



Original Article

Effects of brood and group size on nestling provisioning and resource allocation in a communal bird

Amanda Savagian^{*} and Christina Riehl

Department of Ecology and Evolutionary Biology, Princeton University, 106A Guyot Hall, Princeton, NJ, USA

Received 10 February 2022; revised 20 December 2022; editorial decision 21 February 2023; accepted 7 March 2023

Resource limitations, either due to environmental conditions or constraints on parental provisioning effort, can drive intense competition among offspring. In communal groups, resource availability may increase if parents receive assistance from other group members; however, if those caregivers also produce young, offspring demand may increase at the same time. It is possible, therefore, that the costs of intrabrood competition in large broods may outweigh the benefits of provisioning from additional caregivers. We tested the relationships between group size, brood size, and provisioning rates in the greater ani (*Crotophaga major*), a communally nesting cuckoo in which multiple breeding pairs and nonreproductive helpers cooperatively raise a shared brood. Crucially, brood and group size can vary independently in this species, allowing us to test changes in each variable separately. Using video footage of 2255 prey deliveries across 10 nests, we found that an increase in the number of adult caregivers within a group did not sufficiently offset a corresponding increase in the number of dependent young within a brood: prey availability per average nestling decreased with brood size, regardless of group size. In larger broods, last-hatched nestlings received significantly less prey than their broodmates, in part due to greater hatching asynchrony that exacerbated competitive asymmetries and facilitated inequality in food allocation. Our results indicate that last-hatched ani nestlings suffer a “double cost” in large broods: they must compete with more nestmates, and suffer disproportionately from asynchronous hatching. These costs may contribute to increased parent–offspring conflict and may constrain group size in communal breeders.

Key words: brood reduction, communal breeding, competition, *Crotophaga major*, hatching asynchrony, parental care, provisioning.

INTRODUCTION

In cooperative breeding groups, nonreproductive helpers improve the fitness of breeders by allowing them to conserve energy for future reproduction or to invest greater resources in their present brood (Russell et al. 2007; Cusick et al. 2018; Downing et al. 2020; Downing et al. 2021). Studies of provisioning behavior have documented how breeders respond to the presence of additional caregivers, and how such responses affect nutritional investment in the current brood (Hatchwell 1999; Heinsohn 2004; Johnstone 2011). In some species, breeders may compensate for the extra assistance by decreasing their own provisioning effort, such that resource availability for the present brood remains constant even as group size increases (“load-lightening,” Hatchwell 1999; Legge 2000a; Lu et al. 2011; Koenig and Walters 2012a). In others, breeders may maintain their baseline investment levels, so that contributions from nonbreeding helpers increase the total amount of food delivered to

the brood, and the amount distributed to and consumed by each individual offspring (Clutton-Brock et al. 2001; Liebl, Nomano, et al. 2016). This may reduce competition within the brood and improve overall survival probability for current offspring (Legge 2000b).

Alternatively, total resource availability may increase, but breeders may respond to this additive care by producing more offspring in their present brood (Davies and Hatchwell 1992; Woxvold and Magrath 2005; Lejeune et al. 2016), leading to constant or decreased per-nestling provisioning rates as brood size and group size increase simultaneously (Savage et al. 2013). In these larger broods, there may be emergent costs for which the presence of additional caregivers or greater total resource availability may be unable to compensate. For example, increases in brood size may alter the competitive landscape within a brood, imposing greater physiological costs as offspring compete against more broodmates (Neuenschwander et al. 2003; Naguib et al. 2004) and amplifying competitive asymmetries among them, leading to a potentially

Address correspondence to A. Savagian. E-mail: agsavagian@gmail.com.

the amount of prey actually consumed by each nestling (rather than the amount theoretically available if resources were distributed equally). If an increase in brood size affects the competitive landscape within a nest, potentially through greater hatching asynchrony, we predicted that the distribution of prey among first-, middle-, and last-hatched nestlings would become more skewed as brood size increased.

Third, we evaluated whether increased hatching asynchrony could be a mechanism underlying greater intrabrood competition in larger broods by quantifying the overall relationship between brood size and hatching asynchrony in our study population.

METHODS

Data collection

We leveraged two complimentary datasets in this study, both of which were obtained from the same population of greater anis within the Barro Colorado Nature Monument (BCNM) in central Panama. The BCNM is managed by the Smithsonian Tropical Research Institute and supports a long-term study population of approximately 80 ani breeding groups (Riehl and Jara 2009; Riehl and Strong 2019). Our first dataset contained long-term nest monitoring data collected from 2007–2009 and 2012–2019, and was used to characterize overall relationships between brood size and group size, and between brood size and hatching asynchrony. Detailed descriptions of nest monitoring protocols are given in Riehl and Jara (2009). Briefly, nests were located at the beginning of each breeding season and were checked every 1–3 days during the nesting period. The number of eggs or nestlings in the nest and the number of adults present at the nest were recorded at each visit, and the number of breeding females in each group was confirmed by the pattern and timing of egg laying and/or through genotyping of eggs and nestlings with a panel of 12 highly polymorphic microsatellite loci (Almany et al. 2009; Riehl 2012; Riehl and Strong 2019). For these analyses, group size was defined as the number of breeding adults plus nonbreeding helpers in the nesting group, and brood size was defined as the number of eggs that hatched in the communal nest. We defined hatching asynchrony as the spread of days over which nestlings hatched, and measured this spread as the difference between the first and last calendar days of hatching; a hatch spread of zero indicates that all nestlings hatched on the first day, a spread of one indicates that nestlings hatched over a period of two days, and so on. We analyzed data collected from a subset of years (2007–2009 and 2012–2019), since these were the years for which complete information on group size, brood size, and hatch spread were available. A total of 138 nesting groups were included in the analysis of brood size and group size, and 110 nesting groups in the analysis of brood size and hatching asynchrony.

Our second dataset, used to measure how variation in brood and group size influences prey availability, actual prey distribution, and average adult workload, followed 10 focal groups over a single breeding season from July to August 2018. This dataset used video-recordings to capture precise data on how much prey adults delivered to the nest (and was therefore available to nestlings), and how prey items were actually distributed among individually marked nestlings within the nest. Once hatching began at our 10 focal nests, we visited daily in order to individually mark nestlings with non-toxic paint pens, record their position in the hatch order, and install small video cameras to monitor prey deliveries and distribution. A nestling's position in the hatch order was assigned

based on whether it hatched on the first, a middle, or the last day of the hatch period; multiple nestlings could be assigned to the same position. If nestlings hatched over a 2-day period, they were assigned only to first and last hatch positions.

Video cameras (Contour +2 or Roam3) were attached to external battery packs (Anker Aster E1s) within one foot of the nest and secured using zip ties. We filmed nestlings for 1–5 days after hatching; we did not visit nests after day 6, when nestlings can prematurely fledge if disturbed (Riehl and Jara 2009). Ultimately, we annotated 2–4 days of footage per nest for a minimum of 10 h of footage per group; we avoided first-hatch days when possible and excluded footage with partial broods. We also excluded footage recorded during heavy rainstorms, after 1730 h (when adults feed less frequently), and when researchers were in the camera frame. All procedures were approved by the Institutional Animal Care and Use Committees of Princeton University (protocol #10034) and the Smithsonian Tropical Research Institute (protocol #2017-0626-2020). Time at the nest was kept to a minimum and adults returned to the nest within 17 min (\pm 13 min SD) after researchers left. Paint markings do not influence prey allocation within the nest and adults are not aggressive toward marked nestlings (Savagian and Riehl, unpublished data).

Four observers manually watched and annotated the video files using ELAN software (v5.9; The Language Archive 2020). For every prey delivery, they noted the arrival time and the identity of the nestling who received the prey item; if no nestling was fed (e.g., the adult consumed prey or it escaped from the nest) or we could not confirm the identity of the nestling, we excluded the prey delivery from analysis. They also tallied the total number of prey items delivered to each nest, in order to calculate a single provisioning rate that captured the workload of an average adult in each group. We calculated this average rate by dividing the total number of prey items by the number of adults in each group. Since very few adults in this study population are banded, we were unable to quantify actual delivery rates for individual birds in our focal groups, but data from a pilot study of three fully marked groups show that all breeding adults contribute equally to provisioning, regardless of sex (M. G. Smith and C. Riehl, unpublished data). This suggests that simply dividing total prey deliveries by group size is a reasonable approximation of individual provisioning effort. Helper provisioning rates, based on observations of five banded helpers at three nests, typically fall within the range of variation of breeder provisioning rates, although they can be lower (A. G. Savagian and C. Riehl, unpublished data); we therefore treat helper contributions as functionally equivalent to breeder contributions and include helpers in our value of group size. Using just the number of breeders for our value of group size produced qualitatively similar results as using both breeders and helpers (Supplementary Tables S1–S5).

Nestling diet consists primarily of large invertebrates (Orthoptera, Araneae, Cicadidae, and Blattodea), as well as small vertebrates including several species of amphibian, gecko, and iguana (Riehl and Strong 2015, A. G. Savagian and C. Riehl, unpublished data). Although prey items differ in size, analyses showed that a simple tally of the number of prey items a nestling received each day was tightly correlated with the total amount of food it received (the sum of all prey mass), suggesting that the number of prey items received is an adequate proxy for prey consumption (Supplementary Methods). Because 2018 was a La Niña year, characterized by higher-than-average precipitation and a shorter dry

season in Panama (Leigh et al. 1990; NOAA Climate Prediction Center 2022), invertebrate abundance was likely quite high at our field site, contributing to high nestling survival rates during the 2018 breeding season (Wolda 1978; Levings and Windsor 1984; Riehl and Smart 2022). Within our 10 focal groups, only two out of 57 nestlings starved. Thirteen other nestlings disappeared before fledging (attributed to predation) and one healthy nestling was found dead in the nest of unknown causes.

Statistical analysis and hypothesis testing

All data analysis was performed in R (v4.0.2; R Development Core Team 2020). To address our first question, how variation in brood and group size influence prey availability per average nestling, we ran three generalized linear models with Poisson error distributions predicting 1) brood size as a function of group size, using the long-term nest monitoring data from 2007–2009 and 2012–2019; 2) the number of prey items available to an average nestling at each of our 10 focal nests, as a function of brood and group size; and 3) the number of prey items delivered by an average adult at each of our 10 focal nests, again as a function of brood and group size. The number of prey items available to an average nestling or delivered by an average adult was calculated by dividing the total number of prey items available to an average nestling or delivered by an average adult was calculated by dividing the total number of prey items delivered to each nest during the study period by the number of nestlings in a brood or the number of adults (breeders and helpers) in a group, respectively. These average provisioning rates were rounded to the nearest integer to accommodate a Poisson error distribution, and we included a log-transformed offset term of the number of hours of footage annotated for each group to control for differences in opportunities for prey delivery.

To address our second question, how variation in brood and group size influence the actual distribution of prey among individual nestlings, we modeled the number of prey items distributed to and consumed by each individual nestling in our 10 focal nests as a function of brood size, group size, and a nestling's position in the hatch order, along with all two-way interactions between the predictors and a three-way interaction involving all three. This generalized linear mixed effects model was fit with a Poisson error distribution, included group ID as a random effect, and included a log-transformed offset term of the number of hours of footage annotated for each group. Position in the hatch order was coded as a three-level categorical predictor (first-, middle-, or last-hatched).

Finally, to address our third question, how hatching asynchrony may contribute to intrabrood competition, we used the long-term nest monitoring data from 2007–2009 and 2012–2019 to predict hatch spread as a function of brood size and the number of breeding females within a group (2 or 3), using a generalized linear model with a Poisson error distribution.

Candidate models were evaluated using an information-theoretic approach in which we compared all possible combinations of our predictor variables and identified the resulting “best-subsets” models using Akaike's information criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002). Global models were generated using the package “lme4” (Bates et al. 2015) and candidate models were compared using the “MuMIN” package (Bartoń 2020). Models that were within 2 AICc units of the top model were considered to be best-subsets of the global model, except those that contained only one more parameter than the top model (Arnold 2010). If more than one top model emerged, we used model averaging based on the top models to obtain parameter estimates, again using the “MuMIN” package (Burnham and

Anderson 2002). To reduce structural multicollinearity, we mean-centered all continuous predictors used in interactions (brood size and group size) during the model-selection process (Iacobucci et al. 2016); the resulting variance inflation factors, as calculated using the package “car” (Fox and Weisberg 2019), were all less than 2 (Supplementary Table S6). If no interaction terms were retained in a best-subset model, we subsequently reverted to raw predictor values when summarizing the final model to facilitate interpretation; if interaction terms were retained, we kept the mean-centered values.

RESULTS

Brood size and group size were significantly and positively associated in the long-term nest monitoring dataset, as predicted (GLM: estimate = 0.120; SE = 0.035; $\chi^2 = 3.404$; $P = 0.000663$; 95% CI = 0.050–0.189). However, the relationship was highly variable (Figure 1). For example, although a brood of seven nestlings was most likely to be cared for by a group of four adults, they could also be provisioned by five, six, seven, or even eight caregivers. This variation subsequently allowed us to separately test the effects of brood size and group size on prey availability and distribution within a nest and on adult provisioning rates.

Within our 10 focal groups, as brood size increased, the number of prey items available to an average nestling decreased significantly (Table 1). Brood size was the only predictor retained in the best-subset model of prey availability, suggesting that nestlings in large broods had less prey available to them, per capita, regardless of the number of adults provisioning them (Supplementary Table S7). The provisioning effort of an average adult increased with brood size (Table 1, Figure 2), even though this appeared insufficient to fully meet nestling demand in larger broods. This increase was independent of group size, which was not a significant term in the averaged best-subset model: whether they were assisted by relatively many or relatively few fellow caregivers, the average adult made more provisioning trips as nestling number increased (Table 1).

The actual distribution of prey items among individual nestlings also changed as brood size increased. Overall, last-hatched nestlings received less prey than their middle- and first-hatched counterparts, and this divergence was most pronounced in the largest broods (Table 1, Figure 3). Middle-hatched nestlings also received less than first-hatched nestlings, but significantly more than those who hatched last (Supplementary Table S8). Only position in the hatch order, brood size, and an interaction between them were retained in the best-subset model; group size did not significantly contribute to the observed variation in how resources were allocated among nestlings (Supplementary Table S9). The greater skew in prey distribution within larger focal broods may be explained by the corresponding increase in hatching asynchrony also observed in larger broods in the overall study population (GLM: estimate = 0.140; SE = 0.035; $\chi^2 = 3.994$; $P < 0.0001$; 95% CI = 0.072–0.210; Figure 4, Supplementary Table S10). In summary, therefore, larger broods were associated with increased hatching asynchrony, less equal distribution of prey among nestlings, and a decrease in the amount of food delivered per average nestling, despite increases in adult provisioning effort.

DISCUSSION

In this study, we found that an increase in the number of adult caregivers within a group did not sufficiently offset a corresponding

increase in the number of dependent young within a brood: prey availability per average nestling decreased significantly with brood size, independent of group size. Distribution of that prey within the nest also changed with brood size, potentially due to more pronounced hatching asynchrony in larger broods that further disadvantaged last-hatched nestlings. This persistent brood size effect

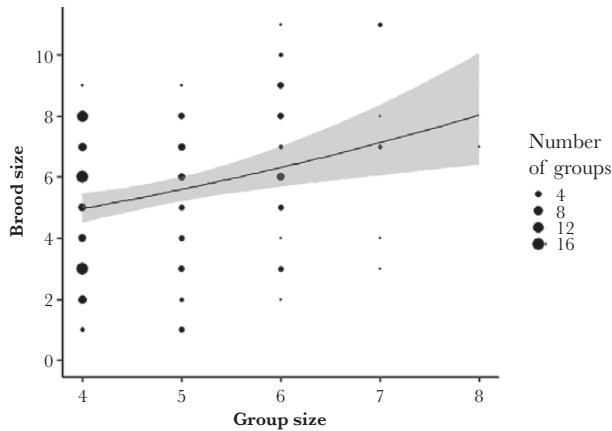


Figure 1

Results of a generalized linear model fit with a Poisson distribution of the relationship between group size (the number of breeders and nonreproductive helpers) and brood size for communally nesting greater anis. Shading indicates 95% confidence intervals. Minimum group size = 4 adults (two breeding pairs). $N = 138$ groups; excludes those with brood size equal to 0.

underscores the usefulness of evaluating variation in brood size and group size separately (e.g., Liebl, Browning, et al. 2016; Sieber et al. 2017). It also highlights the importance of integrating the effects of offspring competition into models of how breeders should respond to the presence of additional helpers or co-breeders within a social group (Savage et al. 2013). A breeding female may be selected to produce fewer supplementary offspring than may otherwise be predicted, once the costs of increased hatching asynchrony, offspring competition, and resource skew are taken into account.

For greater ani nestlings, we found that hatching into a larger brood meant having access to less food, even if more caregivers were present. While adults seemed sensitive to variation in brood size, given that the workload of an average adult and the total amount of prey delivered to the nest increased with the number of nestlings, caregivers did not increase their provisioning effort enough to maintain consistent prey availability per the average nestling across broods. For groups with relatively few caregivers, this may reflect a constraint imposed by the costs to future reproduction on investing more heavily in the present brood (Meade et al. 2010; Lu et al. 2011). However, this result is more puzzling for groups with relatively many caregivers. In cooperative groups, it is not uncommon for caregivers to decrease investment as group size increases, but these declines in individual investment typically maintain a consistent net level of offspring care (Brown 1978; Hatchwell 1999; Yuan et al. 2005; but see van Boheemen et al. 2019). For example, in the groove-billed ani (*C. sulcirostris*), a communal breeder and close relative of the greater ani, per-nestling provisioning rates remain constant regardless of the number of adult provisioners (Vehrencamp 1978). Greater ani adults may reduce or limit their provisioning workload in larger groups because their contribution

Table 1

Results of a series of best-subset generalized linear models and a mixed effects model predicting (A) provisioning effort of an average adult; (B) prey availability per average nestling; and (C) actual prey distribution among individual nestlings

A) Number of prey items delivered by an average adult

Fixed effect	Estimate	SE	ζ	P	95% CI
Brood size	0.121	0.020	5.200	<0.0001	0.075, 0.166
Group size	-0.077	0.071	1.005	0.315	-0.226, 0.073

B) Number of prey items available to an average nestling

Fixed effect	Estimate	SE	ζ	P	95% CI
Brood size	-0.043	0.017	-2.449	0.0143	-0.077, -0.009

C) Number of prey items distributed to each individual nestling

Fixed effect	Estimate	SE	ζ	P	95% CI
Brood size	-0.039	0.016	-2.440	0.0147	-0.073, -0.006
Hatch position (middle)	-0.306	0.066	-4.657	<0.0001	-0.434, -0.176
Hatch position (last)	-0.524	0.059	-8.829	<0.0001	-0.641, -0.408
Brood size \times Hatch position (middle)	0.045	0.022	2.051	0.0403	0.001, 0.087
Brood size \times Hatch position (last)	-0.082	0.021	-3.923	<0.0001	-0.123, -0.041
Random effect	Variance	SD			
Group ID	0.007	0.084			

Models are fit with a Poisson distribution. Position in the hatch order is coded as a three-level categorical variable (first, middle, last), with first-hatched as the reference level. Continuous predictors included in interaction terms are mean-centered. Model (A) parameters were derived through model averaging based on two best-subset models (see Supplementary Tables S11 and 12). $N = 10$ breeding groups containing 57 nestlings.

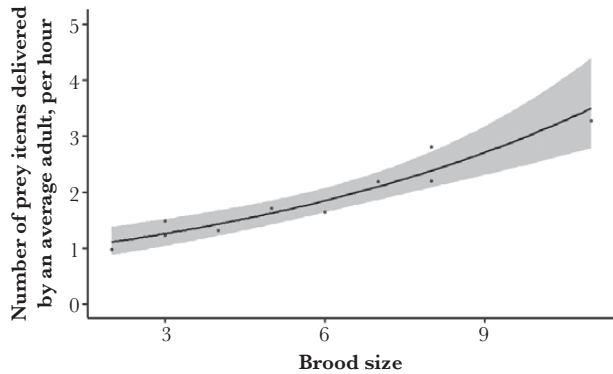


Figure 2

The effect of brood size on the provisioning effort of adult greater ani, as estimated by the most competitive best-subset model (see Supplementary Table S8 for the full set of candidate models) and controlling for variation in the number of adult caregivers. $N = 10$ nests.

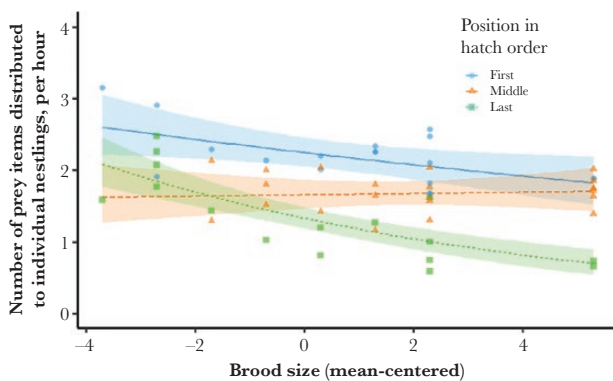


Figure 3

Model-estimated effects of an interaction between position in the hatch order and brood size on the actual distribution of prey items among individual greater ani nestlings within their communal broods. Position in hatch order is coded as a three-level categorical variable (first, middle, last). $N = 57$ nestlings across 10 nests.

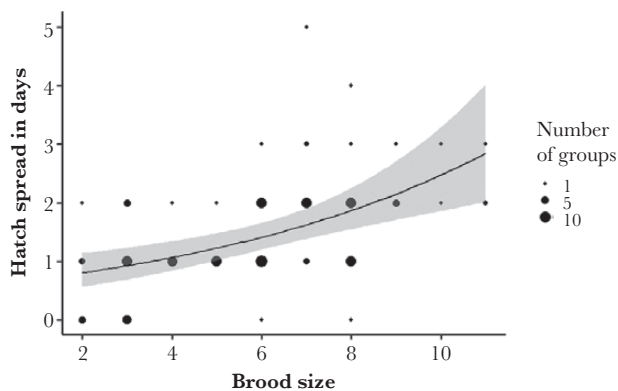


Figure 4

Results of a generalized linear model fit with a Poisson distribution of the relationship between brood size and hatching asynchrony across 110 communal greater ani nests. Nests with only one nestling were excluded.

to the communal brood decreases: a breeder's share of parentage diminishes with the addition of each unrelated co-breeding pair,

potentially reducing fitness incentives to provide care (Riehl 2012). This is in contrast to cooperative groups in which the presence of nonreproductive helpers does not affect breeder parentage, and in contrast to groove-billed anis, for whom parentage is unequally distributed regardless of group size (Vehrencamp 1977). Inclusive fitness benefits may also explain why a study on provisioning effort in the communally breeding Seychelles warbler (*Acrocephalus sechellensis*) found the opposite result: nestlings in communal nests (containing two nestlings and two caregivers) received the same per capita amount of prey as did nestlings in noncommunal nests (containing one nestling and one caregiver; Bebbington et al. 2018). Since co-breeders are typically mother–daughter pairs in this species, caregivers in both communal and noncommunal nests have high inclusive fitness incentives to maintain provisioning effort, even though the share of direct parentage is 50% less in communal nests (Richardson et al. 2002).

In addition to suffering from lower overall resource availability as brood size increased, ani nestlings in larger broods also experienced greater skew in how those resources were distributed. We found that as brood size increased, last-hatched nestlings received significantly less prey than their first- and middle-hatched broodmates. Overall competition for resources is likely to increase with brood size, as nestlings expend more energy to beg or scramble for access to food and as existing asymmetries become amplified (Mock and Lamey 1991; Neuenschwander et al. 2003; Bebbington et al. 2017). In larger ani broods, last-hatched nestlings may have been at a greater disadvantage from the start: our analysis revealed that hatching asynchrony increased with brood size, widening the competitive gap between those who hatched early and those who hatched late. It is likely that the greater hatching asynchrony generally observed in larger broods is the mechanism underlying this despotic prey distribution, as opposed to brood size alone (e.g., Gilby et al. 2011). Last-hatched nestlings thus seem to pay a “double cost” in large broods: there are fewer resources available overall, and, of those resources, they obtain significantly fewer due to competition from their increasingly large broodmates.

Overall, the increased demand and greater hatching asynchrony observed in larger broods appear to be emergent costs for which proportional increases in the number of adult caregivers are unable to compensate. These costs likely explain the higher probability of starvation in larger greater ani broods, and may also offer insight into why three-pair groups consistently experience lower nestling survival rates compared to two-pair groups, despite having more caregivers on average (Riehl and Smart 2022). Considering the effects of within-brood competition on offspring survival is thus crucial to understanding what constrains the number of reproductive pairs within a breeding group, and what selective forces may influence existing group members' decisions to admit another pair (Bebbington et al. 2018).

For greater ani, increased hatching asynchrony in larger broods may be a nonadaptive or even maladaptive consequence of sharing a nest with multiple females. In communal groups, individuals have less control over hatching patterns within the brood, since one female may begin incubating before her co-breeders have finished laying. Synchrony is harder to achieve as the number of females increases, which may partly explain the more asynchronous hatching observed in larger broods; even though the number of laying females did not emerge as a predictor in our model, groups with three females consistently produce larger broods than those with two (Riehl 2012), suggesting that nesting in a larger group could still lead to increased asynchrony. Additionally, larger clutches may be more likely to suffer from uneven incubation, which can also

contribute to asynchronous hatching (Sandercock 1997; Fernández and Reboreda 2007).

However, it remains possible that increased brood reduction in larger, more asynchronous broods could still benefit parents' inclusive fitness, and even that of last-hatched nestlings, if it reduces the predation or starvation risk of the remaining nestlings (O'Connor 1978; Clark and Wilson 1981; Forbes 1993). Hatching asynchrony may minimize the time that offspring are present in the nest, reducing predation and outweighing the cost of brood reduction (Clark and Wilson 1981; Lee and Lima 2017). Since predation is a significant cause of egg loss in greater anis (Riehl and Jara 2009), it may be in adults' best interests to begin incubation before the final egg is laid and to fledge nestlings as soon as possible. A previous study on this population showed that overall nestling survival is highest in synchronous clutches, but the survival analysis only considered nonpredated nests and therefore may not have fully captured the potential benefits of asynchronous hatching under high predation pressure (Riehl 2016). Seemingly costly offspring competition in larger broods may thus be ultimately beneficial for parents, setting up potential conflict between parents and offspring if brood reduction does not also maximize the inclusive fitness of last-hatched nestlings (Trivers 1974; Godfray 1995; Mock 2004).

Whether hatching asynchrony is indeed a cost, and the degree to which this potential cost has played a role in limiting the size of communal breeding groups, is unknown. In the communally breeding Taiwan yuhina (*Yuhina brunneiceps*), asynchronous hatching due to the early onset of incubation also contributes to brood reduction, but under poor ecological conditions, females may be able to manipulate their own laying patterns to improve synchrony and limit overall mortality (Shen et al. 2012). Similar behavioral adaptations may exist in other species and mitigate the emergent consequences of multiple females laying in a shared nest. Broader investigation into the presence and fitness consequences of asynchronous hatching in other communally breeding species will be necessary in order to identify which selective pressures are acting on hatching patterns and to determine how they are likely to have influenced the evolutionary trajectory of communal breeding overall.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at *Behavioral Ecology* online.

We thank Luke Carabbia, Zachariah Smart, Maria Smith, Meghan Strong, and Oliver Whang for assistance in the field, along with Danielle Almstead, Chiti Arvind, Laura Jara, Christa Morris, and Wendy Webber for contributing to the long-term nest monitoring project. We are grateful to Prabhanjana Acharya, Luke Carabbia, and Willow Dalehite for helping to transcribe prey deliveries from video footage. Melissa Cano and the Smithsonian Tropical Research Institute staff provided invaluable logistical support for this project.

AUTHOR CONTRIBUTIONS

Amanda Savagian (Conceptualization-Lead, Data curation-Lead, Formal analysis-Lead, Funding acquisition-Equal, Investigation-Lead, Methodology-Lead, Project administration-Lead, Writing – original draft-Lead, Writing – review & editing-Lead), Christina Riehl (Conceptualization-Supporting, Data curation-Supporting, Formal analysis-Supporting, Funding acquisition-Equal, Investigation-Supporting, Methodology-Supporting, Project administration-Supporting, Writing – original draft-Supporting, Writing – review & editing-Supporting).

FUNDING

This work was supported by the American Philosophical Society, Princeton University (the Department of Ecology and Evolutionary Biology, the Program in Latin American Studies, the High Meadows Environmental Institute, and the Office of Undergraduate Research), and the National Science Foundation (grant numbers IOS-1755279, IOS-184543 to C.R.). A.G.S. was supported by fellowships from the National Science Foundation Graduate Research Fellowship Program and the Princeton Institute for International and Regional Studies.

DATA AVAILABILITY

Analyses reported in this article can be reproduced using the data provided by Savagian and Riehl (2023).

Handling Editor: Jan Komdeur

REFERENCES

- Almany GR, De Arruda MP, Arthofer W, Atallah ZK, Beissinger SR, Berumen ML, Bogdanowicz SM, Brown SD, Bruford MW, Burdine C, et al; Molecular Ecology Resources Primer Development Consortium. 2009. Permanent genetic resources added to molecular ecology resources database 1 May 2009–31 July 2009. *Mol Ecol Resour.* 9:1460–1466.
- Arnold TW. 2010. Uninformative parameters and model detection using Akaike's information criterion. *J Wildl Manage.* 74(6):1175–1178.
- Bartoń K. 2020. MuMIn: multi-model inference. <https://cran.r-project.org/package=MuMIn>
- Bates DM, Mächler M, Bolker BM, Walker SC. 2015. Fitting linear mixed-effects models using lme4. *J Stat Softw.* 67:1–51.
- Bebbington K, Fairfield EA, Spurgin LG, Kingma SA, Dugdale HL, Komdeur J, Richardson DS. 2018. Joint care can outweigh costs of nonkin competition in communal breeders. *Behav Ecol.* 29:169–178.
- Bebbington K, Kingma SA, Fairfield EA, Spurgin LG, Komdeur J, Richardson DS. 2017. Consequences of sibling rivalry vary across life in a passerine bird. *Behav Ecol.* 28(2):407–418.
- Brown JL. 1978. Avian communal breeding systems. *Annu Rev Ecol Syst.* 9:123–155.
- Burnham KP, Anderson DR. 2002. Model selection and multimodel inference. 2nd ed. New York: Springer.
- Cariello MO, Macedo RHF, Schwabl HG. 2006. Maternal androgens in eggs of communally breeding guira cuckoos (*Guira guira*). *Horm Behav.* 49(5):654–662.
- Caro SM, West SA, Griffin AS. 2016. Sibling conflict and dishonest signaling in birds. *Proc Natl Acad Sci USA.* 113(48):13803–13808.
- Clark AB, Wilson DS. 1981. Avian breeding adaptations: hatching asynchrony, brood reduction, and nest failure. *Q Rev Biol.* 56(3):253–277.
- Clutton-Brock TH, Russell AF, Sharpe LL, Brotherton PNM, McIlrath GM, White S, Cameron EZ. 2001. Effects of helpers on juvenile development and survival in meerkats. *Science.* 293(5539):2446–2449.
- Cusick JA, de Villa M, DuVal EH, Cox JA. 2018. How do helpers help? Helper contributions throughout the nesting cycle in the cooperatively breeding brown-headed nuthatch. *Behav Ecol Sociobiol.* 72(3):43.
- Davies NB, Hatchwell BJ. 1992. The value of male parental care and its influence on reproductive allocation by male and female dunlocks. *J Anim Ecol.* 61(2):259–272.
- Dijkstra C, Bult A, Bijlsma S, Daan S, Meijer T, Zijlstra M. 1990. Brood size manipulations in the kestrel (*Falco tinnunculus*): effects on offspring and parent survival. *J Anim Ecol.* 59(1):269–285.
- Downing PA, Griffin AS, Cornwallis CK. 2020. The benefits of help in cooperative birds: nonexistent or difficult to detect? *Am Nat.* 195(6):1085–1091.
- Downing PA, Griffin AS, Cornwallis CK. 2021. Hard-working helpers contribute to long breeder lifespans in cooperative birds. *Philos Trans R Soc Lond B Biol Sci.* 376(1823):20190742.
- Drachmann J, Als TD, Boomsma JJ. 2000. Hatching asynchrony in linnets: the effects of nest predation and food demand of nestlings. *Ornis Fenn.* 77:155–167.
- Fernández GJ, Reboreda JC. 2007. Costs of large communal clutches for males and female greater rheas *Rhea americana*. *Ibis.* 149:215–222.
- Forbes LS. 1993. Avian brood reduction and parent-offspring "conflict." *Am Nat.* 142(1):82–117.

- Fox J, Weisberg S. 2019. An R companion to applied regression. 3rd ed. Thousand Oaks (CA): Sage.
- Gilby AJ, Mainwaring MC, Griffith SC. 2011. The adaptive benefit of hatching asynchrony in wild zebra finches. *Anim Behav*. 82:479–484.
- Godfray HCJ. 1995. Signaling of need between parents and young: parent-offspring conflict and sibling rivalry. *Am Nat*. 146(1):1–24.
- Godfray HCJ, Partridge L, Harvey PH. 1991. Clutch size. *Annu Rev Ecol Syst*. 22:409–429.
- Hatchwell BJ. 1999. Investment strategies of breeders in avian cooperative breeding systems. *Am Nat*. 154(2):205–219.
- Heinsohn RG. 2004. Parental care, load-lightening, and costs. In: Koenig WD, Dickinson JL, editors. *Ecology and evolution of cooperative breeding in birds*. Cambridge: Cambridge University Press. p. 67–80.
- Iacobucci D, Schneider MJ, Popovich DL, Bakamitsos GA. 2016. Mean centering helps alleviate “micro” but not “macro” multicollinearity. *Behav Res Methods*. 48:1308–1317.
- Johnstone RA. 2011. Load lightening and negotiation over offspring care in cooperative breeders. *Behav Ecol*. 22(2):436–444.
- Koenig WD, Walters EL. 2012a. Brooding, provisioning, and compensatory care in the cooperatively breeding acorn woodpecker. *Behav Ecol*. 23:181–190.
- Koenig WD, Walters EL. 2012b. An experimental study of chick provisioning in the cooperatively breeding acorn woodpecker. *Ethology*. 118(6):566–574.
- Lack D. 1954. The significance of clutch size in birds. In: *The natural regulation of animal numbers*. New York: Oxford University Press. p. 21–31.
- The Language Archive. 2020. ELAN. Nijmegen (The Netherlands): Max Planck Institute for Psycholinguistics. <https://archive.mpi.nl/ta/elan>
- Lee JK, Lima SL. 2017. Hatching asynchrony in birds: multiple nesting attempts and the nest failure hypothesis. *Auk*. 134:1–10.
- Legge S. 2000a. Helper contributions in the cooperatively breeding laughing kookaburra: feeding young is no laughing matter. *Anim Behav*. 59(5):1009–1018.
- Legge S. 2000b. Siblicide in the cooperatively breeding laughing kookaburra (*Dacelo novaeguineae*). *Behav Ecol Sociobiol*. 48(4):293–302.
- Leigh EG, Windsor DM, Rand AS, Foster RB. 1990. The impact of the “El niño” drought of 1982–83 on a Panamanian semideciduous forest. *Elsevier Oceanogr Ser*. 52(C):473–486.
- Lejeune L, van de Pol M, Cockburn A, Louter M, Brouwer L. 2016. Male and female helper effects on maternal investment and adult survival in red-winged fairy-wrens. *Behav Ecol*. 27:1841–1850.
- Levings SC, Windsor DM. 1984. Litter moisture content as a determinant of litter arthropod distribution and abundance during the dry season on Barro Colorado Island, Panama. *Biotropica*. 16(2):125–131.
- Liebl AL, Browning LE, Russell AF. 2016. Manipulating carer number versus brood size: complementary but not equivalent ways of quantifying carer effects on offspring. *Behav Ecol*. 27:1247–1254.
- Liebl AL, Nomano FY, Browning LE, Russell AF. 2016. Experimental evidence for fully additive care among male carers in the cooperatively breeding chestnut-crowned babbler. *Anim Behav*. 115:47–53.
- Lu X, Yu T, Ke D. 2011. Helped ground tit parents in poor foraging environments reduce provisioning effort despite nestling starvation. *Anim Behav*. 82:861–867.
- Macnair MR, Parker GA. 1979. Models of parent-offspring conflict. III. Intra-brood conflict. *Anim Behav*. 27:1202–1209.
- Magrath RD. 1990. Hatching asynchrony in altricial birds. *Biol Rev*. 65:587–622.
- Meade J, Nam K-B, Beckerman AP, Hatchwell BJ. 2010. Consequences of “load-lightening” for future indirect fitness gains by helpers in a cooperatively breeding bird. *J Anim Ecol*. 79:529–537.
- Mock DW. 1994. Brood reduction: narrow sense, broad sense. *J Avian Biol*. 25(1):3–7.
- Mock DW. 2004. More than kin and less than kind. Cambridge (MA): Belknap Press.
- Mock DW, Lamey TC. 1991. The role of brood size in regulating egret sibling aggression. *Am Nat*. 138(4):1015–1026.
- Naguib M, Riebel K, Marzal A, Gil D. 2004. Nestling immunocompetence and testosterone covary with brood size in a songbird. *Proc R Soc B*. 271:833–838.
- Neuenschwander S, Brinkhof MWG, Kölliker M, Richner H. 2003. Brood size, sibling competition, and the cost of begging in great tits (*Parus major*). *Behav Ecol*. 14:457–462.
- NOAA Climate Prediction Center. 2022. Southern oscillation index. <https://www.cpc.ncep.noaa.gov/data/indices/soi>
- O’Connor RJ. 1978. Brood reduction in birds: selection for fratricide, infanticide and suicide? *Anim Behav*. 26:79–96.
- R Development Core Team. 2020. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. <https://www.r-project.org/>
- Richardson DS, Burke T, Komdeur J. 2002. Direct benefits and the evolution of female-biased cooperative breeding in Seychelles warblers. *Evolution*. 56(11):2313–2321.
- Ricklefs RE. 1965. Brood reduction in the curve-billed thrasher. *Condor*. 67(6):505–510.
- Riehl C. 2011. Living with strangers: direct benefits favour non-kin cooperation in a communally nesting bird. *Proc R Soc B*. 278:1728–1735.
- Riehl C. 2012. Mating system and reproductive skew in a communally breeding cuckoo: hard-working males do not sire more young. *Anim Behav*. 84:707–714.
- Riehl C. 2016. Infanticide and within-clutch competition select for reproductive synchrony in a cooperative bird. *Evolution*. 70(8):1760–1769.
- Riehl C, Jara L. 2009. Natural history and reproductive biology of the communally breeding greater ani (*Crotophaga major*) at Gatún Lake, Panama. *Wilson J Ornithol*. 121(4):679–687.
- Riehl C, Smart ZF. 2022. Climate fluctuations influence variation in group size in a cooperative bird. *Curr Biol*. 32(19):4264–4269.e3.
- Riehl C, Strong MJ. 2015. Social living without kin discrimination: experimental evidence from a communally breeding bird. *Behav Ecol Sociobiol*. 69:1293–1299.
- Riehl C, Strong MJ. 2019. Social parasitism as an alternative reproductive tactic in a cooperatively breeding cuckoo. *Nature*. 567:96–99.
- Roulin A, Dreiss AN. 2012. Sibling competition and cooperation over parental care. In: Royle NJ, Smiseth PT, Kölliker M, editors. *The evolution of parental care*. Oxford: Oxford University Press. p. 133–149.
- Russell AF, Langmore NE, Cockburn A, Astheimer LB, Kilner RM. 2007. Reduced egg investment can conceal helper effects in cooperatively breeding birds. *Science*. 317:941–944.
- Sandercock BK. 1997. Incubation capacity and clutch size determination in two calidrine sandpipers: a test of the four-egg threshold. *Oecologia*. 110:50–59.
- Savage JL, Russell AF, Johnstone RA. 2013. Maternal costs in offspring production affect investment rules in joint rearing. *Behav Ecol*. 24:750–758.
- Savagian AG, Riehl C. 2023. Effects of brood and group size on nestling provisioning and resource allocation in a communal bird. *Behav Ecol*. doi:10.5061/dryad.ngflvhzq
- Shen S-F, Chen H-C, Vehrencamp SL, Yuan H-W. 2010. Group provisioning limits sharing conflict among nestlings in joint-nesting Taiwan yuhinas. *Biol Lett*. 6:318–321.
- Shen S-F, Vehrencamp SL, Johnstone RA, Chen H-C, Chan S-F, Liao W-Y, Lin K-Y, Yuan H-W. 2012. Unfavourable environment limits social conflict in *Yuhina brunneiceps*. *Nat Commun*. 3(885):1–7.
- Sieber DJ, Paquet M, Smiseth PT. 2017. Joint effects of brood size and resource availability on sibling competition. *Anim Behav*. 129:25–30.
- Stoleson SH, Beissinger SR. 1995. Hatching asynchrony and the onset of incubation in birds, revisited. In: Power DM, editor. *Current Ornithology*. vol 12. New York: Plenum Press. p. 191–270.
- Stouffer PC, Power HW. 1990. Density effects on asynchronous hatching and brood reduction in European starlings. *Auk*. 107:359–366.
- Trivers RL. 1974. Parent-offspring conflict. *Am Zool*. 14(1):249–264.
- van Boheemen LA, Hammers M, Kingma SA, Richardson DS, Burke T, Komdeur J, Dugdale HL. 2019. Compensatory and additive helper effects in the cooperatively breeding Seychelles warbler (*Acrocephalus sechellensis*). *Ecol Evol*. 9:2986–2995.
- Vehrencamp SL. 1977. Relative fecundity and parental effort in communally nesting anis, *Crotophaga sulcirostris*. *Science*. 197(4301):403–405.
- Vehrencamp SL. 1978. The adaptive significance of communal nesting in groove-billed anis (*Crotophaga sulcirostris*). *Behav Ecol Sociobiol*. 4(1):1–33.
- Wolda H. 1978. Seasonal fluctuations in rainfall, food and abundance of tropical insects. *J Anim Ecol*. 47(2):369–381.
- Woxvold IA, Magrath MJL. 2005. Helping enhances multiple components of reproductive success in the cooperatively breeding apostlebird. *J Anim Ecol*. 74:1039–1050.
- Yuan H-W, Shen S-F, Lin K-Y, Lee P-F. 2005. Group-size effects and parental investment strategies during incubation in joint-nesting Taiwan yuhinas (*Yuhina brunneiceps*). *Wilson Bull*. 117(3):306–312.