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Letter

Coordination of care reduces conflict and predation risk in a cooperatively breeding bird

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Abstract

When two or more individuals cooperate to provision a shared brood, each carer may be able to maximize their payoffs by coordinating provisioning in relation to what others are doing. This investment "game" is not simply a matter of how much to invest but also of the relative timing of investment. Recent studies propose that temporal coordination of care in the forms of alternation (i.e., turn-taking) and synchrony (i.e., provisioning together) function to mitigate conflict between carers and reduce brood predation risk, respectively. Such coordination is widespread in biparental and cooperatively breeding birds, yet the fitness consequences have rarely been empirically tested. Here, we use a long-term study of long-tailed tits *Aegithalos caudatus*, a facultative cooperatively breeding bird with active coordination of care, to assess the support for these hypothesized functions for coordination of provisioning visits. First, we found evidence that turn-taking mitigates conflict between carers because, in cooperative groups, provisioning rates and offspring recruitment increased with the level of active alternation exhibited by carers and with the associated increase in provisioning rate parity between carers. In contrast, offspring recruitment did not increase with alternation in biparental nests, although it was positively correlated with parity of provisioning between carers, which is predicted to result from conflict mitigation. Second, synchronous nest visits were associated with a reduced probability of nest predation and thus increased brood survival, especially when provisioning rates were high. We attribute this effect to synchrony reducing carer activity near the nest. We conclude that temporal coordination of provisioning visits in the forms of alternation and synchrony both confer fitness benefits on carers and despite being intrinsically linked, these different kinds of coordination appear to serve different functions.

Keywords: alternation, brood, predation, conflict, cooperation, coordination, synchrony

Lay Summary

Natural selection dictates that individuals should seek to maximize their genetic contribution to future generations. To achieve this goal, many animals provide parental care, which increases the survival and fitness of their offspring. However, providing care is costly so when multiple individuals care for the same young, as is commonplace in birds, each individual should prefer to contribute less and for other carers to invest more. Offspring will receive suboptimal care if carers cannot resolve this conflict. Taking turns to provision a brood (alternation) is hypothesized to mitigate this conflict, allowing each carer to contribute similar amounts so that the optimal level of care for offspring is achieved. Similarly, carers may also optimize their care by provisioning at the same time (synchrony), which is hypothesized to reduce the period of activity near nests and, hence, decrease the risk of advertising the location of a nest to predators. Both forms of carer coordination are widely reported, but their functions have received little attention. Here, we tested these hypotheses by investigating the relationships between coordination and offspring fitness in long-tailed tits, finding that alternation was associated with increased provisioning and offspring recruitment, while greater synchrony of visits corresponded with increased brood survival.

Introduction

Parental care has evolved to increase parents' genetic contribution to future generations (Godfray, 1995; Trivers, 1974), but investment in offspring must be drawn from a finite pool of resources (Clutton-Brock, 1991; Stearns, 1992). Therefore, parents are selected to maximize lifetime reproductive success by optimizing their investment in each breeding event (Stearns, 1989). When multiple individuals care for a shared brood, optimization must account for the care that others provide (Houston & Davies, 1985; Lessells & McNamara, 2011; McNamara et al., 1999, 2003). This investment "game" between carers is not simply a question of how much each should invest but also the relative timing of investment (Johnstone et al., 2014). Biparental care may be strictly coordinated, for example, when one parent must remain at the nest to protect offspring (McCully et al., 2022; Patrick et al., 2020; Schreiber & Burger, 2002). In such cases, successful reproduction relies on predictable timing of investment by both partners, so the function of coordination is clear. However, the

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selective advantages of other forms of parental coordination are poorly understood. Specifically, in recent years two forms of coordinated care have been frequently reported: alternation and synchrony of provisioning visits (Savage & Hinde, 2019; Savage et al., 2020), but there have been few rigorous tests of their hypothesized functions.

Alternation of provisioning visits was proposed by Johnstone et al. (2014) as a means of resolving conflict between parents investing in a shared brood. This model argues that care that is conditional upon observing a partner provision offspring ensures fair investment by each carer, resulting in an alternating pattern of feeds and mutually increased investment. Some alternation occurs by chance in a sequence of provisioning visits (Ihle et al., 2019a; Santema et al., 2019; Schlicht et al., 2016), but greater than expected alternation has been demonstrated in a range of biparental (Bebbington & Hatchwell, 2016; Johnstone et al., 2014; Lejeune et al., 2019) and cooperatively breeding species (Halliwell et al., 2022; Koenig & Walters, 2016; Savage et al., 2017). However, there is limited evidence that individual carers actively adjust their behavior to enhance alternation (Griffioen et al., 2021; Halliwell et al., 2023a; Johnstone et al., 2014; Savage et al., 2017) and, whilst there is some evidence that alternation mitigates conflict (Baldan & Griggio, 2019), evidence that it also increases provisioning rate and offspring fitness is equivocal. Burdick and Siefferman (2020) identified a positive relationship between alternation and offspring growth in eastern bluebirds *Sialia sialis*, given certain conditions, and Trapote et al. (2023) found a positive correlation between alternation and offspring mass in carrion crows *Corvus corone*. However, others have found no effect on offspring condition (Bebbington & Hatchwell, 2016; Griffioen et al., 2019; Iserbyt et al., 2017) or survival (Iserbyt et al., 2017), and Ihle et al. (2019b) even found a negative relationship between alternation and offspring survival in house sparrows *Passer domesticus*.

Synchronous provisioning occurs when two or more carers feed a shared brood within a short time window. Synchrony may be necessary for carers to monitor and hence alternate visits with a partner, but it may also have functions independent of alternation. Synchrony may: (a) reduce the time that carers spend near a nest advertising its location to predators—the predation hypothesis (Sargent, 1993); (b) facilitate efficient distribution of resources among offspring within a brood—the resource distribution hypothesis (Shen et al., 2010); and (c) enable signaling of investment, either to demonstrate quality—the prestige hypothesis (Zahavi, 1977a, b)—or to retain group membership—the pay-to-stay hypothesis (Gaston, 1978; Kokko et al., 2002). Alternatively, synchrony may confer no benefit to a brood but instead results from selection for collective foraging to increase foraging efficiency and/or carer safety from predators (Baldan & van Loon, 2022; Beauchamp, 1998; Lee et al., 2010; Mariette & Griffith, 2015; Smith et al., 2023; Sorato et al., 2012). Of these, the predation hypothesis is supported by studies linking synchrony to reduced carer activity near nests and/or brood predation (Bebbington & Hatchwell, 2016; Khwaja et al., 2019; Leniowski & Węgrzyn, 2018; Raihani et al., 2010). The resource distribution hypothesis is supported by studies linking synchrony to reduced intrabrood mass variation (Lejeune et al., 2019; Mariette & Griffith, 2012, 2015; Shen et al., 2010). By contrast, there is little support for either the prestige (Doutrelant & Covas, 2007) or pay-to-stay (Trapote et al., 2021) hypotheses. However, most studies limited their investigation to a single hypothesis or failed to consider that alternation and synchrony may result from the same behavior(s), so may miss the potentially interconnected functions of coordination.

Here, we investigated provisioning coordination in the long-tailed tit *Aegithalos caudatus*, a facultative cooperative breeder in which failed breeders commonly help raise broods belonging to other pairs (Glen & Perrins, 1988; Hatchwell, 2016). Helpers prefer to help kin (Leedale et al., 2020; Russell & Hatchwell, 2002) and gain indirect fitness by increasing the provisioning and recruitment of helped broods (Hatchwell et al., 2004, 2014; MacColl & Hatchwell, 2002, 2003). In contrast, they derive no direct fitness benefits from helping (Meade & Hatchwell, 2010). Long-tailed tits exhibit greater than expected alternation and synchrony when provisioning biparentally and cooperatively (Bebbington & Hatchwell, 2016; Halliwell et al., 2022). Within-brood conflict is minimal in long-tailed tits as they have remarkably low offspring starvation (Hatchwell et al., 2004), so the resource distribution hypothesis does not apply in this case. In addition, since helpers derive no direct fitness benefits from helping, the pay-to-stay and prestige hypotheses are not applicable either. Therefore, we tested two a priori hypotheses for coordinated provisioning. Hypothesis 1 posits that alternation facilitates conflict resolution between carers over investment. Long-tailed tits experience high annual mortality (Meade et al., 2010) and divorce rates (Hatchwell et al., 2000), so the scope for sexual conflict is high because breeders have little interest in their partner's future fitness. We predicted that greater alternation would result in higher provisioning rates (Prediction 1a), heavier chicks (Prediction 1b), and higher recruitment (Prediction 1c). Hypothesis 2 posits that synchrony reduces brood predation risk. Long-tailed tits experience high brood predation (c.72% of nests; Hatchwell et al., 2013) and synchrony reduced near-nest activity (Bebbington & Hatchwell, 2016). Therefore, we predicted that greater synchrony results in increased brood survival (Prediction 2).

Methods

Study system and general field protocol

Data were collected during the breeding seasons (March–June) of 1994–2022 from an intensively studied wild population of long-tailed tits (Rivelin Valley, UK; c.3 km^2; 53°23′ N, 1°34′ W). Nests were located by following adults building nests, typically in low-lying (≤3 m) shrubs (c.73% of nests; Higgott, 2019) such as *Rubus fruticosus*, but sometimes in inaccessible tree forks. Nests were monitored at 1- to 3-day intervals but daily approaching incubation, hatching, and fledging. Incubation starts once the clutch is complete, lasts c.15 days, and all eggs that hatch do so within 24 hr of the first. After hatching (d0), both parents deliver prey items, such as flies, spiders, and caterpillars. Helpers may join a group at any point between hatching and fledging (d16–18), although helping is more common later in development. Long-tailed tits suffer only minimal chick starvation (0.2% daily per chick; Hatchwell et al., 2004) but lose 71.9% of clutches and broods to predation (Hatchwell et al., 2013), typically by corvids (e.g., Eurasian jay *Garrulus glandarius*) and mammals (e.g., stoat *Mustela erminea*). Therefore, most brood mortality can be attributed to complete depredation events, although broods may occasionally be partially depredated (3.9% of successful nests; 9/233).

Clutch size (median = 10; range 4–12; *N* = 293) in accessible nests was recorded during incubation. Brood size (median = 9; range 1–11; *N* = 275), and the mass (to 0.1 g; mean = 7.4 g ± 0.0142 *SE*; *N* = 1970) and tarsus length (to 0.1 mm; mean = 18.3 mm ± 0.0188 *SE*; *N* = 1970) of nestlings were recorded on d11. Each chick was ringed under British Trust for Ornithology license with a unique combination of color rings. We took 5–20 µl of blood by brachial venipuncture (under UK Home Office license) for genetic sex determination of nestlings using the P2–P8 sex-typing primers (Griffiths et al., 1998). Because clutch and/or brood size were important covariates, we limited our analysis to low nests where these metrics were sampled. The biometrics and sex of every chick was known in 77.7% (185/238) of broods. All applicable international, national, and institutional guidelines for the use of animals were followed, and all regulated procedures were approved by the Animal Welfare and Ethical Review Body at the University of Sheffield.

Successful local recruitment was recorded when a fledgling attempted to breed in the field site in a subsequent year. Long-tailed tits exhibit female-biased dispersal, so 20%–25% of males but <10% of female fledglings recruit locally (Sharp et al., 2008, 2011). Therefore, we estimated recruitment success from resightings of male fledglings breeding in subsequent years. We used the number of fledged males that were (median = 1; range = 0–5; $N = 170$ broods) or were not resighted per brood (median = 3; range = 0–7; $N = 170$) to model the proportion that recruited locally (mean = 0.241 ± 0.0212 *SE*; $N = 170$). In our open population, c.40% of breeders were immigrants to our field site *per annum*; these were captured in mist-nets and ringed. Since the project started, 1,531 individuals have been recorded breeding in the site, but many of these never raised a brood, and only 576 (37.6%) birds were recorded provisioning broods in watches matching our criteria, which included 239 unique breeding females, 227 breeding males, and 171 helpers (61 of which were also breeders).

Calculating coordination

Provisioning watches (hereafter "watches") were typically performed from d2 every other day until nest failure or fledging. Coordination is not possible when females are brooding young chicks (≤d5), so analysis was restricted to watches when both parents provisioned full-time (median = 3 watches per nest; median brood age = d10; range d6–18; $N = 894$). Each season c.95% of carers were identifiable by their unique combination of color rings. If an unringed carer provisioned during a watch (4.36% of watches; 39/894), we assumed all feeds were by the same unringed individual and omitted watches including > 1 unringed birds.

Watch protocol was consistent throughout the study. Following a c.10 min habituation period, watches usually lasted for 1 hr between 04:00 and 19:30 unless curtailed by inclement weather (minimum duration: 30 min). When a carer provisioned the brood its identity and time were recorded to the nearest minute, either by direct observation through binoculars (15–25 m away) or video camera (1–5 m away). Watch duration was the time between the first and last feed (mean = 54 min 1 ± 25 s *SE*; range = 30–117 min; $N = 894$). We excluded any watch where identities of feeds or hatch date were unknown and from nests subjected to experimental manipulation. Long-tailed tits provision their nestlings frequently, with a mean rate of 23.8 feeds/h ± 0.320 SE (range 4.53–69.2; $N = 894$) per group in the sample used in this study. The total number of alternated and synchronized feeds was calculated per watch. An alternated feed was any that occurred following a feed by another carer (median = 15 per watch; range 1–68; $N = 894$), meaning that alternation did not require a consistent pattern of feeds (e.g., A-B-C-A-B-C), just nonconsecutive feeds (e.g., A-B-A-C-B-A). A synchronized feed was any nonconsecutive feed that occurred within 2 min of the previous feed (median = 8 per watch; range 0–55; $N = 894$). This 2-min window was chosen to facilitate comparison with prior studies of coordination in this species, which found that rates of synchrony using different window lengths were highly correlated ($r_p \geq 0.94$; Halliwell et al., 2022) and key results were qualitatively the same (Bebbington & Hatchwell, 2016; Halliwell et al., 2022). In watches where one carer performed >50% of feeds, some cannot be alternated or synchronized, so we calculated the "Maximum possible coordination" (mean = 87.4% ± 0.414 *SE*; $N = 894$) for each watch, which functions as a proxy for provisioning rate parity between carers.

Because some alternation and synchrony are expected by chance (Ihle et al., 2019a; Santema et al., 2019; Schlicht et al., 2016), we used a null model to estimate levels of expected coordination (e.g., Halliwell et al., 2022; Ihle et al., 2019a, b; Johnstone et al., 2014). We randomized the order of each carer's intervisit intervals within a watch 1,000 times, which were then recombined to produce 1,000 randomized sequences, and the median number of alternated and synchronized feeds were the expected levels for that watch. Observed and expected alternation and synchrony were used to generate measures of how much each watch deviated from expected, termed "active alternation score" (mean = 0.0663 ± 0.00499 *SE*; $N = 894$) and "active synchrony score" (mean = 0.206 ± 0.00884 *SE*; $N = 894$), respectively. Alternation scores were calculated from log(observed alternated feeds + 0.5) – log(expected alternated feeds + 0.5), and synchrony scores likewise. Therefore, a positive score means that carers coordinated more than expected by random chance (i.e., if they provisioned independently), while a negative score denotes less coordination than expected, which may occur if carers provision in a manner that actively avoids alternation (i.e., in bouts of successive uninterrupted feeds by the same carer). We added 0.5 to each value to avoid taking the log of zero.

Statistical analysis

Statistical analysis was performed on R version 4.2.3 (R Core Team, 2023). Models were built using lme4 (Bates et al., 2015), coxme (Therneau, 2022), and analyzed with lmerTest (Kuznetsova et al., 2017). Figures were produced using ggplot2 (Wickham, 2016), survminer (Kassambara et al., 2021), and cowplot (Wilke, 2020). When investigating the influence of alternation and synchrony on reproductive success we used "active alternation score" and "active synchrony score," respectively. These were analyzed in separate models because they are intrinsically correlated as synchronized feeds are, by definition, alternated. In addition, because previous studies found that active alternation decreased with helper presence and active synchrony with provisioning rate (Halliwell et al., 2022), we included these terms and their interactions with each coordination score as explanatory terms in our alternation and synchrony analyses, respectively. A significant interaction term indicates that the importance of coordination varied with the presence of helpers ("helped during watch?"—binary factor denoting whether a pair was assisted by helpers in each watch, and "nest helped"—a binary factor denoting whether a pair was helped within the range of watches analyzed) or "(aggregate) provisioning rate"—a continuous numerical variable denoting the number of feeds performed per hour by all carers per watch (or across several watches).

Provisioning rate (Prediction 1a)

We used a normally distributed linear mixed effects model (LMM) to investigate the relationship between alternation and provisioning rate in the *Full sample* of watches ($N = 871$ at 275 nests; Supplementary Figure S1). The response variable was the log-transformed provisioning rate per watch and the explanatory terms of interest were "active alternation score" and its interaction with "helped during watch?". Covariates and random effects used here and throughout are described below.

Chick mass (Predictions 1b)

We fitted normally distributed LMMs to investigate the relationship between alternation and chick mass using a subset of watches taken prior to biometric assessment from nests where all chicks' biometrics and sexes were known (*Chick mass sample sex known*; N = 360 at 185 nests containing 1,533 chicks). The response variable was each chick's mass on d11. Terms of interest were "active alternation score" (aggregated across each appropriate watch) and its interactions with "nest helped?" and "aggregate provisioning rate".

Recruitment rate (Predictions 1c)

We fitted a binomially distributed generalized LMM (GLMM) to investigate the relationship between alternation and recruitment rate, using a subset of watches from successful nests where each chick's sex was known (*Recruit sample*; N = 574 watches at 170 nests containing 719 male chicks). The response variable was a two-column variable (number of males recruited, number of males not recruited), which functions as a measure of proportion recruited. Terms of interest were "aggregate active alternation score" and its interaction with "nest helped?". Because this interaction term was significant, we also repeated this analysis on subsamples of biparental (2 carers) watches (N = 331 at 101 nests containing 420 male chicks) and cooperative (> 2 carers) watches (N = 243 at 69 nests containing 299 male chicks).

Predation and survival (Prediction 2)

To investigate survival time, we used a Cox proportional hazard mixed model (CPHMM) (Therneau, 2022) with the two-column response variable (days until event, fledged or failed) applied to the *Predation sample*, which included watches from nests depredated prior to ringing, for which brood size was assumed equal to clutch size (N = 894 watches at 293 nests). Data were right censored with all fledged broods defined as age 18. Terms of interest were "aggregate active synchrony score" and its interaction with "aggregate provisioning rate".

Covariates and random effects

We controlled for biologically important covariates that could influence provisioning behavior. "Provisioning rate variation"—a continuous numerical variable denoting variation in the provisioning rate during each watch (mean = 0.582 ± 0.00733 *SE*; N = 894); included because as carers' intervisit intervals become more consistent, the null model's ability to disrupt patterns of coordination fundamentally diminishes (Supplementary Tables S1 and S2 and Supplementary Figure S2). "Brood size" (linear and quadratic)—an integer numerical variable denoting the number of live chicks on d11; included because it affects demand on carers. "Watch duration"—a continuous numerical variable denoting the time (minutes) between the first and last recorded feeds per watch; included because the total number of feeds increases with watch duration. "Watch start time" —a continuous numerical variable denoting the time each watch started (mean = 9:54 am ± 5 min *SE*; N = 894); included because long-tailed tits have higher provisioning activity soon after sunrise (Hatchwell et al., 2004; MacColl & Hatchwell, 2002). "Maximum possible coordination"—a continuous numerical variable denoting the highest theoretical percentage of feeds that could be alternated (or synchronized) during a given watch. "Hatch date" (linear and quadratic)—an integer numerical variable denoting the number of days between March 1 and hatching (Median = May 3; range April 15–June 6; N = 293); included to account for within-season environmental variation. "Brood age"—an integer numerical variable denoting the number of days between hatching and a watch; included because provisioning rate increases with age. "Chick sex"—a binary factor denoting whether a chick is male or female; included because male chicks are typically heavier (Nam et al., 2011). "Brood sex ratio"—a continuous numerical variable denoting the ratio of female:male chicks within a given brood (mean = 0.511 ± 0.0124 *SE*; N = 185); included to account for differences in chick mass between broods with different sex ratios. "Tarsus length" (linear and quadratic)—a continuous numerical variable denoting chick tarsal length (mm). "Mean carer number"—a continuous numerical variable denoting the mean number of carers observed provisioning during all watches of a given nest (mean = 3.21 ± 0.0798 *SE*; N = 69, cooperative nests only). Random effects were as follows. "Year"—factor denoting the year a watch was performed. "Nest ID"—factor denoting the identity of a nest. "Pair ID"—factor denoting the unique combination of parents. "Female ID" and "Male ID"—factors denoting the unique identity of each mother and father, respectively. "Rowref"—observation level random effect used to account for overdispersion in Poisson-distributed models. Full model details are available in Supplementary Table S3.

Results

Hypothesis 1: Alternation facilitates conflict resolution

Prediction 1a: Alternation increases provisioning rate

As predicted, we found a significant positive relationship between provisioning rate and alternation (LMM: $p = 0.002$, Table 1; Figure 1A). This effect did not differ significantly between biparental and cooperative breeding groups ($p = 0.096$, Table 1). There were also significant positive effects of maximum possible coordination, i.e., parity of provisioning rates among carers ($b = 0.067 \pm 0.012$ *SE*, $\chi^2 = 33.23$, $p < 0.001$, Supplementary Table S4), brood size (linear) ($b = 0.162 \pm 0.069$ *SE*, $\chi^2 = 5.44$, $p = 0.020$, Supplementary Table S4), and the presence of helpers (b = Yes: 0.078 ± 0.030 *SE*, $\chi^2 = 5.73$, $p = 0.017$, Supplementary Table S4) on provisioning rate, showing that helpers increased total food delivered, as reported previously (Hatchwell et al., 2014; MacColl & Hatchwell, 2003). We also found significant negative effects of watch duration ($p = 0.015$, Supplementary Table S4) and watch start time ($p < 0.001$, Supplementary Table S4); no other term was significant (Supplementary Table S4).

Prediction 1b: Alternation increases chick mass

The prediction that greater alternation would be associated with heavier nestlings was not supported (LMM: $p = 0.285$, Table 1; Figure 1B). However, as expected larger chicks were heavier, chick mass increasing with tarsus length before plateauing ($p < 0.001$; Supplementary Table S5), and male offspring were larger than females ($p < 0.001$; Supplementary Table S5); no other term was significantly related to chick mass (Supplementary Table S5).

Prediction 1c: Alternation increases recruitment rate

Recruitment did not increase with alternation per se, but there was a significant effect on recruitment of the interaction between alternation and whether a nest had helpers (GLMM: $p = 0.021$, Table 1; Figure 1C). This result indicates that in helped broods, recruitment was positively related to alternation, while in biparental broods there was no such effect (Figure 1C). The analyses of biparental and cooperative nests separately supported this

Table 1. Effect of active alternation score and associated interaction terms on provisioning rate at each watch, and offspring condition and reproductive success at each nest.

Response variable	Key terms	Estimates ± *SE*	*df*	χ^2	*p*
Prediction 1a: Alternation increases provisioning rate					
N = 871 watches at 275 nests.					
Log(provisioning rate)	Alternation	0.032 ± 0.012	1,870	9.74	**0.002**
	Alternation * Helped during watch?	Yes: 0.048 ± 0.029	1,870	2.78	0.096
Prediction 1b: Alternation increases chick mass.					
N = 360 watches at 185 nests containing 1,533 chicks.					
Chick mass	Alternation	−0.036 ± 0.031	1,1532	1.14	0.285
	Alternation * Nest helped?	Yes: 0.103 ± 0.078	1,1532	1.73	0.188
Prediction 1c: Alternation increases recruitment rate					
All nests—N = 574 watches at 170 nests containing 719 male chicks.					
Proportion recruited	Alternation	−0.340 ± 0.202	1,169	0.58	0.445
	Alternation * Nest helped?	Yes: 0.929 ± 0.402	1,169	5.36	**0.021**
Biparental nests only—N = 331 watches at 101 nests containing 420 male chicks.					
Proportion recruited	Alternation	−0.401 ± 0.245	1,100	2.37	0.123
Cooperative nests only—N = 243 watches at 69 nests containing 299 male chicks.					
Proportion recruited	Alternation	0.800 ± 0.293	1,68	9.09	**0.003**

Note. Significant values ($p < 0.05$) in bold.

conclusion. At cooperative nests, recruitment increased significantly with alternation (p = 0.003; Table 1) and carer number (b = 0.554 ± 0.252 SE, χ^2 = 5.31, p = 0.021, Supplementary Table S6), meaning that both higher levels of alternation and more helpers independently increased offspring recruitment rate. In contrast, there was no significant effect of any terms on recruitment at biparental nests (Supplementary Table S7). In the overall model, the only other significant term was a positive effect of maximum possible coordination (b = 0.375 ± 0.188 SE, χ^2 = 3.97, p = 0.046, Supplementary Table S8), so male recruitment rate increased with parity of provisioning rate between carers.

Hypothesis 2: Synchrony reduces brood predation risk

Brood survival time, our response variable directly linked to predation risk, was significantly related to the interaction of synchrony and provisioning rate (CPHMM: b = −0.544 ± 0.206 SE, z = −2.64, χ^2 = 6.97, p = 0.008, Supplementary Table S9; Figure 2A), meaning that the effect of synchrony to prolong nest survival increased with provisioning rate. Overall, there was a negative effect of brood size on survival (Figure 2B), although the relationship was quadratic (linear b = −0.966 ± 0.688 SE, z = −1.40, χ^2 = 1.97, p = 0.149; quadratic b = 1.332 ± 0.665 SE, z = 2.00, χ^2 = 4.01, p = 0.045, Supplementary Table S9), with a small initial increase in survival before a larger decrease at large brood size. As expected, brood age (b = −1.156 ± 0.185 SE, z = −6.26, χ^2 = 39.23, p < 0.001, Supplementary Table S9) was significantly related to survival time, but all other terms showed no significant effect on survival time (Supplementary Table S9).

Discussion

In this study, we investigated the role of coordinated provisioning in resolving conflict between carers and reducing brood predation in biparental and cooperatively breeding long-tailed tits. First, we found support for the hypothesis that alternation (i.e., conditional cooperation) facilitates conflict resolution because greater alternation was associated with increased provisioning rate (all nests), parity of investment among carers (all nests), and local recruitment of offspring (cooperative nests only). Second, our results support the hypothesis that synchronous provisioning reduces predation risk because greater synchrony was associated with prolonged nest survival when provisioning rates were high. Viewed together, our results suggest that large, high-activity groups of highly coordinated carers experienced the best reproductive outcomes because their offspring were more likely to fledge and recruit locally.

Since its conception (Johnstone et al., 2014), the conditional cooperation model for provisioning has received much empirical attention, with many studies showing that carers alternate visits more than expected by chance (e.g., Bebbington & Hatchwell, 2016; Halliwell et al., 2022; Johnstone et al., 2014; Koenig & Walters, 2016; Lejeune et al., 2019; Savage et al., 2017). However, the hypothesis that parents alternate provisioning visits to mitigate conflict remains contentious because alternation could be plausibly explained by shared environments rather than conditionality (Ihle et al., 2019a; Santema et al., 2019; Schlicht et al., 2016). A notable exception to this problem is the recent demonstration that long-tailed tits conditionally delayed feeding (i.e., loiter near the nest) in a manner that facilitates alternation (Halliwell et al., 2023a). It is also problematic that evidence for a beneficial effect of alternation is sparse. A prior study of long-tailed tits showed that alternation was positively correlated with provisioning rate (Bebbington & Hatchwell, 2016), and others have shown that alternation was positively related to offspring mass (Trapote et al., 2023) or mass gain (Burdick & Siefferman, 2020). However, no previous study has identified a direct positive effect of alternation on offspring survival or recruitment. Here, we corroborated the link between alternation and provisioning rate and found that provisioning rate increased with parity of effort among carers, suggesting increased investment when conflict between carers was mitigated. Crucially, we also found that alternation was positively correlated with offspring recruitment in cooperative groups, an important component of fitness in this species (MacColl & Hatchwell, 2004).

In contrast to the effect in cooperative nests, offspring recruitment was not significantly related to alternation in biparental nests, although it was positively correlated with parity of provisioning between carers. According to the conditional cooperation hypothesis (Johnstone et al., 2014), alternation optimizes investment by ensuring parity in provisioning rates, suggesting that successful conflict resolution should also benefit offspring raised biparentally. It is possible that the parity term masked an effect of alternation in biparental nests, although it is unclear why this would not also be the case in cooperative nests. Recruitment from biparental nests is also low compared to cooperative nests (Hatchwell et al., 2014), so our capacity to detect effects of provisioning behavior on relatively infrequent recruitment events may be low.

Although alternation was correlated with provisioning and recruitment rates, it did not influence nestling mass significantly. This is surprising given the effect on provisioning rates and the fact that heavier chicks are more likely to recruit locally (Hatchwell et al., 2004; MacColl & Hatchwell, 2002). However, this apparent anomaly is probably because our offspring mass analysis used only watches prior to biometric assessment (i.e., d6–11), whereas our provisioning rate and recruitment analyses utilized watches to the end of the nestling period (i.e., d6–18). If the benefits of alternation and higher provisioning rates occur later in development or are cumulative, as with the effect of brood size on survival, we might not detect an effect on chick mass until after d11.

Long-tailed tits also exhibit prerequisites for the predation hypothesis; they have a short breeding season and raise only one brood per year, despite losing most nests to predators (Hatchwell et al., 2013), so there should be strong selection for strategies to reduce nest conspicuousness. Bebbington and Hatchwell (2016) reported that synchrony reduced the total time that long-tailed tits spent near the nest when provisioning, which can advertise a nest's location to predators (Sahin Arslan & Martin, 2024; Martin et al., 2000; Skutch, 1949). Here, we found that greater synchrony was associated with increased brood survival, particularly when provisioning rates were high. This makes intuitive sense because as the frequency of visits increases, so does the chance of advertising a brood's location to predators. However, we found that nests provisioned more frequently, and smaller broods, both experienced reduced predation even when provisioned asynchronously. This suggests that begging intensity influences predation risk because well-fed groups should be more satiated and thus beg less intensely, while smaller broods inherently produce less noise (Briskie et al., 1999; Haskell, 1994). Synchronous provisioning may reduce overall begging intensity by overlapping carers' near-nest loitering periods prior to feeding, thus limiting the total time that one or more carers are near the nest when begging is loudest (Sargent, 1993). Therefore, long-tailed tits must trade-off potential reproductive output against the risk of brood predation, with synchrony playing an important role in reducing predation risk. On the other hand, it should be noted that in an experiment, carers did not increase synchrony in response to temporarily increased perceived predation risk (Halliwell et al., 2023b), suggesting that synchrony is not dynamically adjusted in response to varying predation risk, but rather is an antipredator strategy performed consistently across the nestling period.

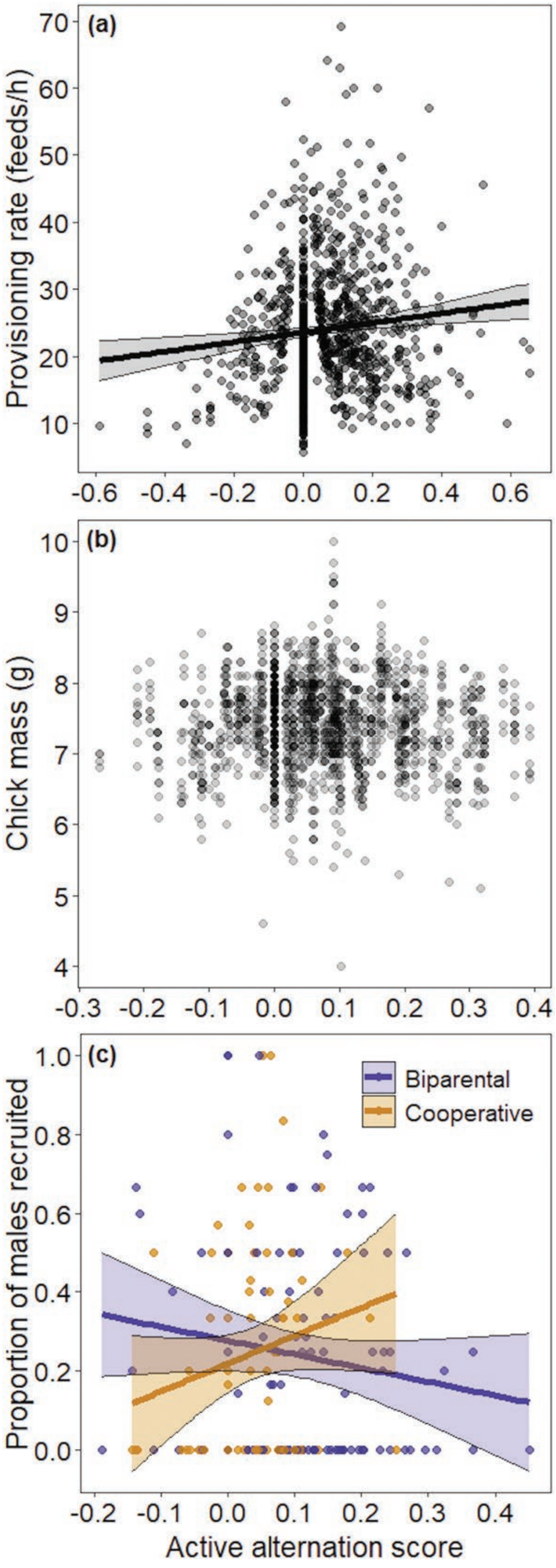

Figure 1. (A) Provisioning rate (feeds/hour) vs. active alternation score per watch from the full sample of watches (N = 871 watches at 275 nests). Note: straight line at X = 0 is where the number of observed alternated visits is equal to expected, and the gap between this line and the rest of the data is due to the lower resolution of the null model (obs. vs. exp.) at low provisioning rates. (B) Chick mass (grams) at d11 vs. aggregate active alternation score per nest from a subsample of watches taken prior to weighing where all chick sexes were known (N = 360 watches at 185 nests containing 1,533 chicks). (C) Proportion of male offspring recruited into the local breeding population vs. the aggregate active alternation score at biparental (N = 331 watches at 101 nests containing 420 male chicks) and cooperative nests (N = 243 watches at 69 nests containing 299 male chicks) that fledged and in which all chick sexes were known. Data points were translucent, so overlapping data points results in darker shades. Predicted relationships (± 95% CI) are fitted from GLMMs, see Table 1.

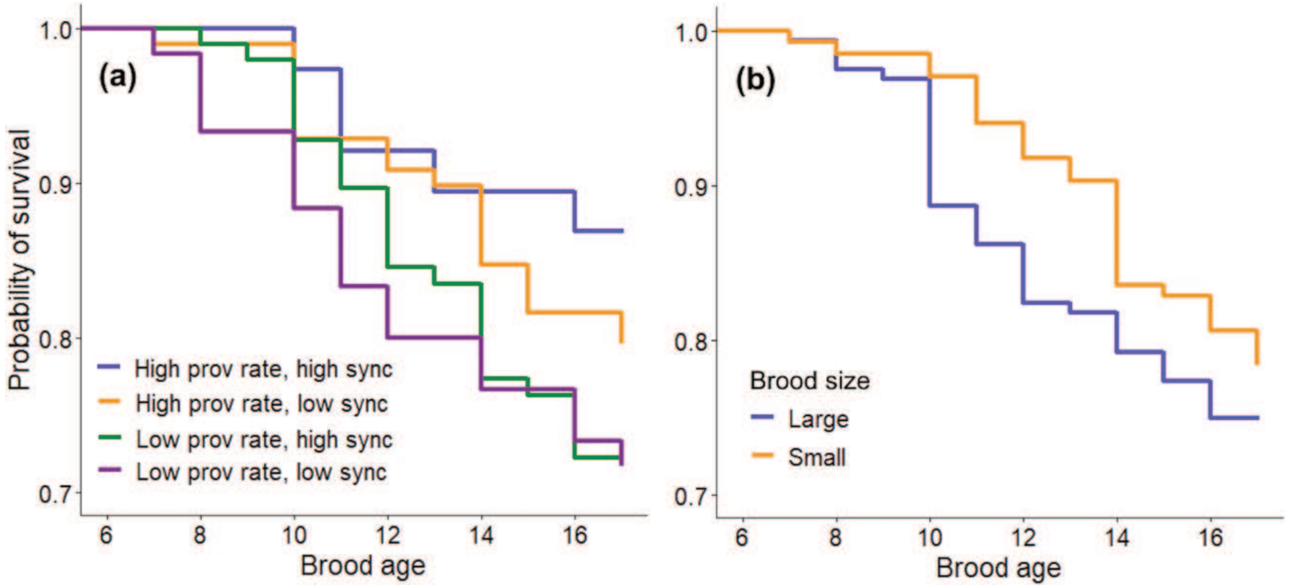

Figure 2. Kaplan–Meier curves for the cumulative probability of brood survival vs. brood age for (A) nests above the mean average aggregate provisioning rate and above the mean average aggregate active synchrony scores (*N* = 151 watches at 38 nests), above average aggregate provisioning rate and below average aggregate active synchrony score (*N* = 339 watches at 98 nests), below average aggregate provisioning rate and above average aggregate active synchrony score (*N* = 238 watches at 97 nests) and below average aggregate provisioning rate and below average aggregate active synchrony score (*N* = 166 watches at 60 nests), and (B) nests with equal to or above the median average brood size (*N* = 482 watches at 159 nests) and nests with below average brood size (*N* = 412 watches at 134 nests).

This begs the question of why carers do not provision broods less frequently with larger loads? The diet of nestling long-tailed tits, small invertebrates delivered to nestlings carried in the bill, means the capacity of carers to adjust provisioning strategy to mitigate predation risk is very limited. Therefore, the best strategy to reduce near-nest activity and associated offspring begging may be to provision synchronously (Sahin Arslan & Martin, 2024; Bebbington & Hatchwell, 2016; Martin et al., 2000; Skutch, 1949). The problem of advertising nests to predators may be particularly acute for cooperative species if extra carers increase activity at the nest, enhancing the need for synchrony to reduce vulnerability to predators. Alternatively, if helpers are effective at nest defense, offspring may be better protected in larger groups, as in Florida scrub jays *Aphelocoma coerulescens* (Mumme, 1992), potentially negating the need for synchrony. To date, there have been insufficient studies of cooperative species to compare levels of coordination across social systems, but we suggest that such studies would be particularly worthwhile.

Our results indicate that although alternation and synchrony are intrinsically linked, they appear to serve independent functions in long-tailed tits. Alternation facilitates conflict resolution between carers (Johnstone et al., 2014), particularly in cooperative groups where the potential for conflict is greater (Savage et al., 2017), while synchrony reduces predation risk. Indeed, these distinct functions are consistent with the notion that they result from different behavioral strategies. Alternation is partly facilitated by carers delaying provisioning if it was not their turn to feed, while synchrony is facilitated by carers arriving back to the nest together, presumably resulting from group foraging (Halliwell et al., 2023a). However, synchrony may have an additional function of facilitating alternation; by overlapping loitering periods, synchrony may limit the amount of time a carer must wait near the nest for another to arrive (e.g., to avoid feeding consecutively). Therefore, scheduling nest visits via synchrony could facilitate efficient negotiation by allowing carers to gather information about the timing of others' last contributions without the need for prolonged loitering periods near the nest, which could advertise its location to predators. Indeed, these two metrics of coordination are positively correlated in long-tailed tits (Bebbington & Hatchwell, 2016) and other species (Mariette & Griffith, 2015), although that does not demonstrate a causal link between the two.

In conclusion, to our knowledge, this is the first study to demonstrate that coordinated provisioning by carers increases the production of recruits, and it joins the short list of studies finding that it reduces brood predation risk (Leniowski & Węgrzyn, 2018; Raihani et al., 2010). We found support for the conditional cooperation hypothesis because higher alternation and parity of provisioning rates corresponded with higher provisioning rates and recruitment of offspring raised cooperatively, and the predation hypothesis because in above average provisioning rate groups, higher synchrony corresponded with increased brood survival. These results support the idea that alternation and synchrony may co-occur while having independent functions. Moreover, our previous studies suggest that each form of coordination results from different behaviors by carers—synchrony arising from collective foraging and alternation through conditionality in nest visits, which is facilitated by overlapped loitering periods prior to provisioning (i.e., synchrony). Finally, we suggest that cooperative breeding systems offer a particularly rich and variable social environment in which to investigate the occurrence and functions of coordinated care.

Supplementary material

Supplementary material is available online at *Evolution Letters*.

Data and code availability

All data and analysis code used in this study are available at Dryad: https://doi.org/10.5061/dryad.9p8cz8wqj.

Author contributions

We used the CrediT framework to categorize each author's contributions, as follows. C.H. performed conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, software, validation, visualization, and writing—original draft. A.P.B. performed supervision, methodology, and writing—review & editing. S.C.P. performed supervision and writing—review & editing. B.J.H. performed conceptualization, data curation, funding acquisition, investigation, project administration, resources, supervision, and writing—review & editing.

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Conflict of interest: The authors declare no conflicts of interest.

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References

Baldan, D., & Griggio, M. (2019). Pair coordination is related to later brood desertion in a provisioning songbird. *Animal Behaviour*, 156, 147–152. https://doi.org/10.1016/j.anbehav.2019.08.002

Baldan, D., & van Loon, E. E. (2022). Songbird parents coordinate offspring provisioning at fine spatio-temporal scales. *Journal of Animal Ecology*, *91*(6), 1316–1326. https://doi.org/10.1111/1365-2656.13702

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48

Beauchamp, G. U. Y. (1998). The effect of group size on mean food intake rate in birds. *Biological Reviews of the Cambridge Philosophical Society*, *73*(4), 449–472. https://doi.org/10.1017/s0006323198005246

Bebbington, K., & Hatchwell, B. J. (2016). Coordinated parental provisioning is related to feeding rate and reproductive success in a songbird. *Behavioral Ecology*, 27(2), 652–659. https://doi.org/10.1093/beheco/arv198

Briskie, J. V., Martin, P. R., & Martin, T. E. (1999). Nest predation and the evolution of nestling begging calls. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 266(1434), 2153–2159. https://doi.org/10.1098/rspb.1999.0902

Burdick, C., & Siefferman, L. (2020). Interspecific density influences the adaptive significance of provisioning coordination between breeding partners. *Frontiers in Ecology and Evolution*, 8, 29.

Clutton-Brock, T. H. (1991). The costs of breeding. In T. H. Clutton-Brock (Ed.), *The evolution of parental care* (pp. 31–47). Princeton University Press.

Doutrelant, C., & Covas, R. (2007). Helping has signalling characteristics in a cooperatively breeding bird. *Animal Behaviour*, 74(4), 739–747. https://doi.org/10.1016/j.anbehav.2006.11.033

Gaston, A. J. (1978). The evolution of group territorial behavior and cooperative breeding. *American Naturalist*, *112*(988), 1091–1100. https://doi.org/10.1086/283348

Glen, N. W., & Perrins, C. M. (1988). Cooperative breeding by long-tailed tits. *British Birds*, *81*, 630–641.

Godfray, H. C. J. (1995). Evolutionary theory of parent-offspring conflict. *Nature*, *376*(6536), 133–138. https://doi.org/10.1038/376133a0

Griffioen, M., Iserbyt, A., & Müller, W. (2021). Turn taking is not restricted by task specialisation but does not facilitate equality in offspring provisioning. *Scientific Reports*, *11*(1), 21884–21884. https://doi.org/10.1038/s41598-021-01298-z

Griffioen, M., Müller, W., & Iserbyt, A. (2019). A fixed agreement—Consequences of brood size manipulation on alternation in blue tits. *PeerJ*, *7*, e6826. https://doi.org/10.7717/peerj.6826

Griffiths, R., Double, M. C., Orr, K., & Dawson, R. J. (1998). A DNA test to sex most birds. *Molecular Ecology*, *7*(8), 1071–1075. https://doi.org/10.1046/j.1365-294x.1998.00389.x

Halliwell, C., Beckerman, A. P., Biddiscombe, S. J., Germain, M., & Hatchwell, B. J. (2023a). Coordination of care is facilitated by delayed feeding and collective arrivals in the long-tailed tit. *Animal Behaviour*, 201, 23–44. https://doi.org/10.1016/j.anbehav.2023.04.005

Halliwell, C., Beckerman, A. P., Germain, M., Patrick, S. C., Leedale, A. E., & Hatchwell, B. J. (2022). Coordination of care by breeders and helpers in the cooperatively breeding long-tailed tit, *Aegithalos caudatus*. *Behavioral Ecology*, 33(4), 844–858. https://doi.org/10.1093/beheco/arac048

Halliwell, C., Beckerman, A. P., Patrick, S. C., & Hatchwell, B. J. (2024). *Coordination of care reduces conflict and predation risk in a cooperative breeding bird*. Dryad Digital Repository. https://doi.org/10.5061/dryad.9p8cz8wqj

Halliwell, C., Biddiscombe, S. J., & Hatchwell, B. J. (2023b). Experimental variation of perceived predation risk does not affect coordination of parental care in long-tailed tits. *Behavior, Ecology and Sociobiology*, *77*(9), 107. https://doi.org/10.1007/s00265-023-03383-x

Haskell, D. (1994). Experimental evidence that nestling begging behavior incurs a cost due to nest predation. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 257, 161–164. https://doi.org/10.1098/rspb.1994.0110

Hatchwell, B. J. (2016). Long-tailed tits: Ecological causes and fitness consequences of redirected helping. In W. D. Koenig & J. L. Dickinson (Eds.), *Cooperative breeding in vertebrates: Studies of ecology, evolution and behavior* (pp. 39–57). Cambridge University Press.

Hatchwell, B. J., Gullett, P. R., & Adams, M. J. (2014). Helping in cooperative breeding long-tailed tits: A test of Hamilton's rule. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 369, 20130565. https://doi.org/10.1098/rstb.2013.0565

Hatchwell, B. J., Russell, A. F., MacColl, A. D. C., Ross, D. J., Fowlie, M. K., & McGowan, A. (2004). Helpers increase long-term but not short-term productivity in cooperatively breeding long-tailed tits. *Behavioral Ecology*, 15, 1–10. https://doi.org/10.1093/beheco/arg091

Hatchwell, B. J., Russell, A. F., Ross, D. J., & Fowlie, M. K. (2000). Divorce in cooperatively breeding long-tailed tits: A consequence of inbreeding avoidance? *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *267*(1445), 813–819. https://doi.org/10.1098/rspb.2000.1076

Hatchwell, B. J., Sharp, S. P., Beckerman, A. P., & Meade, J. (2013). Ecological and demographic correlates of helping behaviour in a cooperatively breeding bird. *Journal of Animal Ecology*, *82*(2), 486–494. https://doi.org/10.1111/1365-2656.12017

Higgott, C. G. (2019). *Evolutionary ecology of avian nest design and function in a variable environment* [PhD thesis]. University of Sheffield.

Houston, A. I., & Davies, N. B. (1985). The evolution of cooperation and life history in the Dunnock, *Prunella modularis*. In R. M. Sibly, & R. H. Smith (Eds.), *Behavioural ecology: Ecological consequences of adaptive behaviour* (pp. 471–487). Blackwell Scientific Publications.

Ihle, M., Pick, J. L., Winney, I. S., Nakagawa, S., & Burke, T. (2019a). Measuring up to reality: Null models and analysis simulations to study parental coordination over provisioning offspring. *Frontiers in Ecology and Evolution*, *7*, 142. https://doi.org/10.3389/fevo.2019.00142

Ihle, M., Pick, J. L., Winney, I. S., Nakagawa, S., Schroeder, J., & Burke, T. (2019b). Rearing success does not improve with apparent pair coordination in offspring provisioning. *Frontiers in Ecology and Evolution*, *7*, 405. https://doi.org/10.3389/fevo.2019.00405

Iserbyt, A., Fresneau, N., Kortenhoff, T., Eens, M., & Müller, W. (2017). Decreasing parental task specialization promotes conditional cooperation. *Scientific Reports*, *7*(1), 6565. https://doi.org/10.1038/s41598-017-06667-1

Johnstone, R. A., Manica, A., Fayet, A. L., Stoddard, M. C., Rodriguez-Gironés, M. A., & Hinde, C. A. (2014). Reciprocity and conditional cooperation between great tit parents. *Behavioral Ecology*, *25*(1), 216–222. https://doi.org/10.1093/beheco/art109

Kassambara, A., Kosinski, M., & Biecek, P. (2021). *_survminer: Drawing Survival Curves using "ggplot2."*. *R package version 0.4.9*. https://CRAN.R-project.org/package=survminer

Khwaja, N., Massaro, M., Martin, T. E., & Briskie, J. V. (2019). Do parents synchronise nest visits as an antipredator adaptation in birds of New Zealand and Tasmania? *Frontiers in Ecology and Evolution*, *7*, 389. https://doi.org/10.3389/fevo.2019.00389

Koenig, W. D., & Walters, E. L. (2016). Provisioning patterns in the cooperatively breeding acorn woodpecker: Does feeding behavior serve as a signal? *Animal Behaviour*, *119*, 125–134. https://doi.org/10.1016/j.anbehav.2016.06.002

Kokko, H., Johnstone, R. A., & Wright, J. (2002). The evolution of parental and alloparental effort in cooperative breeding groups: When should helpers pay to stay. *Behavioral Ecology*, *13*(3), 291–300. https://doi.org/10.1093/beheco/13.3.291

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). Package: Tests in linear mixed effects models. *Journal of Statistical Software*, *82*, 1–26. https://doi.org/10.18637/jss.v082.i13

Lee, J. W., Kim, H. Y., & Hatchwell, B. J. (2010). Parental provisioning behavior in a flock-living passerine, the vinous-throated parrotbill *Paradoxornis webbianus*. *Journal fuer Ornithologie*, *151*, 483–490. https://doi.org/10.1007/s10336-009-0484-1

Leedale, A. E., Lachlan, R. F., Robinson, E. J. H., & Hatchwell, B. J. (2020). Helping decisions and kin recognition in long-tailed tits: Is call similarity used to direct help towards kin? *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 375(1802), 20190565. https://doi.org/10.1098/rstb.2019.0565

Lejeune, L. A., Savage, J. L., Bründl, A. C., Thiney, A., Russell, A. F., & Chaine, A. S. (2019). Environmental effects on parental care visitation patterns in blue tits *Cyanistes caeruleus*. *Frontiers in Ecology and Evolution*, *7*, 356. https://doi.org/10.3389/fevo.2019.00356

Leniowski, K., & Węgrzyn, E. (2018). Synchronisation of parental behaviors reduces the risk of nest predation in a socially monogamous passerine bird. *Scientific Reports*, *8*(1), 7385. https://doi.org/10.1038/s41598-018-25746-5

Lessells, C. M., & McNamara, J. M. (2011). Sexual conflict over parental investment in repeated bouts: negotiation reduces overall care. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1733), 1506–1514. https://doi.org/10.1098/rspb.2011.1690

MacColl, A. D. C., & Hatchwell, B. J. (2002). Temporal variation in fitness payoffs promotes cooperative breeding in long-tailed tits *Aegithalos caudatus*. *American Naturalist*, *160*, 186–194. https://doi.org/10.1086/341013

MacColl, A. D. C., & Hatchwell, B. J. (2003). Sharing of caring: Nestling provisioning behavior of long-tailed tit, *Aegithalos caudatus*, parents and helpers. *Animal Behaviour*, *66*, 955–964.

MacColl, A. D. C., & Hatchwell, B. J. (2004). Determinants of lifetime fitness in a cooperative breeder, the long-tailed tit *Aegithalos caudatus*. *Journal of Animal Ecology*, *73*(6), 1137–1148. https://doi.org/10.1111/j.0021-8790.2004.00887.x

Mariette, M. M., & Griffith, S. C. (2012). Nest visit synchrony is high and correlates with reproductive success in the wild zebra finch *Taeniopygia guttata*. *Journal of Avian Biology*, *43*(2), 131–140. https://doi.org/10.1111/j.1600-048x.2012.05555.x

Mariette, M. M., & Griffith, S. C. (2015). The adaptive significance of provisioning and foraging coordination between breeding partners. *American Naturalist*, *185*(2), 270–280. https://doi.org/10.1086/679441

Martin, T. E., Scott, J., & Menge, C. (2000). Nest predation increases with parental activity: Separating nest site and parental activity effects. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *267*(1459), 2287–2293. https://doi.org/10.1098/rspb.2000.1281

McCully, F. R., Weimerskirch, H., Cornell, S. J., Hatchwell, B. J., Cairo, M., & Patrick, S. C. (2022). Partner intrinsic characteristics influence foraging trip duration, but not coordination of care in wandering albatrosses Diomedea exulans. *Ecology and Evolution*, 12(12). https://doi.org/10.1002/ece3.9621

McNamara, J. M., Gasson, C. E., & Houston, A. I. (1999). Incorporating rules of responding into evolutionary games. *Nature*, *401*(6751), 368–371. https://doi.org/10.1038/43869

McNamara, J. M., Houston, A. I., Barta, Z., & Osorno, J. L. (2003). Should young ever be better off with one parent than with two? *Behavioral Ecology*, *14*, 301–310. https://doi.org/10.1093/beheco/14.3.301

Meade, J., & Hatchwell, B. J. (2010). No direct fitness benefits of helping in a cooperative breeder despite higher survival of helpers. *Behavioral Ecology*, *21*(6), 1186–1194. https://doi.org/10.1093/beheco/arq137

Meade, J., Nam, K.-B., Beckerman, A. P., & Hatchwell, B. J. (2010). Consequences of 'load-lightening' for future indirect fitness gains by helpers in a cooperative breeding bird. *Journal of Animal Ecology*, *79*(3), 529–537. https://doi.org/10.1111/j.1365-2656.2009.01656.x

Mumme, R. L. (1992). Do helpers increase reproductive success? *Behavior, Ecology and Sociobiology*, *31*, 319–328. https://doi.org/10.1007/BF00177772

Nam, K. -B., Meade, J., & Hatchwell, B. J. (2011). Do parents and helpers adjust their provisioning effort in relation to nestling sex in a cooperatively breeding bird? *Animal Behaviour*, *82*(2), 303–309. https://doi.org/10.1016/j.anbehav.2011.05.004

Patrick, S. C., Corbeau, A., Réale, D., & Weimerskirch, H. (2020). Coordination in parental effort decreases with age in a long-lived seabird. *Oikos*, *129*(12), 1763–1772. https://doi.org/10.1111/oik.07404

R Core Team. (2023). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Raihani, N. J., Nelson-Flower, M. J., Moyes, K., Browning, L. E., & Ridley, A. R. (2010). Synchronous provisioning increases brood survival in cooperatively breeding pied babblers. *Journal of Animal Ecology*, *79*(1), 44–52. https://doi.org/10.1111/j.1365-2656.2009.01606.x

Russell, A. F., & Hatchwell, B. J. (2002). Experimental evidence for kin-biased helping in a cooperatively breeding vertebrate.

Proceedings of the Royal Society of London. Series B: Biological Sciences, 268(1481), 2169–2174. https://doi.org/10.1098/rspb.2001.1790

Sahin Arslan, N. S., & Martin, T. E. (2024). Visual predators and diurnal nest predation provide support for the Skutch Hypothesis and explain evolved incubation behaviors in a montane tropical bird community. *Ornithology*, *141*, 1–13. https://doi.org/10.1093/ornithology/ukad047

Santema, P., Schlicht, E., & Kempenaers, B. (2019). Testing the conditional cooperation model: What can we learn from parents taking turns when feeding offspring? *Frontiers in Ecology and Evolution*, *7*, 94. https://doi.org/10.3389/fevo.2019.00094

Sargent, S. (1993). Nesting biology of the yellow-throated Euphonia: Large clutch size in a neotropical frugivore. *Wilson Bulletin*, 105, 285–300.

Savage, J. L., Browning, L. E., Manica, A., Russell, A. F., & Johnstone, R. A. (2017). Turn-taking in cooperative offspring care: By-product of individual provisioning behavior or active response rule? *Behavior, Ecology and Sociobiology*, *71*(11), 162. https://doi.org/10.1007/s00265-017-2391-4

Savage, J. L., & Hinde, C. A. (2019). What can we quantify about carer behavior? *Frontiers in Ecology and Evolution*, *7*, 418. https://doi.org/10.3389/fevo.2019.00418

Savage, J. L., Hinde, C. A., & Johnstone, R. A. (2020). Cooperation and coordination in the family. *Frontiers in Ecology and Evolution*, *8*, 614863. https://doi.org/10.3389/fevo.2020.614863

Schlicht, E., Santema, P., Schlicht, R., & Kempenaers, B. (2016). Evidence for condition cooperation in biparental care systems? A comment on Johnstone et al. *Behavioral Ecology*, *27*(3), e2–e5. https://doi.org/10.1093/beheco/arw036

Schreiber, E., & Burger, J. (2002). Biology of marine birds. *Boca Raton*, Florida: CRC Press.

Sharp, S. P., Simeoni, M., & Hatchwell, B. J. (2008). Dispersal of sibling coalitions promotes helping among immigrants in a cooperatively breeding bird. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 275(1647), 2125–2130. https://doi.org/10.1098/rspb.2008.0398

Sharp, S. P., Simeoni, M., McGowan, A., Nam, K. B., & Hatchwell, B. J. (2011). Patterns of recruitment, relatedness and cooperative breeding in two populations of long-tailed tits. *Animal Behaviour*, *81*(4), 843–849. https://doi.org/10.1016/j.anbehav.2011.01.021

Shen, S. -F., Chen, H. -C., Vehrencamp, S. L., & Yuan, H. -W. (2010). Group provisioning limits sharing conflict among nestlings in joint-nesting Taiwan yuhina. *Animal Behaviour*, 6, 318–321. https://doi.org/10.1098/rsbl.2009.0909

Skutch, A. F. (1949). Do tropical birds rear as many young as they can nourish? *IBIS*, *91*(3), 430–455. https://doi.org/10.1111/j.1474-919x.1949.tb02293.x

Smith, M. G., Savagian, A. G., & Riehl, C. (2023). Caregivers in a communally nesting bird do not consistently synchronize nest visits. *Behavior, Ecology and Sociobiology*, *77*(7), 84. https://doi.org/10.1007/s00265-023-03361-3

Sorato, E., Gullett, P. R., Griffith, S. C., & Russell, A. F. (2012). Effects of predation risk on foraging behaviour and group size: Adaptations in a social cooperative species. *Animal Behaviour*, *84*(4), 823–834. https://doi.org/10.1016/j.anbehav.2012.07.003

Stearns, S. C. (1989). Trade-offs in life-history evolution. *Functional Ecology*, 3(3), 259–268. https://doi.org/10.2307/2389364

Stearns, S. C. (1992). *The evolution of life histories* (Vol. 249, p. xii). Oxford University Press.

Therneau, T. M. (2022). *_coxme: Mixed Effects Cox Models_. R package version 2.2-18.1*. https://CRAN.R-project.org/package=coxme

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

Trapote, E., Moreno-González, V., Canestrari, D., Rutz, C., & Baglione, V. (2023). Fitness benefits of alternated chick provisioning in cooperatively breeding carrion crows. *Journal of Animal Ecology*, 93(1), 95–108. https://doi.org/10.1111/1365-2656.14033

Trivers, R. L. (1974). Parent-offspring conflict. *American Zoologist*, 14(1), 249–264. https://doi.org/10.1093/icb/14.1.249

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag. https://CRAN.R-project.org/web/packages/ggplot2

Wilke, C. (2020). *cowplot: Streamlined Plot Theme and Plot Annotations for "ggplot2."* https://CRAN.R-project.org/package=cowplot

Zahavi, A. (1977a). The cost of honesty (further remarks on the handicap principle). *Journal of Theoretical Biology*, *67*(3), 603–605. https://doi.org/10.1016/0022-5193(77)90061-3

Zahavi, A. (1977b). Reliability in communication systems and the evolution of altruism. In B. Stonehouse, & C. Perrins (Eds.), *Evolutionary ecology* (pp. 253–259). Macmillan Press.