ORIGINAL ARTICLE

Caregivers in a communally nesting bird do not consistently synchronize nest visits

Maria G. Smith[1] · Amanda G. Savagian[1] · Christina Riehl[1]

Abstract

Several hypotheses propose that parent birds might synchronize their visits to the nest, but field studies have historically overlooked the temporal pattern of parental care. Either synchrony or asynchrony could provide adaptive benefits; alternatively, any observed synchrony could simply be a byproduct of other coordinated behavior among caregivers. Few studies have quantified visit synchrony in cooperatively breeding birds with multiple caregivers. We tested whether visits to the nest are more or less synchronized than expected by chance in the communally nesting greater ani (*Crotophaga major*), a tropical bird that breeds in groups of four to eight adult caregivers. Across 27 breeding groups, anis did not consistently synchronize nest visits more than expected by chance; however, six groups (22%) did exhibit significant synchrony (up to 44% of visits). Nest visit synchrony was not associated with fledging success or brood size, as would be predicted by two common adaptive hypotheses, and instead might be a byproduct of synchronized foraging.

Significance statement

Various hypotheses may explain why birds either synchronize or evenly space their visits to the nest. Such coordination could increase fitness; however, its prevalence and consequences remain poorly understood, particularly in cooperative breeders. We tested whether nest visits were more or less synchronized than expected by chance in a communally nesting bird, the greater ani, which forms breeding groups of four to eight adults. While some breeding groups synchronized nest visits more than expected, most did not. Further, groups with more synchronized visits did not have increased fledging success, suggesting that the synchrony we observed might not provide a fitness benefit but rather could be a byproduct of adult social behavior away from the nest.

Introduction

Parental care is essential for offspring growth and survival in many taxa (Clutton-Brock 1991; Alonso-Alvarez and Velando 2012), and, when more than one caregiver raises young, parents or social group members must cooperate and coordinate to ensure offspring survival (Griffith 2019). While the overall investment by different providers of parental care has received much attention in the past few decades

(e.g., males vs. females or parents vs. non-breeding helpers; Clutton-Brock 1991; Royle et al. 2012), the temporal pattern of parental care and its potential fitness implications were largely overlooked until recently (Raihani et al. 2010; Johnstone et al. 2014; Savage et al. 2020). The timing of caregivers' bouts of offspring care could be more clumped (hereafter "more synchronized") or more evenly dispersed (hereafter "less synchronized") than expected by chance. Various adaptive and non-adaptive hypotheses for the temporal distribution of parental care have recently been proposed (e.g., Raihani et al. 2010; Shen et al. 2010), but empirical evidence for synchrony is mixed: in some species, parental care bouts appear to be synchronized (e.g., Raihani et al. 2010; Shen et al. 2010; Mariette and Griffith 2012; Halliwell et al. 2022), whereas other species do not show such synchrony (e.g., Khwaja et al. 2019; Enns and Williams 2021).

Communicated by M. Leonard

✉ Maria G. Smith
mgsmith@princeton.edu

1 Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, USA

In birds, the most prominent adaptive hypothesis to explain non-random timing of feeding visits posits that synchrony reduces the risk of nest predation (Sargent 1993; Raihani et al. 2010). Several studies have found evidence to support this hypothesis (Raihani et al. 2010; Bebbington and Hatchwell 2016; Leniowski and Węgrzyn 2018). Parental activity at the nest can attract predators (Muchai and du Plessis 2005; Matysioková and Remeš 2018), possibly through increased frequency of nestling begging calls (Haskell 1994; Haff and Magrath 2011). Synchronizing nest visits is one way that parents can decrease predation risk for their broods, either by concentrating begging bouts temporally or simply by decreasing the total amount of time during which there is parental activity near the nest (Skutch 1949; Raihani et al. 2010). Several other adaptive hypotheses for nest visit synchrony have been proposed but have received limited attention. For example, synchronized feeds might decrease competition among nestlings and lead to a more even distribution of food among them (Shen et al. 2010), or caregivers might decrease their own risk of predation by synchronizing visits (Foster and Treherne 1981; Raihani et al. 2010; Mainwaring and Griffith 2013). Nest visit synchrony also could provide social signaling benefits when non-breeding helpers pay to stay (Trapote et al. 2021; but see McDonald et al. 2008; Nomano et al. 2015; Koenig and Walters 2016), or when individuals signal information about their own quality to groupmates (Doutrelant and Covas 2007; but see McDonald et al. 2008; Koenig and Walters 2016). Finally, by observing the feeding contributions of other caregivers, synchrony might provide adults with the opportunity to better determine their own optimal levels of investment in the brood (Bebbington and Hatchwell 2016). To date, there is either limited or contradictory evidence supporting any one of these hypotheses.

Some studies have failed to find any fitness consequences of nest visit synchrony (van Rooij and Griffith 2013; Ihle et al. 2019b). Synchrony might instead occur as a non-adaptive byproduct of other coordinated behaviors of adults, which could occur for adaptive reasons that are not contingent on visiting the nest synchronously. For example, if caregivers benefit from spending time in close proximity to each other, for example to increase foraging success or decrease predation risk (Beauchamp 1998; McDonald et al. 2008; Mariette and Griffith 2012; Sorato et al. 2012), then nest visits might often be synchronized simply as a byproduct of this adult social behavior. Alternatively, adults might synchronize their behavior due to shared environmental conditions; for example, if the weather impacts foraging conditions, adults might tend to feed nestlings at the same time after poor conditions improve (Schlicht et al. 2016; Ihle et al. 2019a).

The possibility that nest visits could be less synchronized than expected by chance has received little attention, with the only tests in seabirds (Wojczulanis-Jakubas et al. 2018; Grissot et al. 2019), but it is a possibility in other species. Evenly spaced visits might improve nestling digestive efficiency: when parents feed at close intervals, nestlings are overfed, and food is retained in the gut for less time, rendering digestion less efficient (Karasov and Wright 2002). If offspring digestive efficiency is maximized, this is expected to increase offspring growth rates and could even decrease predation risk by allowing nestlings to fledge earlier (Martin et al. 2018). Alternatively, evenly spaced visits, like synchronous visits, actually could decrease nestling predation risk under some circumstances. For example, if visually oriented predators are much more likely to notice multiple birds visiting the same location than single birds, then less synchronized visits could decrease nest conspicuousness to those predators.

Despite the growing literature on nest visit synchrony, most of the work has focused on species with biparental care. However, several of the above hypotheses predict that cooperative breeders, in which more than two adults care for offspring (Cockburn 2006), should experience greater selection pressure to evolve nest visit synchrony. Compared to species with biparental care, cooperative breeders have more caregivers and often larger broods and, consequently, usually have higher feeding rates, which might increase nest conspicuousness to predators (Muchai and du Plessis 2005; Matysioková and Remeš 2018). Additionally, signaling of one's own contributions or assessing the contributions of others via nest visit synchrony could be more important in larger, cooperative groups than in a biparental system (Nomano et al. 2015; Koenig and Walters 2016). However, it is also possible that coordination of synchrony is more difficult with more individuals, which could constrain the evolution of synchrony in cooperative groups. Despite the prediction that visit synchrony should be under increased selection in cooperative breeders, only a few studies have investigated the possibility of synchrony and its potential fitness consequences in these social systems, and they have produced mixed evidence (Raihani et al. 2010; Shen et al. 2010; Koenig and Walters 2016; Nomano et al. 2019; Halliwell et al. 2022). Our understanding of nest visit synchrony in birds therefore remains incomplete, especially in cooperative breeders.

In this study, we quantified synchrony of nest visits in communally nesting greater anis (*Crotophaga major*), which breed in groups containing two or three breeding pairs and non-reproductive (unpaired) helpers. Each group therefore contains between four and eight adult caregivers (Riehl and Jara 2009; Riehl and Strong 2019). While we lacked the data to test all predictions for all relevant hypotheses for visit synchrony, we were able to test a subset of predictions for two hypotheses that were suited to our data set and the natural history of this species. We expected greater ani breeding

groups to exhibit more synchrony than expected by chance, potentially explained by the predation risk hypothesis or the nestling competition hypothesis. First, nest predation is the most frequent cause of reproductive failure (approximately 70% of nests are depredated, and 78% of all nest failures are attributable to predation; CR, unpublished data). Therefore, we would expect selection to favor antipredator strategies in this species. Second, nestlings in greater ani broods are produced by unrelated breeders (Riehl 2011) and therefore might experience high intrabrood competition. It is plausible that synchronous feedings could be used to evenly distribute food among nestlings, as in the communally nesting Taiwan Yuhina (*Yuhina brunneiceps*), which has a similar breeding system (Shen et al. 2010). We asked whether the amount of visit synchrony observed was positively correlated with fledging success, which served as a test of one of the predictions of the predation risk hypothesis. We also asked whether brood size was positively correlated with synchrony, as would be expected according to the nestling competition hypothesis.

Methods

Study system and data collection

We studied the greater ani (hereafter "ani") in the Barro Colorado Nature Monument, central Panama, from June to September of 2017–2019. Anis are communal nesters in which two or three unrelated, socially monogamous pairs cooperate to raise young in a shared nest; single pairs have never been recorded to raise young successfully (Riehl and Jara 2009; Riehl and Strong 2019). About 15–20% of breeding groups also include one or two non-breeding helpers, which can be either related to one breeding pair or unrelated to all breeders (Riehl and Jara 2009; Riehl and Smart 2022). All group members contribute to feeding the young medium to large arthropods, such as katydids and spiders, and some small vertebrates, such as lizards (Riehl and Jara 2009; Riehl and Strong 2015). Ani nestlings can leave the nest as early as 5 or 6 days of age (Riehl and Jara 2009), so our data collection was restricted to the first 6 days of the nestling stage to prevent premature fledging.

Anis nest on the shorelines of lakes or in emergent vegetation in the water, so we monitored nests by boat. We typically found nests during the building or laying stages then visited them every day or every other day during the nestling stage to film nests and to note hatching dates, brood sizes, and the fates of all nestlings. We used small cameras (Contour Roam 3 (Contour, LLC, Provo, UT) or GoPro Hero 5 (GoPro, San Mateo, CA)) outfitted with external battery packs (Anker Power Bank (Anker Innovations Co., Ltd., Changsha, China) or GoPro ActionPack Extended Battery (Re-Fuel by Digipower, Avenel, NJ)) to extend filming time

to up to 9 or more hours. Filming generally began between 0600 and 1100 h; however, due to weather or logistical difficulties, some footage began later in the day. Video footage lasted until dark or until the battery was spent. Footage from 2018 was also analyzed in studies of nestling begging and feeding behavior (Savagian and Riehl 2022, 2023). It was not possible to record data blind because our study involved focal animals in the field.

For our analyses, we selected a subset of the available video recordings that occurred as late as possible in the nestling stage to minimize the time adults spent brooding nestlings. Footage therefore typically was taken when the oldest nestlings were 4 days old (mean $\pm$ SE = 3.8 $\pm$ 0.1 days, range = 2–6 days, N = 54 footage-days). We used footage from a day in which one or more nestlings hatched on only two occasions and never used footage from a day during which most nestlings in a brood hatched. We acquired 2 days of video footage for each of 27 nests—17 small groups (two breeding pairs) and 10 large groups (three breeding pairs)—for a total of 332 h of footage. Each day of footage lasted a mean of 6.0 h ($\pm$ 0.2 h (SE), range = 1.5–8.7 h, N = 54 footage-days) and included a mean of 70 visits ($\pm$ 5 visits (SE), range = 10–180 visits). Brood size ranged from 1 to 11 (mean $\pm$ SE = 5.2 $\pm$ 0.4, N = 54 footage-days) and was consistent between the 2 days filmed at each nest in all but one instance, in which two of eight nestlings were depredated overnight between filming days.

We manually coded each video beginning after a 10-min acclimation period to allow the birds to resume normal behavior after we set up the camera. We noted the following: start time of all visits to the nest (when the adult arrived on the nest rim or in the nest cup or perched near the nest but began feeding a nestling from that location) and the behavior of the visiting adult (bringing food for nestlings; brooding, with start and end times; bringing a leaf or twig to the nest; and/or interacting with another feeding adult). Most adults filmed were not individually marked, so we were unable to quantify the behavior of specific birds.

Despite having few marked birds in our study population, we were able to confirm that most breeding groups filmed were distinct. Most nests filmed over the 3 years of our study were in different territories, and ani breeding groups tend to remain in the same territories across years (Riehl and Strong 2018). By observing as many territories as possible, we minimized our chances of collecting data on the same breeding group in multiple years (pseudoreplication). However, to maximize our sample size of nests that survived until the late nestling stage, we included in our analysis four groups that were observed in two different years. For three of these four groups, we inferred that there was a change in group composition (we documented at least one additional or replaced group member) across years using genetic information (see Riehl and Strong 2019 for details). In the fourth group,

most nestlings were depredated, so it was not possible to determine whether all six breeders were the same across the two years, but we included this group in our analyses.

Prior to analysis, we further restricted the data set to exclude periods of time in which nest visit rates were low, as our statistical methods assumed that nest visit rates were fairly constant (see below). Because birds typically brood nestlings during rain (Beintema and Visser 1989; Rosa and Murphy 1994) and because a brooding adult is excluded from the pool of potential visitors during that time (Bebbington and Hatchwell 2016), we removed periods of time for which it rained or an adult brooded for more than 10 min. If two periods of rain or of brooding were separated by < 10 min, we combined them, including the intervening time, to create one longer period to exclude. To remove additional time periods during which visit rates were lower than usual (Savagian and Riehl 2023), we also restricted our analyses to nest visits before 1700 h (~ 1.5 h before the earliest sunset of the breeding season).

Statistical analyses

We conducted all analyses in R v. 4.1.2 (R Core Team 2021). Using the final data set, we defined nest visit synchrony as the proportion of inter-visit intervals (IVIs) that were 1 min or less (Bebbington and Hatchwell 2016; Leniowski and Węgrzyn 2018). We defined an IVI as the time between one bird's arrival at the nest and the subsequent arrival time, as in similar studies (Johnstone et al. 2014; Bebbington and Hatchwell 2016; Ihle et al. 2019b). We consider 1 min to be a biologically relevant period of time (Ihle et al. 2019a), given that 1 min is greater than the duration of a typical nest visit (median 18 s, $N = 2615$ visits at 15 nests) and much less than the time between visits by the same individual (median 24.1 min, $N = 521$ visits for a subset of three nests at which all birds were individually marked). In other words, during a 1-min period, there is enough time for the first bird to leave before the second arrives (in case the second is waiting to feed alone), and it is not likely that the same bird will be returning within the same minute. We also conducted the analyses using a 2-min synchrony window (Ihle et al. 2019a; Khwaja et al. 2019; see Supplementary Material), although given the short median visit duration in anis, we believe that a 1-min window is more biologically relevant (Enns and Williams 2021). When periods of rain or brooding were removed from the data set, the observation period effectively was given a new start time, and we did not calculate IVIs that included the time excluded due to rain or brooding. Our overall measure of observed nest visit synchrony reported is the proportion of a given nest's IVIs that were 1 min or less. Therefore, the theoretical maximum synchrony is 1, while the theoretical minimum synchrony is 0.

It is important to account for synchronized nest visits that can occur by chance, especially given that the breeding groups in our sample vary in visit rate and group size. With a higher visit rate, there is a higher probability of synchrony occurring simply by chance rather than through active coordination among birds. While various randomization methods have been suggested when individual identities are known (Ihle et al. 2019a), we used an approach similar to that of Khwaja et al. (2019) because our birds were mostly unmarked. There is evidence that birds' visits to nests approximately follow a Poisson process, especially when multiple birds are considered together, as this decreases the potential impact of any refractory period that could exist between visits (Pick et al. 2023). The temporal pattern of nest visits therefore can be modeled by an exponential distribution, which is described by one parameter: the visit rate (Khwaja et al. 2019; Pick et al. 2023). We confirmed that the observed IVIs for each nest generally followed an exponential distribution (Fig. S1). This simulation approach also assumes that the visit rate remains relatively constant throughout the day and between the 2 days of footage used for each nest, since they were combined for the main analyses. We confirmed that this assumption generally held (see Supplementary Material); however, we also report analyses conducted for each day of footage separately.

For each nest, we calculated the overall visit rate (excluding long bouts of rain and brooding, as described above) and used this as the rate parameter for a simulated exponential distribution with sample size equal to the observed number of IVIs for that nest. We simulated such a distribution a total of 10,000 times per nest and each time calculated the proportion of IVIs that were synchronized (within 1 min, as described above). Finally, we compared the observed proportion of synchronized IVIs to the distribution of expected IVIs if visits occurred randomly and calculated the associated two-tailed P-value. Our α level was 0.05: 0.025 in the lower tail of the expected distribution, such that an observed value in this tail was considered significantly less synchronized than expected by chance, and 0.025 in the upper tail, such that an observed value in this tail was significantly more synchronized than expected by chance (Araya-Salas et al. 2017; Kern and Radford 2018). It is important to consider non-feeding visits to nests, if they occur, because hypotheses for nest visit synchrony can apply to either all nest visits or just visits involving nestling feeding. We therefore conducted these analyses for two data sets: one with all nest visits and one with only feeding visits. A few visits could not be confirmed to involve feedings because they occurred at the edge of the camera frame ($N = 28$ visits from two nests). Since the majority (93%; $N = 3834$) of nest visits documented at all other nests involved feeding, we assumed that these 28 unseen visits involved feeding and therefore included them in the feeding-only data set.

For an additional comparison, we calculated a synchrony index for each nest: the observed synchrony minus the median expected synchrony (Khwaja et al. 2019). If this synchrony index was greater than 0, then the birds at that nest tended to synchronize visits more than expected; if the index was less than 0, then the birds tended to synchronize visits less than expected. We compared all synchrony indices to 0 with a one-sample t-test to determine whether visits across all nests were more or less synchronized than expected. While this method does not address whether observed synchrony at a given nest differed significantly from the expected synchrony, it provides an overall sense of whether observed synchrony was generally either more or less synchronized than expected, even if by only a small margin.

Finally, although we generally lacked data to test all predictions of relevant hypotheses for visit synchrony and therefore focused on testing simply for the presence or absence of synchrony, we did have the data to test predictions of two hypotheses (predation risk and nestling competition). We acknowledge that, with our small sample size, it might be difficult to detect such correlations and therefore consider our analyses to be fairly exploratory. We asked whether an increased synchrony index was correlated with lower nest failure, as predicted by the predation risk hypothesis. All nestling mortality during data collection at our focal nests was due to predation; we observed no starvation of focal nestlings. Nest failure was therefore a measure of predation risk in this case. We constructed a binomial generalized linear model (GLM) with whether a nest fledged any young as the response variable. Because ani nestlings can survive outside the nest as early as 6 days old, we stopped checking nests at this age and considered young to be fledged if they survived to day 6. We included synchrony index and group size as predictors because nest success is known to be correlated positively with group size in the greater ani (Riehl and Smart 2022). We also tested whether visit synchrony was positively correlated with brood size, as predicted by the nestling competition hypothesis. We constructed a linear model with synchrony index as the response variable and brood size as a predictor.

Results

When we considered all nest visits ($N = 3679$ IVIs), visits at 6 of 27 nests (22%) were more synchronized than expected by chance, while visits at one nest (4%) were less synchronized than expected by chance (Fig. 1(a); Table S1). The mean observed visit synchrony was 0.24 (± 0.02 (SE), range = 0.09–0.44), the mean observed synchrony of nests whose visits were more synchronized than expected by chance was 0.30 (± 0.03 (SE), range = 0.24–0.44), and

that of the nest whose visits were less synchronized than expected by chance was 0.27. Overall, the synchrony indices (observed synchrony minus the median synchrony from the 10,000 simulations) for each nest were significantly different from 0, with most being positive (one-sample t-test: $t_{26} = 3.448$, $P = 0.002$, mean = 0.036). When we analyzed each day of footage separately, we still observed that visits on 6 of the 54 days were more synchronized than expected (Fig. S2). These 6 days were from the same 6 nests as in the data set with days combined; none of these nests had visits more synchronized by chance on both days observed.

For the second set of analyses, we removed visits that did not involve bringing a food item for nestlings ($N = 261$ visits). Behaviors observed during non-feeding visits included brooding or shading nestlings (26% of visits), bringing a leaf (nest lining) or twig to add to the nest or maintaining the nest (16%), interacting with a feeding adult directly or indirectly (including handling food brought by another adult; 8%), a combination of these behaviors (4%), or no obvious behaviors other than sitting at or in the nest (45%).

When we considered feeding visits only ($N = 3432$ IVIs), visits at 4 of 27 nests (15%) were more synchronized than expected by chance, while visits at one nest (4%) were less synchronized than expected by chance (Fig. 1(b); Table S2). The main difference between these results (considering only feeding visits) and the first results (considering all visits) was that two nests (19 and 24, as numbered in Fig. 1) were no longer more synchronized than expected by chance. The mean observed visit synchrony was 0.22 (± 0.01 (SE), range = 0.04–0.33), the mean observed synchrony of nests whose visits were more synchronized than expected by chance was 0.25 (± 0.01 (SE), range = 0.23–0.27), and that of the nest whose visits were less synchronized than expected by chance was 0.27. As with the analysis of all visits, the synchrony indices for each nest were significantly different from 0, with most being positive (one-sample t-test: $t_{26} = 3.390$, $P = 0.002$, mean = 0.031). When we analyzed each day of footage separately, we observed that visits on 6 of the 54 days were more synchronized than expected (Fig. S3). These 6 days were from 5 of the same 6 nests as in the analysis of all visits with days combined (all but nest 24, which still did not exhibit more synchrony than expected when days were analyzed separately).

We repeated the analysis of all visits with a definition of synchrony as the proportion of IVIs that were 2 min or less. As with the analysis using a 1-min synchrony window, visits were more or less synchronized than expected by chance for few nests (see Supplementary Material; Fig. S4; Table S3). Visits at 2 of 27 nests (7%) were more synchronized than expected by chance, while visits at one nest (4%) were less synchronized than expected by chance (see Supplementary Material for additional details). When we analyzed each day of footage separately, we observed
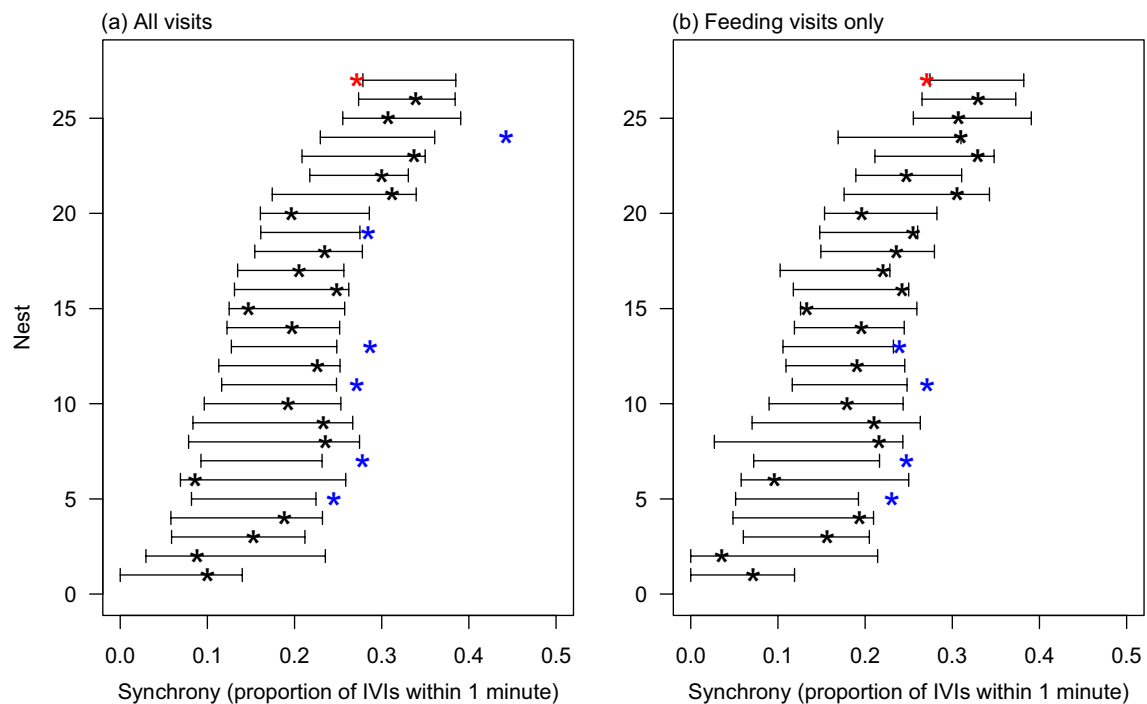
Fig. 1 Observed (asterisks) and expected 95% confidence intervals from 10,000 simulations (bars) of nest visit synchrony for (**a**) all visits and (**b**) feeding visits only to 27 nests, with synchrony defined as the proportion of inter-visit intervals (IVIs) less than or equal to 1 min. Blue asterisks denote observed synchrony values significantly higher than expected by chance, while red asterisks denote observed synchrony values significantly lower than expected by chance. Black asterisks denote nests for which observed synchrony did not differ statistically from expected synchrony. Nests in (**a**) are ordered from lowest to highest observed visit rate from bottom to top; nests in (**b**) are ordered as in (**a**) for ease of comparison

that visits on only 2 of the 54 days were more synchronized than expected (Fig. S5). One of these days was from the same nest as in the data set with days combined. The nest with less synchrony than expected when days were combined also exhibited less synchrony when days were analyzed separately, but only on one of the days observed.

Finally, we tested predictions of two hypotheses for feeding synchrony: predation risk and nestling competition. For all the following analyses, synchrony indices calculated from the data set with all visits (with days combined) were used. Synchrony index was not significantly correlated with fledging success, which increased with increasing group size (Fig. 2; GLM: synchrony index: -11.51 ± 11.08, $z = -1.04$, $P = 0.30$; group size: 1.47 ± 0.74, $z = 1.99$, $P = 0.05$; $N = 27$ nests). Only 8 of 27 nests in our sample (30%) failed to fledge any young. Synchrony index was not significantly correlated with brood size (Fig. 3; linear model: brood size: -0.005 ± 0.004, $t = -1.32$, $P = 0.20$; $N = 27$ nests). In addition, synchrony index was not significantly correlated with group size (see Supplementary Material; Fig. S6).

Discussion

We did not find strong evidence that nest visits were more or less synchronized than expected by chance in the greater ani. We found a significantly positive overall synchrony index across nests, indicating that nests tended to show higher observed synchrony than median expected synchrony. However, the magnitude of this difference was generally small, as evidenced by only six (full data set) or four (feeding-only data set) nests out of 27 whose visits were significantly more synchronized than expected by chance when comparing observed synchrony to a 95% confidence interval of expected synchrony (rather than to median expected synchrony in the *t*-test). Given that the 95% confidence intervals of expected synchrony had a mean spread of 0.14 and that the overall difference between mean observed synchrony and median expected synchrony was only 0.04, comparing observed synchrony to the median expected synchrony (rather than to the confidence interval calculated in our simulations) is a less robust test for active synchrony, although it provides a

Fig. 2 Fledging success (whether a nest fledged any young) vs. synchrony index for communally nesting groups ($N = 27$). The correlation was not significant
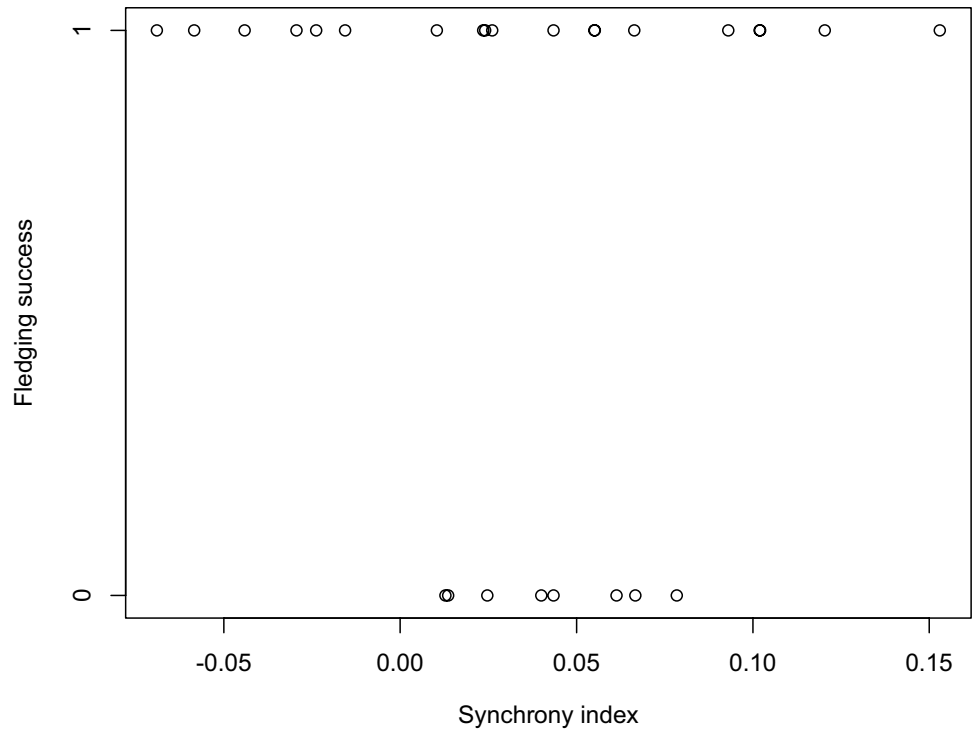
Fig. 3 Synchrony index vs. brood size (number of nestlings) for communally nesting groups ($N = 27$). The correlation was not significant
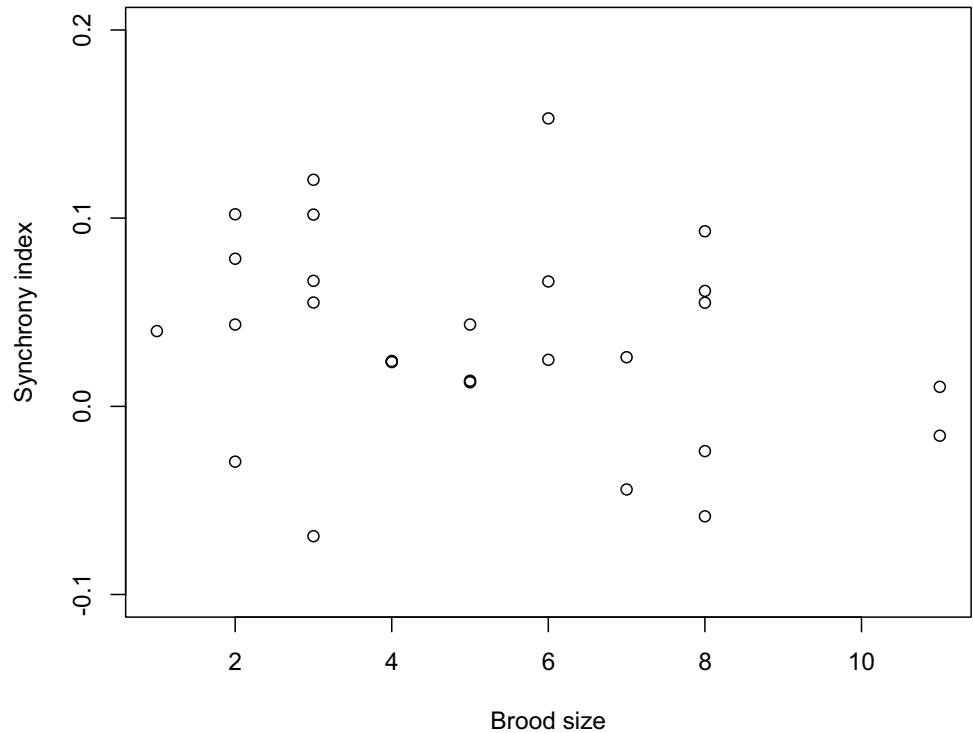
convenient test of the general trend across all nests. We therefore conclude that, because a minority of nests (22% when all visits were included) showed significantly more synchrony than expected when comparing observed synchrony to 95% confidence intervals of expected synchrony, greater ani groups did not consistently synchronize nest visits.

The lack of obvious and consistent visit synchrony in the greater ani contrasts with other work on cooperatively

breeding birds, which generally has found more widespread synchrony in nest visits than expected (Raihani et al. 2010; Shen et al. 2010; Halliwell et al. 2022; but see Nomano et al. 2019). Although it is difficult to compare directly across species, as synchrony will depend on group size and feeding rate, the average proportion of synchronized visits that we observed was lower than that in other species studied, such as cooperatively breeding southern pied-babblers (*Turdoides bicolor*, 41% of visits, Raihani et al. 2010) and Taiwan yuhinas (89.5% of visits, Shen et al. 2010) and biparental Eurasian blackcaps (*Sylvia atricapilla*, 57% of visits, Leniowski and Węgrzyn 2018). When considering only feeding visits rather than all nest visits, we found even less evidence for visit synchrony, and our results also differed when using a 2-min synchrony window instead of a 1-min window. Furthermore, when we analyzed the 2 days of footage for each nest separately, no nest ever showed more (or less) synchrony than expected on both days filmed. This inconsistency between results highlights an important caveat, which was that our nest-specific results were somewhat dependent on the data set, definition of synchrony, and timescale used, further suggesting that the few instances of statistically significant synchrony that we observed might not be biologically relevant or important for fitness.

While the results were largely similar when comparing the data set with all visits to that with only feeding visits, two nests (19 and 24) had visits more synchronized than expected by chance in the full data set but did not when non-feeding visits were excluded. It is likely that one of these cases can be explained simply by a decrease in sample size, while the other may be linked to the importance of non-feeding visits in determining synchrony. Despite the change in statistical significance, observed visit synchrony at nest 19 was similar in the two data sets, decreasing from 0.28 to 0.26 when non-feeding visits were excluded ($N = 15$ of 211 (7%) visits removed), suggesting that the change was due to the decrease in sample size. By contrast, nest 24 had the highest observed visit synchrony (0.44) in the full data set, and when non-feeding visits were removed from the data set ($N = 41$ of 183 (22%) visits removed), observed synchrony dropped to 0.31. This large decrease suggests that non-feeding visits were important in contributing to synchronized nest visits. Anecdotally, at nest 24, we recorded many instances of breeders arriving at the nest while either of the two helpers was attempting to feed. Sometimes the adults directly interfered by taking food from helpers and feeding it to nestlings themselves. In greater anis, 8% of non-feeding visits involved solely these types of intragroup feeding interactions, as did many feeding visits in which the feeding adult stayed at the nest to interact with other caregivers arriving with food (Savagian and Riehl 2022). While these interactions between caregivers have not been well documented in the literature to our knowledge, they

may represent an important subset of nest visits, especially in cooperative breeders, and therefore may be important to consider in future analyses of the synchrony of nest visits.

Our results also differed when we defined synchrony using a 2-min window compared to a 1-min window: even fewer nests exhibited more synchrony than expected using a 2-min window. We believe that a 1-min window is more biologically relevant than a 2-min window in this species, but we used both windows to assess the robustness of our results. In contrast to other studies that compared different synchrony windows (Ihle et al. 2019a; Halliwell et al. 2022), the overall prevalence of significant synchrony in our study changed with different windows. This dependence of the results on the definition of synchrony chosen has been discussed by others (Ihle et al. 2019a; Enns and Williams 2021), and we agree that more rigorous selection of species-specific synchrony windows would be beneficial. Ideally, synchrony windows would be determined based on behavioral observations and would be placed in the context of the hypothesis for synchrony being tested.

Although we do not have strong evidence for widespread nest visit synchrony in the greater ani, a few nests consistently had visits more synchronized than expected by chance. An adaptive explanation for this synchrony is unlikely given its low prevalence, the fact that more synchronized visits were never documented on both days of footage for a given nest when days were analyzed separately, and the lack of correlations between synchrony index and fledging success and between brood size and synchrony index. While our sample size was small and biased toward nests that had already survived until the late nestling stage and therefore might not have been sufficient to detect any correlations, we saw no indication of trends in the data and therefore suggest that fledging success and brood size are unlikely to be correlated with visit synchrony in this population. However, we acknowledge that we lacked the data to test all possible hypotheses for visit synchrony and therefore cannot completely rule out adaptive hypotheses for the patterns we observed.

Alternatively, visit synchrony could occur consistently at this subset of nests as a byproduct of social behavior. Greater ani breeding groups remain on territory year round and form relatively stable groups across years (Riehl and Strong 2018). Anis within a group therefore spend much of their time together. While we have not quantified the amount of time they forage together or perch together near the nest, both social activities seem common (Riehl 2012) and therefore could explain some of the observed nest visit synchrony. The lack of synchrony observed at the majority of nests could be due to a lack of adaptive value or because synchrony is too costly to evolve. Caregivers can suffer opportunity costs while waiting with food for another group member to arrive so that visits can be synchronized (Raihani et al. 2010; Khwaja et al. 2019), and

such coordination could be too complex to achieve due to either logistical or cognitive constraints.

In summary, we did not find evidence that greater ani group members consistently synchronize visits to the nest, in contrast to several other cooperatively breeding species. The visit synchrony we observed at some nests might arise as a byproduct of adult social behavior. We encourage further work on the temporal pattern of nest visits in additional species, particularly cooperative breeders, with careful data collection and testing of relevant hypotheses for synchrony, to improve our understanding of the prevalence and importance of nest visit synchrony in birds.

Data availability All data generated or analyzed during this study are included in this published article and its supplementary information files.

Declarations

Ethics approval All methods were approved by the Institutional Animal Care and Use Committees of Princeton University (2114F-17-19) and the Smithsonian Tropical Research Institute (2015-0601-2018, 2018-0403-2021). All applicable international, national, and/or institutional guidelines for the use of animals were followed.

Competing interests The authors declare no competing interests.

Disclaimer Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation.

References

Alonso-Alvarez C, Velando A (2012) Benefits and costs of parental care. In: Royle NJ, Smiseth PT, Kölliker M (eds) The evolution of parental care. Oxford University Press, Oxford, pp 40–61

Araya-Salas M, Wojczulanis-Jakubas K, Phillips EM, Mennill DJ, Wright TF (2017) To overlap or not to overlap: context-dependent coordinated singing in lekking long-billed hermits. Anim Behav 124:57–64. https://doi.org/10.1016/j.anbehav.2016.12.003

Beauchamp G (1998) The effect of group size on mean food intake rate in birds. Biol Rev 73:449–472. https://doi.org/10.1017/S0006323198005246

Bebbington K, Hatchwell BJ (2016) Coordinated parental provisioning is related to feeding rate and reproductive success in a songbird. Behav Ecol 27:652–659. https://doi.org/10.1093/beheco/arv198

Beintema AJ, Visser GH (1989) The effect of weather on time budgets and development of chicks of meadow birds. Ardea 77:181–192

Clutton-Brock TH (1991) The evolution of parental care. Princeton University Press, Princeton

Cockburn A (2006) Prevalence of different modes of parental care in birds. Proc R Soc Lond B 273:1375–1383. https://doi.org/10.1098/rspb.2005.3458

Doutrelant C, Covas R (2007) Helping has signalling characteristics in a cooperatively breeding bird. Anim Behav 74:739–747. https://doi.org/10.1016/j.anbehav.2006.11.033

Enns J, Williams TD (2021) Paying attention but not coordinating: parental care in European starlings (*Sturnus vulgaris*). Anim Behav 193:113–124. https://doi.org/10.1016/j.anbehav.2022.09.009

Foster WA, Treherne JE (1981) Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. Nature 293:466–467. https://doi.org/10.1038/293466a0

Griffith SC (2019) Cooperation and coordination in socially monogamous birds: moving away from a focus on sexual conflict. Front Ecol Evol 7:455. https://doi.org/10.3389/fevo.2019.00455

Grissot A, Araya-Salas M, Jakubas D, Kidawa D, Boehnke R, Błachowiak-Samołyk K, Wojczulanis-Jakubas K (2019) Parental coordination of chick provisioning in a planktivorous Arctic seabird under divergent conditions on foraging grounds. Front Ecol Evol 7:349. https://doi.org/10.3389/fevo.2019.00349

Haff TM, Magrath RD (2011) Calling at a cost: elevated nestling calling attracts predators to active nests. Biol Lett 7:493–495. https://doi.org/10.1098/rsbl.2010.1125

Halliwell C, Beckerman AP, Germain M, Patrick SC, Leedale AE, Hatchwell BJ (2022) Coordination of care by breeders and helpers in the cooperatively breeding long-tailed tit. Behav Ecol 33:844–858. https://doi.org/10.1093/beheco/arac048

Haskell D (1994) Experimental evidence that nestling begging behaviour incurs a cost due to nest predation. Proc R Soc Lond B 257:161–164. https://doi.org/10.1098/rspb.1994.0110

Ihle M, Pick JL, Winney IS, Nakagawa S, Burke T (2019a) Measuring up to reality: null models and analysis simulations to study parental coordination over provisioning offspring. Front Ecol Evol 7:142. https://doi.org/10.3389/fevo.2019.00142

Ihle M, Pick JL, Winney IS, Nakagawa S, Schroeder J, Burke T (2019b) Rearing success does not improve with apparent pair coordination in offspring provisioning. Front Ecol Evol 7:405. https://doi.org/10.3389/fevo.2019.00405

Johnstone RA, Manica A, Fayet AL, Stoddard MC, Rodriguez-Gironés MA, Hinde CA (2014) Reciprocity and conditional cooperation between great tit parents. Behav Ecol 25:216–222. https://doi.org/10.1093/beheco/art109

Karasov WH, Wright J (2002) Nestling digestive physiology and begging. In: Wright J, Leonard ML (eds) The evolution of begging. Kluwer Academic Publishers, Dordrecht, pp 199–219

Kern JM, Radford AN (2018) Experimental evidence for delayed contingent cooperation among wild dwarf mongooses. P Natl Acad Sci USA 115:6255–6260. https://doi.org/10.1073/pnas.1801000115

Khwaja N, Massaro M, Martin TE, Briskie JV (2019) Do parents synchronise nest visits as an antipredator adaptation in birds of New Zealand and Tasmania? Front Ecol Evol 7:389. https://doi.org/10.3389/fevo.2019.00389

Koenig WD, Walters EL (2016) Provisioning patterns in the cooperatively breeding acorn woodpecker: does feeding behaviour serve

as a signal? Anim Behav 119:125–134. https://doi.org/10.1016/j.anbehav.2016.06.002

Leniowski K, Węgrzyn E (2018) Synchronisation of parental behaviours reduces the risk of nest predation in a socially monogamous passerine bird. Sci Rep 8:7385. https://doi.org/10.1038/s41598-018-25746-5

Mainwaring MC, Griffith SC (2013) Looking after your partner: sentinel behaviour in a socially monogamous bird. PeerJ 1:e83. https://doi.org/10.7717/peerj.83

Mariette MM, Griffith SC (2012) Nest visit synchrony is high and correlates with reproductive success in the wild zebra finch *Taeniopygia guttata*. J Avian Biol 43:131–140. https://doi.org/10.1111/j.1600-048X.2012.05555.x

Martin TE, Tobalske B, Riordan MM, Case SB, Dial KP (2018) Age and performance at fledging are a cause and consequence of juvenile mortality between life stages. Sci Adv 4:eaar1988. https://doi.org/10.1126/sciadv.aar1988

Matysioková B, Remeš V (2018) Evolution of parental activity at the nest is shaped by the risk of nest predation and ambient temperature across bird species. Evolution 72:2214–2224. https://doi.org/10.1111/evo.13580

McDonald PG, te Marvelde L, Kazem AJN, Wright J (2008) Helping as a signal and the effect of a potential audience during provisioning visits in a cooperative bird. Anim Behav 75:1319–1330. https://doi.org/10.1016/j.anbehav.2007.09.005

Muchai M, du Plessis MA (2005) Nest predation of grassland bird species increases with parental activity at the nest. J Avian Biol 36:110–116. https://doi.org/10.1111/j.0908-8857.2005.03312.x

Nomano FY, Browning LE, Savage JL, Rollins LA, Griffith SC, Russell AF (2015) Unrelated helpers neither signal contributions nor suffer retribution in chestnut-crowed babblers. Behav Ecol 26:986–995. https://doi.org/10.1093/beheco/arv023

Nomano FY, Savage JL, Browning LE, Griffith SC, Russell AF (2019) Breeding phenology and meteorological conditions affect carer provisioning rates and group-level coordination in cooperative chestnut-crowned babblers. Front Ecol Evol 7:423. https://doi.org/10.3389/fevo.2019.00423

Pick JL, Khwaja N, Spence MA, Ihle M, Nakagawa S (2023) Counter culture: causes, extent and solutions of systematic bias in the analysis of behavioural counts. PeerJ 11:e15059. https://doi.org/10.7717/peerj.15059

R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/

Raihani NJ, Nelson-Flower MJ, Moyes K, Browning LE, Ridley AR (2010) Synchronous provisioning increases brood survival in cooperatively breeding pied babblers. J Anim Ecol 79:44–52. https://doi.org/10.1111/j.1365-2656.2009.01606.x

Riehl C (2011) Living with strangers: direct benefits favour non-kin cooperation in a communally nesting bird. Proc R Soc Lond B 278:1728–1735. https://doi.org/10.1098/rspb.2010.1752

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. https://doi.org/10.1016/j.anbehav.2012.06.028

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 121:679–687. https://doi.org/10.1676/09-017.1

Riehl C, Smart ZF (2022) Climate fluctuations influence variation in group size in a cooperative bird. Curr Biol 32:4264–4269. https://doi.org/10.1016/j.cub.2022.07.057

Riehl C, Strong MJ (2015) Social living without kin discrimination: experimental evidence from a communally breeding bird. Behav Ecol Sociobiol 69:1293–1299. https://doi.org/10.1007/s00265-015-1942-9

Riehl C, Strong MJ (2018) Stable social relationships between unrelated females increase individual fitness in a cooperative bird. Proc R Soc B 285:20180130. https://doi.org/10.1098/rspb.2018.0130

Riehl C, Strong MJ (2019) Social parasitism as an alternative reproductive tactic in a cooperatively breeding cuckoo. Nature 567:96–99. https://doi.org/10.1038/s41586-019-0981-1

Rosa SM, Murphy MT (1994) Trade-offs and constraints on eastern kingbird parental care. Wilson Bull 106:668–678

Royle NJ, Smiseth PT, Kölliker M (eds) (2012) The evolution of parental care. Oxford University Press, Oxford

Sargent S (1993) Nesting biology of the yellow-throated euphonia: large clutch size in a Neotropical frugivore. Wilson Bull 105:285–300

Savage JL, Hinde CA, Johnstone RA (2020) Editorial: cooperation and coordination in the family. Front Ecol Evol 8:614863. https://doi.org/10.3389/fevo.2020.614863

Savagian AG, Riehl C (2022) Begging is an honest signal of hunger in a communally nesting bird with low genetic relatedness. Behav Ecol Sociobiol 76:146. https://doi.org/10.1007/s00265-022-03252-z

Savagian AG, Riehl C (2023) Effects of brood and group size on nestling provisioning and resource allocation in a communal bird. Behav Ecol. https://doi.org/10.1093/beheco/arad020. (published online)

Schlicht E, Santema P, Schlicht R, Kempenaers B (2016) Evidence for conditional cooperation in biparental care systems? A comment on Johnstone et al. Behav Ecol 27:e2–e5. https://doi.org/10.1093/beheco/arw036

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. https://doi.org/10.1098/rsbl.2009.0909

Skutch AF (1949) Do tropical birds rear as many young as they can nourish? Ibis 91:430–455. https://doi.org/10.1111/j.1474-919X.1949.tb02293.x

Sorato E, Gullett PR, Griffith SC, Russell AF (2012) Effects of predation risk on foraging behaviour and group size: adaptations in a social cooperative species. Anim Behav 84:823–834. https://doi.org/10.1016/j.anbehav.2012.07.003

Trapote E, Canestrari D, Baglione V (2021) Female helpers signal their contribution to chick provisioning in a cooperatively breeding bird. Anim Behav 172:113–120. https://doi.org/10.1016/j.anbehav.2020.12.011

van Rooij EP, Griffith SC (2013) Synchronised provisioning at the nest: parental coordination over care in a socially monogamous species. PeerJ 1:e232. https://doi.org/10.7717/peerj.232

Wojczulanis-Jakubas K, Araya-Salas M, Jakubas D (2018) Seabird parents provision their chick in a coordinated manner. PLoS ONE 13:e0189969. https://doi.org/10.1371/journal.pone.0189969