The Role of Sibling Competition and Parental Provisioning on Food Distribution among Ferruginous Hawk Nestlings

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THE ROLE OF SIBLING COMPETITION AND PARENTAL PROVISIONING ON FOOD DISTRIBUTION AMONG FERRUGINOUS HAWK NESTLINGS

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Abstract.—Parent-offspring conflicts arise through the competing efforts of the parents (to optimize their reproductive success) and the offspring (to secure maximum resources for themselves to enhance survival). Competition among siblings in a brood plays a key role in each nestling's relative fitness, particularly in avian species that hatch asynchronously. Previously published research has shown that the first-hatched nestling secures the most food, often at an energetic cost to its siblings. However, few researchers have simultaneously investigated competition and parental allocation behaviors to determine their effects on food distribution among raptor nestlings. We found that Ferruginous Hawk (*Buteo regalis*) parents delivered the same number of prey to nests, regardless of brood size. Contrary to our expectations, all nestlings consumed a similar amount of food within individual feeding events. Importantly, neither nestling competition nor parental allocation was the dominant process responsible for equal food distribution. Instead, the first-hatched and second-hatched nestling gained more food by competition, and the third-hatched nestling gained more food through parental allocation. Although each nestling attempted to optimize its food consumption relative to its siblings, resulting in unequal competitive outcomes, parents altered their allocation behavior to offset sibling competition. Ultimately parents provided the last-hatched nestling with more food, and thereby controlled food distribution to maximize their reproductive output. Future work should explore the role of nestling competition and parental allocation on food distribution using supplementation at nests when prey abundance in the environment is low.

Key Words: *Ferruginous Hawk*; Buteo regalis; *breeding ecology*; *competitive hierarchy*; *feeding behavior*; *raptor*; *sibling conflict.*

ROL DE LA COMPETENCIA ENTRE HERMANOS Y DEL APROVISIONAMIENTO PARENTAL EN LA DISTRIBUCIÓN DE ALIMENTOS ENTRE POLLUELOS DE *BUTEO REGALIS*

Resumen.—Los conflictos entre progenitores y crías surgen a través de los esfuerzos competitivos de los progenitores (para optimizar su éxito reproductivo) y de las crías (para asegurarse el máximo de recursos para aumentar su supervivencia). La competencia entre hermanos en una nidada juega un papel clave en la eficacia biológica relativa de cada polluelo, particularmente en especies de aves que eclosionan asincrónicamente. Investigaciones publicadas previamente han mostrado que el primer polluelo eclosionado se queda con la mayor parte de los alimentos, usualmente con un coste energético para sus hermanos. Sin embargo, pocos investigadores han investigado simultáneamente los comportamientos de competencia y de asignación parental para determinar sus efectos en la distribución de alimentos entre los hermanos en aves rapaces. Encontramos que los progenitores de *Buteo regalis* aportaron el mismo número de

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presas a los nidos, independientemente del tamaño de la nidada. Contrariamente a nuestras expectativas, todos los polluelos consumieron una cantidad similar de alimento dentro de los eventos individuales de alimentación. Es importante destacar que ni la competencia de los polluelos ni la asignación de los progenitores fue el proceso dominante responsable de una distribución pareja de los alimentos. En cambio, el primer polluelo eclosionado y el segundo polluelo eclosionado obtuvieron más alimentos por competencia, y el tercer polluelo eclosionado obtuvo más alimento a través de la asignación de los progenitores. Aunque cada polluelo intentó optimizar su consumo de alimentos en relación a sus hermanos, generando resultados competitivos desiguales, los progenitores alternaron su comportamiento de asignación para compensar la competencia entre hermanos. En última instancia, los progenitores aportaron más alimento al último polluelo eclosionado, y por ende controlaron la distribución de alimentos para maximizar su producción reproductiva. El trabajo futuro debería explorar los roles de la competencia entre polluelos y de la asignación parental en la distribución de alimentos usando suplementación en los nidos cuando la abundancia de presas en el ambiente es baja.

[Traducción del equipo editorial]

INTRODUCTION

Hatching asynchrony in avian species creates a dominance hierarchy in which earlier-hatched nestlings are larger in size and better able to compete for food (Mock and Parker 1997, Valderrábano-Ibarra et al. 2007). However, a nestling's fitness depends on its ability to compete for food relative to its siblings, which is influenced by relative body size and developmental maturity, mostly determined by the hatching order (Ploger and Mock 1986). When food is limited, asynchronous hatching can create greater fitness differences among siblings (Bortolotti 1986, Byholm et al. 2011). Differences in offspring fitness are further exacerbated when aggressive behaviors among siblings increase as the total food available for distribution to nestlings decreases (Drummond and Chavelas 1989, Machmer and Ydenberg 1998). Large inequities in food acquisition between the first and last sibling to hatch can result in a decrease in fitness or even death due to sustained stress on the younger nestling through sibling aggression, thereby decreasing reproductive output and thus fitness of the parents (Bortolotti 1986, Martinez-Padilla et al. 2004, Ploger and Medeiros 2004). The phenomenon whereby offspring make decisions to optimize their own success at the expense of other offspring, and consequently reduce the fitness of their parents, is known as a "parent-offspring conflict" (Rodríguez et al. 2008, Byholm et al. 2011).

To offset conflict among siblings, and maintain their own fitness, parents can alter their food-provisioning strategy. Birds of prey have been shown to alter their parental behavior in response to nestling age, growth rate, and food abundance in their breeding grounds (Dewey and Kennedy 2001, Steen et al. 2012). Parental allocation can mediate the degree to which sibling competition determines the amount of food that each nestling secures (Gardner and Smiseth 2011). For instance, parents may preferentially feed first-hatched nestlings, reflecting an investment in growth of the oldest nestling at a cost to the younger ones (Davis et al. 1999). Parents may feed the last-hatched preferentially to equalize overall prey distribution in highly competitive nests (Ploger and Medeiros 2004). Alternatively, parents may provision food randomly, or in response to nestling begging behavior (Kacelnik et al. 1995, Ostreiher 1996). Thus, to reveal mechanistically how nestling behavior drives parental provisioning strategies, food distribution should be evaluated alongside nestling competition to understand its relative influence on the provisioning of food among nestlings.

Ferruginous Hawks (*Buteo regalis*) are an ideal species for studying sibling competition and parental provisioning behaviors. Breeding pairs raise semialtricial nestlings in clutch sizes of one to six nestlings from May to July (Semenchuk 1992, Schmutz et al. 2008). As in many raptors, nestlings hatch asynchronously, resulting in older nestlings that are larger and more developed than their younger siblings. This allows an investigation of how sibling competition and parental allocation influence food distribution among nestlings. In Alberta, decreased abundance of prey such as Richardson's ground squirrel (*Urocitellus richardsonii*) can limit population growth (Schmutz et al. 2008). Research on this population's feeding behavior will contribute to determining how hatching order might influence nestling energetic intake and how parents maximize their reproductive success through allocation strategies.

Past research on the parent-offspring conflict in raptors has largely focused on how asynchronous

hatching influences competition within the nest, but generally has not addressed the role of parental provisioning on nestling food consumption in the same investigation (but see Watson and Ritchison 2018). Our goal was to determine the effects of both nestling competition and parental allocation on nestling food consumption in Ferruginous Hawks by addressing four specific objectives. (1) We compared the quantity of food allocated per capita to nestlings in different brood sizes, a metric that might indicate an association between prey delivery rate and brood size. (2) We quantified the frequency of competitive behaviors among siblings, and whether these frequencies were higher for siblings that hatched earliest or latest. (3) We evaluated the frequency with which parents distribute prey to each nestling during feeding events, to determine whether parents allocated food preferentially to nestlings of a certain hatching order, equally among nestlings, or without a discernable pattern. (4) We quantified the amount of food each nestling consumed during feeding events, independent of whether they secured the food through sibling competition or parental allocation. Comparing nestling consumption to parental allocation rates enabled us to determine the relative importance of both processes on the ability of nestlings of each hatching-rank to secure food.

We predicted that there would be less food allocated to nestlings per capita in larger broods (Giovanni et al. 2007). We expected that competitive behaviors would decline as nestlings become satiated throughout the course of each day (Cook et al. 2000). We predicted that the first-hatched nestling would exhibit aggressive competitive behaviors more frequently than the second- and third-hatched nestling (Valderrábano-Ibarra et al. 2007). We also expected that parents would allocate food equally among nestlings (Steen 2010), resulting in the first-hatched nestling securing the greatest amount of food. Therefore, we expected food consumption among nestling to be unequal based on hatching order, and that sibling competition would be the dominant process responsible for determining food distribution among nestlings.

METHODS

Nest Locations and Video Monitoring. We studied Ferruginous Hawks nesting in southeastern Alberta and southwestern Saskatchewan, Canada, during three breeding seasons, 2011–2013. We used digital camera systems to collect data on prey deliveries, feeding behavior, and nestling behavior at nests. We installed closed circuit television (CCTV) cameras when nestlings were a minimum of 7 d old, to minimize the risk of parental abandonment, in compliance with our research permits. We installed two cameras near each nest, one to record a wide-angle view of the entire nest and a second positioned to get a closer view of the nestlings for identification of hatching order. Data were recorded using digital video recorder (DVR) systems, and both cameras and DVRs were powered using deep cycle marine batteries. We visited the nests every 5–7 d, to change batteries and replace the hard drives if necessary. Additional details are available (Nordell 2016).

For this study, we used a subset of 18 nests, out of 58 nests that were being monitored as part of a broader research effort. We chose nests that met the following criteria: (1) the nest contained one to three nestlings, (2) the nest had continuous video data available during the period when the nestlings were age 21 d to 41 d, and (3) the camera angles allowed clear viewing of prey deliveries and competitive behavior. We collected data from 18 total nests in the three breeding seasons; two in 2011, eight in 2012, and eight in 2013. No nests were studied for more than one year in this investigation. Recording was terminated after the nestlings fledged the nest at approximately age 7 wk.

Data Collected from Recordings. We recorded how many feeding events occurred during one day for all 18 nests. Because we were interested in investigating how allocation and competition influenced relative food distribution to nestlings, we focused our observations on feeding events. However, to investigate whether brood size or nest age changed the amount of food allocated to nestlings over the sum of a day, we sampled each nest for one entire recorded day to account for variation in the number of prey delivered daily. To achieve both goals simultaneously, we observed every prey delivery and subsequent feeding event from 0500 H to 2200 H for each nest for one day. We designated the day the first nestling hatched as Day 1 for each nest, and we defined nest age as the age of the oldest nestling. We randomly selected one day between Day 21 and Day 41 for analysis. For this study we were interested in determining food allocation during the period that nestlings still depended on adults to feed them. We sampled nests older than 21 d, because after this point the relative ages of the nestlings were easily discernable. Since Ferruginous Hawk nestlings hatch asynchronously, we sampled nests younger

than 41 d old so that nestlings of all hatching orders were considered with similar variability in maturity (i.e., youngest nestling age ranged from 18–38 d while the oldest ranged from 21–41 d old), and so that our study was reflective of the nestling period (Ng et al. 2020).

We identified the hatching order of each nestling based on their degree of feather tract development: the youngest had the most down feathers, and the oldest had the darkest contour feathers. The relative ages of nestlings in broods of two and three were clearly identifiable. There was less difference among nestlings' feather development in broods of four, making it difficult to identify their relative ages accurately. For this reason, we did not include nests with four nestlings in our analyses. Past work in Alberta and Saskatchewan showed that Ferruginous Hawks produce nests with an average brood size of 2.7 nestlings (Schmutz et al. 2008). Thus, our analysis of broods of two and three nestlings was representative of typical brood sizes within this Ferruginous Hawk breeding population.

We identified the most common competitive behaviors among nestlings and categorized them into four groups. First, we evaluated which nestling (as classified by its rank) was closest to the parent providing the food (hereafter "feeder") during a given feeding event. Then, we counted the frequency of pecking behaviors that each nestling performed within each feeding event; we defined pecking as an aggressive use of one nestling's beak to directly target another nestling. Likewise, we counted the frequency that each nestling stole a piece of food from another nestling's beak. We counted the frequency that each nestling blocked another nestling from the feeder, either by stepping directly in front of the other nestling to intercept a piece of food or using a wing to block access to the feeder. It was often unclear which nestling the competitive action targeted, so for this reason we did not record which nestling was recipient of the aggression and instead focused on which nestling was performing the behavior. All nestling behaviors were recorded by nestling rank: first-hatched, second-hatched, or third-hatched.

We quantified two measures of food distribution to nestlings within feeding events. First, we counted each piece that the feeder took from the prey item, without any regard to size, and recorded each as one single food piece. This measure was used to account for the possibility that raptor adults considered the number of pieces fed rather than the amount of

energy per food piece. Next, we evaluated food proffered by the amount, in which each food piece was categorized as one of three sizes: half the size, the same size, or 1.5 times the size of the feeder's beak. Food pieces that exceeded 1.5 times the size of the feeder's beak were classified as multiples of that category. For reference, the average beak length of three adult female museum specimen was 20.3 ± 0.9 mm, which is within the general range the genus *Buteo* (Slagsvold et al. 2010). Because the individual feeding event was considered the sampling unit, only the size of the food piece (and the feeder's beak) needed to remain consistent within feeding events to provide a relative measure of food distribution among siblings. The amount of food per nestling was calculated by multiplying the number of food pieces by the size of each piece, then calculating the sum of food for each nestling within a feeding event. This measure was used primarily to evaluate the net amount of food each nestling gained relative to its siblings, as the size of the piece is important energetically for a nestling and could therefore influence its behavior based on satiation.

We used both measures to compare food allocated as well as food consumed for each nesting rank. We defined allocation as an offering of food from the feeder to a nestling, regardless of whether that nestling secured it. Consumption referred to any food the nestling secured and consumed, regardless of whether the nestling was allocated the piece by the feeder. In this way, by comparing the number of food pieces that a given nestling hatch-rank was allocated to the number of food pieces that nestling consumed, we could determine any difference, which was due to nestling competition (i.e., stealing behaviors). This allowed us to evaluate the relative importance that each process—parental allocation and nestling competition—had on each nestling's ability to secure food.

Statistical Analyses. All following analyses were performed in R version 3.5.3 (R Core Team 2020).

Prey delivery rate and brood size. We determined the difference in amount of food provisioned to nestlings within our dataset in two ways. Using a linear regression, we tested the difference in the amount of food provisioned to nests in a day between broods of two and three nestlings, and among years. Then we tested whether the average amount of food each nestling received in a day differed among brood sizes, which would indicate whether broods of three received less food per capita relative to broods of one or two nestlings. We

also tested whether nest age influenced how much food was allocated to nests in a day using a linear regression. These analyses were necessary to determine whether we needed to control for variation in the amount of food distributed to nestlings by brood size, year, and nest age in the following analyses.

Nestling competitive behavior. For all following competition food distribution metrics, we used a linear mixed model approach with a Poisson distribution to account for our count data. Because we watched every feeding event in a day for the selected nests, feeding events were not all independent. We controlled for our grouped study design by including feeding events within nest identities as a random effect in every competition and food distribution analysis.

We quantified whether the frequency of competitive behaviors differed among nestlings of different hatching orders, and how the frequency of these behaviors changed throughout a day. We fit six generalized mixed models, controlling for variation within individual nests and nest age as random effects. All models were evaluated at the feeding event level. First, to evaluate how competitive behaviors changed throughout a day, we tested whether the sum of all competitive behaviors was predicted by the sequential ordering of feeding events (e.g., first feeding in the day, second feeding in the day, etc.). Because brood size may influence the frequency and type of competitive behaviors, the following models were performed separately for broods of two and three nestlings (Machmer and Ydenberg 1998). To evaluate which nestling was overall most competitive, the sum of all three competitive behaviors (i.e., stealing, pecking, blocking) was predicted by nestling hatching order. The final four models evaluated each behavior separately, predicted by nestling hatching order: the total time spent closest to the feeder (for broods of three only), the sum of stealing behaviors, the sum of pecking behaviors, and sum of blocking behaviors.

To determine how competitive behaviors (stealing, pecking, blocking) varied among nestlings based on hatching order, we ran type III ANOVAs on our generalized mixed models. To assess differences in frequency of each competitive behavior among nestlings of different ranks, we compared their pairwise marginal linear means as evaluated in the regression, using a log-likelihood ratio test.

Parental allocation. To evaluate how parents allocated food to nestlings within feeding events, we performed two separate glme models: one for the number of food pieces, and another for the amount of food allocated. For both measures of food allocation, the best fitting glme model was determined by corrected AIC using the MuMIn package (Barton 2019). They both contained nestling rank as the only fixed effect, and the same random effects to control for nest identity and nest age. To compare the number of food pieces and amount of food allocated between each sibling pair, we performed a Tukey HSD post-hoc analyses in the emmeans package (Lenth 2019).

Role of nestling competition and parental allocation on nestling consumption. We quantified the amount of food that each nestling (identified by hatching order) consumed, so that we could identify any disparity between the food allocated to each nestling and food consumed by each nestling, as influenced by competition. We used an ANOVA to determine whether nestling hatching order predicted the food consumed in a feeding event. The generalized mixed model of best fit as determined by stepwise AICc contained hatching order as the fixed effect, and controlled for feeding events grouped by nests, and nest age as random effects. To compare the means of both food consumption measures among nestlings of different ranks, we used a Tukey HSD post-hoc analyses.

We determined the relative effect that each process (nestling competition and parental allocation) had on the amount of food consumed by nestlings within feeding events. To address this, first we calculated "food gained" by subtracting the amount of food allocated from the amount of food consumed, for each observation. For example, if a nestling was allocated five food units by the feeder, but ate seven units in this feeding event, food gain would be $7 - 5 = 2$, indicating that the nestling gained an additional two food units by stealing from its siblings. If a nestling was allocated seven food units by the feeder, but it consumed only two units, then food gain would be $2 - 7 = -5$, indicating that the nestling lost five food units due to sibling competition. We tested the difference in mean food gained using an ANOVA on a generalized mixed effects model in which nestling hatching order was the fixed effect, and feeding events within nests, nest age, and brood size were random effects. Any value of "food gained" that did not equal zero was due to nestling competition; i.e., the nestling that was

Table 1.   Behaviors performed by Ferruginous Hawk nestlings of each hatching order in broods of two and three nestlings during a feeding event (mean ± SE; $n = 72$). n_{fe} = the number of feeding events; n_{nest} = the number of nests.

		COMPETITIVE BEHAVIORS		
BROOD SIZE	NESTLING	BLOCK	PECK	STEAL
Two ($n_{fe} = 16$, $n_{nest} = 4$)	1st-hatched	NA	1.67 ± 0.33	2.50 ± 0.92
	2nd-hatched	1.00 ± 0.0	3.17 ± 1.47	3.50 ± 1.38
Three ($n_{fe} = 56$, $n_{nest} = 11$)	1st-hatched	1.70 ± 0.33	3.22 ± 0.43	3.62 ± 0.53
	2nd-hatched	1.56 ± 0.29	4.61 ± 0.59	4.86 ± 0.59
	3rd-hatched	1.38 ± 0.18	2.33 ± 0.46	3.35 ± 0.47

allocated the food was not the same nestling that consumed it. Throughout we present results as mean ± SE.

RESULTS

We reviewed 323 hr of recordings for this study, and in doing so, observed 72 feeding events for nests with broods of two ($n = 16$, over four nests) or three nestlings ($n = 56$, over 11 nests). To address how the number of prey deliveries changed with brood sizes, we included an additional three nests with broods of a single nestling. In total, 18 nests were evaluated for 1 d each. Within multi-nestling broods, stealing behavior was the most common competitive behavior, occurring in 81.9% of feeding events, followed by pecking in 76.4% of feeding events, and blocking in 29.2% ($n = 72$, Table 1). On average, there were 5.2 ± 0.5 feeding events per day ($n = 15$). Each nestling was fed an average of 120.4 ± 19.0 pieces of food per day, and 21.9 ± 2.1 pieces of food within a feeding event. Each nestling ate an average amount of 70.2 ± 10.5 adult-beak-size food units in a day and 12.5 ± 1.2 adult-beak-size food units within a feeding event (Table 2). The number of pieces (size not considered) and the amount of food (size considered) were highly correlated ($r_{allocation} = 0.98$, $r_{consumption} = 0.97$). For purposes of clarity, we present the amount of food as the number of adult-beak-size units to address differences in allocation and consumption between nestlings, as it provides more information regarding the relative distribution of energy between nestlings than count of food pieces alone.

Prey Delivery Rate and Brood Size. Overall, broods of three nestlings were allocated less food per nestling during a day than smaller brood sizes ($F = 9.96$, df = 1, $P = 0.003$, $n = 18$), and there was no significant change in the number of feeding events in a day among brood sizes ($F = 0.57$, df = 1, $P = 0.45$, $n = 18$). Less food was allocated to each nestling in older nests than younger nests ($F = 7.37$, df = 1, $P = 0.01$, $n = 18$; Fig. 1). Therefore, we controlled for nest age and brood size in our food distribution models, to focus on the relative amount of food allocated and consumed by nestlings of different hatching orders within feeding events. There was no significant difference in the amount of food allocated per nestling among years ($F = 0.07$, df = 1, $P = 0.79$, $n = 18$).

Nestling Competitive Behaviors. We found that throughout a day, the frequency of all competitive behaviors pooled was highest during earlier feeding events ($\chi^2 = 82.29$, df = 1, $P < 0.001$; Fig. 2). In broods of two nestlings, the second-hatched nestling

Table 2.   The amount of food distributed to Ferruginous Hawk nestlings in broods of three within feeding events ($n = 56$). The amount of food was measured by adult-beak-size units by comparing food to the beak of the feeding parent. Sample sizes indicate the number of feeding events in which each nestling was fed/consumed food. The third-hatched was allocated significantly more food than the first-hatched, yet there was no difference detected in the amount of food nestlings consumed. n = the number of feeding events.

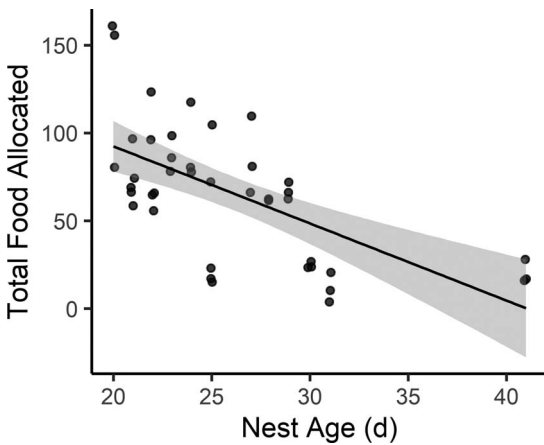|	AMOUNT OF FOOD (ADULT-BEAK-SIZE UNITS)		
FOOD MEASUREMENT	1ST-HATCHED NESTLING ($n = 56$)	2ND-HATCHED NESTLING ($n = 56$)	3RD-HATCHED NESTLING ($n = 55$)
Food allocated	11.0 ± 1.2	12.6 ± 1.5	13.0 ± 1.3
Food consumed	11.1 ± 1.2	12.7 ± 1.4	12.2 ± 1.2

Figure 1. The total amount of food (adult-beak-sized pieces) allocated to each nestling per day decreases with nest age, defined as the number of days since the first nestling hatched. Data includes nests of one ($n=3$), two ($n=4$), and three ($n=11$) nestlings for a total of 44 nestlings. Shaded area represents the standard error.

performed an overall higher frequency of competitive behaviors than the first-hatched within feeding events ($\chi^2=4.14$, df = 1, $P=0.042$, $n=16$; Table 1). However, when we analyzed each behavior separately we found no differences between the number of times the first-hatched and second-hatched nestlings stole prey ($\chi^2 = 3.31$, df = 1, $P = 0.068$), pecked siblings ($\chi^2 = 1.71$, df = 1, $P = 0.19$), or performed blocking behaviors ($\chi^2=0.30$, df=2, $P=0.86$) within feeding events.

In broods of three nestlings, the second-hatched nestling performed an overall higher frequency of competitive behaviors compared to both its siblings ($\chi^2=27.30$, df=2, $P < 0.001$, $n=56$). We found that all nestlings were positioned closest to the feeder on average the same percentage of time ($\chi^2=0.67$, df=2, $P = 0.72$, $n = 56$). The frequency of stealing and pecking behaviors were both predicted by nestling hatching order ($\chi^2=9.61$, df=2, $P=0.008$, $n=56$; $\chi^2=18.45$, df=2, $P < 0.001$; Fig. 3). We found that the second-hatched nestling stole more frequently than the third-hatched nestling ($t = 2.92$, df = 102, $P = 0.012$), but not more than the first-hatched nestling ($t = 2.19$, df = 102, $P=0.079$). The second-hatched nestling engaged in more pecking behavior than the first-hatched nestling ($t = 2.55$, df = 73, $P = 0.034$) and the third-hatched nestling ($t=4.15$, df=73, $P < 0.001$), but the frequency of pecking behavior did not differ between the third- and first-hatched
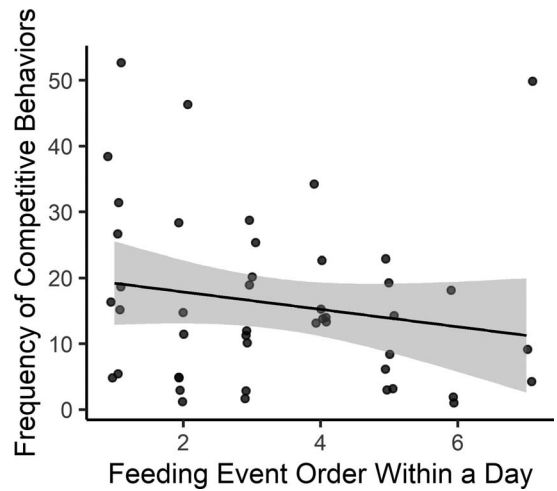

Figure 2. The sum of all competitive behaviors (stealing from siblings, pecking, and blocking siblings from the feeder) performed by nestlings within a feeding event decreases with the number of feeding events in that day. Competitive behaviors were observed in 81.9% of feeding events ($n = 72$) containing brood sizes of two and three nestlings. Shaded area represents the standard error.

nestling ($t = 1.84$, df = 73, $P = 0.16$). The frequency of blocking behaviors did not differ among nestlings ($\chi^2 = 0.30$, df = 2, $P = 0.86$).

Parental Allocation of Food. Nestling hatching order had a significant effect on the amount of food allocated to nestlings during feeding events ($\chi^2 = 8.44$, df = 2, $P = 0.014$, $n = 72$). The first-hatched nestling was allocated a smaller amount of food than the third-hatched nestling ($t = -2.90$, df = 192, $P = 0.010$). However, there was no difference in the amount of food allocated to the first-hatched nestling and the second-hatched nestling ($t = -1.18$, df = 192, $P = 0.47$), or between the third-hatched nestling and the second-hatched nestling ($t = 1.85$, df = 192, $P=0.16$).

Role of Nestling Competition and Parental Allocation on Nestling Consumption. We found that the amount of food nestlings consumed during a feeding event did not differ significantly by hatching order ($\chi^2 = 288$, df = 2, $P = 0.24$). Our post-hoc comparison of means confirmed that there were no significant differences in the amount of food consumed between the first-hatched and second-hatched nestlings ($t=-1.56$, df = 192, $P=0.22$), the first-hatched and third-hatched nestling ($t = -1.02$, df = 192, $P = 0.57$), and the second-hatched and third-hatched nestlings ($t=0.47$, df = 192, $P=0.89$).
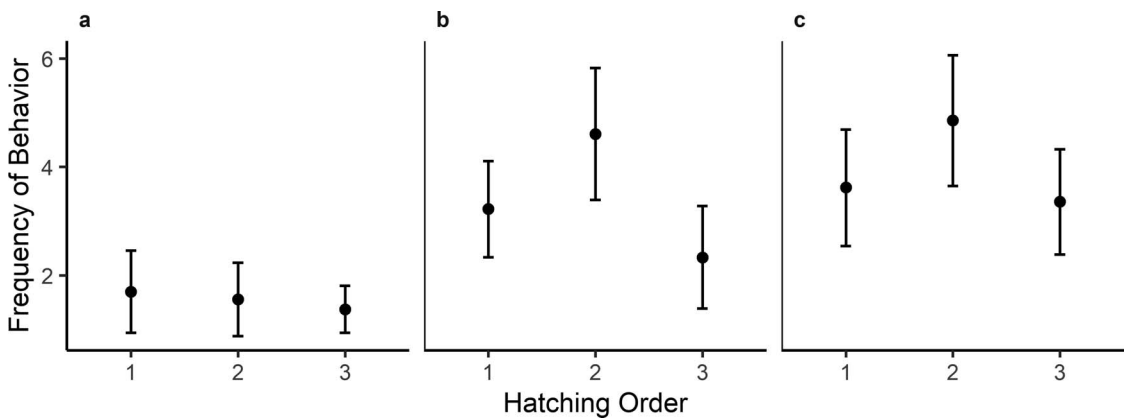
Figure 3. The average number of (a) blocking behaviors, (b) pecking behaviors, and (c) stealing behaviors performed by nestlings of each hatching order per feeding event ($n = 56$ feeding events; 1 = first-hatched nestling, 2 = second-hatched nestling, 3 = third-hatched nestling). Data shown are for broods of three nestlings. Error bars are 95% CIs.

We calculated the difference between how much food each nestling was allocated and how much food that nestling consumed using the "food gained" metric (i.e., food consumed—food allocated per observation), as an indication of whether nestlings gained food or lost food due to sibling competition. We then calculated the mean of this metric per nestling over the course of a day in broods of three ($n = 11$) to account for the possibility that nestlings of certain hatching orders were fed at different times throughout a day. Food gained differed significantly among the young, averaging +2.7 ± 2.5 adult-beak-sized units per for the first-hatched nestling, +1.5 ± 2.3 for the second-hatched nestling and −5.3 ± 2.2 for the third-hatched nestling ($F = 3.90$, df = 2, $P = 0.028$; Fig. 4); the third-hatched nestling lost significantly more food than both the first-hatched nestling ($t = -2.51$, df = 41, $P = 0.042$) and second-hatched nestling gained ($t = -2.50$, df = 41, $P = 0.044$). Between the first- and second-hatched nestling the amount of food gained did not differ ($t = 0.066$, df = 41, $P = 0.99$).

DISCUSSION

Overall, we found that as both brood size and nest age increased, nestlings received less food per capita in a day than nestlings in smaller or younger nests (Fig. 1). Among siblings, food distribution within Ferruginous Hawk nests depended on both sibling competition and parental allocation, such that patterns of unequal food distribution from one process were offset by the other. There were no
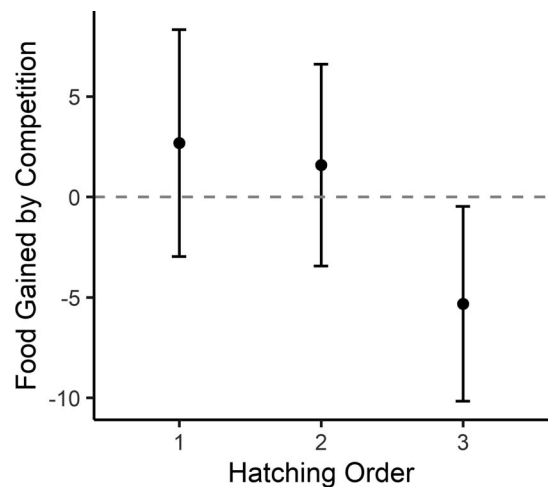

Figure 4. Average cumulative amount of food gained per day ($n_{nest} = 11$) for each nestling in broods of three, by hatching order. The amount of food (adult-beak-sized pieces) allocated by the parents was subtracted from the amount of food each nestling consumed, for each observation, resulting in food gained exclusively by competition. Numerical means ± SE for each nestling by hatching order are shown above the plot. The horizontal line at the zero intercept indicates that the nestling consumed the same amount of food as was allocated by the parents. Negative values indicate that the nestling lost food it was allocated due to competition, and positive values indicate that the nestling gained food due to competition. The error bars are 95% CIs.

detectable differences in the amount of food that each nestling consumed within feeding events, even though the second-hatched nestling tended to exhibit the most competitive behaviors, followed closely by the first-hatched nestling (Fig. 3). Contrary to our prediction, in broods of three the feeder allocated the last-hatched nestling with more food on average. In sum, we found that the last-hatched nestling lost a portion of the food that it was allocated due to stealing by its siblings, and that the first- and second-hatched nestlings gained more food than they were allocated through stealing behaviors (Fig. 4).

Prey Delivery Rate and Brood Size. Our results supported our prediction that nestlings in broods of three would be allocated less food per capita than nests of two. One possible explanation is that Ferruginous Hawk parents may limit the amount of time they spend foraging during the day, to optimize the amount of time they spend on brooding behaviors, regardless of brood size. Past research on the same breeding population of Ferruginous Hawks showed that parents increase the amount of time spent on brooding behaviors when storms are approaching; however, they do not compensate for lost foraging time by supplementing prey to the nest after the storm (Laux et al. 2016). Hawks may be limited in the number of prey they can retrieve in a day by the time they must spend on the nest protecting and brooding or shading their nestlings. This hypothesis could be explored in future studies by quantifying the ratio of time parents spend on brooding behavior and time spent foraging, especially when young nestlings are most limited in their thermoregulatory capacities (<21 d old), for nests of different brood sizes.

Nestlings in nests with older young were allocated less food per capita than nestlings in younger nests (Fig. 1). Ferruginous Hawk nestlings fledge from the nest between 38 and 50 d old and attempt to feed themselves as early as 16 d old (Ng et al. 2020). Based on our video observations, although nestlings could swallow small pieces of prey left in the nest between adult feedings, they were rarely able to pull prey items into smaller pieces at ages younger than 35 d old. As we considered nests between the ages of 21 d and 41 d old, the pattern of decreased food allocation in nests with older young may be due to decreased dependence on adults for feeding. Although the difference in the total amount of food distributed differed among brood sizes and nest ages, the relative pattern of food allocation within

nests did not differ among broods or through this period. Thus, the results of our study pertain to broods of two and three Ferruginous Hawk nestlings age 21–41 d old, when they are mostly unable to feed themselves.

Nestling Competitive Behavior. We predicted that nestlings would compete unequally and that the first-hatched nestling would perform the most competitive behaviors. We did find that nestlings competed unequally, but the second-hatched nestling performed the most competitive behaviors overall in both broods of two and three, followed closely by the first-hatched. The third-hatched nestling performed the fewest competitive behaviors (Fig. 3). Viñuela (1999) found that competition was more common between first-hatched and second-hatched Black Kite (*Milvus migrans*) nestlings, rather than against the third-hatched nestling. We did not record which nestling was the target of competitive behaviors; however, because the first- and second-hatched nestlings were able to gain more food than they were allocated, and the third-hatched nestling lost food on average, we can infer that the third-hatched was most often the target of stealing behaviors by its siblings (Fig. 4). This inference is consistent with past findings that the last-hatched nestling is the subordinate competitor (Ploger and Mock 1986). For both broods of two and three, our analyses showed that nestlings performed more competitive behaviors during the earlier feeding events of the day (Fig. 2). Assuming nestlings are hungriest after a night without feeding, our results were consistent with a previously reported link between nestling hunger and aggression (Drummond and Chavelas 1989, Machmer and Ydenberg 1998).

In broods of three, we found the second-hatched nestling performed more overall competitive behaviors than the first-hatched, yet there were no differences between these two nestlings when each behavior type was tested separately. Additionally, both of these nestlings gained food through competition more so than parental allocation, with a trend towards the first-hatched having gained the most food overall (Fig. 4). As such, the first-hatched may have been more successful in gaining food or may have stolen larger pieces of food per competitive attempt than the second-hatched. By contrast the second-hatched might exhibit more behavioral posturing to make up for its smaller body size. Future work could tease apart any meaningful differences between the two older nestlings by

analyzing the energetic costs associated with competition (e.g., blocking or pecking). Within Great Tits (*Parus major*) and European Starlings (*Sturnus vulgaris*), one nestling's monopolization of the space closest to the feeder increased food intake for that nestling (Kacelnik et al. 1995, Kölliker et al. 1998). However, we found all nestlings spent a similar amount of time closest to the feeder (within feeding events).

In broods of two nestlings, the second-hatched nestling performed more overall competitive behaviors than the first-hatched, but we could not detect a relationship between the frequency of specific behaviors (i.e., stealing, pecking, and blocking) and hatching order. These apparently opposing results may be due to the low sample size of competitive behaviors in broods of two (such behaviors were only present in 10 out of 16 feeding events; 62.5%). However, the relative low frequency of competitive interactions we recorded in broods of two is not unlike that observed for small broods in other species. Northern Goshawk nestlings had less nestling competition under higher food abundance, which could arise from more per capita food in broods of two nestlings (Byholm et al. 2011).

Parental Allocation of Food. Our prediction that parents would distribute food equally among nestlings was not supported. Instead, we found evidence that the last-hatched nestling was allocated overall a larger amount of food relative to its siblings, but the difference was only significant compared to the first-hatched nestling (Table 2). Our results are consistent with findings for asynchronously hatching Black Kites, in which parents behaved to minimize nestling competition by preferentially feeding the last-hatched nestling (Viñuela 1999). Preferentially feeding the smallest nestling in a size hierarchy could be a strategy to maximize the parents' reproductive success in an unpredictable environment (Du et al. 2012). Similarly, Great Egrets (*Ardea alba*) provide more food to the second-hatched nestlings in comparison to the first-hatched in broods of three (Ploger and Medeiros 2004), suggesting parental behavior plays an important role in nestling food consumption.

When examining food consumption (independent of the effects of competition or allocation), we found no statistical difference among nestlings' consumption, but with a trend toward lower consumption by the first-hatched nestling (Table 2). Thus, considering the third-hatched nestling lost the most food to competition, yet parents allocated

the most food to the third-hatched, we infer that parents distributed food in a manner that offset competitive dominance to some degree. Other research presents evidence that when food is scarce parents may change their provisioning strategy. For example, Northern Goshawk (*Accipiter gentilis*) parents spend more time foraging and less time protecting the nest during years with low prey abundance, leaving the nestlings more vulnerable to predation (Dewey and Kennedy 2001). Parental allocation strategies may shift to a preferential investment in the first-hatched nestling during severe food limitation, potentially resulting in lower fitness or death of other brood members (Davis et al. 1999, Du et al. 2012). Our finding that Ferruginous Hawks provisioned food to the last-hatched nestling through all three years of our study (2011–2013) suggests that either environmental prey abundance did not vary significantly, or if prey abundance did fluctuate throughout those years, it did not alter the hawks' food allocation behavior.

Ferruginous Hawk parents may preferentially feed the last-hatched nestling more food in response to hunger cues from the nestlings, as in Barn Owls (*Tyto alba*; Roulin 2004). An experimental study on American Kestrels (*Falco sparverius*) found that parents increase their prey provisioning rates to nests when nestlings are food-deprived, as indicated by a high intensity of begging behavior (Watson and Ritchison 2018). Fargallo et al. (2003) demonstrated that researchers watching silent videos could approximate the amount of begging behaviors by Eurasian Kestrel (*F. tinnunculus*) nestlings by measuring the mouth-gaping behavior of the nestling closest to the parent. Ferruginous Hawk nestlings in our study rarely performed open-mouth begging behavior (M. Szojka unpubl. data); however, subtle vocalized cues that we could not perceive on silent video recordings may be used to communicate hunger levels to parents. Microphones/acoustic recording units and digital video recording units should be used in conjunction in future studies investigating food distribution in raptors, to capture both overt and subtle begging cues.

Parental provisioning strategies for broods of two and three nestlings were similar in our study. Broods of four nestlings or more were not included in this study as it was challenging to accurately identify all of the nestlings visually as they were unmarked, and differentiation of nestlings relied on the researcher's ability to keep track of each individual. In future studies of Ferruginous Hawks, researchers should

mark individual nestlings to target nests with broods of four and five young to examine whether provisioning and competitive outcomes match those found in our study. Parents on average deliver the same number of prey per day to nests of two and three young, and we rarely observed more than seven prey delivered per day. If the amount of food per capita is lower to nestlings in larger broods, food distribution patterns may lead to alternate provisioning strategies by the parents. Food supplementation experiments could also be conducted with nests that experience natural food limitation to determine how food allocation strategies may change. These future directions would provide further insight into how parental allocation strategies may change with relatively lower food consumption by the last-hatched nestling.

Role of Nestling Competition and Parental Allocation on Nestling Consumption. Our prediction that nestlings would consume unequal amounts of food, due to differential competitive abilities related to hatch-rank, was only partially supported. Our data suggested that the first-hatched nestlings gained more food through nestling competition but was allocated less food by the feeder compared to the last-hatched (Table 2). The second-hatched nestling did not differ significantly from its siblings in terms of food allocated nor food gained via competition, indicating that it may benefit from both processes to secure resources. The last-hatched nestling in broods of three lost food through competition with its siblings but was fed preferentially by parents, at least in comparison to the first-hatched (Fig. 4; Table 2). In sum, our data suggested that there was little difference in the approximate amount of food that nestlings of each hatch-rank consumed across feeding events, although outcomes of allocation and competition tended to vary among them. Our results provided evidence that provisioning strategies of parents and stealing behaviors of siblings influence each nestling's ability to secure food to different degrees, depending on their hatching order. All together, our study suggested that parental allocation offset the competitive disadvantage experienced by the last-hatched nestling such that competitive differences did not reflect the final food distribution of nestlings, at least for brood sizes of two or three nestlings.

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