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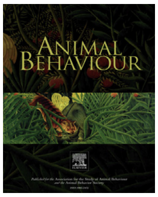

Coordination of care is facilitated by delayed feeding and collective arrivals in the long-tailed tit

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When multiple carers invest in a shared brood, there is likely to be conflict among individuals over how much each carer invests. This conflict results in suboptimal investment to the detriment of all carers. It has been proposed that conditional cooperation, that is, ‘turn taking’ or ‘alternation’, may resolve this conflict by preventing exploitation. This contentious idea has received some empirical support, but distinguishing active alternation from that expected via passive processes has proved challenging. The aim of this study was to use detailed observations of provisioning to examine whether carers at biparental (parents only) and cooperative (parents and helpers) nests of the long-tailed tit, *Aegithalos caudatus*, behave in a context-dependent manner that increases the level of alternation. First, we show that carers that had been the last to feed waited near the nest (loitering) for longer before feeding when they next arrived at the nest and allowed others to feed first, thus facilitating alternation. Second, we found that the arrival of carers near the nest and their subsequent feeds were tightly synchronized, with overlapping loitering periods, allowing them to monitor the effort of other carers. Finally, we show that measures of coordination were influenced by carers arriving in a status-dependent order, with breeding females consistently arriving first and helpers last. Together, these results show how patterns of alternation and synchrony arise in long-tailed tits, and reveal the behavioural mechanisms underpinning coordination of care.

Parental care is near-ubiquitous among birds, with posthatching care observed in >98% of species (Cockburn, 2006). It enhances the direct fitness of parents by increasing the probability that their offspring survive to breed themselves (Godfray, 1995; Godfray & Johnstone, 2000; Hinde et al., 2010; Trivers, 1974). Additionally, in cooperative breeders, where nonparents help to raise offspring, helpers may accrue direct benefits by increasing their own likelihood of breeding in the future (Dickinson & Hatchwell, 2004; Kokko et al., 2001, 2002; Zahavi, 1977a,b) and/or indirect fitness by increasing the productivity of their relatives (Hamilton, 1964). However, (allo)parental care is also costly to both parents and helpers, with experimental studies showing that carers suffer costs from their investment, for example reduced fecundity or immune function (Dijkstra et al., 1990; Gustafsson & Pärt, 1990; Nilsson & Svensson, 1996; Visser & Lessells, 2001). Therefore, in systems of biparental and cooperative care, where benefits are shared but costs are borne individually, carers can maximize their benefit-to-cost ratio by allowing the other carer(s) to bear more of the burden (Trivers, 1972). This creates a temptation to defect and hence conflict between carers over investment in their shared brood, so systems with multiple carers must be resilient against the threat of exploitation (Hinde et al., 2010; Houston & Davies, 1985). Despite this conflict, systems of shared care are widespread, being found in ca. 90% of all bird species (Cockburn, 2006).

To determine how this conflict is managed, studies have modelled how carers may respond to changes in a partner's provisioning effort, both in evolutionary time, where a stable equilibrium is reached via multiple generations of selection on individuals based on their different fixed levels of care (i.e. the sealed bid model: Houston & Davies, 1985) and in behavioural time, where a stable equilibrium is reached by individuals plastically adjusting their level of care in real time in response to care provided by their partner(s) (i.e. the negotiation model: McNamara et al., 1999). Both models predict that individuals should respond to a reduction in a partner's effort by incomplete compensation. While this is broadly

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supported by experimental studies (Harrison et al., 2009), there are many exceptions where carers showed either no response to changes in partners' effort (e.g. Schwagmeyer et al., 2002; Tajima & Nakamura, 2003) or matched their changes (e.g. Hinde, 2006; Meade et al., 2011). Furthermore, these models predict that the stable equilibrium of parental provisioning effort is below the optimum level to maximize brood fitness (Houston & Davies, 1985; Lessells & McNamara, 2012; McNamara et al., 1999, 2003). Therefore, the threat of exploitation limits the ability of carers to optimize their level of shared care and resulting fitness, unless exploitation can be otherwise prevented (McNamara et al., 2003; Royle et al., 2002, 2004, 2006). Johnstone et al. (2014) proposed a solution to this problem, suggesting that carers actively take turns to feed their brood, ensuring that any reduction in provisioning rate by one individual is matched immediately by a reduction in effort by their partner(s). This system of conditional cooperation, known as alternation, prevents individuals from gaining advantage by reducing their personal effort, thus enabling carers to more closely achieve their optimum level of brood care without the risk of exploitation (Johnstone et al., 2014). The logic of this mechanism for conflict resolution extends to cooperative systems in which broods are provisioned by three or more individuals, all of whom benefit from increased brood productivity. For example, in kin-selected cooperative breeding systems helpers benefit from enhanced survival of a shared brood, just as parents do (Hamilton, 1964; Hatchwell, 2009; Hatchwell et al., 2014). Therefore, in such systems, coordination could prevent breeders reducing their investment too much in response to helping, so that helpers still benefit from increased total care for the brood (Savage et al., 2017).

Many studies have sought to identify alternation behaviour; however, a certain level of alternation is expected by random chance, that is, ‘passive’ alternation, even if no active turn-taking behaviour occurs. Moreover, factors such as weather, predation threat and resource abundance may affect all carers at a nest, and thereby increase the level of passive alternation (Ihle et al., 2019a; Santema et al., 2019; Schlicht et al., 2016). To account for such effects, studies have compared observed alternation to expected values generated through a variety of null model randomization and simulation approaches to infer the true level of ‘active’ alternation (e.g. Baldan & Griggio, 2019; Halliwell et al., 2022; Ihle et al., 2019b; Johnstone et al., 2014; Khwaja et al., 2019). While many of these found that observed alternation was greater than expected, even when using the most conservative randomization approach (Halliwell et al., 2022; Ihle et al., 2019b; Johnstone et al., 2014; Lejeune et al., 2019; Savage et al., 2017), this does not provide definitive evidence of active alternation behaviour, because null models may not fully account for expected alternation through passive provisioning processes. More convincing evidence for active alternation would be the demonstration of provisioning behaviours that are conditional on sequences of visits by carers and that increase the level of alternation (Johnstone et al., 2014; Savage et al., 2017).

Continuous time Markov models have been used to show that an individual's provisioning rate following its own feed was lower than that following the feed of another carer in both biparental (Johnstone et al., 2014) and cooperative (Savage et al., 2017) systems, thereby providing a mechanism by which individuals could facilitate alternation. Similarly, Iserbyt et al. (2019) showed that when a carer was captured during an experiment, its partner waited six times longer to feed again than usual, although this approach can be criticized for the social disruption caused by the experiment. Active alternation requires that carers adjust their provisioning behaviour in response to the actions (or inactions) of others at the nest, even though they may themselves be foraging away from the nest. The models of Johnstone et al. (2014) and Johnstone and Savage (2019) allow for imperfect monitoring, but a reliable mechanism for regular updates on the actions of other carers is still required, not only to allow a carer to match any reduction in effort by a potential defector, but also to inform them that their own attempts to cheat have been noticed. For example, the cooperatively breeding chestnut-crowned babbler, *Pomatostomus ruficeps*, often forages solitarily far from the nest, limiting their ability to reliably monitor other carers' efforts and enforce conditional cooperation (Savage et al., 2017). Therefore, it has been suggested that alternation of provisioning visits may be facilitated by another form of coordination by carers, namely synchrony.

Synchronous provisioning has several proposed functions such as reducing nest conspicuousness to predators (Khwaja et al., 2019; Leniowski & Węgrzyn, 2018; Mariette & Griffith, 2012; Raihani et al., 2010) and reducing the capacity for more competitive chicks to monopolize food (Mariette & Griffith, 2012, 2015; Shen et al., 2010). Alternatively, it may have no benefit for the brood, but may instead be a consequence of carers foraging together and hence tending to return to the nest to provision a brood synchronously (Baldan, 2019; Baldan & Van Loon, 2022; Mariette & Griffith, 2015). None of these functions require that feeds should also be alternated. However, it has also been suggested that synchronous provisioning may allow carers to monitor the care of others to ensure alternation and prevent exploitation (Baldan, 2019; Baldan & Van Loon, 2022; Bebbington & Hatchwell, 2016; Mariette & Griffith, 2015). Importantly, this function is distinct from the others as it also predicts that carers returning synchronously to the nest should actively take turns provisioning the brood. This might be achieved by individuals that were last to feed actively delaying their next feed until other carers have fed. Here, we term the time carers spent near the nest prior to feeding the ‘loitering’ period. To our knowledge, no previous study has investigated whether alternation is facilitated by variation in loitering behaviour by carers that is conditional on whether they were the last carer to feed a brood.

In this study, we investigated the behaviours that facilitate coordination of care in a facultative cooperative breeder, the long-tailed tit, *Aegithalos caudatus*. Long-tailed tits coordinate their provisioning of broods, with greater than expected levels of synchrony and alternation of visits in biparental and cooperative nests (Bebbington & Hatchwell, 2016; Halliwell et al., 2022). Halliwell et al. (2022) used a conservative randomization approach to control for passive processes that may drive coordination, but, as described above, not all potential drivers of passive coordination may be incorporated in null models. Therefore, the overall aim of this study was to use detailed behavioural observations of the timing of arrivals and feeds of carers at biparental and cooperative nests to determine whether carers adjust their behaviour in a manner that facilitates the alternation and synchrony of feeds.

First, we examined support for the hypothesis that carers loiter near the nest before feeding to facilitate alternation of feeds (Hypothesis 1: ‘loitering facilitates alternation’). We tested two specific predictions of this hypothesis: (1A) an arriving carer that had been the last bird to feed would loiter near the nest longer than carers that had not been the last to feed; and (1B) arriving carers that had been the last to feed a brood would wait until another carer had fed before doing so themselves.

Second, we assessed support for the hypothesis that synchronous feeds are facilitated by collective foraging trips that allow carers to monitor the care provided by others (Hypothesis 2: ‘collective arrivals facilitate synchrony’). Here, we predicted: (2A) carers would arrive in the vicinity of nests synchronously; and (2B) carers would feed a brood while another carer loitered nearby.

Our final objective was to determine whether measures of coordination were influenced by variation in provisioning behaviour among carers of different status. In a previous study of long-tailed tits, feed synchrony was greatest in helpers, followed by breeding males then breeding females (Halliwell et al., 2022). One interpretation of this result is that helpers synchronize more to signal their effort to gain direct benefits of helping, for example increased social standing (Zahavi, 1977a,b) or as payment of rent (Kokko et al., 2002). However, no direct benefits to helpers have been identified in long-tailed tits (Hatchwell, 2016; Meade & Hatchwell, 2010), so it was instead suggested that this apparent variation in synchrony among carers of different status could be caused by status-dependent order effects, breeders tending to lead and helpers to follow (Halliwell et al., 2022). An order effect of this nature has been reported in the biparental great tit, *Parus major*, where synchronous visits to the nest tend to be led by the female (Baldan, 2019). Therefore, we tested the hypothesis that order effects might drive differences between carers in measures of coordination (Hypothesis 3: 'status-dependent order of visits'). Here, we predicted: (3A) breeding females, breeding males and helpers would fill specific positions (e.g. first, middle and last) within sequences of feeds during synchronized bouts; and (3B) there would be preferred associations among carers of different status, reasoning that if coordination is driven primarily by the behaviour of one carer in particular (e.g. the mother) then other carers will more often be found to associate with this carer. Together, these analyses will provide a detailed understanding of how patterns of alternation and synchrony arise, providing novel insights into the behavioural mechanisms underpinning coordination.

METHODS

Study System and Data Collection

Field work was conducted in 2020–2021 on 23 breeding pairs of long-tailed tits in an intensively monitored population in the Rivelin Valley, Sheffield, U.K. (53°23′N, 1°34′W) as part of a long-term study running since 1994. The ca. 3 km^2 field site is primarily composed of deciduous woodland, agricultural pasture and scrub. Individuals were identified by a unique combination of two colour rings which were applied, along with a BTO metal ring (under British Trust for Ornithology licence), to nestlings for birds hatched within the field site or upon capture in mist-nets for adult immigrants (see Ethical Note below). Nests were found by following adults gathering nest material and once located were checked every 2 days, with daily checks as nests approached incubation and hatching. Nests were typically built <2 m from the ground within brambles, *Rubus fruticosus*, gorse, *Ulex* spp., rose, *Rosa* spp., holly, *Ilex* spp., or >3 m from the ground in the forks of tree branches, although only nests within reach of observers, where clutch and brood size could be readily measured, were used for this study. Clutch size (median 10, range 7–11, $N = 23$) was measured once laying had ceased and incubation started. Incubation lasts ca. 15 days (Hatchwell, 2016), and all eggs that hatch typically do so on the same day (day 0). Brood size (median 9, range 6–11, $N = 23$) was recorded on day 11 and was assumed to remain constant for the full duration of provisioning observation (day 6–16; Hatchwell et al., 2004).

Provisioning watches (hereafter 'watches') were performed every other day from day 6 until fledging (ca. day 16), because for ca. 5 days after hatching nestlings are brooded by their mothers for much of the time and provisioned indirectly by fathers which pass food to the mother on the nest, so no coordination of carer visits is possible until day 6. Long-tailed tits are facultative cooperative breeders, so nests may be provisioned biparentally (two parents) or cooperatively (two parents and one or more helpers). Our data set included 101 unique watches with two to six active carers per watch, with 49% of watches being biparental and 32%, 9%, 7% and 4% watches from cooperative nests with three, four, five and six carers, respectively. Watches were conducted at 23 unique nests, including 21 unique breeding females (hereafter 'females'), 23 unique breeding males (hereafter 'males') and 25 unique helpers. Watches were performed between 0700 and 1630 hours and started after a 10 min habituation period to minimize observer disturbance. Watches were typically conducted for 60 min following the first observed feed, with the final watch duration recorded as the time between first and last feeding visits (mean duration ± SD = 58.5 ± 5.9 min, range 41.2–78.3, $N = 101$ watches). We omitted one watch of duration <30 min.

The protocol during watches was to record the identity of a carer and the time, to the nearest second, they arrived near the nest (within 15 m) and then provisioned the brood. Prior to beginning a watch, a video camera was placed ca. 2 m from the nest, recording the nest entrance so that the identity of carers and time of feed, to the nearest second, could be determined by video review. Meanwhile, an observer sat ≥20 m from the nest, where they identified carers arriving near the nest, recording the identity and time of arrival to the nearest second. The time a carer spent near the nest prior to feeding is hereafter referred to as the 'loitering' period. The order of arrivals near the nest was important for our analysis, so when carers arrived simultaneously observers recorded the arrival times as equal but noted which carer was identified first. After 7.1% ($N = 2470$) of arrivals the carers left the area without provisioning, so these instances were excluded. Watches were conducted only at nests with good visibility of surroundings, but 5.3 ± 6.1% (SD) of arrivals that resulted in a feed (recorded by video) were missed (range 0–21%, $N = 101$ watches); one watch where more than 25% of arrivals were missed was omitted. Gaps were filled by substituting time first seen on camera for arrival time, reasoning that the longer a carer loitered the lower the chance that it would be missed, so missed arrivals would likely have preceded very short loitering periods. Observations were conducted by three observers: 73/101 watches were conducted by C.H. and the remainder by S.J.B. (13) and M.G. (15), with distance estimation standardized in joint watches before data collection started.

Ethical Note

Adult and nestling long-tailed tits were ringed by B.J.H. and S.J.B. under British Trust for Ornithology (BTO) licence with two colour rings (size code: XF) on one leg and a BTO metal ring on the other. Adult birds were captured using mist-nets and nestlings in accessible nests were temporarily removed from nests and ringed on day 11 posthatching. Mist-nets were watched continuously during trapping and birds extracted and processed as soon as they were caught. During processing of nestlings half the brood was removed at a time to ensure that adults still had offspring to feed in the nest, and to reduce the time that chicks spent out of the nest. For this study, 69 unique wild adult birds were sampled, including 21 breeding females, 23 breeding males and 25 helpers (20 males, three females and two unknown). A total of 199 nestlings were ringed from nests used in this study.

Nest monitoring was conducted by noninvasive observation whenever possible. To determine lay date and hatch date nests were checked by an observer carefully inserting a single finger into the nest when the parents were absent to check for the presence of eggs or chicks. Completed nests were checked every 2 days and the first egg lay date was determined by counting back assuming that one egg was laid per day. During incubation, nests were checked every 2 days, predominantly by observation of the nest from a distance to avoid disturbance, but occasionally by hand if predation was suspected from a lack of activity at the nest. From day 12 of the incubation period, nests were checked daily to ensure hatch date (typically after 13–15 days of incubation) was recorded to within 24 h. Once a brood had hatched (day 0) provisioning data were collected every other day, starting at day 2, until either the nest failed or fledged (ca. day 16–18). Provisioning watches necessitated a brief period of nest disturbance (ca. 1 min) while the observer set up a camera on a tripod ca. 2 m from the nest.

Calculating Coordination

Alternation and synchrony were analysed as the absolute number of alternated and synchronized visits performed within each provisioning watch. An alternated feed was defined as any feed that avoided consecutive feeds by the same individual, ensuring turn taking between two or more carers. For example, the sequence A–B–A–C–B–C avoids consecutive feeds by the same carer, so all these would be considered alternated (except the first); note that in cooperative nests alternation did not require repeated patterns of feeds by all carers, for example A–B–C–A–B–C, simply nonconsecutive feeds. A synchronized feed was defined as any alternated feed that occurred within a brief time window of the previous feed, for example if three feeds occurred within quick succession after a gap in provisioning (e.g. A–B–C) then feeds B and C are considered synchronized, but feed A is not because it did not occur within the synchrony window of the previous feed. We investigated the synchrony of arrivals near the nest and feeds using two different synchrony window lengths: long (2 min) and short (30 s), a synchronized arrival being any that occurred within the specified window of the previous arrival by another carer. The long (2 min) window was chosen to match previous studies of coordination (Bebbington & Hatchwell, 2016; Halliwell et al., 2022; Ihle et al., 2019a) which measured feed times to the nearest minute and produced qualitatively the same results with 1 min, 2 min and 3 min synchrony windows. In this study, since we recorded feed and arrival times to the nearest second, we utilized this increased resolution to compare the level of active synchrony using a long (2 min) and a short (30 s) window; a difference between them could indicate whether arrivals or feeds were more or less tightly synchronized than previously shown.

A certain level of passive coordination (alternation and synchrony) is expected by chance (Ihle et al., 2019a; Santema et al., 2019; Schlicht et al., 2016), and factors such as predator threat, local resource abundance and changing weather can increase apparent coordination through their common effect on all carers at a watch. Refractory periods (the foraging time needed to obtain food for chicks) may also contribute to apparent coordination as they create a period during which a consecutive visit is not possible, but an alternated visit is. Therefore, to determine the extent to which observed coordination was due to active coordination behaviours we compared observed coordination metrics to an expected passive level of coordination generated through null model randomization. We used a modified version of the within-watch, within-individual intervisit interval randomization procedure (Fig. 1a, c) that randomized the times between an individual carer's feeds within a given watch, that is, the intervisit intervals (e.g. Halliwell et al., 2022; Ihle et al., 2019b; Johnstone et al., 2014; Savage et al., 2017; Fig. 1c). Here, we split the intervisit interval into ‘time away’ (mean duration ± SE: 357.6 ± 7.3 s, $N = 2010$) from and ‘time near’ (loitering; 50.3 ± 1.5 s, $N = 2307$) the nest (Fig. 1a). We found no correlation between ‘time away’ and ‘time near’ (Pearson correlation: $r_{100} = 0.137$, $P = 0.171$), so we randomized these time periods independently of one another (Fig. 1b). This approach more precisely defines the length of the refractory period, which is now contained within ‘time away’, thus creating a more biologically

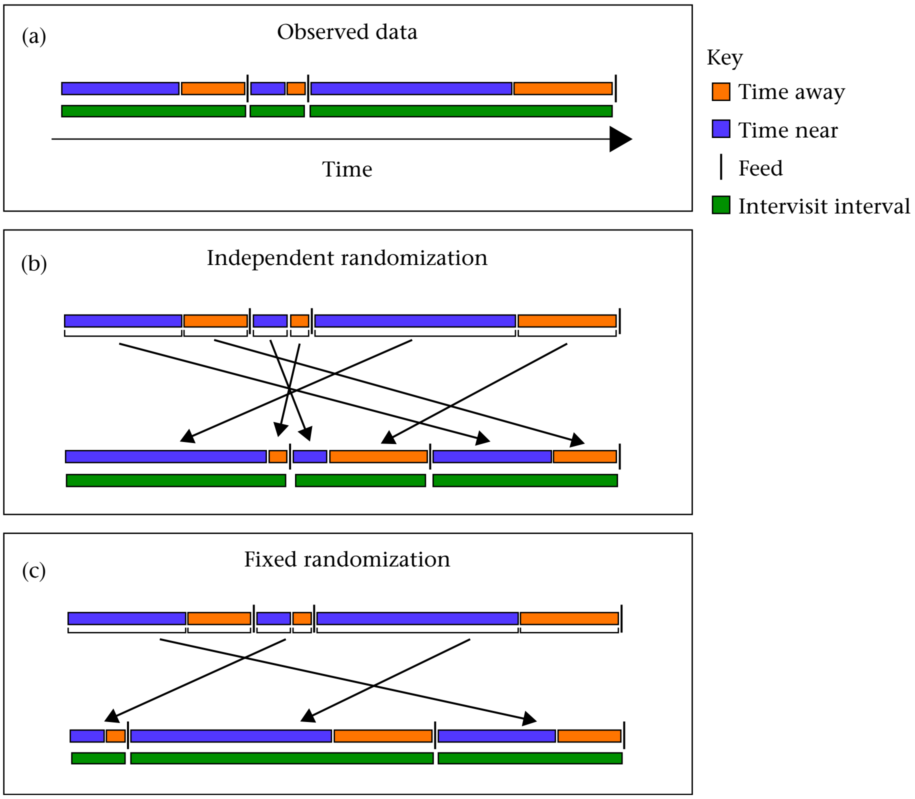

Figure 1. Demonstration of how (a) an observed sequence of feeds by an individual is randomized by: (b) our modified approach which randomized ‘time away’ and ‘time near’ independently and (c) the approach detailed in Ihle et al. (2019a) which randomized ‘time away’ and ‘time near’ together as fixed blocks.

realistic approximation of the level of apparent coordination expected by chance. We applied our null model to the observed data set, generating 1000 randomized sequences which we used as a framework for generating expected values for a given metric of coordination. For example, to test whether carers alternated more than expected by chance, we calculated the median 'expected' number of alternated feeds per watch from these 1000 randomized sequences and compared that to the 'observed' number of alternated feeds seen in that watch. The difference between these observed and expected values is hereafter referred to as 'active' coordination.

Hypothesis 1: loitering facilitates alternation

To test predictions of the delayed feeding hypothesis we calculated several metrics of coordination directly from provisioning watches (observed) and the median number from 1000 randomized sequences (expected) as follows. First, we calculated the number of feeds where a carer waited to ensure alternation, defined as the number of visits where, upon arrival near the nest, a carer that had been the last to feed waited for another carer to feed before them in the current bout. Second, we calculated the mean loitering time for carers when, upon arrival, they were the last carer to feed previously, and the mean loitering time when they were not. Similarly, we calculated the number of instances where another carer fed during the loitering period of the focal carer when, upon arrival, they were the last to feed, and the number of instances another carer fed when they were not last to feed.

Hypothesis 2: collective arrivals facilitate synchrony

To test the predictions of the collective arrival hypothesis we first calculated the observed and expected numbers of instances of synchronous arrivals and synchronous feeds during a given watch (using both long and short synchrony windows). Second, we calculated the number of observed and expected cases when the focal carer arrived near the nest with another carer already present, and when another carer fed during the loitering period of the focal carer. For this analysis all measures were calculated as the total number of cases by all carers present during a given watch.

Hypothesis 3: status-dependent order of visits

To test the predictions of the status-dependent arrival hypothesis, first we calculated the observed and expected number of instances where the focal carer arrived near the nest with another carer already nearby. These metrics were calculated for each individual carer, allowing comparison of the number of these cases between carers of different status.

Second, we quantified the orders in which carers arrived and fed during synchronized bouts. We restricted this investigation to biparental (two carers: male (M) and female (F)) watches and cooperative watches with one helper (three carers: M, F and helper (H)) which together made up 80% of our watches, because as the number of carers increases, the number of possible orders in which carers may arrive or feed in increases exponentially, from two possible orders with two carers (F–M and M–F), six with three carers, 24 for four carers and so on. For these analyses we considered only 'isolated' synchronized bouts (2 min window). For a synchrony bout to be isolated it must be separated from the previous bout by at least 2 min to avoid one bout influencing another. For example, if a biparental nest has a female-first synchronized feed bout (F–M) followed shortly by another synchronized bout then the female is more likely to arrive first in the subsequent bout because feeding first in the previous bout afforded her a head start. For these analyses our null expectation was that carers of different status would occupy randomly each position within a sequence, that is, 50% per position for biparental watches and 33.3% per position for cooperative watches.

For biparental watches, we determined the number of female-first and male-first arrival and feed sequences per watch, our model structure accounting for multiple bouts from the same watch with random effect terms. In total we identified 294 synchronized bouts from 46 biparental watches (median = 6 per watch); three watches contained no suitable bouts. For cooperative watches, we determined the position within arrival and feed sequences by females, males and helpers. We identified 82 synchronized bouts from 27 cooperative watches (median = 3 per watch); five watches contained no suitable bouts. Of the 82 bouts, in three instances the same carer arrived twice within the synchronized bout, so these bouts were omitted from the arrival order analysis. For analysis of cooperative bouts, we determined the number of times carers of each status occupied a position (first, middle and last) for both arrivals and feeds. Finally, to investigate whether carers at cooperative nests were more closely associated with other specific carers, we determined the number of times a carer synchronized with one other carer only during isolated synchronized bouts (i.e. F&M, F&H and M&H) regardless of the order of arrivals or feeds. In total, we found 102, 96 and 58 instances of a female, male and helper synchronizing with another carer, respectively.

Statistical Analysis

All statistical analysis was performed on R version 4.0.2 (R Core Team, 2020), and applied to the data set Halliwell et al. (2023). All models were built using lme4 (Bates et al., 2015) and analysed using lmerTest (Kuznetsova et al., 2017). Where applicable, post hoc testing was performed using the package emmeans (Lenth et al., 2019). Figures were produced using the packages ggplot2 (Wickham, 2016) and cowplot (Wilke, 2020).

Model framework and covariates

All models employed the following fixed-effect covariates (see Appendix and Table 1 for term definitions): 'Provisioning rate' (collective or individual), 'Carer number', 'Watch duration', 'Brood size', 'Watch start time', 'Brood age', 'Hatch date' and 'AMax' (or SMax), with 'Data type' (i.e. observed or expected) or associated interaction used to determine whether the metric differed significantly from that expected by chance. We also used the following random effects: 'Year', 'Nest', 'Watch ID' and 'Rowref' for Poisson-distributed models (Table 1). In the sample of nests used for this study only two birds bred in both years, but with different partners, and only two helpers were recorded as helping at multiple nests. Therefore, for 19 of 23 nests the Carer ID terms are completely synonymous with Watch ID, so, for collective level analyses we used the random effects of Year, Nest ID and Watch ID only. However, in the individual level analyses of the effect of carer status on coordination, a 'Carer ID' term was used to control for consistent differences between carers that featured in multiple watches of the same nest. Full details of each model's structure, including terms of interest, covariates, error distribution and random effects used are available in Appendix Table A1. Full outputs, including estimates and *P* values for all model terms, including covariates are available in Appendix Tables A2–A14.

Hypothesis 1: loitering facilitates alternation

Before testing explicit predictions of the hypothesis that loitering facilitates alternation, we first tested whether alternation occurred more than expected by chance, as reported for a much larger data set by Halliwell et al. (2022). To do so we built a generalized mixed-effects model (GLMM) with a Poisson

Table 1
Details of random and fixed effects applied throughout analyses

	Description
Random effects	
Year	Unique factor designating the 2020 or 2021 breeding season
Nest ID	Unique factor designating which nest was watched
Watch ID	Unique factor designating each provisioning watch
Rowref	Observation level random effect to account for overdispersion in Poisson-distributed models, i.e. each watch, both observed and expected, was given a unique number corresponding to its row
Carer ID	Unique factor designating carer identity used in individual level analysis
Provisioning rate ratio (FH, MH, FM)	Continuous numerical variable, designating the ratio of feeds by other carers at the watch (e.g. male:helper ratio for female analysis) applied as a random slope term with Nest and Watch ID for association models only
Fixed effects	
Provisioning rate (collective)	Continuous numerical variable representing total hourly provisioning rate by all carers during a watch (mean: 22.7 feeds/h; range 4.72–59.6)
Provisioning rate (individual)	Continuous numerical variable representing the hourly provisioning rate by a given carer during a watch (mean: 8.02 feeds/h; range 0.822–33.6)
Carer number	Ordinal factor designating the number of carers seen provisioning during a watch (6 > 5 > 4 > 3 > 2)
Watch duration	Continuous numerical variable representing the length of time (min) between the first arrival and the last feed at each watch
Brood size	Integer variable representing the number of live chicks on day 11. This value was used for all watches at the same nest
Watch start time	Continuous numerical variable representing the time (h) since the start of a given day on which a watch was started
Brood age	Integer variable representing the number of days since hatching (day 0) on which a watch was performed
Hatch date	Integer variable representing the number of days since 1 March each year (median: 29 April; range 19 April–1 June)
AMax (or SMax)	Continuous numerical variable representing the highest theoretical percentage of visits during a watch that could be alternated (or synchronized). Acts as proxy for provisioning rate disparity between carers, as a visit can only be alternated (or synchronized) if there are sufficient visits by other carers to alternate (or synchronize) with
Data type	Binary factor designating whether data were from field observations (observed) or generated by null model randomization (expected). The difference between observed and expected values is the level of 'active' coordination
Last to feed	Binary factor designating whether upon its arrival near the nest the focal bird provisioned the chicks most recently
Synchrony window	Binary factor designating whether a synchronized visit was from the 2 min or 30 s synchrony window
Arrival or feed	Binary factor designating an arrival or a feed
Carer status	Three-level factor designating whether an individual carer is a breeding male, a breeding female or a helper. Used in individual level analysis
Order	Binary factor designating whether an arrival or a feed was male first (M–F) or female first (F–M). Used in biparental watches
Position	Three-level factor designating the relative position of arrivals or feeds occupied by a carer when all three carers synchronize (first, middle, last). Used in cooperative watches
Association	Binary factor designating the status of the other carer a given carer synchronized with during a synchronized bout, regardless of order

M: male; F: female; H: helper.

distribution, the key term of interest being 'Data type', that is, observed alternation versus expected alternation. Then, to test the two predictions of the hypothesis that carers loitered to facilitate alternation we built a general linear mixed-effects model (LMM) and two generalized linear mixed-effects models (GLMMs), as follows.

Prediction 1A: loiter longer if last to feed. To test the prediction that arriving carers that had been the last to feed a brood should loiter longer than expected before feeding the brood, we built an LMM with a normal distribution. The response term was the log-transformed mean loitering period by carers per watch. For each watch we calculated the mean loitering time for carers which, upon arrival near the nest, were the most recent carer to feed; and the mean loitering time for carers which, upon arrival, were not the most recent carer to feed. These two conditions were distinguished by the term 'Last to feed', a binary factor indicating whether, upon arrival, the focal bird was last to feed or not. The key term of interest in this model was the two-way interaction term of 'Data type' and 'Last to feed', which tested whether the difference between loitering times when a carer was versus was not last to feed, was greater than expected by chance.

Prediction 1B: loiter to allow alternation. To test the prediction that arriving carers that were the last to feed should loiter until another carer had fed before feeding themselves, we used a GLMM with Poisson distribution. The response variable was the number of feeds per watch where the focal carer was the last to feed upon arrival, but allowed another carer to feed before themselves feeding, and in this case the term of interest was 'Data type', testing whether the focal carer was more likely than expected to loiter until another bird had fed the brood if they had been the last carer to feed. In a second test of this prediction, we also examined whether another carer was more likely to feed during a focal bird's loitering period when the focal bird was the last carer to feed compared to when it was not. In this case, the response variable was the number of feeds per watch where another carer fed during the loitering period of the focal carer. For each watch we calculated the number of instances where another carer fed during the focal carer's loitering period when the focal carer was, upon arrival near the nest, the most recent carer to feed; and the number of instances where another carer fed during the focal carer's loitering period when the focal carer was not, upon arrival, the most recent carer to feed. These two conditions were again distinguished using the term 'Last to feed' (see above). The term of interest in the model was the interaction between 'Data type' and 'Last to feed', which tested whether the focal carer was more likely to allow another carer to feed during their loitering period when they were versus were not last to feed, than expected by chance.

Hypothesis 2: collective arrivals facilitate synchrony

To test the hypothesis that synchronous feeds are a consequence of coordinated foraging, with birds arriving back at the nest synchronously and hence feeding synchronously, we tested two predictions.

Prediction 2A: carers arrive synchronously. First, we examined whether arrivals and feeds were more synchronous than expected by chance, also comparing the degree of synchrony between arrivals and feeds. We built a GLMM with Poisson distribution with a response variable of the number of synchronous arrivals and feeds per watch. Our field protocol allowed us to investigate synchrony at higher resolution than in Halliwell et al. (2022), so in these analyses we used two measures of synchrony: birds arriving and feeding within 30 s of each other and within 2 min of each other, denoted by the term ‘Synchrony window’. The key terms of interest in this model were ‘Data type’ (i.e. whether synchrony was greater than expected), ‘Arrival or feed’ (i.e. a binary factor indicating whether it was an arrival or feed order) and ‘Synchrony window’, and their interactions. The interaction terms are informative in different ways. For example, a two-way interaction of ‘Data type’ and ‘Arrival or feed’ indicates whether the active synchrony of arrivals is different from feeds, while an interaction of ‘Data type’ and ‘Synchrony window’ indicates whether active synchrony differed using alternative time windows. Estimates of whether observed synchrony was greater than expected for arrivals and feeds separately, at both synchrony intervals, were calculated by Tukey's honestly significant difference (HSD) post hoc test, using the package emmeans (Lenth et al., 2019).

We also tested this prediction by examining whether a carer was more likely than expected to arrive at a nest when another carer was already present, using a GLMM with Poisson distribution. The response variable in this analysis was the number of occasions within a watch when a focal carer arrived back at the nest when another carer was present, and the key term of interest was ‘Data type’, indicating whether the observed frequency was greater than expected by chance.

Prediction 2B: carers feed while another loiters. This prediction was tested in a GLMM with Poisson distribution. The response term was the number of feeds per watch where the focal carer fed while another carer was loitering nearby, and the term ‘Data type’ indicated whether the observed level was greater than expected by chance.

Hypothesis 3: status-dependent order of visits

Finally, we examined the hypothesis that variation in coordination among carers of different status is a consequence of consistent orders of visits, testing two predictions.

Prediction 3A: carers arrive and feed in consistent sequence. This prediction was tested in two sets of analysis. First, we used a GLMM with Poisson distribution to investigate whether carers of specific status (female, male and helper) were more likely than expected by chance to arrive back at the nest first. The response variable for this model was the number of visits where another carer was present upon the focal carer's arrival at a nest per individual per watch. The term of interest in this model was the two-way interaction of ‘Data type’ and ‘Carer status’, a three-level factor designating whether an individual was a female, male or helper (Table 1). Results reported by Halliwell et al. (2022) suggested that females may be more likely to return to the nest first and helpers last, so we used this interaction term to investigate whether males and helpers were more likely to arrive with another carer already present, than expected by chance.

Second, we investigated the sequences of arrivals and feeds during isolated synchronized bouts with two Poisson-distributed GLMMs, one for biparental nests and one for cooperative nests. In the biparental model, the response variable was the order of arrival and feed sequences during synchronized bouts by the parents at biparental nests (F—M and M—F). The term of interest was ‘Order’; a binary factor designating whether a bout was male or female first. We speculated that females should arrive and feed first, so we expected that female-first orders (F—M) should be overrepresented in both arrival and feed sequences, which we tested by post hoc analysis. We also included a two-way interaction term between ‘Order’ and ‘Arrival or feed’ to examine whether there was any difference between the two behaviours. Similarly, in the cooperative sequence model the response variable was the relative position upon arrival and feed during synchronized bouts where all three carers (male, female, helper) fed at cooperative (three carers) nests. Here, we investigated the three-way interaction term of ‘Carer status’, ‘Arrival or feed’ and ‘Position’, which was a three-level factor indicating whether a carer was in the first, middle or last position. Post hoc analysis was used to determine whether certain carer statuses were overrepresented in certain positions within the sequence for arrivals and feeds.

Prediction 3B: preferential associations among carers. Finally, to test the prediction that carers of a particular status preferentially synchronized with carers of another particular status we built three Poisson-distributed GLMMs. These models investigated the frequency that each carer status (female, male, helper) synchronized with each carer type during two-carer synchronized bouts at cooperative (three carers) nests using the binary factor ‘Association’. To account for the effect that different provisioning rates by each carer would have on the likelihood of association we included the ratio of feed rates by other carers during that watch as a random slope term; inclusion of this term as a fixed effect instead produced quantitatively the same results for ‘Association’.

RESULTS

Hypothesis 1: Loitering Facilitates Alternation

Before testing explicit predictions of the hypothesis that loitering facilitates alternation, we first investigated whether active alternation occurred in the data set collected for this study. Observed alternation was significantly greater than expected by chance (GLMM: $P = 0.041$; Table 2, Fig. 2a), as reported previously (Bebbington & Hatchwell, 2016; Halliwell et al., 2022). To assess support for the hypothesis that alternation is facilitated by carers

Table 2
Models investigating the hypothesis that loitering facilitates alternation

Response variable	Fixed effects	Estimates ± SE	*df*	χ^2	*P*
Number of alternated visits per watch	Data type	Observed: 0.062 ± 0.061	1, 184	4.19	**0.041**
Prediction 1A: loiter longer if last to feed					
Ln(mean loiter time)	Data type∗Last to feed	Observed, Yes: 0.156 ± 0.061	1, 377	6.55	**0.010**
Prediction 1B: loiter to allow alternation					
Number of visits where carer waited to ensure alternation per watch	Data type	Observed: 0.873 ± 0.203	1, 181	34.65	**<0.001**
Number of visits, per watch, where another carer fed while focal carer loitered	Data type∗Last to feed	Observed, Yes: 0.458 ± 0.155	1, 377	8.70	**0.003**

Significant values ($P < 0.05$) are in bold.

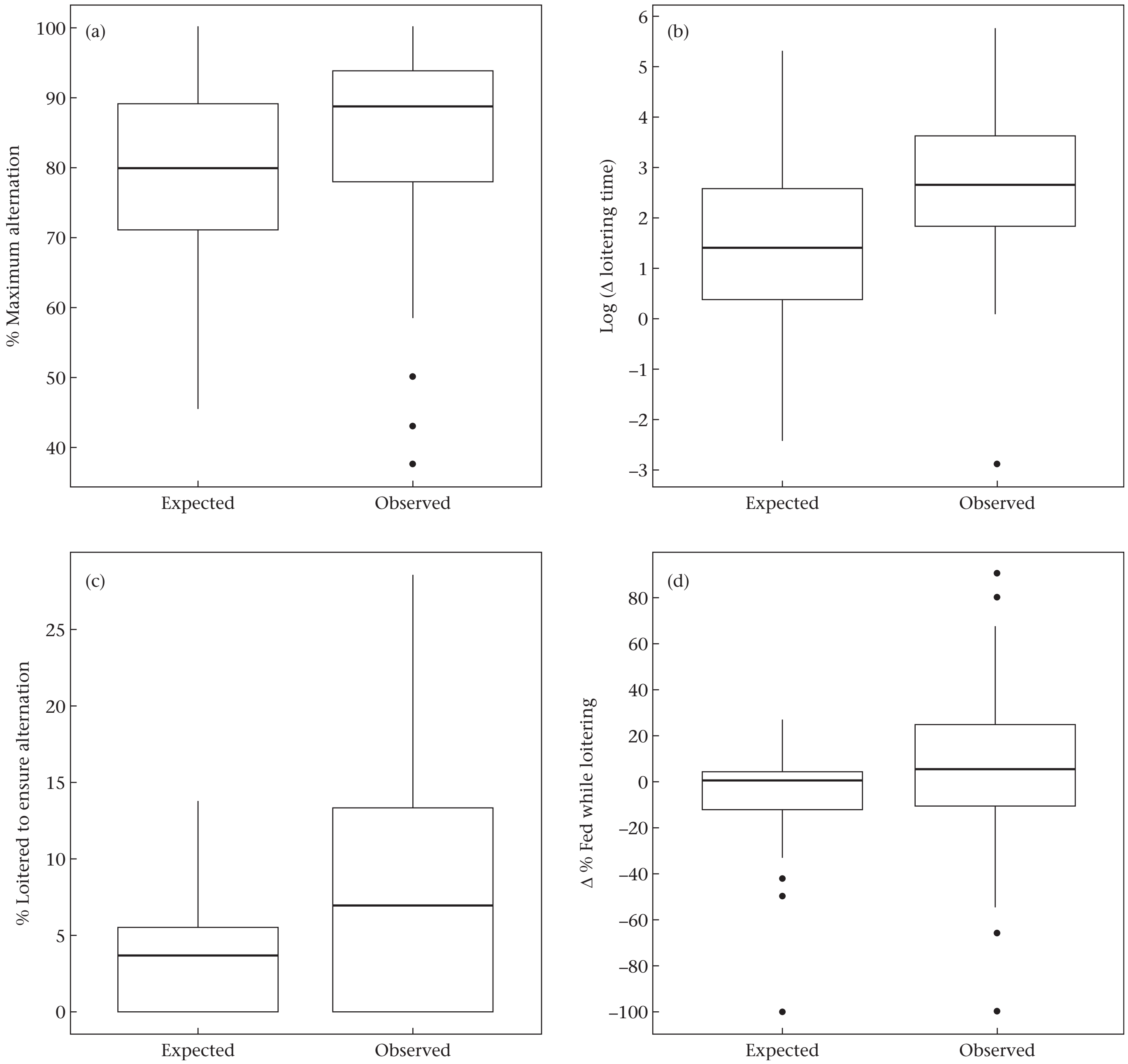

Figure 2. Plots of observed and expected results for (a) the percentage of maximum theoretical alternation achieved by carers during a given watch, (b) the log-transformed difference in mean loitering time between when the focal carer was versus was not last to feed, per watch, (c) the percentage of visits where a carer loitered to ensure alternation per watch and (d) the difference in percentage of visits where another carer fed while the focal carer loitered, between when the focal carer was versus was not last to feed, per watch. Bold lines in boxes represent the median values. Lower and upper boundaries of boxes represent lower and upper quartile values, respectively. Upper and lower boundaries of tails represent the maximum observed value within the upper fence (third quartile + 1.5 × interquartile range) and minimum observed value within the lower fence (first quartile − 1.5 × interquartile range), respectively. Points represent outliers (values outside lower–upper fence range). Total $N = 101$ watches from 23 nests.

delaying their feeding visits if they were last to feed, we tested two predictions.

Prediction 1A: loiter longer if last to feed

The prediction that an arriving carer that had been the last bird to feed previously would loiter near the nest longer than birds that had not been the last to feed was supported. The interaction term of ‘data type’ and ‘last to feed’ was significant, showing that carers loitered for longer if feeding immediately would have resulted in a nonalternated feed (LMM: $P = 0.011$; Table 2, Fig. 2b).

Prediction 1B: loiter to allow alternation

We tested the prediction that arriving carers that had been the last to feed previously would wait until another carer had fed before doing so themselves in two analyses. First, we found that the number of instances where carers waited to allow alternation was significantly greater than expected by chance (GLMM: $P < 0.001$;

Table 2, Fig. 2c). Second, another carer was more likely to feed during a focal carer's loitering period if, upon arrival, the focal carer had previously been the last bird to feed (GLMM: $P = 0.003$; Table 2, Fig. 2d). These results show that carers arriving in the proximity of nests to provision chicks behaved in a manner that increased the probability of alternated feeds.

Hypothesis 2: Collective Arrivals Facilitate Synchrony

We tested two predictions derived from the hypothesis that active synchrony is facilitated by carers' collective arrival at the nest.

Prediction 2A: carers arrive synchronously

First, the prediction that carers synchronized arrivals near the nest as well as nestling feeds was supported, because the number of observed synchronous feeds was significantly greater than expected by chance for both the 2 min (Tukey's HSD: $P < 0.001$; Fig. 3a) and 30 s synchrony windows (Tukey's HSD: $P < 0.001$; Fig. 3a), as was the number of observed synchronous arrivals for both 2 min (Tukey's HSD: $P < 0.001$; Fig. 3b) and 30 s synchrony windows (Tukey's HSD: $P < 0.001$; Fig. 3b). There was no significant difference in the level of active synchrony between arrivals and feeds (GLMM: $P = 0.740$; Table 3, Fig. 3). Interestingly, the level of active synchrony was significantly greater for the 30 s window than the 2 min window (GLMM: $P < 0.001$; Table 3, Fig. 3), suggesting that both arrivals and feeds were more tightly synchronized than previously thought. Furthermore, this disparity in active synchrony between the 2 min and 30 s windows did not differ significantly between arrivals and feeds (GLMM: $P = 0.321$; Table 3, Fig. 3), indicating that arrivals and feeds were equally tightly synchronized.

Synchronous arrival would also result in carers having overlapping loitering periods, so we tested the prediction that there would be significantly more arrivals at the nest when another carer was present, than expected by chance. This prediction was supported (GLMM: $P < 0.001$; Table 3, Fig. 4a), showing that synchronous arrivals caused carers to actively overlap in their loitering periods.

Prediction 2B: carers feed while another loiters

Finally, we found support for the prediction that carers were more likely to feed while another carer was loitering nearby, as the number of instances where this occurred was greater than expected by chance (GLMM: $P < 0.001$; Table 3, Fig. 4b). Together these results suggest that synchronous feeds of nestlings are a consequence of synchronous arrival near the nest, indicative of collective foraging behaviour.

Hypothesis 3: Status-dependent Order of Visits

Halliwell et al. (2022) reported that carers of different status exhibited differences in their level of active synchrony, with helpers being more synchronous than males, and males more than females. They hypothesized that this could result from collective arrivals where breeders tend to lead and helpers follow. To assess support for this hypothesis, we tested two predictions.

Prediction 3A: carers arrive and feed in consistent sequence

First, we found support for the prediction that females arrive at the nest first, as males and helpers were more likely than females to arrive in the vicinity of the nest when another carer was already present (GLMM: $P = 0.033$; Table 4, Fig. 5). This was true for both biparental nests, where first arrivals at the nest were strongly in favour of females (Tukey's HSD: $P = 0.032$; Fig. 6a) and cooperative nests, where females were more likely to arrive in the first position than the last (Tukey's HSD: $P = 0.033$; Fig. 6b). Moreover, helpers were more likely to arrive in the last position than either the first (Tukey's HSD: $P = 0.033$; Fig. 6b) or middle position (Tukey's HSD: $P = 0.006$; Fig. 6b).

In contrast, there was no support for the prediction that females also fed first during synchronized bouts. At biparental nests, the order of arrivals was significantly different from the order of feeds (GLMM: $P = 0.019$; Table 4, Fig. 6a, c), but neither males nor females were more likely to feed first (Tukey's HSD: $P = 0.251$; Fig. 6c). At

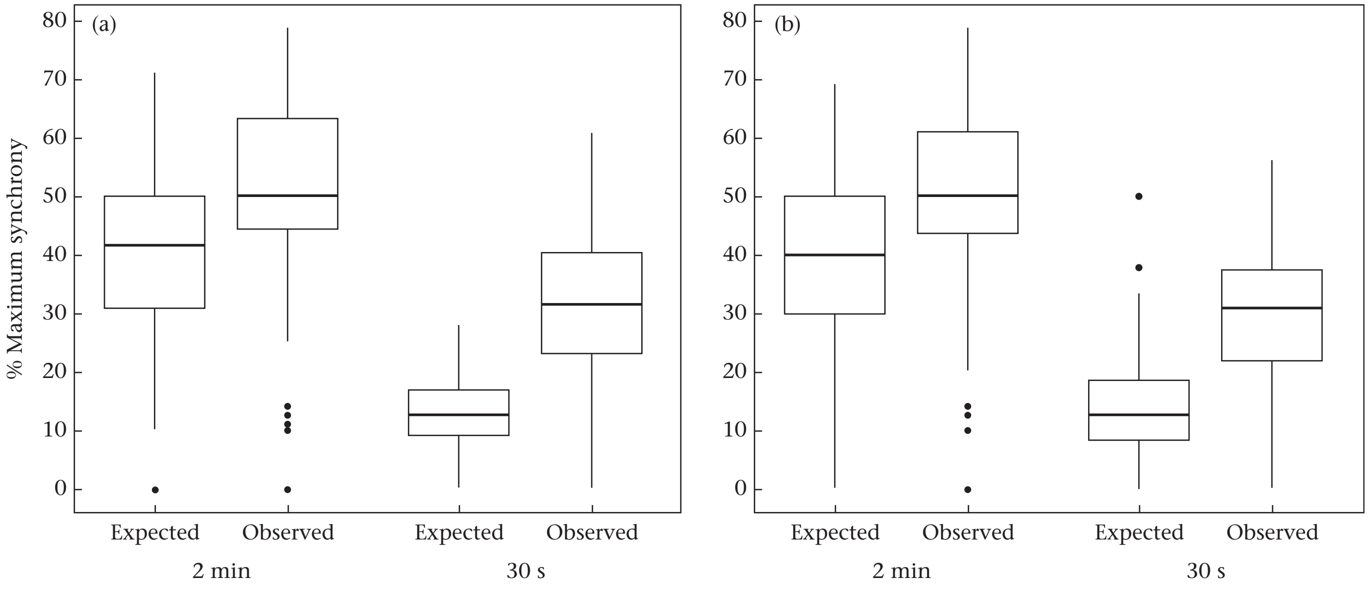

Figure 3. Plots of observed and expected percentage of maximum theoretical (a) feed and (b) arrival synchrony achieved per watch for 2 min and 30 s synchrony windows. Bold lines in boxes represent the median values. Lower and upper boundaries of boxes represent lower and upper quartile values, respectively. Upper and lower boundaries of tails represent the maximum observed value within the upper fence (third quartile + 1.5 × interquartile range) and minimum observed value within the lower fence (first quartile − 1.55 × interquartile range), respectively. Points represent outliers (values outside lower−upper fence range). Total $N = 101$ watches from 23 nests per figure.

Table 3
Models investigating the hypothesis that collective arrivals facilitate synchrony

Response variable	Fixed effects	Estimates ± SE	*df*	χ^2	*P*
Prediction 2A: carers arrive synchronously					
Number of synchronized arrivals and feeds per watch	Data type ∗ Synchrony window ∗ Feed or arrival	Observed, Feed, 2 min: −0.117 ± 0.118	1, 781	0.98	0.321
	Data type ∗ Feed or arrival	Observed, Feed: 0.065 ± 0.099	1, 781	0.11	0.740
	Data type ∗ Synchrony window	Observed, 2 min: 0.451 ± 0.085	1, 781	75.38	**<0.001**
Number of visits, per watch, where the focal carer arrived back with another carer loitering	Data type	Observed: 0.588 ± 0.116	1, 181	39.73	**<0.001**
Prediction 2B: carers feed while another loiters					
Number of visits, per watch, where focal carer fed while another loitered	Data type	Observed	1, 181	39.93	**<0.001**

Significant values ($P < 0.05$) are in bold.

cooperative nests, the order of arrivals was not significantly different from the order of feeds (GLMM: $P = 0.123$; Table 4, Fig. 6b, d), and the only difference between carer statuses in likelihood of feeding in a particular position was a nonsignificant trend for females to feed in the middle position more than helpers (Tukey's HSD: $P = 0.061$; Fig. 6d).

Prediction 3B: preferential associations among carers

Finally, we found mixed support for the prediction of preferential association between carers of different status at cooperative nests. Males were significantly more likely to synchronize with females than with helpers (GLMM: $P < 0.001$; Table 4), and females were significantly more likely to synchronize with males than with helpers (GLMM: $P = 0.005$; Table 4). However, helpers showed no active preference for synchronizing with either males or females (GLMM: $P = 0.576$; Table 4).

DISCUSSION

In this study we used detailed observations of provisioning behaviour to record when carers arrived near the nest and provisioned the brood. This enabled us to quantify loitering periods between arrival and provisioning which we used to test a series of hypotheses regarding the mechanisms by which ‘active’ coordination of care may be facilitated. First, we showed that the time carers spent loitering near the nest facilitated alternation, with arriving carers that had been the last to feed loitering for longer and being more likely to have another carer feed during their loitering period, than expected by chance. Second, we demonstrated that synchronous feeds were facilitated by collective arrival of carers near the nest, with carers showing a greater than expected level of arrival and feed synchrony and being more likely to arrive and to feed during the loitering period of another carer than expected. Finally, we found mixed support for the hypothesis that visit order (and hence measures of coordination) was determined by carer status. While breeding females were more likely to arrive back to the nest first at biparental and cooperative nests and helpers were more likely to arrive back last, these trends were not reflected in feed order. Furthermore, we found that breeders preferentially synchronized together at cooperative nests, but helpers showed no active preference for synchronizing with either member of the breeding pair.

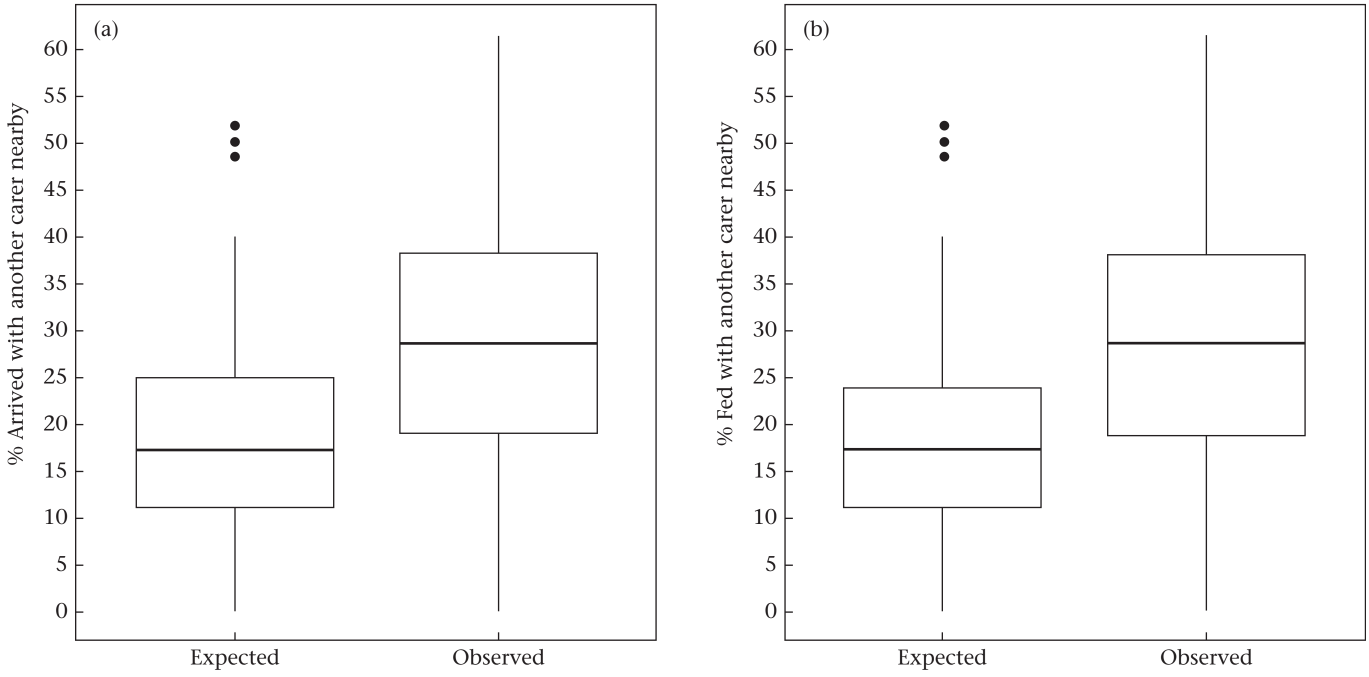

Figure 4. Plots of observed and expected percentage of visits, per watch, where the focal carer (a) arrived and (b) fed while another carer was nearby. Bold lines in boxes represent the median values. Lower and upper boundaries of boxes represent lower and upper quartile values, respectively. Upper and lower boundaries of tails represent the maximum observed value within the upper fence (third quartile + 1.5 × interquartile range) and minimum observed value within the lower fence (first quartile − 1.5 × interquartile range), respectively. Points represent outliers (values outside lower–upper fence range). Total $N = 101$ watches of 23 nests.

Table 4
Models investigating the hypothesis that carers exhibit status dependent orders of visits

Response variable	Fixed effects	Estimates ± SE	*df*	χ^2	*P*
Prediction 3A: carers arrive and feed in consistent sequence					
Number of visits, per watch, per individual, where the focal carer arrived back with another carer loitering	Data type∗Carer status	Observed, helper: 0.396 ± 0.181 Observed, male: 0.356 ± 0.154	2, 553	6.85	**0.033**
Frequency of each order (male first & female first), per watch, during synchronized arrivals and feeds (biparental)	Order∗Arrival or feed	Male first, Feed: 0.396 ± 0.169	1, 173	5.46	**0.019**
Frequency that each carer occupied each position (first, middle, last), per watch, during synchronized arrivals and feeds (cooperative)	Carer status∗Position∗Feed or arrival	Feed, Middle, M: −0.919 ± 0.525 Feed, Middle, H: −0.810 ± 0.568 Feed, Last, M: 0.616 ± 0.579 Feed, Last, H: 0.919 ± 0.525	4, 452	7.26	0.123
Prediction 3B: preferential associations among carers					
Frequency that males synchronized with each other carer, per watch, during cooperative synchronized bouts	Association	MH: −0.936 ± 0.272	1, 45	11.82	**<0.001**
Frequency that helpers synchronized with each other carer, per watch, during cooperative synchronized bouts	Association	MH: −0.163 ± 0.319	1, 33	0.26	0.609
Frequency that females synchronized with each other carer, per watch, during cooperative synchronized bouts	Association	FM: 0.814 ± 0.290	1, 43	7.87	**0.005**

Significant values ($P < 0.05$) are in bold.

Hypothesis 1: Loitering Facilitates Alternation

Johnstone et al.'s (2014) hypothesis that alternation (turn taking) of provisioning visits could be a means by which carers resolve conflict over care via conditional cooperation remains contentious because even the most conservative null model may not accurately replicate passive provisioning processes (Santema et al., 2019). Instead, it has been suggested that alternation may be caused by covarying environmental factors (Ihle, et al., 2019a; Santema et al., 2019; Schlicht et al., 2016). Johnstone et al. (2014) proposed that alternation could be facilitated by individuals dynamically adjusting their provisioning rate depending on whether they were or were not last to provision the brood, decreasing their rate following their own feed and increasing after the feed of another. While this mechanism was supported by studies of both biparental (Johnstone et al., 2014) and cooperative (Savage et al., 2017) species, there remain questions over the precise mechanism by which carers monitor the actions of others and adjust their behaviour. Therefore, our findings that carers that had been last to provision when they next arrived near the nest loitered for longer and allowed another carer to feed the chicks before they fed the brood themselves provide, for the first time, clear evidence that carers exhibit condition-dependent (last to feed versus not last to feed) behaviour that facilitates alternation of care. Building on the idea of Johnstone et al. (2014) we therefore provide a plausible mechanism through which carers dynamically adjust their behaviour in real time so that any change in effort by one carer is reciprocated by their partner(s), resulting in conditional cooperation and hence alternation.

Hypothesis 2: Collective Arrivals Facilitate Synchrony

Synchrony of provisioning visits is another characteristic of carer coordination, with several hypothesized functions. Some explanations such as reduced predator exposure (Khwaja et al., 2019; Leniowski & Węgrzyn, 2018; Mariette & Griffith, 2012; Raihani et al., 2010), prevention of food monopolization by some chicks in a brood (Mariette & Griffith, 2012, 2015; Shen et al., 2010) and signalling effort or quality to other carers (Doutrelant & Covas, 2007; Trapote et al., 2021; Zahavi, 1977a,b) do not require active alternation per se. However, synchrony has also been hypothesized to enable alternation by increasing the overlap of time spent near the nest by different carers, thereby allowing for accurate and reliable adjustment of behaviour facilitating alternation (Baldan, 2019; Baldan & Van Loon, 2022; Bebbington & Hatchwell, 2016; Mariette & Griffith, 2015). Mariette and Griffith (2015) found that zebra finches, *Taeniopygia guttata*, synchronized attendance at feeding stations as well as at the nest, and they proposed that synchronous nest visits result from collective foraging behaviour that was an adaptation to reduce predation risk for carers. Similarly, studies using lightweight radiotransmitters to track the time and location of foraging great tits found that parents coordinated their foraging behaviour in time and space (Baldan, 2019; Baldan & Van Loon, 2022). Furthermore, several other species found to synchronize nest visits also forage collectively (e.g. Doutrelant & Covas, 2007; Shen et al., 2010); thus, synchronous nest visits may simply be a by-product of collective foraging in some species. Indeed, previous studies of coordinated care in long-tailed tits also suggested that synchronous feeding visits may be a consequence of collective foraging behaviour (Bebbington & Hatchwell, 2016; Halliwell et al., 2022). This study supports that hypothesis, with carers synchronizing both arrivals and feeds. Utilizing the increased resolution for timing of visits in the present study, we found that the levels of active synchrony for both arrivals and feeds were greater for the 30 s than the 2 min synchrony window, suggesting that visits were even more tightly synchronized than previously thought. Additionally, carers were more likely to arrive and to feed during the loitering period of another carer than expected by chance, indicating overlap of time near the nest. Thus, it is important to consider the factors that may select for collective foraging independently of coordinated care.

Collective foraging occurs across many taxa (e.g. Ioannou & Dall, 2016; Lemanski et al., 2019; Palacios-Romo et al., 2019), including birds (Beauchamp, 1998). Theoretical and empirical studies show that group size is often associated with increased foraging

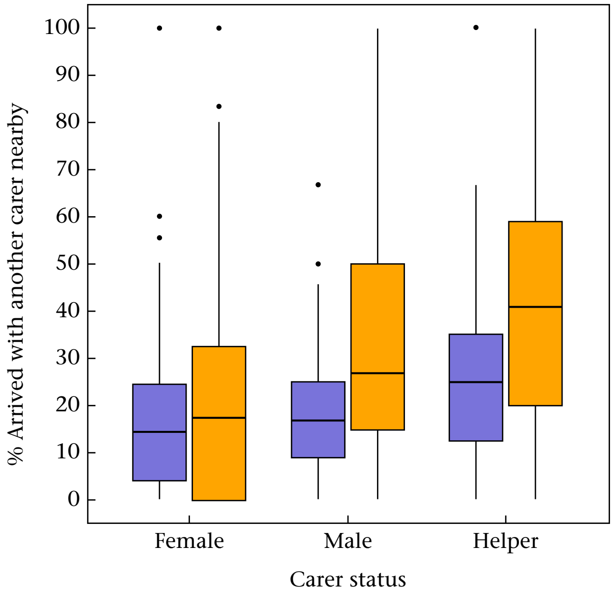

Figure 5. Plot of observed (orange) and expected (blue) percentage of visits, per individual, per watch, where the focal carer arrived with another carer nearby for each carer status. Bold lines in boxes represent the median values. Lower and upper boundaries of boxes represent lower and upper quartile values, respectively. Upper and lower boundaries of tails represent the maximum observed value within the upper fence (third quartile + 1.5 × interquartile range) and minimum observed value within the lower fence (first quartile − 1.5 × interquartile range), respectively. Points represent outliers (values outside lower–upper fence range). Total $N = 289$ individual samples from 101 watches of 65 individuals at 23 nests.

efficiency (Beauchamp, 1998; Caraco, 1981; Lihoreau et al., 2017) or reduced predation risk (Hamilton, 1971; Sorato et al., 2012). Long-tailed tits spend most of the year in large flocks that forage and roost together, splitting up into pairs only during their short breeding season (Ellison et al., 2020; Hatchwell et al., 2001; McGowan et al., 2006, 2007; Napper & Hatchwell, 2016). Furthermore, when breeding, members of a pair typically forage together except during incubation when males forage alone while females incubate, although even at this stage pairs typically reunite when females leave the nest to forage (Hatchwell et al., 1999). The survival rate of long-tailed tits in relation to flock size and composition is unknown, but these observations suggest that there is a strong selection for foraging in groups throughout the year. Therefore, synchronous provisioning may simply be a consequence of collective foraging, but that does not rule out other potential adaptive functions, including to facilitate alternation. Indeed, our findings on loitering behaviour and alternation indicate that carers could make use of their overlapping loitering periods to negotiate conditional cooperation.

Hypothesis 3: Status-dependent Order of Visits

We also hypothesized that coordination may be influenced by leader–follower dynamics within groups of foragers. Halliwell et al. (2022) showed that helpers had the highest levels of active synchrony, followed by breeding males and then breeding females. This could be interpreted as helpers signalling their effort as part of a ‘pay-to-stay’ system, as suggested in carrion crows, *Corvus corone* (Trapote et al., 2021), but no direct benefits of helping have been identified in long-tailed tits (Meade & Hatchwell, 2010), so there is no obvious advantage to a helper of signalling its effort to conspecifics. Instead, Halliwell et al. (2022) suggested that this variation in active synchrony among carers of different status could be a consequence of a consistent visit order. Evidence from mammals suggests that foraging trips may be led by particular individuals (Anand & Radhakrishna, 2022) that are often females (e.g. Barelli et al., 2008; Fischhoff et al., 2007; Pyritz et al., 2011; Trillmich et al., 2004; Van Belle et al., 2013), but among birds evidence for female-led collective foraging is limited (Baldan, 2019). If females are more likely to lead than males and helpers to follow (i.e. F–M–H), then our measure of synchrony (defined by the time interval since the last feed by another carer), would result in the highest active synchrony by helpers and the least by females, with males intermediate, as reported by Halliwell et al. (2022).

We tested this hypothesis by investigating arrival and feed orders at biparental nests and cooperative nests with one helper. We found evidence of status-dependent arrival orders, because females were overrepresented in the first arrival position at both biparental and cooperative nests, and helpers were overrepresented in the last arrival position at cooperative nests. Helpers were also most likely to arrive at the nest with another carer already present, with females being the least likely. However, this arrival order (F–M–H) did not translate into the same conserved feed orders, with no carer status significantly overrepresented in any position within feed sequences. We suggest two potential explanations for this contrast with the results of Halliwell et al. (2022). First, and most likely, is the small sample size ($N = 73$ watches) for feed sequence analysis used here, compared to 795 watches in Halliwell et al. (2022). Second, systematic feed orders may be more pronounced at nests with more helpers. The present analysis included nests with just one helper, and it is possible that a status-dependent feed order effect is driven by larger groups of carers.

As a further test of the hypothesis that carers have status-dependent visit orders we investigated synchrony between dyads of carers at cooperative nests. If females tend to lead, then both males and helpers should synchronize with females most. Interestingly, while this was the case for males, helpers showed no apparent preference for either breeder, even when accounting for differences in provisioning rate. We interpret this as evidence that when two birds synchronize visits at cooperative nests it is usually the breeding pair, while helpers more often synchronize as part of a group of three or more. This is compatible with our hypothesis that synchrony is driven by collective foraging, but with the added detail that males typically follow females and that helpers follow the breeding pair, rather than any specific carer.

Why should the observed leader–follower dynamics (F–M–H) occur within caring groups of long-tailed tits? It is unlikely to be dominance related because within nonbreeding flocks of long-tailed tits, males are dominant over females in contests over food and roost positions (Napper et al., 2013), and it is not clear why social status should be reversed during breeding. It is also unlikely to be related to either age or breeding experience because in the redirected helping system of long-tailed tits, there is no effect of age on the probability of helping or breeding (Roper et al., 2022). Instead, we suggest that familiarity with the immediate surroundings of the nest and transit to and from the nest may play a role. Females are likely to be more familiar with these than males because while nest building and provisioning duties are shared, only females incubate, with frequent breaks to forage. Helpers, on the other hand, are likely to be least familiar with the nest surroundings because they join a nest as helpers only during the nestling period (Hatchwell et al., 2004). While this explanation is speculative, it is important to stress that measures of coordination may be influenced by such behaviours, and so they should be considered where possible.

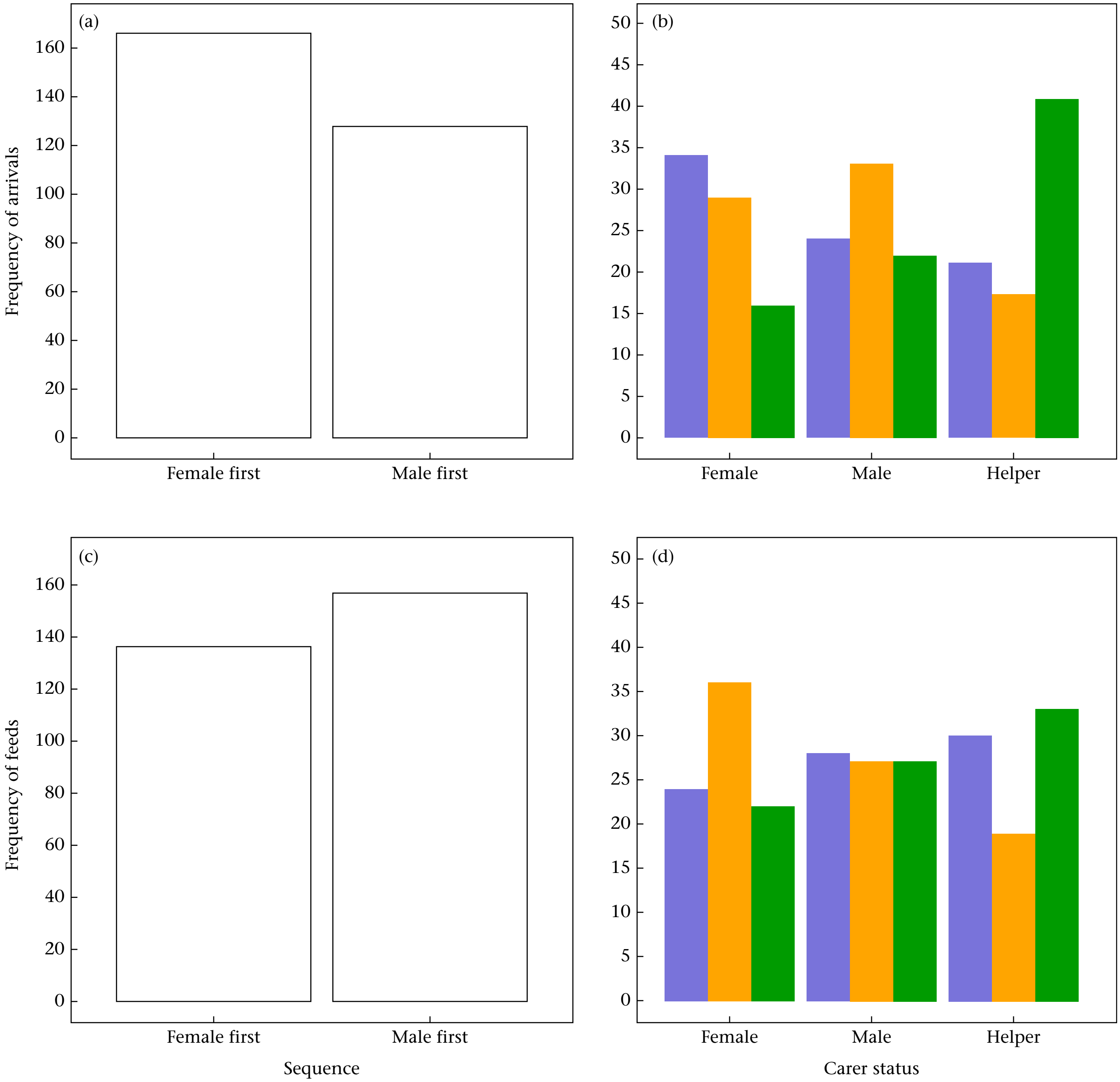

Figure 6. Plots of the frequency of (a) female and male first arrival orders at biparental nests, (b) each carer's arrival position (first: blue; middle: orange; last: green) at cooperative (three carers) nests, (c) female and male first feed orders at biparental nests and (d) each carer's feed position at cooperative (three carers) nests. Total $N = 294$ synchronized bouts from 46 watches of 13 nests for (a) and (c), $N = 82$ synchronized bouts from 27 watches of 10 nests for (b) and (d).

Synthesis

Coordination of care is typically investigated by analysing both alternation and synchrony. These behaviours do not necessarily serve the same function (Halliwell et al., 2022; Lejeune et al., 2019), but they are intrinsically linked because synchronized visits are also, by definition, alternated. In this study, we have investigated the proximate behaviours that facilitate alternation and synchrony, so it is important to reconcile our findings with each other and with previous studies on the same species (Bebbington & Hatchwell, 2016; Halliwell et al., 2022) by proposing a mechanism for coordination that is consistent with all findings.

Synchronized nest visits may inevitably lead to alternated visits because all feeds within a synchronized bout by several carers, except the first, are necessarily alternated. This effect will be stronger if carers feed in a conserved order because all visits are alternated if the order is perfectly conserved across all bouts of feeding. However, this idea that alternation arises from the purely passive process of conserved feed orders in synchronized bouts of nest visits is not consistent with the loitering behaviours that we observed. Rather, loitering behaviour that is conditional on whether a carer was the last bird to feed or not indicates that alternation is an active process which, when coupled with collective arrivals, may result in synchronous feeds with a conserved feed order. On the other hand, this mechanism alone does not necessarily predict that carers would also arrive at the nest synchronously and with a conserved order.

Instead, we suggest a coordination system in which carers tend to forage collectively, often being led by the female when returning to the nest, with inconsistencies that could potentially lead to a carer exceeding its optimum investment being amended by delaying feeding if the carer were last to feed. Of course, information on the frequency and timing of other carers' visits is unlikely to be perfect, introducing noise into the pattern of alternation and the conserved sequence of feeds (Johnstone & Savage, 2019). This suggested behavioural mechanism of coordination is consistent with Halliwell et al.'s (2022) finding that active alternation declined with group size, because in larger groups the ability of carers, and perhaps their incentive, to maintain strict alternation decreases. Thus, alternation in larger groups may be driven more by collective arrivals rather than context-dependent loitering, offering a plausible explanation for why helpers exhibit greater active synchrony than breeders (Halliwell et al., 2022). This mechanism is also consistent with results from an experimental study of long-tailed tits, which demonstrated that parents match increased provisioning effort by their partner when they were induced to feed more frequently using playback of begging calls (Meade et al., 2011).

Finally, we consider causes of variation in carer coordination between nests. In blue tits, *Cyanistes caeruleus*, synchrony but not alternation varied between different habitats (Lejeune et al., 2019). Additionally, in long-tailed tits active alternation was repeatable within nests while active synchrony was repeatable within individuals (Halliwell et al., 2022). These findings seemingly suggest that alternation and synchrony have independent functions. How then do we reconcile this with our proposed mechanism of coordination caused by collective arrivals and context-dependent loitering? One explanation is that nests vary consistently in the ability of carers to monitor the care of others and hence adjust their loitering behaviour, causing repeatable alternation at a given nest. Alternatively, individuals within groups of carers may be consistent in their leading or following behaviour, resulting in more, or less, alternation at different nests. Repeatable synchrony within individuals could result from carers varying consistently in the extent to which they show risk-averse or risk-prone behaviour that influences their tendency to forage collectively or solitarily. Aplin et al. (2014) found that individual variation in personality in great tits influenced an individual's foraging behaviour, with more reactive individuals feeding collectively while more proactive individuals tended to feed on the periphery of the flock. This is compatible with Halliwell et al. (2022)'s finding that active synchrony was repeatable between multiple watches of the same individual. To investigate this idea, it would be interesting to manipulate carers' perceived risk of predation to test whether collective foraging or other measures of coordination are affected.

Conclusion

To our knowledge this is the first study to investigate the proximate behavioural mechanism facilitating alternation using analysis of loitering periods prior to feeding. We found support for the hypotheses that carers loiter to ensure alternation and that synchrony is facilitated by collective foraging behaviour, showing for the first time that carers actively perform behaviours leading to alternation of visits. We also found limited support for the hypothesis that carer status determines the order of visits, with our analysis showing status-dependent arrival orders, although evidence for status-dependent feed orders remains equivocal (Halliwell et al., 2022). We therefore proposed a model for coordination of care, in which alternation is facilitated by both context-dependent delayed feeding and collective arrivals, with the latter partially enabling the former. While we have also shown that synchrony is facilitated by collective arrivals near the nest, thus enabling alternation, we have not directly addressed the question of what the likely benefits of collective foraging are. Nevertheless, it facilitates monitoring of other carers' efforts and hence could be a product of selection for conditional caring (Johnstone et al., 2014). A detailed examination of the fitness consequences of variation in coordination among individuals and among nests is needed to provide further insights into such questions. Given the large interspecific variation in how carers change provisioning rate in response to manipulations of their partner(s) (Harrison et al., 2009), it is also very likely that coordination of care will vary substantially across species in mechanism and function depending on their ecology and life history.

Author Contributions

Chay Halliwell: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Visualization, Writing – Original draft, Writing – Review & editing. **Andrew P. Beckerman**: Conceptualization, Investigation, Supervision, Visualization, Writing – Review & editing. **Sarah J. Biddiscombe**: Data curation, Investigation, Project administration. **Marion Germain**: Data curation, Investigation, Writing – Review & editing. **Ben J. Hatchwell**: Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Visualization, Writing – Review & editing.

Data Availability

Data are available at https://doi.org/10.5061/dryad.37pvmcvpq. See Halliwell et al. (2023).

Declaration of Interest

None.

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Appendix. Covariate Justifications

Provisioning rate was included because as the number of feeds increases, intrinsically so does the number of coordinated feeds. Therefore, we must control for total provisioning rate (either individual or collective) and all variables that may influence provisioning rate (e.g. brood size, hatch date) to attain a measure of coordination independent of provisioning rate.

Carer number was included because as the number of carers increases so does the provisioning rate and the level of alternation. If there are more carers with which to coordinate, the level of both observed and expected coordination should increase with carer number, although not necessarily by the same amount (Halliwell et al., 2022).

Watch duration was included because the longer a watch is the more feeds will be possible within that time. As we wanted to calculate measures of coordination independent of provisioning rate or watch duration, we included this term.

Brood size was included because we expected, based on previous studies, that the provisioning rate would increase with the number of live chicks. Therefore, we controlled for brood size to isolate the level of coordination, independent of factors that may modulate provisioning rate.

Watch start time was included because previous research suggests that provisioning rate may change during the day, being greatest in the period immediately after sunrise (Hatchwell et al., 2004; MacColl & Hatchwell, 2002).

Brood age was included because a brood's energetic demand may vary throughout their development; thus, brood age may influence provisioning rate.

Hatch date was included because the time in a season when a brood is being provisioned may influence provisioning rate by mediating the availability of invertebrate prey.

AMax (or SMax) was included to account for disparities in provisioning rates between carers which could render coordinating a certain number of feeds impossible. For example, if one carer delivers more than half the total number of feeds then for a certain number of their feeds alternation and synchrony are impossible because there are not enough other feeds to coordinate with. This term is therefore used as a proxy for provisioning rate asymmetry often used in studies of biparental provisioning systems (Bebbington & Hatchwell, 2016), but applicable to a cooperative breeding system. We note that AMax and SMax are always the same value.

Table A1
Full details of all models used, including response variables, terms of interest, covariates, random effects, error distribution and sample sizes

Response variables	Terms of interest	Covariates	Random effects	Error distribution	No. of watches
Collective loitering period models					
Number of synchronized arrivals and feeds	Data type*Synchrony window*Feed or arrival	Data type* (Total feed rate + Carer number + Watch duration + Brood size + Watch start time) + Brood age + Hatch date + AMax	(1|Year) + (1|NestID) + (1|WatchID) + (1|Rowref)	Poisson	101
Number of alternated feeds	Data type				101
Number of visits where a carer waited to ensure alternation					101
Number of feeds where another carer was present upon a carer's arrival					101
Number of feeds where a carer fed while another bird was nearby					101
Log(mean loitering time)	Data type*Last to feed		(1|Year) + (1|NestID) + (1|WatchID)	Normal	101
Number of visits where another carer fed during a carer's loiter			(1|Year) + (1|Nest) + (1|WatchID) + (1|Rowref)	Poisson	101
Individual loitering period models					
Number of feeds where another carer was present upon a carer's arrival	Data type*Carer status	Data type* (Indiv feed rate + Carer number + Watch duration + Brood size + Watch start time) + Brood age + Hatch date + AMax	(1|Year) + (1|NestID) + (1|WatchID) + (1|CarerID) + (1|Rowref)	Poisson	101
Synchronized runs sequence analysis					
Frequency of each sequence (F–M & M–F) from biparental nest watches	Order*Feed or arrival	Total feed rate + Watch duration + Brood size + Watch start time + Brood age + Hatch date + AMax	(1|WatchID) + (1|NestID) + (1|Rowref)	Poisson	46
Frequency of each position (first, middle & last) occupied by each carer status for both feeds and arrival	Position*Feed or arrival*Carer status		(1|WatchID) + (1|NestID) + (1|CarerID) + (1|Rowref)		27
Synchrony association analysis					
Frequency of female synchronizing with another carer (male or helper)	Association	Indiv feed rate + Watch duration + Brood size + Watch start time + Brood age + Hatch date + AMax	(MH_ratio |WatchID) + (MH_ratio |NestID) + (1|CarerID) + (1|Rowref)	Poisson	26
Frequency of male synchronising with another carer (female or helper)			(FH_ratio|WatchID) + (FH_ratio|NestID) + (1|CarerID) + (1|Rowref)		27
Frequency of helper synchronising with another carer (female or male)			(FM_ratio|WatchID) + (FM_ratio|NestID) + (1|CarerID) + (1|Rowref)		21

Table A2
Outputs of the model investigating levels of alternation per watch

Parameter	*df*	Estimate ± SE	χ^2	*P*
Intercept	**1, 184**	**2.51 ± 0.044**		**<0.001**
Data type (relative to expected)	**1**	**Observed: 0.062 ± 0.061**	**4.19**	**0.041**
Provisioning rate (collective)	**1**	**0.376 ± 0.029**	**326.74**	**<0.001**
Carer number (relative to 2 carers)	**4**	**3: 0.089 ± 0.066** **4: 0.282 ± 0.090** **5: 0.230 ± 0.105** **6: 0.347 ± 0.130**	**25.38**	**<0.001**
Watch duration	**1**	**0.066 ± 0.030**	**10.47**	**0.001**
Brood size	1	−0.006 ± 0.041	0.28	0.600
Watch start time	**1**	**−0.087 ± 0.028**	**14.13**	**<0.001**
Brood age	1	0.003 ± 0.020	0.02	0.893
Hatch date	1	−0.053 ± 0.030	3.13	0.077
AMax	**1**	**0.204 ± 0.034**	**35.07**	**<0.001**
Data type*Provisioning rate (collective)	1	0.019 ± 0.034	0.25	0.618
Data type*Carer number	4	Obs, 3: 0.043 ± 0.084 Obs, 4: −0.035 ± 0.120 Obs, 5: −0.064 ± 0.142 Obs, 6: −0.016 ± 0.172	0.80	0.939
Data type*Watch duration	1	0.005 ± 0.049	0.01	0.907
Data type*Brood size	1	−0.021 ± 0.049	0.19	0.661
Data type*Watch start time	1	0.029 ± 0.038	0.58	0.445

Estimates and *P* values for fixed effects on the number of alternated visits per provisioning watch from a GLMM; *N* = 202 from 101 watches at 23 nests. Significant values are in bold.

Table A3
Outputs of the model investigating mean loitering times per watch

Parameter	*df*	Estimate ± SE	χ^2	*P*
Intercept	**1, 377**	**3.87 ± 0.182**		**<0.001**
Data type (relative to ‘expected’)	**1**	**Observed: −0.206 ± 0.054**	**6.71**	**0.010**
Last to feed (relative to ‘no’)	1	Yes: −0.075 ± 0.043	0.01	0.941
Provisioning rate (collective)	**1**	**−0.415 ± 0.076**	**30.54**	**<0.001**
Carer number (relative to 2 carers)	4	3: 0.221 ± 0.167 4: 0.022 ± 0.233 5: 0.215 ± 0.280 6: 0.356 ± 0.355	4.30	0.367
Watch duration	1	0.050 ± 0.058	0.29	0.590
Brood size	1	0.024 ± 0.118	0.13	0.723
Watch start time	1	0.012 ± 0.057	0.22	0.642
Brood age	1	0.043 ± 0.059	0.55	0.458
Hatch date	1	0.103 ± 0.107	0.92	0.337
AMax	1	0.004 ± 0.074	<0.01	0.959
Data type∗Last to feed	**1**	**Observed, yes: 0.156 ± 0.061**	**6.55**	**0.010**
Data type∗Provisioning rate (collective)	1	0.012 ± 0.037	0.11	0.742
Data type∗Carer number	4	Obs, 3: 0.023 ± 0.072 Obs, 4: 0.120 ± 0.112 Obs, 5: 0.303 ± 0.133 Obs, 6: 0.332 ± 0.184	8.08	0.089
Data type∗Watch duration	1	−0.041 ± 0.032	1.68	0.195
Data type∗Brood size	1	0.034 ± 0.039	0.74	0.389
Data type∗Watch start time	1	0.028 ± 0.032	0.78	0.376

Estimates and *P* values for fixed effects on the mean loitering time per provisioning watch, subdivided by whether the focal carer was last to feed, from an LMM; $N = 400$ from 101 watches at 23 nests. Significant values are in bold.

Table A4
Outputs of the model investigating number of feeds where a carer loitered to ensure alternation per watch

Parameter	*df*	Estimate ± SE	χ^2	*P*
Intercept	**1, 181**	**−0.198 ± 0.176**		**<0.001**
Data type (relative to ‘expected’)	**1**	**Observed: 0.873 ± 0.203**	**34.65**	**<0.001**
Provisioning rate (collective)	**1**	**0.288 ± 0.129**	**16.12**	**<0.001**
Carer number (relative to 2 carers)	4	3: −0.191 ± 0.260 4: 0.507 ± 0.458 5: 0.700 ± 0.582 6: −1.95 ± >10.00	11.48	0.119
Watch duration	1	0.141 ± 0.124	0.30	0.586
Brood size	**1**	**−0.127 ± 0.162**	**5.08**	**0.024**
Watch start time	1	−0.121 ± 0.115	0.25	0.618
Brood age	1	0.486 ± 0.075	<0.01	0.949
Hatch date	**1**	**−0.290 ± 0.114**	**6.51**	**0.012**
AMax	**1**	**0.437 ± 0.125**	**12.27**	**<0.001**
Data type∗Provisioning rate (collective)	1	0.059 ± 0.143	0.17	0.678
Data type∗Carer number	4	Obs, 3: −0.227 ± 0.292 Obs, 4: 0.095 ± 0.519 Obs, 5: −0.174 ± 0.671 Obs, 6: 1.85 ± >10.00	0.77	0.943
Data type∗Watch duration	1	−0.148 ± 0.146	1.03	0.311
Data type∗Brood size	1	−0.174 ± 0.175	0.99	0.320
Data type∗Watch start time	1	0.061 ± 0.135	0.25	0.624

Estimates and *P* values for fixed effects on the number of visits where carers loitered to ensure alternation per provisioning watch from a GLMM; $N = 202$ from 101 watches at 23 nests. Significant values are in bold.

Table A5
Outputs of the model investigating number of feeds where another carer fed during the focal carer's loitering period per watch

Parameter	*df*	Estimate ± SE	χ^2	*P*
Intercept	**1, 377**	**0.286 ± 0.132**		**<0.001**
Data type (relative to 'expected')	**1**	**Observed: 0.632 ± 0.143**	**57.34**	**<0.001**
Last to feed (relative to 'no')	**1**	**Yes: −1.04 ± 0.126**	**99.55**	**<0.001**
Provisioning rate (collective)	**1**	**0.357 ± 0.075**	**32.81**	**<0.001**
Carer number (relative to 2 carers)	4	3: 0.357 ± 0.075 4: 0.648 ± 0.231 5: 0.803 ± 0.264 6: 1.22 ± 0.313	21.78	<0.001
Watch duration	1	0.105 ± 0.074	3.17	0.075
Brood size	1	−0.055 ± 0.113	0.05	0.822
Watch start time	1	−0.093 ± 0.068	0.41	0.522
Brood age	1	0.006 ± 0.048	0.01	0.903
Hatch date	1	−0.131 ± 0.080	2.67	0.102
AMax	**1**	**0.257 ± 0.081**	**10.08**	**0.001**
Data type*Last to feed	**1**	**Observed, yes: 0.458 ± 0.155**	**8.70**	**0.003**
Data type*Provisioning rate (collective)	1	−0.062 ± 0.079	0.62	0.433
Data type*Carer number	4	Obs, 3: −0.256 ± 0.174 Obs, 4: −0.359 ± 0.241 Obs, 5: −0.457 ± 0.285 Obs, 6: −0.106 ± 0.307	4.43	0.351
Data type*Watch duration	1	−0.027 ± 0.083	0.11	0.742
Data type*Brood size	1	0.053 ± 0.100	0.28	0.594
Data type*Watch start time	1	0.098 ± 0.077	1.63	0.202

Estimates and *P* values for fixed effects on the number of visits where another carer fed during the focal carer's loitering period per provisioning watch, subdivided by whether the focal carer was last to feed, from a GLMM; $N = 400$ from 101 watches at 23 nests. Significant values are in bold.

Table A6
Outputs of the model investigating levels of synchrony per watch

Parameter	*df*	Estimate ± SE	χ^2	*P*
Intercept	**1, 781**	**0.614 ± 0.086**		**<0.001**
Data type (relative to 'expected')	**1**	**Observed: 0.848 ± 0.083**	**195.99**	**<0.001**
Feed or arrival (relative to arrival)	**1**	**Feed: 0.043 ± 0.082**	**5.48**	**0.019**
Synchrony window (relative to 30 s)	**1**	**2 min: 1.07 ± 0.068**	**729.03**	**<0.001**
Provisioning rate (collective)	**1**	**0.592 ± 0.040**	**220.18**	**<0.001**
Carer number (relative to 2 carers)	**4**	**3: 0.074 ± 0.083** **4: 0.242 ± 0.115** **5: 0.499 ± 0.143** **6: 0.473 ± 0.175**	**10.61**	**0.031**
Watch duration	**1**	**0.077 ± 0.035**	**7.58**	**0.006**
Brood size	1	0.006 ± 0.060	0.02	0.882
Watch start time	**1**	**−0.092 ± 0.031**	**6.29**	**0.012**
Brood age	**1**	**0.069 ± 0.029**	**5.45**	**0.020**
Hatch date	**1**	**−0.099 ± 0.050**	**4.01**	**0.045**
AMax	**1**	**0.261 ± 0.048**	**29.96**	**<0.001**
Feed or arrival*Synchrony window	1	Feed, 2 min: 0.034 ± 0.094	0.11	0.470
Data type*Feed or arrival	1	Obs, feed: 0.065 ± 0.099	0.11	0.740
Data type*Synchrony window	**1**	**Obs, 2 min: −0.451 ± 0.085**	**75.38**	**<0.001**
Data type*Provisioning rate (collective)	**1**	**−0.096 ± 0.029**	**10.77**	**0.001**
Data type*Carer number	4	Obs, 3: −0.058 ± 0.064 Obs, 4: −0.104 ± 0.092 Obs, 5: −0.251 ± 0.109 Obs, 6: −0.210 ± 0.134	6.50	0.165
Data type*Watch duration	1	<0.000 ± 0.034	<0.01	0.997
Data type*Brood size	1	−0.022 ± 0.038	0.34	0.559
Data type*Watch start time	1	0.046 ± 0.029	2.55	0.110
Data type*Feed or arrival*Synchrony window	1	Obs, Feed, 2 min: −0.117 ± 0.118	0.98	0.321

Estimates and *P* values for fixed effects on the number of synchronized arrivals and visits at both 2 min and 30 s synchrony windows, per provisioning watch from a GLMM; $N = 808$ from 101 watches at 23 nests. Significant values are in bold.

Table A7

Outputs of the model investigating the number of feeds where the focal carer arrived while another carer was nearby per watch

Parameter	*df*	Estimate ± SE	χ^2	*P*
Intercept	**1, 181**	**0.950 ± 0.113**		**<0.001**
Data type (relative to 'expected')	**1**	**Observed: 0.588 ± 0.116**	**39.73**	**<0.001**
Provisioning rate (individual)	**1**	**0.307 ± 0.071**	**30.35**	**<0.001**
Carer number (relative to 2 carers)	**4**	**3: 0.445 ± 0.160**	**13.89**	**0.008**
		4: 0.560 ± 0.213		
		5: 0.749 ± 0.242		
		6: 1.05 ± 0.296		
Watch duration	1	0.076 ± 0.065	2.43	0.119
Brood size	1	−0.078 ± 0.105	0.24	0.622
Watch start time	1	−0.026 ± 0.061	0.11	0.739
Brood age	1	0.017 ± 0.046	0.13	0.739
Hatch date	1	−0.056 ± 0.080	0.49	0.484
AMax	**1**	**0.246 ± 0.075**	**10.75**	**0.001**
Data type∗Provisioning rate (individual)	1	−0.005 ± 0.072	0.01	0.940
Data type∗Carer number	4	Obs, 3: −0.234 ± 0.155	4.51	0.341
		Obs, 4: −0.282 ± 0.210		
		Obs, 5: −0.378 ± 0.246		
		Obs, 6: −0.409 ± 0.277		
Data type∗Watch duration	1	−0.005 ± 0.073	<0.01	0.947
Data type∗Brood size	1	0.054 ± 0.087	0.38	0.536
Data type∗Watch start time	1	0.018 ± 0.067	0.07	0.794

Estimates and *P* values for fixed effects on the number of visits where the focal carer arrived with another carer loitering per provisioning watch from a GLMM; $N = 202$ from 101 watches at 23 nests. Significant values are in bold.

Table A8

Outputs of the model investigating the number of feeds by the focal carer where another carer was present per watch

Parameter	*df*	Estimate ± SE	χ^2	*P*
Intercept	**1, 181**	**0.951 ± 0.114**		**<0.001**
Data type (relative to 'expected')	**1**	**Observed: 0.588 ± 0.116**	**39.93**	**<0.001**
Provisioning rate (collective)	**1**	**0.294 ± 0.072**	**26.90**	**<0.001**
Carer number (relative to 2 carers)	**4**	**3: 0.438 ± 0.161**	**11.39**	**0.023**
		4: 0.507 ± 0.208		
		5: 0.683 ± 0.247		
		6: 0.999 ± 0.302		
Watch duration	1	0.078 ± 0.066	2.36	0.124
Brood size	1	−0.080 ± 0.106	0.31	0.577
Watch start time	1	−0.029 ± 0.061	0.13	0.719
Brood age	1	0.025 ± 0.047	1.29	0.599
Hatch date	1	−0.065 ± 0.081	0.65	0.422
AMax	**1**	**0.248 ± 0.076**	**10.72**	**0.001**
Data type∗Provisioning rate (collective)	1	−0.001 ± 0.072	<0.01	0.906
Data type∗Carer number	4	Obs, 3: −0.231 ± 0.155	4.63	0.328
		Obs, 4: −0.243 ± 0.213		
		Obs, 5: −0.428 ± 0.251		
		Obs, 6: −0.405 ± 0.281		
Data type∗Watch duration	1	−0.009 ± 0.073	0.02	0.906
Data type∗Brood size	1	0.047 ± 0.087	0.29	0.588
Data type∗Watch start time	1	0.021 ± 0.067	0.10	0.750

Estimates and *P* values for fixed effects on the number of visits where another carer was loitering as the focal carer provisioned the chicks per provisioning watch from a GLMM; $N = 202$ from 101 watches at 23 nests. Significant values are in bold.

Table A9
Outputs of the model investigating the number of feeds where the focal carer arrived while another carer was nearby per individual per watch

Parameter	*df*	Estimate ± SE	χ^2	*P*
Intercept	**1, 553**	**−0.234 ± 0.157**		**<0.001**
Data type (relative to ‘expected’)	**1**	**Observed: 0.482 ± 0.164**	**50.04**	**<0.001**
Carer status (relative to female)	**2**	**H: 0.052 ± 0.139** **M: 0.116 ± 0.120**	**19.67**	**<0.001**
Provisioning rate (collective)	**1**	**0.488 ± 0.066**	**90.22**	**<0.001**
Carer number (relative to 2 carers)	4	3: 0.391 ± 0.189 4: 0.354 ± 0.257 5: 0.579 ± 0.287 6: 0.741 ± 0.362	2.59	0.628
Watch duration	1	0.097 ± 0.070	2.58	0.108
Brood size	1	−0.089 ± 0.118	0.35	0.556
Watch start time	1	−0.045 ± 0.066	0.16	0.691
Brood age	1	−0.002 ± 0.051	<0.01	0.963
Hatch date	1	−0.026 ± 0.095	0.08	0.783
AMax	**1**	**0.240 ± 0.081**	**8.84**	**0.003**
Data type ∗ Carer status	**2**	**Obs, H: 0.396 ± 0.181** **Obs, M: 0.356 ± 0.154**	**6.85**	**0.033**
Data type ∗ Provisioning rate	1	−0.356 ± 0.070	0.17	0.681
Data type ∗ Carer number	4	Obs, 3: −0.319 ± 0.172 Obs, 4: −0.392 ± 0.237 Obs, 5: −0.604 ± 0.261 Obs, 6: −0.580 ± 0.310	7.01	0.135
Data type ∗ Watch duration	1	−0.021 ± 0.074	0.08	0.776
Data type ∗ Brood size	1	0.043 ± 0.086	0.24	0.621
Data type ∗ Watch start time	1	0.039 ± 0.069	0.33	0.567

Estimates and *P* values for fixed effects on the number of visits where the focal carer arrived with another carer loitering per individual per provisioning watch from a GLMM; $N = 578$ from 101 watches at 23 nests. Significant values are in bold.

Table A10
Outputs of the model investigating the number times each feed order occurred within a synchronized feed bout per watch (biparental only)

Parameter	*df*	Estimate ± SE	χ^2	*P*
Intercept	**1, 173**	**1.11 ± 0.086**		**<0.001**
Order (relative to F–M)	1	M–F: −0.258 ± 0.120	0.483	0.483
Feed or arrival (relative to arrival)	1	Feed: −0.192 ± 0.118	<0.01	0.998
Provisioning rate (collective)	**1**	**0.293 ± 0.061**	**23.45**	**<0.001**
Watch duration	1	0.014 ± 0.049	0.08	0.777
Brood size	1	−0.071 ± 0.078	0.83	0.363
Watch start time	**1**	**−0.168 ± 0.047**	**12.64**	**<0.001**
Brood age	1	0.027 ± 0.051	0.28	0.597
Hatch date	**1**	**−0.177 ± 0.082**	**4.61**	**0.032**
AMax	**1**	**0.317 ± 0.065**	**23.78**	**<0.001**
Order ∗ Feed or arrival	**1**	**M-F, feed: 0.396 ± 0.169**	**5.46**	**0.019**

Estimates and *P* values for fixed effects on the number of each order of synchronized bouts per provisioning watch at biparental nests from GLMM; $N = 184$ from 46 watches at 13 nests. F: female; M: male. Significant values are in bold.

Table A11

Outputs of the model investigating the number of times each carer occupied a given relative position within a synchronized feed bout per watch (three carers only)

Parameter	*df*	Estimate ± SE	χ^2	*P*
Intercept	**1, 452**	**0.102 ± 0.184**		**<0.001**
Position (relative to first)	2	Middle: −0.159 ± 0.251 Last: −0.754 ± 0.302	0.08	0.962
Feed or arrival (relative to arrival)	1	Feed: −0.372 ± 0.265	0.02	0.881
Carer status (relative female)	2	M: −0.348 ± 0.265 H: −0.482 ± 0.276	0.13	0.939
Provisioning rate (collective)	1	0.081 ± 0.137	0.35	0.555
Watch duration	1	−0.181 ± 0.119	2.30	0.129
Brood size	1	0.231 ± 0.125	3.41	0.065
Watch start time	1	−0.074 ± 0.090	0.69	0.408
Brood age	1	−0.022 ± 0.095	0.05	0.820
Hatch date	1	0.028 ± 0.115	0.06	0.806
AMax	**1**	**0.276 ± 0.111**	**6.19**	**0.013**
Position ∗ Feed or arrival	2	Middle, feed: 0.564 ± 0.362 Last, feed: 0.667 ± 0.421	<0.01	1.00
Position ∗ Carer status	**4**	**Middle, M: 0.565 ± 0.363** **Middle, H: −0.052 ± 0.411** **Last, M: 0.667 ± 0.421** **Last, H: 1.42 ± 0.403**	**21.74**	**<0.001**
Feed or arrival ∗ Carer status	2	Feed, M: 0.502 ± 0.383 Feed, H: 0.705 ± 0.388	<0.01	1.00
Position ∗ Feed arrival ∗ Carer status	4	Feed, Middle, M: −0.919 ± 0.525 Feed, Middle, H: −0.810 ± 0.568 Feed, Last, M: −0.616 ± 0.579 Feed, Last, H: −0.919 ± 0.525	7.26	0.123

Estimates and *P* values for fixed effects on the number of times each carer status occupied a certain position within arrival or feed sequences at synchronized bouts per provisioning watch at cooperative (three carers) nests from a GLMM; *N* = 477 from 27 watches at 10 nests. Significant values are in bold.

Table A12

Outputs of the model investigating the number of times each breeding male synchronized with another carer per watch (three carers only)

Parameter	*df*	Estimate ± SE	χ^2	*P*
Intercept	**1, 45**	**0.746 ± 0.179**		**<0.001**
Association (relative to MF)	**1**	**MH: −0.936 ± 0.272**	**11.82**	**<0.001**
Provisioning rate (individual)	1	0.281 ± 0.195	2.08	0.149
Watch duration	1	−0.070 ± 0.191	0.13	0.714
Brood size	1	−0.292 ± 0.182	2.59	0.108
Watch start time	1	0.025 ± 0.164	0.02	0.879
Brood age	1	0.012 ± 0.173	<0.01	0.945
Hatch date	1	−0.040 ± 0.194	0.04	0.838
AMax	1	−0.014 ± 0.171	0.01	0.933

Estimates and *P* values for fixed effects on the number of times each breeding male synchronized visits with females and helpers per provisioning watch at cooperative (three carers) nests from a GLMM; *N* = 54 from 27 watches of 10 males at 10 nests. M: male; F: female. Significant values are in bold.

Table A13

Outputs of the model investigating the number of times each helper synchronized with another carer per watch (three carers only)

Parameter	*df*	Estimate ± SE	χ^2	*P*
Intercept	1, 33	0.157 ± 0.249		0.539
Association (relative to FH)	1	MH: −0.163 ± 0.319	0.26	0.609
Provisioning rate (individual)	**1**	**0.553 ± 0.233**	**5.65**	**0.018**
Watch duration	1	0.216 ± 0.233	0.86	0.354
Brood size	1	−0.206 ± 0.281	0.54	0.464
Watch start time	1	−0.126 ± 0.185	0.46	0.497
Brood age	1	−0.157 ± 0.240	0.43	0.513
Hatch date	1	−0.189 ± 0.308	0.38	0.540
AMax	1	−0.191 ± 0.263	0.53	0.469

Estimates and *P* values for fixed effects on the number of times each helper synchronized visits with females and males per provisioning watch at cooperative (three carers) nests from a GLMM; *N* = 42 from 21 watches of 9 helpers at 9 nests. F: female; H: helper. Significant values are in bold.

Table A14

Outputs of the model investigating the number of times each breeding female synchronized with another carer per watch (three carers only)

Parameter	*df*	Estimate ± SE	χ^2	*P*
Intercept	**1, 43**	**−0.081 ± 0.252**		**<0.001**
Association (relative to FH)	**1**	**FM: 0.814 ± 0.290**	**7.87**	**0.005**
Provisioning rate (individual)	**1**	**0.438 ± 0.204**	**4.59**	**0.032**
Watch duration	1	0.093 ± 0.231	0.16	0.688
Brood size	1	−0.218 ± 0.239	0.84	0.360
Watch start time	1	−0.066 ± 0.163	0.16	0.685
Brood age	1	−0.017 ± 0.201	0.01	0.932
Hatch date	1	−0.089 ± 0.221	0.16	0.687
AMax	1	0.040 ± 0.174	0.05	0.819

Estimates and *P* values for fixed effects on the number of times each breeding female synchronized visits with males and helpers per provisioning watch at cooperative (three carers) nests from GLMM; *N* = 52 from 26 watches of 9 females at 9 nests. F: female; H: helper. Significant values are in bold.