinson 1979, Mock et al. 1990, Morandini and Ferrer 2015). Thus, evaluating the relationship between aggression and food consumption is important for understanding brood reduction by siblicide and ultimate drivers of behavior (Morandini and Ferrer 2015). Our study on the behavior of Red-shouldered Hawks showed that nestling hatch rank was an important predictor of the amount of aggression exhibited by nestlings, supporting our prediction. The oldest nestling exhibited significantly more aggressive behavior than younger siblings, even though nestlings' age differences in this species are relatively small (0.6–2.4 d; Miller et al. 2020). Broods of three had higher aggression rates than broods of two, and aggression decreased from week 2 to week 3 post-hatching. However, hatch rank was not as important in determining nestling food consumption; the most parsimonious model included only brood age and brood size as predictors, and food consumption did not differ significantly among nestlings of different ranks. Similarly, the overall (brood-level) rates of food consumption were not related to rates of brood aggression, which was

Table 4. Effect of the amount of food consumed (g) on the number of aggressive acts at the nestling and brood levels in Red-shouldered Hawk ($n = 70$ nestlings from 16 nests) in Cincinnati, Ohio, in 2011–2012. Models were zero-inflated negative binomial mixed models, with nest ID as a random effect, and a combination of brood age, brood size, and hatch rank as fixed effects based on the best aggression model identified in Table 3. Italicized and bolded models are the best (i.e., $\Delta AIC_c \leq 2$) models.

Level Considered	Model	K^a	AIC_c^b	ΔAIC_c^c
Nestling level	*Age+Size+Rank*	7	***447.2***	***0.0***
	Age+Size+Rank+Food	8	449.7	2.5
Brood level	*Age+Size*	5	***228.3***	***0.00***
	Age+Size+Food	6	231.7	3.4

[a] K is the number of parameters in the model.
[b] AIC_c is the Akaike Information Criterion corrected for small samples.
[c] $\Delta AIC_c = AIC_c - \min AIC_c$.

contrary to our prediction and suggests that the relationship between food consumption, aggression, and hatch rank is complicated.

Food Consumption and Aggression. Nestling rank was the most important predictor for determining the differences in the number of aggressive acts displayed by each nestling. Consistent with other raptor studies (Gerhardt et al. 1997, Townsend 2006, Morandini and Ferrer 2015), we found that the first-hatched Red-shouldered Hawk nestlings exhibited the most aggressive behavior compared to later-hatched nestlings. At the brood level, brood age and brood size together predicted the total amount of aggression within a nest. Increasing aggression with increasing brood size (Morandini and Ferrer 2015) and decreasing aggression as nestlings age (Viñuela 1999, Soravia et al. 2021) is supported by previous studies. However, our analyses of the relationship between food and aggression showed no statistical relationship between the amount of food consumed and nestling aggression at the nestling and brood levels, and this finding differed from those of several other studies (Viñuela 1999, Morandini and Ferrer 2015, Soravia et al. 2021).

Overall, our finding that levels of nestling aggression were related to hatch rank were consistent with those of Townsend (2006). However, some differences between the studies are clear; in that study, food supplementation decreased the aggression of the first-hatched nestling (Townsend 2006). Specifically, at supplemented nests, first-hatched nestlings committed a mean of 0.29 aggressive acts/nestling/hr compared with un-supplemented nests with mean 2.26 aggressive acts/nestling/hr. Townsend's (2006) results suggested a threshold effect; when a first-hatched young reached a point of satiation, it became less aggressive toward its siblings. By contrast, we found no evidence of a relationship between food consumption and nestling aggression. The differences in the experimental methodology and ecological conditions of the two studies may help explain the differing results. Townsend (2006) studied a population of Red-shouldered Hawks exploiting a natural bottomland forest habitat in Arkansas, whereas Red-shouldered Hawks in our study hunted in a developed suburban area of southwestern Ohio. Unlike Townsend (2006), we accounted for brood age and brood size in addition to hatch rank, but we studied nestlings only in week 2–3 post-hatching. Finally, because Townsend (2006) experimentally supplemented nests, that extra food provided may have been greater than

the amount parents can normally provide and enough to satiate the nestlings, thereby reducing aggression of the first-hatched nestlings. Provisioning by adults in our study may not have approached the amount of food supplemented at the nests in Townsend's (2006) study.

In our study, nestling aggression decreased from week 2 to week 3, although the proportion of all aggressive acts that occurred during feeding increased from week 2 (33.1%) to week 3 (49.3%; Miller 2013). Perhaps, a change in feeding behavior as the young age may have influenced the level and timing of aggression (Gonzalez-Voyer et al. 2007, Morandini and Ferrer 2015, Redondo et al. 2019); nestling Red-shouldered Hawks do not feed themselves during week 2 but begin to feed themselves during week 3 (Dykstra et al. 2003), which may facilitate more opportunities for aggressive interactions. Prey type/size may also theoretically influence aggression incidence, as small prey items may be more easily monopolized by a single nestling (Morandini and Ferrer 2015, Redondo et al. 2019). We found some evidence of a difference in prey type/size between weeks 2 and 3, as small invertebrates made up 17% of the prey items (by frequency) in week 2 but 44% in week 3 (Table S2). The finding that the first-hatched nestling is the most aggressive, combined with the decreasing number of aggressive acts as nestlings age, supports the idea that the larger and more developed first-hatched nestling establishes dominance at the beginning of the nestling period (Drummond et al. 1986) to gain an advantage over its siblings (Meyburg 1974, Hahn 1981). This dominance might allow first-hatched nestlings to gain preferential access to food in some cases, although we did not find evidence of that for Red-shouldered Hawks in Cincinnati. An advantage gained by dominance may be expressed as faster growth rate or larger fledging size; our study protocol did not allow us to detect either of these, but this question should be addressed in future research.

Other raptor species with facultative siblicide exhibit different relationships between aggression rates and food consumption. Young first-hatched and second-hatched Black Kite nestlings fight aggressively and attack the third-hatched nestling, but the female parent preferentially allocates food to the third-hatched (Viñuela 1999). Szojka et al. (2020) found that among a small sample of Ferruginous Hawk (*Buteo regalis*) nests, the second-hatched nestling is the most aggressive, the first- and

second-hatched nestling gain food by competition (aggression and stealing), whereas the last-hatched loses food to its siblings but is allocated more by parents, resulting in no difference in food consumption among the nestlings. Byholm et al. (2011) reported that Northern Goshawk females feed all nestlings evenly when they are young, and sibling aggression (during feeding sessions) does not begin until nestlings start to self-feed and increases as nestlings age. Similarly, Broad-winged Hawk (*Buteo platypterus*) nestlings seem to exhibit sibling aggression mainly after the young can feed themselves, based on observations of a limited number of nests (Matray 1974). Osprey nestlings vary their aggressiveness based on the mass asynchrony of their siblings; senior nestlings are more aggressive when siblings are near the same mass, possibly because such aggression is necessary to maintain greater access to food when siblings might have been more capable (Machmer and Ydenberg 1998).

The occurrence of facultative siblicide suggests an inherent measure of adaptability in a species, so it is not surprising that different species developed different strategies around the relationship of food consumption and sibling aggression. Even different populations of the same species sometimes exhibit differing strategies (Morandini and Ferrer 2015), demonstrating phenotypic plasticity in sibling brood behavior. Hence it is important to study this topic in numerous locations and species to develop a more complete understanding of how sibling aggression is related to access to food and of its influence on the ecology, demography, and fitness of raptors.

Prey Types and Delivery Rates. The proportions of bird prey items (17.6% of identified prey) and invertebrate prey items (34.1%) delivered to Red-shouldered Hawk nests in our study are among the highest documented in Red-shouldered Hawk diet studies (reviewed by Strobel and Boal 2010, Dykstra et al. 2020). One early study in Michigan reported a higher proportion of birds (28%; unspecified non-pellet method; Craighead and Craighead 1956), but 11 other studies reported 0–9% birds (Strobel and Boal 2010, Dykstra et al. 2020). Both the proportion and the biomass (28.3%) of bird prey in our study were higher than previously reported for this same population (both were 6.9% in Dykstra et al. 2003). Video monitoring likely allowed for more accurate identification of both birds and invertebrates than reported in Dykstra et al. (2003). The high proportion of bird prey may reflect the suburban nature of the landscape, which seems to facilitate predation of songbird nests by Red-shouldered Hawks (23.1% of the identified bird prey were clearly nestling or fledgling songbirds; S. Miller unpubl. data). Other generalist urban/suburban raptors also consume more avian prey than their rural counterparts (Bierregaard 2018, Dykstra 2018).

According to a meta-analysis of Red-shouldered Hawk diet, there is a relationship between latitude and the proportions of amphibians or mammals in the diet, with mammals more common in northern studies (Strobel and Boal 2010). The diet we recorded in this study did not conform to the patterns identified by Strobel and Boal (2010) because of the high proportions of invertebrates and birds relative to other studies (reviewed by Dykstra et al. 2020). Although possibly a result of different investigation methods (e.g., direct observations, cameras, pellet analysis), this divergence in diet composition may also reflect local differences in prey abundance and availability due to the suburban nature of our study area. Other than Dykstra et al.'s (2003) report from our same study area, no other Red-shouldered Hawk diet studies reviewed occurred within an urban/suburban environment (Dykstra et al. 2020).

Red-shouldered Hawks delivered more prey per hour (1.02 ± 0.56 prey items/hr) than previously recorded for this population (0.85 items/hr), but the mean biomass in this study was lower (22.4 ± 6.0 g/hr vs. 29 g/hr in Dykstra et al. 2003). These differences may be partly explained by the greater number of small prey items documented in this study. Our current analysis also includes only weeks 2 and 3 of the nestling phase, a time when nestling energy requirements may be lower than during later stages as the nestlings grow. The differences between studies probably also reflect that we calculated biomass using only the amount of food actually consumed by nestlings and did not include food delivered to the nest that was subsequently carried away or consumed by the parent, whereas most other studies that used direct observation to quantify Red-shouldered Hawk diet include total biomass delivered (Howell and Chapman 1998, Dykstra et al. 2003, Townsend 2006, Strobel 2007). Parental resource allocation (between offspring and self-maintenance) is rarely incorporated into studies of sibling aggression and food provisioning but may play a role in the determination of reproductive outcomes and should be further studied (Morandini and Ferrer 2015).

Documentation of prey types and sizes is important because prey type/size may be linked with sibling aggression levels. Some researchers have

proposed that species' propensity toward large, infrequently delivered prey facilitates greater sibling aggression (Drummond 2002, Gonzalez-Voyer et al. 2007, Redondo et al. 2019), especially during the earliest stages of nestling development, when the female parent directly feeds the young. However, evidence addressing this hypothesis is mixed. Redondo et al. (2019) found that low provisioning rates (i.e., fewer but larger food items) were linked to higher sibling aggression levels across 65 raptor species. Conversely, an earlier meta-analysis showed no relationship between food parcel size and nestling aggression among 69 avian species (Gonzalez-Voyer et al. 2007). To our knowledge, whether this proposed relationship may explain intraspecific differences among broods has not been tested. Overall, Red-shouldered Hawks tend to deliver fairly small items relatively frequently, but express relatively high levels of sibling aggression (Redondo et al. 2019). Comparing prey size to sibling aggression was outside the original scope of our research and our data are not structured to address it, but we recommend future studies examine this topic.

Conclusions. Red-shouldered Hawks in our suburban study area fed their young more birds and invertebrates than expected based on the diet documented in studies elsewhere (Strobel and Boal 2010, Dykstra et al. 2020), a finding that may reflect food availability in their suburban environment. Nestling Red-shouldered Hawks frequently behaved aggressively toward younger siblings, establishing their dominance early during the brood-rearing period. Nestling hatch rank was the most important predictor of the amount of aggression exhibited by individual nestlings. The oldest nestling exhibited significantly more aggressive behavior than younger siblings, but rates of food consumption were not statistically associated with rates of aggression. For a species with facultative siblicide, the relationship between food consumption, aggression, and hatch rank is a complicated one that requires additional investigation, and we encourage further study in other regions of the Red-shouldered Hawk's range, and for other similar raptor species.

SUPPLEMENTAL MATERIAL (available online). Table S1: Calculations of grams/bite of different prey types used to estimate food consumed by Red-shouldered Hawk nestlings in Cincinnati, Ohio in 2011 and 2012, based on unpublished prey mass data compiled by Dykstra et al. (2003). Table S2: Prey types delivered to each Red-shouldered Hawk nest by brood age. Table S3: Aggression acts by Red-shouldered Hawk nestlings, recorded by type of aggressive act and brood age. Figure S1: Tail patterns of individual Red-shouldered Hawks, used to distinguish male and female parents.

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