**Cooperation, conflict, and the coordination of care in the long-tailed tit, *Aegithalos caudatus***

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Thesis submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy

Ecology and Evolutionary Biology

Department of Biosciences

University of Sheffield

**September 2023**

A drawing of birds and a nest

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**General summary**

Parental care is costly to carers, so when multiple carers raise the same offspring, each is selected to maximise their benefit-to-cost ratio at the expense of others, causing conflict between carers over relative investment. Coordinated provisioning is hypothesised to resolve this conflict and to mitigate the costs of care. In this thesis, I investigated whether, how, and why pairs and cooperative groups of long-tailed tits, *Aegithalos caudatus*, performed two forms of coordinated care, alternation (i.e. taking turns) and synchrony (i.e. feeding together). In chapter 2, I used a long-term database of provisioning watches to determine whether carers coordinate their provisioning. Carers alternated and synchronised more than expected by chance, and helpers were more synchronous than breeders, although their level of coordination was not influenced by relatedness to the parents. In chapter 3, I investigated the behavioural mechanisms underlying coordination, finding that alternation was facilitated by carers actively delaying feeding near the nest if it was not their turn to feed. Synchronised feeds were facilitated by synchronous arrivals near the nest, typically led by breeding females, indicating collective foraging. In chapters 4 and 5, I conducted an experiment and analysed long-term data to test several hypotheses for the adaptive function of coordination. A high level of alternation was associated with higher provisioning rates and greater breeding productivity, as predicted by the hypothesis that conditional cooperation mitigates conflict among carers. Synchrony of nest visits across the nestling period was associated with a reduced brood predation risk in the long-term dataset, although the experimental manipulation of perceived predation threat did not cause a temporary increase in synchrony. I conclude that coordinated care in long-tailed tits is adaptive; alternated provisioning functions to resolve conflict between carers, thereby preventing exploitation, and synchronous provisioning reduces the chance that a brood’s location is advertised to predators.

**Acknowledgements**

First and foremost, I would like to thank my supervisor Ben Hatchwell for providing me the opportunity to be part of his amazing long-tailed tit research group, and for his incredible support and guidance throughout my PhD. Ben has been an inspiration to me, and time after time I’ve found myself in awe of his ingenuity, passion, and commitment to high quality scientific research. Thank you also to my co-supervisors Andrew Beckerman and Samantha Patrick for all their support throughout, particularly for their invaluable guidance in statistics, coding, and data analysis which has been vital to the success of my thesis and to my development as a researcher.

I am grateful to everyone who has contributed to the long-tailed tit project before my PhD, thanks to them I had decades of rigorously collected data which were essential for many of my analyses. Thank you also to the current research group, particularly to Sarah Biddiscombe for her tireless organisation during field seasons, incredible nest finding ability, and great sense of humour. Sarah worked beaverishly in the lab and the field throughout my PhD and was vital to successful data collection in all of our mutual field seasons. Thank you also to Marion Germain, without whom my thesis, and overall PhD experience would not have been the same. Marion contributed to field work, analysis, and interpretation in several of my data chapters, and was also a source of great advice and support when I needed it most.

Thanks also to Caroline Milsom, Jamie Thompson, and everyone else who contributed to field work throughout my PhD, it was a pleasure to share my time with you and thank you for your hard work in the field. I am grateful to Francesca Dawson-Pell and Caitlin Higgot for their advice and support when I first started my PhD, and to Francesca for her amazing positive outlook and lively office chat. Thank you to Amy Leedale and Katy Maher for helping me learn to use CERVUS and Kingroup, and to David Douglas and Malcolm Burgess for their guidance and supervision during my placement project with the RSPB.

Thank you also to my project supporters Terry Burke and David Edwards, and to the reviewers and editors who handled my manuscripts; their feedback improved my manuscripts and helped to develop my scientific writing skills. Thank you also to the friendly and understanding residents and homeowners of the Rivelin valley, as well as Yorkshire Water and the Sheffield City Council for access to their land.

I am grateful to everyone in Sheffield, and elsewhere, who brought a sense of community to my PhD, including everyone from the departmental football league, LHB journal club, and fellow patrons of the University Arms. Finally, a huge thanks to my close friends and family for their unwavering support, without you I never would have made it this far. Thank you for living every twist and turn with me, and for giving me the strength to persevere throughout and achieve my goals. This PhD was funded by the Natural Environment Research Council (NE/S00713X/1).

**Statement of intellectual contributions**

Data chapters (2–5) are formatted and presented as manuscripts for publication, so benefited from collaboration and discussion with colleagues as well as comments from reviewers and journal editors. All data were collected as part of the ongoing long-tailed tit project established and managed by my primary supervisor Ben Hatchwell. Andrew Beckerman and Samantha Patrick co-supervised this project. Data were collected by both past and present members of the long-tailed tit project, including myself (2019–2022). Contributions to each data chapter are outlined below, all other work is my own. Study species illustration was by Sophia Anderson.

Chapter 2: Data for this chapter were collected by various researchers and field assistants from 1994–2019. Some of these data had been digitised by Kat Bebbington, but the majority I digitised myself. I expanded upon a social pedigree network first constructed by Amy Leedale to include additional years and filled gaps using genetic loci data extracted at the University of Sheffield NERC Biomolecular Analysis Facility with support from Terry Burke and Deborah Dawson. I designed the study with Ben Hatchwell and Andrew Beckerman. I performed all analyses myself with support from Ben Hatchwell, Andrew Beckerman, Samantha Patrick, and Marion Germain, all of whom also supplied comments on the manuscript. This study also benefited from discussions with James Savage.

Chapter 3: Data for this chapter were collected by myself, Ben Hatchwell, Sarah Biddiscombe, and Marion Germain from 2020–2021. Jamie Thompson, and Caroline Milsom contributed to field work but were not directly involved with data collection for this study. I designed this study with Ben Hatchwell, who along with Andrew Beckerman and Marion Germain also supplied comments on the manuscript.

Chapter 4: Data for this chapter were collected from experiments I conducted from 2021–2022. Ben Hatchwell and Sarah Biddiscombe collected nest data which was used in this study. Marion Germain, Caroline Milsom, and Jamie Thompson contributed to field work but were not directly involved with data collection for this study. I designed this study with Ben Hatchwell, who also supplied comments on the manuscript.

Chapter 5: Data for this chapter were collected by past and present members of the long-tailed tit research project (1994–2022). I designed the study with Ben Hatchwell. I performed all analyses myself, with help via discussion with Ben Hatchwell, Andrew Beckerman, and Samantha Patrick, who all also supplied comments on the manuscript.

**1. General introduction**

**1.1 Parental care**

**1.1.1 Benefits and costs of care**

Since Darwin (1859) first proposed the principle of evolution by natural selection, much attention has been paid to behaviours where animals appear to behave contrary to their own interests. One such behaviour is parental care, raising the question of why would an ultimately selfish organism sacrifice its own condition for even their own offspring? According to selfish gene theory (Dawkins 1976), the principle of “survival of the fittest” applies not to the individual organism performing a behaviour (i.e. the vehicle) but to their genes underpinning that behaviour (i.e. the replicator). Investing in the production and survival of their offspring (i.e. parental investment) is the mechanism by which most organisms propagate copies of their own genes to future generations, thus maximising their lifetime fitness.

Most animals reproduce sexually and have a diploid genetic structure, so each of a parent’s genes stand a 50% chance of being inherited by their offspring (Hamilton 1964). Therefore, parental investment acts as an intergenerational transfer of resources, where it is to the advantage of each individual gene to sacrifice the condition of their own host to propagate of copies of themselves in others. For example, semelparous organisms such as pink salmon, *Oncorhynchus gorbuscha*, breed only once and die shortly after (Groot and Margolis 1991). To maximise their effective contribution to the next generation, the salmon is under selection simply to maximise the productivity of their single breeding event (Young 1981). However, parental investment also comes at a cost to carers proportional to their investment (Clutton-Brock 1991, Stearns 1992), so in iteroparous species overinvestment in a breeding attempt may increase mortality risk and/or reduce fecundity in later life (Nilsson and Svensson 1996, Visser and Lessells 2001). Likewise, underinvestment may confer an opportunity cost if the organism does not survive to breed again. Therefore, organisms that breed multiple times are selected to optimise their investment across each breeding attempt within their lifetime (Williams 1966). This is supported by the phenomenon of terminal investment, where carers increase investment in their final breeding attempt because they cannot spend any residual investment in the future, so like semelparous organisms they expend all their residual investment in their final breeding attempt to maximise their contribution to future generations (Clutton-Brock 1984, Creighton et al. 2009).

Parental investment includes physiological processes essential to the production of viable offspring (e.g. egg production in birds, foetal gestation in mammals) and parental care behaviours (e.g. incubation or provisioning in birds). In altricial birds, much of their parental investment occurs postnatally (Godfray and Johnstone 2000), and a period of provisioning between hatching and fledging is a near-ubiquitous feature of their parental care systems (Cockburn 2006). The benefits of parental investment to offspring are well documented, with offspring that receive more investment generally experiencing increased survival chances and/or fitness in later life (Trivers 1974, Godfray 1995, Hinde et al. 2010). It should be noted that parental investment may also confer risk to offspring, for example by advertising their location to predators, so carers may also optimise the way they provide care (Skutch 1949, Martin et al. 2000).

**1.1.2 Conflict within the family**

An individual’s investment decisions are further complicated when multiple carers cooperate to raise the same offspring. In lifelong monogamous breeders, where two individuals breed together throughout their lifetimes, the interests of both parents are closely aligned, so they collaboratively optimise their investment such that their collective fitness is maximised over their lifetimes (Westneat and Sargent 1996). However, in species with high rates of adult mortality or divorce, a carer may breed with multiple individuals throughout their life, so they face a further decision over how much to contribute to each breeding attempt versus how much to save for potential future reproduction with a different partner (Trivers 1972). In this case, each parent must trade-off collective benefits (i.e. success of their offspring) with individual costs (i.e. reduced residual investment), leading to conflict between parents over their relative contribution to each breeding attempt (Westneat and Sargent 1996). This conflict incentivises each to maximise their partner’s investment in each breeding attempt, relative to their own, thus saving their residual investment for future reproduction (Stearns 1989). However, this could result in both parents reducing investment, to the detriment of their offspring, because the stable level of parental investment is below their offspring’s optimum (Lessells 2012, Lessells and McNamara 2012), and may even result in lower overall investment by two parents than would be provided by a single parent (Royle et al. 2002a, 2004, 2006, McNamara et al. 2003).

This conflict also applies when carers have different genetic stakes in the brood, such as when fathers share brood paternity (Griffith et al. 2002) or when parents are assisted by alloparental helpers (i.e. cooperative breeding) (Hatchwell 1999, Johnstone 2011). When a female engages in extrapair copulations, her social partner has a reduced share of the brood’s paternity. However, even if males are unable to distinguish kin from non-kin, they may still help raise the brood if the (now reduced) genetic payoffs outweigh the costs (Rabenold 1985, Walters 1990, Margraf and Cockburn 2013). In cooperative breeders, helpers may receive genetic payoffs from successfully rearing indirect kin, though their genetic stake halves with each step they are removed from the offspring (relatedness coefficient (r) = 0.5 for sons and daughters, 0.25 for nieces, nephews, and grandoffspring, ≤0.125 for more distant kin). Whether it is ultimately evolutionarily beneficial for helpers to raise indirect kin is determined by Hamilton’s rule (rB > C; Hamilton 1964); here, helping is advantageous when the costs of care to the helper (C) are less than the benefits to their kin (B) multiplied by the coefficient of relatedness (r).

Empirical tests of Hamilton’s rule have found broad support for the idea that investment decisions are governed by the relative costs, benefits, and relatedness between different cooperating parties (Hatchwell et al. 2014, Green et al. 2016). Helpers may benefit from their apparent altruism by augmenting the productivity of a relative’s breeding attempt, however, to maximise payoffs, parents could reduce their investment equal to the amount provided by helpers (i.e. load-lightening; Crick 1992, Hatchwell 1999). If so, helpers may not benefit from their investment (i.e. exploitation), thereby rendering cooperative care evolutionarily inviable, unless load-lightening is constrained or if helpers derive other benefits of care. Despite this, systems of shared care, both biparental and cooperative, are found throughout the animal kingdom, particularly in birds, where they occur in >90% of all known species (Cockburn 2006). Therefore, there must be a mechanism by which this conflict is resolved and shared care is incentivised. Biparental care may be enforced if offspring require more resources than a single carer can provide (e.g. Congdon et al. 2005, Grissot et al. 2019), though parents are still in conflict over investment, so may engage in a ‘race to abandon’ (a.k.a. ‘desertion’) if broods can be raised uniparentally after a certain time (e.g. Winkler 1991, Székely et al. 1999, van Dijk et al. 2007). However, intercarer conflict and desertion are still costly to parents as they could achieve mutually increased payoffs if they cooperated without the threat of exploitation (i.e. the prisoners dilemma; Rapoport and Chammah 1965). In some cooperative species, helpers are thought to derive delayed direct benefits of their investment by increasing their chances of breeding in the future, either by increasing their social standing or perceived quality (i.e. prestige hypothesis; Zahavi 1977a,b) or as payment for group or territory membership until they eventually achieve breeder status (i.e. pay-to-stay; Gaston 1978, Kokko et al. 2002). In these scenarios, rather than helping to increase the survival and fitness of the brood, helpers instead signal their contribution to others to increase their future direct benefits. Whilst signalling may explain cooperation in some cases, there are many shared care systems where carers’ only benefit of investment is the success of the brood (Hatchwell and Komdeur 2000, Dickinson and Hatchwell 2004), so there must be another mechanism by which this conflict is resolved.

Several theoretical studies have modelled how this conflict might be resolved and shared care selected for. Houston and Davies (1985)’s model assumed that two parents enter into each partnership with a fixed level of investment allocated to each breeding attempt (i.e. sealed bid), here, selection acts to stabilise parents’ investment decisions over several generations. However, many empirical studies have shown that parents’ efforts were sensitive to experimental changes in their partner’s provisioning rate, refuting a key assumption of this model. So, McNamara et al. (1999) and others (e.g. Johnstone 2011, Lessells and McNamara 2012) later developed so-called ‘negotiation’ models, where each parent responds to changes in their partner’s effort in behavioural time. Though, both sealed bid and negotiation models predict that parents reach a stable level of investment, and exploitation is prevented by parents responding to changes in their partner’s investment with incomplete compensation, either in real time (negotiation) or over several generations (sealed bid). This prediction was generally supported by experimental studies that manipulated one parent’s investment, with incomplete compensation by their partner being the mean response (meta-analysis: Harrison et al. 2009). However, there are several empirical studies which do not conform to this prediction, with responses ranging from complete compensation (e.g. Wright and Cuthill 1990, Sanz et al. 2000) to no response (e.g. Schwagmeyer et al. 2002, Tajima and Nakamura 2003), and some even matching their partner’s changes (e.g. Hinde 2006, Meade et al. 2011). Although both models allow for a stable investment equilibrium to be reached, there is still a cost of conflict as their investment is below the brood’s optimum level, so parents would both benefit if they could mutually increase their investment.

**1.2 Coordination of care**

**1.2.1 Types of coordination**

Johnstone et al. (2014) proposed a model for parental investment based on conditional cooperation between carers in which continued investment depends on regularly observing their partner provisioning. Here, each parent avoids exploitation by refusing to feed consecutively, thus enforcing a system of strictly coordinated turn-taking between carers (i.e. perfect alternation; figure 1.1a). Note that conditional cooperation is not restricted to provisioning but can apply whenever organisms continuously cooperate to perform shared tasks (e.g. Keser and van Winden 2000, Frey and Meier 2004). A key feature of conditional cooperation is that, rather than performing cooperative tasks simultaneously (i.e. coaction), cooperators engage in reciprocal exchange separated by distinct time gaps, which is thought to be harder to evolve and maintain because each individual must trust that their efforts will be later reciprocated. Despite this, Taborsky and Riebli (2020) found compelling evidence of temporally delayed conditional cooperation in nest building and defence behaviours between unrelated individuals of a cooperatively breeding cichlid fish, *Neolamprologus pulcher*.

Conditional cooperation could enable provisioning birds to mutually increase their investment to more closely match their brood’s optimum, though they must follow unrealistically strict turn-taking rules as cooperation breaks down when one parent misses their partner’s feed, because they each believe it is the other’s turn (Johnstone et al. 2014). Furthermore, this model predicted matching as the only possible response to changes in their partner’s provisioning rate and thus provides no explanation for empirical studies finding (in)complete compensation. Johnstone and Savage (2019) later refined this model by incorporating imperfect monitoring, time dependent costs and benefits, shared costs of care, as well as asymmetries in accuracy of monitoring and payoffs between carers. This enabled parents to engage in imperfect alternation of visits, making the model more biologically realistic, and recovered the prediction that parents respond with incomplete compensation when the costs of care are sufficiently asymmetric between them.

Conditional cooperation can also apply to cooperative breeding systems when offspring are raised by parents with assistance from alloparental helpers with a shared interest in the success of the brood (Savage et al. 2017), because it may limit how much parents can reduce investment in response to help; thereby allowing helpers to increase total group investment, instead of just replacing the parents’ investment. Although helpers typically have a lower genetic stake in the brood than parents, their interests may still be closely aligned with those of the parents. For example, long-tailed tits, *Aegithalos caudatus*, lose most of their broods to predators (Hatchwell et al. 2013), so only a minority of individuals ever successfully rear their own offspring to fledging (MacColl and Hatchwell 2004). Therefore, helpers instead increase their fitness by augmenting the productivity of their relatives, propagating their genes indirectly via second and third order kin. In support of this, helping has been shown to increase the likelihood that offspring survive to recruitment in the local breeding population; a large component of fitness in this bird species (MacColl and Hatchwell 2002, McGowan et al. 2003, Hatchwell et al. 2004, 2014).

Conditional cooperation is not the only form of coordinated care that has been hypothesised in birds. Many species are also thought to coordinate their contribution to parental care behaviours such as incubation and brooding (e.g. Spoon et al. 2006, Al-Rashidi et al. 2010, Boucaud et al. 2016, Storey et al. 2020). Here, carers coordinate via efficient division of labour, as they must trade-off the demands of their clutch or brood against the personal cost of prolonged nest attendance. Some species mitigate this cost by delivering food to the carer as they incubate the eggs and brood the chicks (Hatchwell et al. 1999a). Others, such as the cockatiel, *Nymphicus hollandicus*, share incubation duties and carefully coordinate their timing such that the clutch is sufficiently attended and both parents effectively maintain their own condition, and pairs with greater incubation coordination also experienced greater hatching and overall reproductive success (Spoon et al. 2006).

Likewise, many pelagic seabird species must strictly coordinate their parental investment to successfully raise offspring. In addition to coordinating their incubation and brooding (Patrick et al. 2020, McCully et al. 2022), many seabirds also strictly coordinate provisioning such that starvation risk, to both offspring and parents, is minimised (Congdon et al. 2005, Tyson et al. 2017). Seabirds are usually lifelong monogamous breeders, so their coordinated provisioning has not evolved as a mechanism of conflict mitigation, but because it is essential for successful reproduction. For example, the little auk, *Alle alle*,is a biparental seabird which must forage far from their nest to provide food for their offspring. However, if their chick goes too long without food they will starve. Constrained by this, parents engage alternately in short (~2h) foraging bouts to provision the chick and long (~13h) foraging bouts to replenish their own energy reserves (Wojczulanis-Jakubas et al. 2018, Grissot et al. 2019). If carers simultaneously engage in long self-feeding bouts the chick could starve, so parents strictly coordinate foraging such that one provisions the chick while the other self-forages before swapping roles (i.e. coordinated dual foraging; figure 1.1b).

In contrast to dual foraging strategies of seabirds, many other bird species are hypothesised to coordinate their provisioning by delivering food simultaneously. This form of coordinated provisioning, known as synchrony (figure 1.1c,d), is hypothesised to facilitate conditional cooperation by enabling carers to reliably monitor the provisioning visits of their partner(s) (Mariette and Griffith 2015, Bebbington and Hatchwell 2016). However, synchrony also has several other hypothesised functions which pre-date the conditional cooperation hypothesis for provisioning.

Firstly, synchrony may reduce the risk that carers advertise their brood’s location to predators when provisioning the brood (predation hypothesis; Sargent 1993). As discussed, parental care is beneficial to offspring, but could risk advertising a brood’s location to predators, either directly by their activity near the nest (Skutch 1949, Martin et al. 2000), or indirectly by inducing offspring begging calls (Haskell 1994, Briskie et al. 1999). Begging calls can attract a predator’s attention, and several bird species have evolved specific alarm calls that instruct offspring to stop begging for a time when a predator is nearby (Greig-Smith 1980, Knight and Temple 1986). Synchrony could reduce this risk by overlapping carers’ near-nest periods, thus carers may increase the amount of food provisioned per time spent near the nest (Raihani et al. 2010, Bebbington and Hatchwell 2016, Leniowski and Węgrzyn 2018).

Secondly, synchrony is hypothesised to facilitate a more efficient distribution of parental investment among offspring in a brood (intrabrood conflict hypothesis; Shen et al. 2010). Many bird species produce large clutches and broods, but their productivity is reduced when a chick starves prior to fledging. Every organism is selected to survive and reproduce at the expense of their competition, even when in competition with siblings (Kilner and Johnstone 1997, Royle et al. 1999). Therefore, each offspring should prioritise their own survival and condition above that of their siblings, whereas parents are selected to optimise the overall fitness of their brood. This creates conflict between siblings, and between offspring and parents (Trivers 1974, Godfray and Johnstone 2000, Kilner and Drummond 2007, Mock et al. 2011). In birds, the distribution of resources among the brood during each bout is largely determined by the relative position and begging intensity of offspring (Redondo and Castro 1992, Mondloch 1995). Begging is energetically costly to offspring (Kilner 2001), so is typically an honest signal of need (Royle et al. 2002b), with hungrier chicks receiving greater benefits per food item delivered; so, hungrier chicks are expected to beg louder and are therefore more likely to be fed (Kilner and Johnstone 1997, Johnstone and Kilner 2011). Whilst this mechanism ensures a degree of parity between offspring in a brood, over time more well-fed offspring will grow larger, so can produce longer and/or louder begging calls and thus receive more food, reinforcing their advantage. Synchronous provisioning could limit the ability of highly competitive chicks to monopolise resources because, by delivering multiple food items within a short period of time, the first fed chick may be satiated or even still processing the food item by the delivery of the next, and so will be less likely to receive food (Shen et al. 2010). This ensures that food is delivered to less competitive offspring, reducing the risk of maladaptive brood reduction via starvation.

Thirdly, synchrony could help signal a carer’s (allo)parental effort to others. In some cooperative breeding systems, helpers derive direct benefits from their investment; increasing their chances of breeding in the future either by advertising their quality to potential future mates (prestige hypothesis; Zahavi 1977a,b) or as payment for membership to a group where they may eventually achieve breeder status (pay-to-stay hypothesis; Gaston 1978, Kokko et al. 2002). Here, helpers are expected to maximise the visibility of their provisioning visits, particularly to the individual(s) from whom they derive their benefits (e.g. dominant breeders or potential partners).

Finally, synchrony may confer no direct benefits to carers but could instead be a consequence of other behaviours that do, such as collective (or group) foraging (collective foraging hypothesis; Beauchamp 1998). Collective foraging could benefit carers by increasing foraging efficiency, particularly when certain carers are more well-informed about brood demand or local resource distribution, because other carers can use cues from this individual to inform their foraging decisions (Valone 1989, Lee and Cowlishaw 2017, Palacios-Romo et al. 2019). Additionally, collective foraging may reduce the risk that carers are preyed upon when foraging, as larger groups of birds may be harder to attack (i.e. confusion effect; Landeau and Terborgh 1986), less likely to be attacked (Sorato et al. 2012) and/or individuals within the group may be less likely to be targeted (i.e. dilution effect; Foster and Treherne 1981, Sorato et al. 2012). Whilst collective foraging alone may explain the observed patterns of nest visit synchrony, it does not rule out other adaptive functions of synchrony. In fact, collective foraging may be the mechanism by which synchrony is facilitated even if it provides another adaptive function, such as to reduce brood predation risk or mitigate intrabrood conflict.

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Figure 1.1. Illustration of sample sequences of nest visits by a pair of provisioning carers, a female (orange) and male (blue), exhibiting a different form of coordination as follows: (a) alternation, (b) dual foraging, (c) synchrony, and (d) synchrony with a conserved feed order (i.e. synchronous alternation).

**1.2.2 Evidence of alternation**

When attempting to identify evidence of coordination many empirical studies have investigated coordination directly from sequences of feeds (e.g. Koenig and Walters 2016, Savage et al. 2017), while others have investigated these hypotheses’ predicted outcomes (e.g. Leniowski and Węgrzyn 2018, Lejeune et al. 2019). A difficulty experienced when investigating coordination patterns directly is that certain levels of both alternation and synchrony are expected to occur by random chance even if no active coordination behaviours are performed (Schlicht et al. 2016, Ihle et al. 2019a, Santema et al. 2019). So, many studies have used a variety of null model approaches to estimate whether observed levels of alternation and/or synchrony are higher than expected by chance in both biparental and cooperatively breeding bird species. Most found that observed alternation (biparental: Johnstone et al. 2014, Bebbington and Hatchwell 2016, Leniowski and Węgrzyn 2018, Baldan et al. 2019a,b, Baldan and Griggio 2019, Lejeune et al. 2019, Ihle et al. 2019a, Baldan and Quyang 2020, Griffioen et al. 2021; cooperative: Koenig and Walters 2016, Savage et al. 2017) and synchrony (biparental: Mariette and Griffith 2012, van Rooij and Griffith 2013, Lejeune et al. 2019, Ihle et al. 2019a; cooperative: McDonald et al. 2008a, Koenig and Walters 2016) were greater than was expected by chance, though these findings were not universal (Khwaja et al. 2017, 2019, Enns and Williams 2022). Early approaches generated crude estimates of expected coordination using equations which assumed unrealistic provisioning rules (e.g. Mariette and Griffith 2012, van Rooij and Griffith 2013), so these approaches probably substantially underestimate the true level of expected coordination. Subsequently, increasingly biologically realistic null models were developed which utilised either; more advanced equations (e.g. Baldan and Griggio 2019), data simulated from observed parameters (e.g. Bebbington and Hatchwell 2016), or randomised observed data (e.g Johnstone et al. 2014). Several of these approaches were compared in Ihle et al. (2019a) and within-watch, within-carer intervisit interval randomisation (as used in: Johnstone et al. 2014, Savage et al. 2017, Lejeune et al. 2019) was found to be the most rigorous and conservative approach.

Johnstone et al. (2014) and others (Savage et al. 2017, Griffioen et al. 2021) attempted to identify alternation by using continuous time Markov models to determine whether carers’ return rate to the nest was faster following the feed of another carer (λ) than following their own feed (μ). Whilst this was usually supported (Johnstone et al. 2014, Savage et al. 2017, Griffioen et al. 2021; but see; Enns and Williams 2022), critics highlight how faster return rates following the feed of others, and greater than ‘expected’ coordination, could instead be plausibly explained by refractory periods when foraging (i.e. minimum time to prey capture) and/or carers responding mutually to changes in environmental conditions (Schlicht et al. 2016; but see Johnstone et al. 2016). Refractory periods are generally accounted for in the most robust randomisation approaches (Johnstone et al. 2014, Savage et al. 2017), however if carers experience chronic (e.g. gradually increasing/decreasing rainfall) or acute (e.g. predator nearby) changes in conditions that influence provisioning behaviour during a watch, then they may exhibit temporal autocorrelation (a.k.a. ‘correlated temporal heterogeneity’) in their provisioning rates (i.e. simultaneously increasing/decreasing provisioning rates). This can induce apparent patterns of coordination (particularly alternation) without the need for any active coordination behaviour but is not accounted for in any null model approach to date. In fact, Santema et al. (2019) simulated provisioning data by independently acting, uncoordinated carers exhibiting both chronic and acute temporal autocorrelation. They then applied the most conservative null model randomisation technique to these provisioning watches (hereafter ‘watches’), finding that temporal autocorrelation alone was sufficient to induce greater than expected alternation even though the carers were simulated provisioning in an uncoordinated manner. Although, the degree of chronic temporal autocorrelation necessary to cause this was far higher than was recorded in natural conditions (Johnstone et al. 2016). Note that uncoordinated carers may still exhibit apparent ‘active’ alternation if they experience acute and/or particularly strong chronic autocorrelation during a provisioning watch (Santema et al. 2019).

Baldan et al. (2019b) attempted to isolate coordination due to active behaviours by swapping provisioning sequences between great tit, *Parus major*,pairs taken from concurrent watches of different nests to create ‘pseudo pairs’. Whilst this accounted for some of the apparent coordination due to general environmental effects (18%), they could not distinguish whether the residual apparent coordination (74%) was from active coordination behaviours or nest specific environmental effects (e.g. offspring begging or predator nearby). Therefore, it appears unlikely that true behavioural coordination can be confirmed simply by comparing observed levels of alternation and synchrony with those expected by chance, or by comparing return rates following others vs oneself. However, these techniques may still be useful when used in conjunction with experimental or observational approaches to test the predictions of coordination hypotheses. For example, some studies make inferences about the function of coordination by comparing levels of alternation and synchrony in different conditions, whether observational (e.g. Savage et al. 2017, Lejeune et al. 2019) or experimentally induced (e.g. Griffioen et al. 2021, Enns and Williams 2022).

Given that expected coordination may be underestimated by even the most robust and conservative null models, the collection of studies demonstrating greater than expected alternation alone are not definitive evidence of conditional cooperation. Additionally, other sources of evidence for this hypothesis are circumstantial or could be plausibly explained by other means. For example, Iserbyt et al. (2019) found that when a blue tit, *Cyanistes caeruleus*,parent was captured during the critical provisioning stage, their partner waited six times longer than usual to provision the brood. Though, this finding could also result from observer disturbance near the nest, and the remaining partner instead delayed feeding because they perceived an increased risk of mortality to themselves and/or their brood.

To date, the most compelling evidence of conditional cooperation comes from studies that have sought to identify the consequences of alternation. For example, Bebbington and Hatchwell (2016) found a significant positive correlation between ‘active’ alternation and a group’s overall provisioning rate in long-tailed tits, suggesting that conditional cooperation enables carers to mutually increase their parental investment. Furthermore, Burdick and Siefferman (2020) identified a positive correlation between alternation and offspring mass gain during a critical provisioning stage in eastern bluebirds, *Sialia sialis*,and Lejeune et al. (2019) found a negative relationship between alternation and intrabrood mass variation in blue tits; suggesting that conditional cooperation benefits offspring by increasing the amount of food delivered or efficiency of delivery. Finally, Baldan and Griggio (2019) found that rock sparrow, *Petronia petronia*, parents with higher levels of alternation were less likely to exhibit parental desertion (one parent only) prior to fledging, suggesting that conditional cooperation facilitates conflict resolution between carers. However, several other studies have not detected a significant effect of alternation (either observed or ‘active’) on offspring condition (Bebbington and Hatchwell 2016, Iserbyt et al. 2017, Griffioen et al. 2019a) or survival (Iserbyt et al. 2017), and Ihle et al. (2019b) found a negative relationship between active alternation score and offspring survival to fledging in house sparrows, *Passer domesticus*. Additionally, Enns and Williams (2022) found that European starlings, *Sturnus vulgaris*, did not exhibit greater than expected alternation and, in fact, found that carers took longer to feed consecutively if the preceding visit was by the other carer (i.e. M-F-F) than if it was by the same carer (i.e. F-F-F), suggesting that they do not engage in conditional cooperation over provisioning.

Other studies also found interesting results regarding alternation, although their interpretations are less straightforward. Iserbyt et al. (2017) found that alternation increased in fife canary, *Serinus canaria*, pairs throughout development as each parent’s duties become more similar. Griffioen et al. (2019b) found that blue tit mothers increased their provisioning rate and reduced their level of alternation in response to wing clipping of their partner, even though the males did not adjust their provisioning rate or alternation in response to their handicapping. Griffioen et al. (2021) found that blue tit females exhibited greater turn-taking (λ/μ) than males and increased alternation under experimentally cooled conditions. Further, Baldan and Quyang (2020) found that house wren, *Troglodytes aedon*, parents alternated more and had heavier offspring in rural environments than suburban ones but did not produce more fledglings. Finally, Baldan et al. (2019b) found that active alternation was higher in experimentally reduced broods than control or enlarged broods in great tits; however, applying a similar protocol Griffioen et al. (2019a) found no effect of brood size manipulation on alternation in blue tits. Whilst the findings of these studies are difficult to interpret, they do highlight that different species may apply different provisioning rules (e.g. flexible vs fixed, female vs male led) and that the conditional cooperation hypothesis may apply to some species, but not others.

**1.2.3 Evidence of synchrony**

Just as with alternation, a certain level of provisioning synchrony is expected by chance, and temporal autocorrelation in provisioning rates could theoretically lead to null models underestimating the true level of apparent synchrony expected by chance. However, unlike alternation (Santema et al. 2019), no prior studies have quantified the level of active synchrony expected from temporally autocorrelated simulated provisioning data, so it is not known whether shared environmental conditions alone are sufficient to induce the level of apparent synchrony observed in natural provisioning watches. Therefore, studies demonstrating greater than expected synchrony make a stronger case for true behavioural synchrony than similar findings do for alternation. Nonetheless, there are several mutually compatible hypotheses for synchronous provisioning, so the demonstration that carers synchronise their nest visits is just the first step to understanding this phenomenon. More informative would be the demonstration that carers facilitate synchrony for a specific purpose or that synchrony confers benefits that are compatible with one or more of the hypothesised functions; I address support for each of these hypotheses below.

Firstly, synchrony is hypothesised to facilitate accurate monitoring of other carers that is necessary for conditional cooperation. This hypothesis is difficult to test because alternation and synchrony are inherently linked; indeed, by most definitions all synchronous visits are also necessarily alternated. Alternation inherently results from synchronous provisioning if carers feed in a conserved order (figure 1.1d), so disentangling alternation and synchrony may not be possible even if they perform different adaptive functions. Empirical support for this hypothesis is limited to studies which found that significant levels of active alternation and synchrony co-occurred in several species (Koenig and Walters 2016, Baldan and Griggio 2019, Ihle et al. 2019a, Baldan and Quyang 2020), and in some cases were even positively correlated (Bebbington and Hatchwell 2016, Leniowski and Węgrzyn 2018). However, there is some evidence that alternation and synchrony may perform different functions even in species where they co-occurred. Specifically, Lejeune et al. (2019) found that levels of alternation were negatively correlated with altitude and intrabrood mass variation in blue tits, but synchrony was not. Further, unlike alternation, synchrony was greater in woodland-pasture edges than within woodlands and was positively correlated with chick mass, suggesting that alternation and synchrony may be independently influenced by different environmental factors and may confer subtly different benefits to offspring.

Secondly, synchrony is hypothesised to reduce the risk of offspring predation during provisioning by reducing the total time that carers spend near the nest and/or duration of offspring begging, both of which could advertise a brood’s location to predators (Skutch 1949, Haskell 1994). Raihani et al. (2010) found compelling support for this hypothesis as pied babbler, *Turdoides bicolor*,carers actively waited for a partner before returning to the nest area with food, and synchronous provisioning conferred reduced brood predation risk. They also found that synchrony increased with brood age, presumably because older chicks beg louder. Similarly, Leniowski and Węgrzyn (2018) found that synchrony reduced the total time that blackcap, *Sylvia atricapilla*, carers were active near the nest, thus reducing brood predation risk. However, synchrony also decreased with brood age, although this effect could result from different energetic demands of young poikilothermic chicks versus older endothermic chicks. Bebbington and Hatchwell (2016) also found that synchrony reduced near-nest activity and identified a positive relationship between alternation and nest survival in long-tailed tits, which may instead result from the relationship between synchrony and predation risk, particularly if carers also feed in a conserved order as this may inherently lead to an apparent tendency for turn-taking. Additionally, in a multispecies comparative study, Khwaja et al. (2019) found that New Zealand bellbirds, *Anthornis melanura*, from areas with brood predators, either historically or presently, exhibited higher levels of active synchrony than those from areas which were predator free. However, most species sampled did not synchronise more than was expected by chance, and several other findings from this study did not support the predation hypothesis. Surprisingly, bird species introduced from Europe and Tasmania, which historically experienced brood predation, showed a non-significant tendency to synchronise less than species native to New Zealand, which was historically free of brood predators; further, birds from islands where invasive predators had been experimentally removed overall did not synchronise less than those from islands where predators remained.

Thirdly, synchrony is hypothesised to reduce the costs of intrabrood conflict by facilitating a more even distribution of resources among offspring in a brood. Several studies have identified compelling evidence in support of this hypothesis. Shen et al. (2010) found that cooperatively breeding Taiwan yuhinas, *Yuhina brunneiceps*, distributed food more evenly among their offspring during large-party provisioning bouts than during small-party bouts. Likewise, Mariette and Griffith (2012, 2015) found mixed support for this hypothesis as there was a significant positive relationship between foraging synchrony, but not nest visit synchrony, and offspring mass in Australian zebra finches, *Taeniopygia castanotis* (formerly: *T. guttata*). Also nest visit synchrony increased with brood size (Mariette and Griffith 2012, van Rooij and Griffith 2013), supporting this hypothesis as offspring starvation risk should be greatest in large broods. Additionally, comparing synchrony across different days from the same nest revealed that food was distributed more evenly on days where parents provisioned more synchronously. However, this effect was not observed when comparing overall synchrony between pairs (Mariette and Griffith 2015), suggesting some limited support for the intrabrood competition hypothesis in this species. Likewise, Lejeune et al. (2019) identified a positive correlation between nest visit synchrony and offspring mass in blue tits breeding in woodland interiors, and a negative relationship between alternation and intrabrood mass variation, suggesting that coordinated provisioning, in some form, resulted in a change in distribution of resources to offspring. Baldan and Quyang (2020) also found that house wrens breeding in rural environments were more synchronous and had higher offspring mass than their suburban counterparts, although this is circumstantial as both effects could instead result from differences between environments. Not all studies support this hypothesis, notably Ihle et al. (2019b) did not identify a significant effect of synchrony (or alternation) on offspring mass, intrabrood mass variation, or fledging success in house sparrows, and van Rooij and Griffith (2013) found no effect of synchrony on intrabrood mass variation, intrabrood condition variation, or fledging success in long-tailed finches, *Poephila acuticauda*; all of which are key predictions of the intrabrood conflict hypothesis.

Fourthly, synchrony is hypothesised to enable carers to maximise the visibility of their contribution. Since its conception (Zahavi 1977a,b) the hypothesis that helpers signal their alloparental investment has often been used to explain seemingly altruistic behaviours between unrelated individuals. However, despite much empirical attention (e.g. McDonald et al. 2008a,b, Nomano et al. 2013, 2015), evidence that carers signal their (allo)parental investment either to advertise their quality as a mate (i.e. prestige hypothesis), or to retain group or territory membership (i.e. pay-to-stay hypothesis) is rare (Doutrelant and Covas 2007, Trapote et al. 2021). Nonetheless, there have been some studies that support the notion that helpers synchronise their nest visits to signal their contribution others. Doutrelant and Covas (2007) found that sociable weaver, *Philetairus socius*,helpers waited near the nest before provisioning for longer than breeders did, particularly when they were holding a large food item and when food was less abundant, and they were also more likely to feed after an increase in audience size. These results suggest that helpers actively signal their contribution to shared care, though it was not known whether this was to advertise their quality or as payment for group membership, as helpers did not preferentially synchronise their visits with breeders or opposite sex helpers. Likewise, Trapote et al. (2021) found that female carrion crow, *Corvus corone*, helpers, which may one day attain breeder status in their group, preferentially synchronised their nest visits with dominant breeders, and there was a positive relationship between frequency of overlap with dominants and their likelihood of retaining group membership, supporting the pay-to-stay hypothesis. However, most studies that investigated the potential signalling function of synchrony found no support for either hypothesis because helpers typically did not take actions to increase the visibility of their efforts to dominants (Nomano et al. 2015, Koenig and Walters 2016) or potential mates (Nomano et al. 2013, Koenig and Walters 2016), and did not decrease synchrony in response to the removal of potential audience members (McDonald et al. 2008a,b).

Finally, synchronous nest visits may themselves confer no direct benefit, but could result from other behaviours that do, such as collective foraging. Collective foraging has been reported in several taxa (e.g. Ioannou and Dall 2016, Lemanski et al. 2019, Palacios-Romo et al. 2019), including birds (Beauchamp 1998) and its benefits are supported by both theoretical and empirical studies demonstrating that larger groups of foraging birds exhibited increased foraging efficiency (Caraco 1981, Beauchamp 1998, Lihoreau et al. 2017) and/or reduced predation risk (Hamilton 1971, Sorato et al. 2012). However, these functions are independent of any benefits of synchronous provisioning, meaning collective foraging could cause synchrony even if synchronous returns to the nest confer no direct advantage, making it a potentialnull hypothesis to explain synchrony if no direct function is detected. Alternatively, collective foraging could be a means by which adaptive synchronous nest visits are facilitated even if collective foraging itself confers no other direct benefit. There is circumstantial support for the link between collective foraging and synchrony as many synchronously provisioning bird species are also known to forage together (e.g. Doutrelant and Covas 2007, Shen et al. 2010), and Mariette and Griffith (2015) found that zebra finch synchrony at feeding stations was highly positively correlated with nest visit synchrony. Most compellingly, by radio-tracking the location of great tit parents during provisioning, Baldan and van Loon (2022) showed that great tit pairs’ foraging decisions were highly spatio-temporally correlated and foraging coordination was positively correlated with provisioning rate; there was also some support for the notion that the female typically leads these foraging trips, while the male follows (Baldan 2019). However, not all studies support the link between collective foraging and synchrony, in fact, Lee et al. (2010) found that the level of synchrony decreased with local breeding density and increased with nearest neighbour distance in the flock-living, collectively foraging, vinous-throated parrotbills, *Suthora webbiana* (formerly: *Paradoxornis webbiana*). This suggests that pairs foraged together when their nest location was isolated from conspecifics, resulting in a high rate of synchrony, or as part of a flock(s) when centrally located, which counterintuitively results in a lower rate of synchrony because each parent may forage with a different flock. The latter case appears favourable, as local breeding density was positively correlated with provisioning rate, which in turn was associated with increased offspring mass. Perhaps the difference in synchrony between isolated and well-connected pairs reflects an increased importance for isolated pairs to forage together as they lack conspecific foraging cues and/or safety in numbers that foraging as part of a large flock affords.

**1.3 The Long-tailed tit *Aegithalos caudatus***

**1.3.1 Breeding system and ecology**

Long-tailed tits are small (7–8g; Snow et al. 1998), short lived, sexually monomorphic, primarily insectivorous passerine birds of the family *Aegithalidae* (Figure 1.2; Hatchwell 2016). Their longitudinal range extends from Western Europe to Japan and latitude from Siberia to Arabia. Long-tailed tits are common throughout the British Isles, where they breed annually from March–June each year. During the non-breeding season, they live in flocks of 10–20 individuals which roost and forage together (McGowan et al. 2007, Napper and Hatchwell 2016). In February–March of each year flocks disband as individuals form monogamous breeding pairs, usually with an unrelated member of their flock (Leedale et al. 2020a).

Each pair constructs a nest together (Figure 1.2), usually <3m from the ground in shrubs such as bramble *Rubus fruticosus*, gorse *Ulex spp.*, holly *Ilex spp.*, hawthorn *Crataegus spp.*, or rose *Rosa spp.* (73% of nests; Higgot 2019), but sometimes also >3m from the ground in the forks of tree branches (e.g. birch *Betula spp.*, conifer *Pinus spp*.). Nests are built from tightly interwoven fibres of spider silk, moss, and small amounts of other vegetation covered with lichen flakes for camouflage (Higgot 2019). Each nest is lined internally with up to 2,500 feathers, and once completed are typically 15cm high and 10cm wide. First nests take ~38 days to complete, but in the event of nest destruction replacement nests are built much faster, usually taking just 11 days to complete, though they are typically smaller and of lower quality (Hatchwell 2016). Once nests are complete (typically March–April), the female lays a clutch of 7–12 eggs (median 10) at a rate of one egg per day, before incubating the completed clutch for ~15 days (Hatchwell et al. 1999a). After incubation, all eggs that hatch typically do so within 24h of the first. After hatching (day 0), both parents provision the chicks with small invertebrates (e.g. spiders, caterpillars, flies), though females also brood the chicks for ~5 days post-hatching, while the male feeds the chicks directly, and indirectly via the brooding female. Following the end of brooding (~d6) both parents provision offspring directly until either nest failure or fledgling, typically on d16–18.

Despite having large broods (up to 12 chicks), long-tailed tits experience extremely low rates of offspring starvation (0.2% daily starvation rate per chick; Hatchwell et al. 2004). The primary cause of pre-fledging mortality is predation, typically by corvids (e.g. Eurasian jay, *Garrulus glandarius*) or mammals (e.g. stoat, *Mustela ermina*). Complete predation events (all eggs or chicks dead or missing) are most common, with 72% of all clutches and broods failing due to predation (Hatchwell et al. 2013), though they may also suffer partial predation events (~3%). If a nest is destroyed early in the season and prior to hatching, the pair will usually attempt to build a replacement nest; however, if a nest is destroyed late in the season or after hatching, the pair may abandon breeding and redirect their investment by helping provision a relative’s brood (MacColl and Hatchwell 2002), particularly the males. Rates of extrapair paternity and intraspecific brood parasitism are both very low (Hatchwell et al. 2002), and helpers suffer a personal cost of helping (Meade and Hatchwell 2010a) but appear to gain no direct personal benefit (Hatchwell 2016).

In the facultative cooperative breeding system of long-tailed tits, helpers usually assist kin (Glen and Perrins 1988, Nam et al. 2010, Leedale et al. 2020b), although other factors may influence helper decisions (Leedale et al. 2018, Sturrock et al. 2022). Helpers are thought to derive only indirect, kin-selected benefits from their helping; the addition of helpers to a group increases offspring mass (MacColl and Hatchwell 2002, Hatchwell et al. 2004), probability of recruitment (MacColl and Hatchwell 2002, McGowan et al. 2003, Hatchwell et al. 2004, 2014) and partially reduces the burden on the breeding pair (Meade et al. 2010b). Helpers’ investment decisions, both in who to help and how hard to work, are broadly consistent with Hamilton’s rule (Hatchwell et al. 2014) and are ultimately determined by their relatedness to a breeding bird (usually the male; Leedale et al. 2018, 2020b). The mechanism by which this kin-discrimination occurs is their call patterns, which are learnt from their social parents during development (Sharp et al 2005, Sharp and Hatchwell 2006). Related individuals typically have similar calls and when an individual helps non-kin (30–50% of cases; Leedale et al. 2018, 2020b), they usually have similar calls, suggesting that such instances result from recognition errors. Of individuals with non-zero lifetime inclusive fitness, ~20% derive fitness benefits only from helping their relatives (MacColl and Hatchwell 2004), so helping in long-tailed tits is thought to be a strategy by which failed breeders make the best of a bad lot, because late in the season even the relatively small fitness gains from helping outweigh those from attempting to renest (MacColl and Hatchwell 2002). Therefore, as helpers are thought not to derive any direct benefits of their investment, the signalling-based hypotheses (prestige and pay-to-stay) are likely not applicable to this species, so throughout this thesis I focus my analysis on the other hypotheses for coordinated provisioning which are compatible with the breeding system of long-tailed tits.

In recent decades, long-tailed tits have been an important study species for investigating several behavioural phenomena, including coordination of parental care. Their unusual facultative cooperative breeding system makes them an excellent species for investigating the dynamics of (allo)parental care behaviour. Unlike many cooperative breeders, because helpers are redirected failed breeders rather than retained offspring, there is unlikely to be a confounding effect of territory quality on helper number, so any effect of helpers on reproductive success is likely a truly causal effect. Bebbington and Hatchwell (2016) used a large sample of watches to make several useful inferences about coordinated provisioning in long-tailed tits. Key results were that alternation occurred more than expected by chance (using a simulation approach) and was positively correlated with provisioning rate and nest survival, while synchrony was positively correlated with alternation and associated with reduced near-nest activity, suggesting a lower risk of advertising a nest’s location to predators. Whilst this study was informative, the analysis was restricted to biparental (unhelped) nests, limiting the scope of their interpretation, and subsequent studies have highlighted how their modelling approach may underestimate the level of expected alternation and thus generate spurious results (Ihle et al. 2019a).

A bird in a nest

Description automatically generated

Figure 1.2. Long-tailed tit, *Aegithalos caudatus*, sat in their nest constructed from spider silk and moss, lined internally with feathers and externally with lichen flakes. Photograph by Marion Germain.

**1.3.2 Study population**

Since 1994, a wild population of long-tailed tits (25–72 breeding pairs) has been intensively studied in the Rivelin Valley, near Sheffield, UK (*53°23′N*, *1°34′W*). The field site is a ~3km2 area primarily comprised of deciduous woodland, agricultural pasture, and scrub. Most individuals (~95%) in the field site were individually identifiable from a unique combination of two colour rings (size code: XF), which along with a metal BTO ring (under British Trust for Ornithology licence), were applied to nestlings if they hatched within the study site, or to adult immigrants upon capture via mist-netting. Nests were usually located by following an individual or pair as they gather nest material (33–148 nests per year). Note that each year a small number of nests (~5%) were not found, usually because they were short lived and failed before they were located. During construction each nest was checked at 1–3 day intervals, and once completed was checked every other day to ensure that first lay date can be recorded; long-tailed tits lay one egg per day so lay date could be easily deduced. In the event of nest failure, the pair were searched for, and their replacement nest found as soon as possible. During incubation, clutches were carefully removed from each nest and counted before being returned. Following this, nests were typically sampled non-intrusively (i.e. by observing female attendance through binoculars) to minimise disturbance, although intrusive checks were sometimes necessary to confirm nest failure. As nests approached the end of incubation (~15 days) nests were checked daily to ensure precise recording of hatch date (d0).

Provisioning watches were usually performed every other day from hatching to fledging or failure (d0, d2, d4, d6 etc.) after a brief (10 min) habituation period. Watch protocol remained fundamentally the same from 1994–2019; the time (to the nearest minute) and identity of each carer recorded upon each observed nest visit was either recorded by an observer with binoculars, or a HD video camera, positioned ~2m from the nest for subsequent video review. Subsequently (2020–2022), watch protocol was changed to record the time of arrival back the nest area (15m) and the time each carer fed (to the nearest second). Watches typically lasted one hour, but may be shorter when curtailed by inclement weather, or longer when an experiment was conducted. When visibility was poor, shorter observation periods were performed to determine the presence and identity of helpers at the nest. For nests within reach, on d11 an observer performed biometric assessment of each brood, as follows. Half of the brood was carefully removed and placed in a soft and insulated bird-bag, each chick was then weighed (to the nearest 0.1g) with digital scales, their tarsus length measured (to the nearest 0.1mm) using a calliper, ringed with a unique combination of colour rings on one leg and a metal BTO on the other, and 5–20µl of their blood taken by brachial venepuncture (under UK Home Office licence) for later genotyping and sex determination. These chicks were then returned to the nest and the process then repeated with the remaining half of the brood, this minimised the time that each chick was out of the nest and ensured that carers never returned to an empty nest. Because brood and/or clutch size was used as a covariate throughout my analyses, only nests in reach of an observer were used in my analyses. As nests approached fledging (d16–18), daily checks were performed to ensure that fledge date was precisely recorded. After fledging, each nest was checked to count dead chicks and check for signs of damage; if no damage was detected the number of fledglings was assumed equal to the brood size at d11 minus any dead chicks found in the nest. If the nest was damaged, suggesting predation, the number of fledglings was confirmed by locating and counting the fledged group. The number of local recruits was also calculated by subsequent observations of birds ringed as chicks within the field site attempting to breed in subsequent years.

**1.4 Thesis aims and structure**

The overall aim of this thesis was to investigate the dynamics of the provisioning behaviour of a facultative cooperatively breeding bird. Specifically, whether, how, and why long-tailed tit carers (parents and helpers) temporally coordinate their nest visits, by quantifying the amount non-random provisioning patterns (i.e. alternation and synchrony), the factors influencing their prevalence, and their potential effects on reproductive success.

The primary objective of chapter 2 was to determine whether long-tailed tits actively coordinate their provisioning visits more than is expected by chance. Here, I used the most robust and conservative null model approach to date (Ihle et al. 2019a) to quantify the difference between observed and expected alternation and synchrony (i.e. the level of active coordination) for each individual carer and for the group as a whole during each provisioning watch. I then investigated how these levels of active alternation and synchrony were influenced by key factors such as: the number of carers, brood size, provisioning rate, carer status (i.e. breeding female, breeding male, helper), and relatedness of helpers to the breeding pair.

In chapter 3, I used detailed observations of provisioning sequences to determine the mechanism by which alternation and synchrony may be facilitated. Here, data were collected using a provisioning watch protocol where the time that each carer arrived (to the nearest second) within 15m of the nest was recorded as well as the time that each carer fed the brood. This allowed me to determine whether carers arrived, as well as fed synchronously, and whether the period of loitering prior to provisioning plays an important role in ensuring accurate alternation. Additionally, I investigated whether biparental and cooperative groups of carers arrive and/or feed in a status dependent manner by investigating their relative position within the feeding order during synchronous provisioning bouts.

The aim of chapter 4 was to experimentally test the hypothesis that carers coordinate provisioning as an antipredator measure to reduce the risk of brood predation. Here, I compared several different metrics of provisioning, such as provisioning rate, alternation, synchrony, overlap of loitering periods, and time spent loitering prior to provisioning between control watches and watches following presentation of predatory and non-predatory model birds. I also compared these metrics between different sections of each watch to investigate the potential fine-scale adjustments in provisioning behaviour, particularly coordination, exhibited after model presentations.

In chapter 5, I developed an explicit *a priori* hypothesis-prediction framework to test three hypotheses of coordinated provisioning by investigating the consequences of coordination for parents and offspring. Specifically, I tested key predictions of the conditional cooperation, intrabrood conflict, and predation hypotheses by using ‘active alternation scores’ and ‘active synchrony scores’ to quantify the effect of coordination on provisioning rate, offspring mass, intrabrood mass variation, nest survival, and offspring recruitment rate from a long-term sample of breeding attempts.

Finally, in chapter 6 I synthesise and interpret the findings of my data chapters inclusively with prior research of long-tailed tits and avian coordination of care generally, discuss potential alternative explanations for my findings, and suggest potentially insightful avenues for future research.

**Chapter 2**

**Coordination of care by breeders and helpers in the cooperatively breeding long-tailed tit, *Aegithalos caudatus***

Chapter published as:

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

**2.1 Abstract**

In species with biparental and cooperative brood care, multiple carers cooperate by contributing costly investment to raise a shared brood. However, shared benefits and individual costs also give rise to conflict among carers over investment. Coordination of provisioning visits has been hypothesised to facilitate the resolution of this conflict, preventing exploitation, and ensuring collective investment in the shared brood. We used a 26-year study of long-tailed tits, *Aegithalos caudatus*, a facultative cooperative breeder, to investigate whether care by parents and helpers is coordinated, whether there are consistent differences in coordination between individuals and reproductive roles, and whether coordination varies with helper relatedness to breeders. Coordination takes the form of turn-taking (alternation) or feeding within a short time interval of another carer (synchrony), and both behaviours were observed to occur more than expected by chance, i.e. ‘active’ coordination. First, we found that active alternation decreased with group size while active synchrony occurred at all group sizes. Secondly, we show that alternation was repeatable between observations at the same nest, while synchrony was repeatable between observations of the same individual. Active synchrony varied with reproductive status, with helpers synchronising visits more than breeders, although active alternation did not vary with reproductive status. Finally, we found no significant effect of relatedness on either alternation or synchrony exhibited by helpers. In conclusion, we demonstrate active coordination of provisioning by carers and conclude that coordination is a socially plastic behaviour depending on reproductive status and the number of carers raising the brood.

**2.2 Introduction**

Parental care is observed in some form in most bird species (Cockburn 2006). In altricial species, much of the burden of care occurs postnatally (Godfray and Johnstone 2000) and typically involves a shared caring system, with either biparental or cooperative brood care, in which helpers assist with raising a brood (Cockburn 2006). The benefits of parental care to offspring are well documented (Trivers 1974, Godfray 1995, Godfray and Johnstone 2000, Hinde et al. 2010), as are the fitness costs to parents, including accelerated senescence (Gustafsson and Pärt 1990), reduced survival (Dijkstra et al. 1990, Visser and Lessells 2001) and lower future reproductive success (Nilsson and Svensson 1996). Therefore, in both biparental and cooperative breeding systems there exists a fundamental conflict over individuals’ relative level of investment in the current brood. Shared benefits of increased offspring survival and condition must be traded-off against individual costs of reduced future fitness (Trivers 1974, Hinde et al. 2010). This conflict means that optimal parental care behaviours that maximise lifetime reproductive success are dependent on the actions of others, so carers should use information from their social environment to adjust their own behaviour (Houston and Davies 1985, McNamara et al. 1999, Johnstone and Hinde 2006). Recent work has hypothesised that coordination of care may have a crucial function as a mechanism for negotiating investment between carers, gathering information about others’ effort, building trust, and therefore resolving this conflict so that carers more closely match their optimal level of (allo)parental investment (Johnstone and Hinde 2006, Johnstone et al. 2014, Johnstone and Savage 2019).

Coordination can take the form of two, non-mutually exclusive behaviours: alternation, which is the act of feeding in turn with another carer(s) such that each carer avoids consecutive visits, and synchrony, which is the act of feeding within a short interval of another carer’s feed (Figure 2.1). Previous studies of parental coordination have investigated biparental (e.g. Bebbington and Hatchwell 2016, Leniowski and Węgrzyn 2018, Baldan and Griggio 2019, Baldan et al. 2019a, Ihle et al. 2019a,b, Lejeune et al. 2019) and cooperative care (e.g. Raihani et al. 2010, Koenig and Walters 2016, Khwaja et al. 2017, Savage et al. 2017). The results, so far, are mixed, with many demonstrating a higher than expected level of alternation (Johnstone et al. 2014, Savage et al. 2017, Baldan et al. 2019a, Ihle et al. 2019a), synchrony (Raihani et al. 2010, Mariette and Griffith 2015) or both (Bebbington and Hatchwell 2016, Koenig and Walters 2016, Leniowski and Węgrzyn 2018, Lejeune et al. 2019), while another reported no apparent coordination (Khwaja et al. 2017).

An important message emerging from these studies is that researchers must account for a degree of passive coordination expected by chance due to common factors, such as localised predator risk, weather conditions, and resource abundance, that potentially influence all carers’ provisioning refractory periods (Schlicht et al. 2016, Ihle et al. 2019a, Santema et al. 2019). Refractory periods, which are the minimum times it takes carers to gather food and return to the nest, are hypothesised to inflate levels of alternation and synchrony because they create a short period of time after a feeding visit in which a consecutive visit by the same individual is not possible, but alternated and synchronised visits are (Ihle et al. 2019a). For example, if intervals between feeds were consistent and identical for all carers at a nest, the pattern of visits would resemble perfect alternation even in the absence of coordination behaviour. To account for passive coordination, randomisation and simulation techniques derived from observed behavioural parameters are required to evaluate the level of observed coordination relative to that expected by chance from passive processes (e.g. Johnstone et al. 2014, Baldan and Griggio 2019, Baldan et al. 2019a, Khwaja et al. 2019). Ihle et al. (2019a) reviewed the different null models used to evaluate coordination. They showed that randomisation at the scale of within-nest, within-individual and inter-visit was the most conservative approach (Figure S2.1, supplementary material), because these conserve provisioning refractory periods. The difference between observed and expected coordination can then be measured, hereafter termed ‘active coordination’.

In cooperative breeding systems, additional factors such as the number of carers, carer status, and relatedness of carers to the brood must also be considered when determining an individual’s optimal behaviour (Crick 1992, Hatchwell 1999, Savage et al. 2013a,b, Savage et al. 2015, Green et al. 2016). Most previous studies have identified some form of coordination, but few have investigated the role of variable numbers of carers on coordination behaviour (Savage et al. 2017). Since alternation is hypothesised to facilitate cooperation between carers (Johnstone et al. 2014), variation in the level of coordination between nests with different numbers of carers may inform our understanding of how and why birds coordinate. For example, a change in active coordination between group sizes may represent: (i) a change in the importance of coordination, perhaps due to reduced costs of parental care resulting from load lightening in large groups (Crick 1992); (ii) a change in the ability of carers to monitor one another; or (iii) a change in the potential for analyses to detect active coordination behaviour.

The status of individual carers within groups might also influence their coordination. For example, fathers, mothers, and helpers may provision broods differently (Harrison et al. 2009, Green et al. 2016), and Savage et al. (2017) suggested that alternation was most prominent in breeders and helpers that invested more highly in broods. Synchronous feeding has also been proposed as a means of signalling effort to other carers (Doutrelant and Covas 2007, Koenig and Walters 2016, Trapote et al. 2021), so this hypothesis predicts that if signalling confers direct benefits to helpers, such as in a pay-to-stay system (Gaston 1978, Kokko et al. 2002), more active synchrony should be performed by helpers. Alternatively, synchrony may be a result of collective foraging behaviour that causes carers to return to the nest synchronously (Mariette and Griffith 2012, 2015). Moreover, if coupled with a leader-follower relationship, for example, if helpers are more likely to follow a breeder back to the nest, this may result in greater synchrony by helpers.

In this study, we investigated how levels of coordination varied with the number and status of carers in the long-tailed tit, *Aegithalos caudatus*. Long-tailed tits are short-lived passerine birds, with a facultative cooperative breeding system in which failed breeders redirect their care to help raise the offspring of other breeders, to which they are typically related (Hatchwell et al. 2014, Hatchwell 2016). About half of all broods in our study population are raised by their parents alone, the remainder being fed by their parents assisted by helpers. Helping is a kin-selected adaptation that allows failed breeders to gain indirect fitness benefits by caring for their relatives’ offspring, thereby increasing relatives’ breeding success (Hatchwell et al. 2004, 2014). Previous studies have shown that the care provided by helpers varies with relatedness. First, helpers show an active preference for helping kin rather than non-kin (Russell and Hatchwell 2001, Leedale et al. 2018). Second, helpers provision at a higher rate when they are more closely related to a brood (Nam et al. 2010, Leedale et al. 2020b).

Given that a helper’s relatedness influences their investment decisions we might also expect that it would influence coordination behaviour. For example, if carer coordination benefits the brood, less related helpers may coordinate less due to their lower genetic investment in the brood (Savage et al. 2017). Alternatively, the shared interest of parents and helpers in the brood may be lower for more distantly related helpers, resulting in greater conflict and hence a greater need for coordination. This cooperative breeding system with variable numbers of carers and variable relatedness between carers and the shared brood is well suited for testing whether carers coordinate their care and the factors influencing the level of coordination.

Bebbington and Hatchwell (2016) reported that long-tailed tit parents provisioning at biparental nests coordinate their care so that observed alternation and synchrony were higher than expected by chance. That study, however, utilised a null model that did not fully account for expected alternation and synchrony caused by refractory periods (Ihle et al. 2019a). In this study, we build on the findings of Bebbington and Hatchwell (2016) by investigating the impact of the number of carers, carer status, and relatedness of helpers on coordination of care, using a more conservative approach to analyse a larger sample of biparental nests, as well as cooperative nests with up to three helpers. Our first objective was to investigate whether carers working in different group sizes coordinated their provisioning by comparing observed alternation and synchrony to that expected by passive processes (Ihle et al. 2019a). Secondly, we investigated individual variation in coordination, examining the extent of within-individual and within-nest repeatability in the level of active coordination, and whether levels of active alternation and synchrony varied in relation to the status of the carer (male breeder, female breeder, or helper). Finally, we examined variation in the degree of coordination by helpers to determine whether either alternation or synchrony was influenced by their relatedness to the brood.

**2.3 Methods**

**2.3.1 Study system and data collection**

We used data from a long-term study of a population of long-tailed tits in the Rivelin Valley, Sheffield, UK (53°23′N, 1°34′W) from 1994 to 2019. The field site is ~3km2 with a population of 25–72 breeding pairs (Hatchwell 2016). Each year ~95% of adult birds were marked (under British Trust for Ornithology licence) with a unique combination of two colour rings (size code: XF) on one leg and a BTO metal ring on the other. The adult annual mortality rate is ~50% (Meade and Hatchwell 2010), and ~20% of new recruits into the adult population were ringed as nestlings in the study site, while the remaining ~80% of new recruits were unringed adult immigrants that dispersed into the population. Unringed birds were captured in mist-nests during the nest-building period and DNA samples collected (under Home Office licence) for genotyping and social pedigree reconstruction. Nests were found by following adults and once located, were monitored every 2–3 days, with daily visits around the expected hatch date. Median clutch size is 10 eggs (range: 4–12), which are incubated for ~15 days (Hatchwell 2016). Hatching is extremely synchronous within clutches, with all chicks typically hatching within 24 hours of the first. Initial hatch date was recorded as day 0, and chicks were ringed and counted on day 11*.* Protocols for provisioning watches (hereafter ‘watches’) were broadly consistent throughout the study. In most cases, watches of duration ~60 minutes were carried out every other day, starting on day 2, either by direct field observation or by video camera, for later review (69% of watches were between 45 and 65 minutes). Watches were carried out between 04:00 and 18:00, with 89% starting between 06:00 and 14:00. Watches were performed until a nest was predated, abandoned or chicks fledged, typically on day 16–18.

For ~5 days post-hatching nestlings are brooded regularly by their mothers, who provision offspring only occasionally, while fathers either feed the offspring directly or give food to the mother, who then feeds the chicks. We restricted our analysis, therefore, to watches at day 6 and older, when both parents provision offspring directly. Long-tailed tits exhibit facultative cooperative breeding (Lack and Lack 1958, Hatchwell 2016), meaning nests may be uniparental (1 carer, in the rare event of a parent dying), biparental (2 carers) or cooperative (>2 carers). For this study we restricted analysis to watches of biparental and cooperative nests with up to 5 carers (i.e. social parents and up to 3 helpers). Our dataset contained 65% (516) of watches from biparental nests and 21% (171), 11% (88), and 3% (20) from nests with 3, 4, and 5 carers, respectively. Before starting a watch, ~10 minutes was usually allowed for birds to recover from observer disturbance and we restricted analysis to watches of total duration ≥30.0 minutes and ≤180.0 minutes, with duration defined as the time between first and last observed feeds. Mean watch duration (± SD) was 54.8 ± 14.4 minutes (range 30–118 minutes, *N* = 795 watches). We omitted watches where the identity of any provisioning visit was unknown, and from nests that were manipulated for other behavioural studies (e.g. Meade et al. 2011). Watches were used from 24 years between 1994 and 2019, with 2007 and 2009 excluded because experiments conducted in those years meant that they contained no watches matching our criteria. In total, our dataset included 795 watches performed at 250 unique nests, involving 192 different breeding males, 203 breeding females and 144 helpers.

**2.3.2 Calculating coordination**

We analysed alternation and synchrony as the absolute number of alternated and synchronised feeding visits in a provisioning watch, respectively. We defined an alternated visit as any non-consecutive provisioning visit (i.e. a visit occurring after the provisioning visit of any carer other than itself) and a synchronised visit as an alternated visit occurring within 2-minutes of the previous feed (Figure 2.1). We chose an interval of 2-minutes in accordance with previous studies (Mariette and Griffith 2015, Bebbington and Hatchwell 2016, Ihle et al. 2019a), and further analyses revealed that number of synchronised visits was highly correlated for 1, 2, and 3-minute intervals (Pearson correlations: 1 v. 2 min, r = 0.97, df = 793, *P* < 0.001; 2 v. 3 min, r = 0.97, df = 793, *P* < 0.001; 1 v. 3 min, r = 0.94, df = 793, *P* < 0.001), and analyses of synchrony with different intervals produced qualitatively the same results.

We calculated observed alternation and synchrony directly from visit sequences and times recorded through field observation, generating coordination measures per watch and for each individual carer present in each watch (Figure 2.1). We generated expected data by null model randomisation of observed data, with the binary factor ‘Data type’ specifying whether data were observed or expected. In accordance with the most conservative method of calculating expected alternation and synchrony recommended by Ihle et al. (2019a), our null models used a within-watch, within-individual randomisation procedure in which the order of provisioning visits within a watch was randomised in a manner that preserved the length and identity of each period between feeding visits (inter-visit intervals) (Figure S2.1; supplementary material). We calculated expected numbers of alternated and synchronised visits, both for group total and for individual carers, from the median of 1000 iterations of the null model applied to each provisioning watch. We used median values to preserve integer values for subsequent analysis in Poisson-distributed linear models; mean and median values were highly positively correlated (Pearson correlations: alternated visits, r = 0.99, df = 793, *P* < 0.001; synchronised visits, r = 0.99, df = 793, *P* < 0.001).

A diagram of a graph

Description automatically generated with medium confidence

Figure 2.1. Illustration of sequence of feeding visits at a hypothetical provisioning watch. Breeding male visits in blue, breeding female visits in red, and helper 1 visits in yellow. Alternated and synchronised visits denoted by asterisk (**\***) and triangle (▼), respectively.

**2.3.3 Calculating kinship**

To calculate pairwise values of pedigree relatedness of helpers to parents we constructed an additive relationship matrix using the R package NADIV (Wolak 2012), partially reconstructed using molecular genetic data from up to 17 microsatellite loci to perform offspring-parent reconstruction on CERVUS v. 3.0.7 (Kalinowski et al. 2007) and sibling-sibling reconstruction on KINGROUP v.2 (Konovalov et al. 2004). Building on the social pedigree and protocol used in Leedale et al. (2018, 2020b) we expanded the pedigree to include 2018 and 2019 data. Our study population is open, so even after reconstruction the social pedigree remained incomplete; therefore, where necessary we omitted data with incomplete pairwise relatedness metrics to either social parent.

**2.3.4 Statistical analysis**

All statistical analysis was performed in R version 4.0.2 (R Core Team 2020). All models were built and analysed using the lme4 package (Bates et al. 2015) and lmerTest (Kuznetsova et al. 2017), except for our repeatability models which were built and analysed using the rptR package (Stoffel et al. 2017).

**Collective coordination models (Alt-C and Sync-C)**

To investigate collective alternation and synchrony performed by all carers at a nest we defined two Poisson-distributed generalised linear mixed effects models (GLMM) named ‘Alt-C’ and ‘Sync-C’, respectively. The response variables to these models were the number of alternated visits (collective) and synchronised visits (collective) by all carers at each watch, respectively. To control for observation and population structure, these models were built with the following random effects: ‘Year’, ‘Nest ID’, ‘Watch ID’, ‘Male ID’, ‘Female ID’, ‘Helper1 ID’, ‘Helper2 ID’, ‘Helper3 ID’, ‘Collective Carer IDs’, and ‘Row reference’ (see Table 2.1 for explanation). The fixed effects tested were as follows: ‘Data type’ (observed vs. expected values of alternation and synchrony), ‘Provisioning rate (collective)’, ‘Carer number’, ‘Watch duration’, ‘Brood size’, ‘Time of day’, ‘Brood age’, ‘Hatch date’, and ‘AMax (or SMax)’ (Table 2.1). We focused our analysis on ‘Data type’ and 2-way interactions with other fixed effect terms, as a disparity between observed and expected data represents the level of active coordination performed.

**Individual coordination models (Alt-I and Sync-I)**

To investigate the effect of carer status on alternation and synchrony performed by a given carer, we built two Poisson-distributed GLMMs named ‘Alt-I’ and ‘Sync-I’, respectively. The response variables to these models were the number of alternated visits (individual) and synchronised visits (individual), respectively. These models were built with the following random effects: ‘Year’, ‘Nest ID’, ‘Watch ID’, ‘Carer ID’, and ‘Row reference’ (Table 2.1). The fixed effects tested were as follows: ‘Data type’, ‘Carer status’, ‘Provisioning rate (individual)’, ‘Carer number’, ‘Watch duration’, ‘Brood size’, ‘Time of day’, ‘Brood age’, ‘Hatch date’, and ‘AMax’ or ‘SMax’ (Table 2.1). In this analysis, the focus was on the interaction of ‘Data type’ with ‘Carer status’ because this term represents the disparity in active coordination between carers of different breeding status.

**Repeatability models (Alt-R and Sync-R)**

To investigate the repeatability of active alternation and synchrony within nests and within individuals we constructed two normally distributed GLMMs named ‘Alt-R’ and ‘Sync-R’, respectively. In these models, response variables were the number of actively alternated (individual) and actively synchronised (individual) visits by an individual during a watch, respectively (active alternation range: -3 to 6; active synchrony range: -7 to 9). We used these metrics because repeatability analyses required active coordination to be the response variable, rather than using interaction terms with ‘Data type’ as in our other models. To control for the effect of confounding factors on active coordination we included all fixed effects previously found to significantly influence either individual alternation or synchrony (‘Alt-I’, ‘Sync-I’) and, using the rptR function, ran models with 1000 bootstrapped simulations and 1000 permutations. We investigated both within-nest repeatability (‘Nest ID’) and within-individual repeatability (‘Carer ID’) in the same models. Additionally, we included ‘Year’ as a random effect to account for between-year variation. As active coordination was the response variable and a normal error distribution was used, ‘Watch ID’ and the ‘Row reference’ random effects were not required for these models. We present our repeatability results as values of R and extracted 2.5% and 97.5% confidence intervals (CIs) in addition to *P*-values.

In our dataset many individuals were observed provisioning at only one nest, potentially confounding repeatability of an individual’s behaviour with the potential effect of common nest factors. Therefore, we ran the repeatability analysis on a subset of data, restricted to carers observed provisioning at two or more nests (Table S2.2, supplementary material). Results from these models were qualitatively the same as those for the full dataset for both within-nest and within-individual repeatability for both alternation and synchrony models.

**Kinship models (Alt-K and Sync-K)**

To investigate the effect of kinship to the breeding pair on alternation and synchrony performed by helpers we constructed two Poisson-distributed GLMMs named ‘Alt-K’ and ‘Sync-K’, respectively. Just as with ‘Alt-I’ and ‘Sync-I’, the response variables to these models were the number of alternated visits (individual) and synchronised visits (individual) performed by an individual during a watch, respectively, however analysis was restricted to helpers whose pedigree kinship with breeders was known. These models were built with the same random and fixed effects as ‘Alt-I’ and ‘Sync-I’ but with the addition of three fixed effects: ‘Sex’, ‘Kinship with father’, and ‘Kinship with mother’ (Table 2.1). We focused our analysis on the interactions of ‘Data type’ with our kinship terms as these represent the relationship between the level of active coordination and relatedness.

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| Table 2.1. Details of response variables, fixed effects, random effects used in models and non-model terms. | |
| **Response variables** | **Description** |
| Alternated or synchronised visits (collective) | The absolute number of alternated or synchronised provisioning visits performed by all carers in a group during a watch. |
| Alternated or synchronised visit (individual) | The absolute number of alternated or synchronised provisioning visits performed by a given carer during a watch. |
| Active alternated or active synchronised visits (individual) | The absolute number of actively alternated or synchronised visits performed by a given carer during a given watch, calculated by subtracting a carer’s expected values from their observed values for each watch. |
| **Random effects** | **Description** |
| Year | The unique identifier for which field season year the provisioning watch was performed in. Included to account for variation caused by site wide environmental factors between years. |
| Nest ID | The unique identifier for each nest. Because multiple watches were performed at the same nest, this was included to account for variation caused by factors specific to the local environment e.g. invertebrate abundance and microclimate. |
| Watch ID | The unique identifier for each nest watch. Included to account for similarity between observed and expected data from the same watch. |
| Row reference | Observation level random effect, included as per recommendation from Ihle et al. (2019a) to account for overdispersion in Poisson-distributed models. |
| Individual Carer IDs | The unique identity of each individual carer present during a watch (‘Male ID’, ‘Female ID’, ‘Helper1 ID’, ‘Helper2 ID’, and ‘Helper3 ID’). Included as random effects to account for between individual variation in provisioning behaviour because some individuals were observed provisioning over multiple watches and nests (MacColl and Hatchwell 2003, Adams et al. 2015). However, 37/795 watches (4.7%) featured visits by a single unringed carer, these individuals could therefore not be distinguished with a unique Carer ID. Repeating analyses with these watches omitted produced qualitatively the same results in all cases. |
| Collective Carer ID | The unique identifier for a particular combination of carers seen provisioning during a given watch. Few pairs persist across years due to high annual mortality (Meade et al. 2010b) and divorce rate (Hatchwell et al. 2000) and carer combinations may change daily as helpers join and leave, so ‘Collective Carer ID’ was included to account for between group variation in provisioning coordination. |
| **Fixed effects** | **Description** |
| Data type | Factor designating whether data were observed (from field data) or expected (generated by null model). As we used expected values as our baseline level of coordination ‘Data type’ was therefore a proxy for the level of active coordination performed. Our assessment of whether other terms significantly impact active coordination was investigated by looking at their interaction with ‘Data type’. |
| Provisioning rate (collective) | The total number of provisioning visits performed by all carers during a given watch per hour, modelled as continuous numerical values (mean: 24.1; range: 5.8–69.2). |
| Provisioning rate (individual) | The total number of provisioning visits performed by a given carer during a provisioning watch per hour, modelled as continuous numerical values (mean: 9.6; range: 0.5–34.3). |
| Brood size | The number of live chicks recorded at the nest on day 11, modelled as integer values (median: 8; range 1–12). Included because prior studies have shown that brood size influences provisioning behaviour by mediating brood demand (Meade et al 2010b).We used a single recorded measure of brood size, rather than recording brood size after each watch to minimise nest disturbance and because brood reductions are rare in long-tailed tits, having only a 0.2% daily chick mortality rate via starvation (Hatchwell et al. 2004). |
| Carer number | The number of adult birds that provisioned chicks during a given provisioning watch, modelled as an ordinal factor: 5>4>3>2. |
| Watch duration | The length of time in minutes between the first and last feeding visit during a provisioning watch, included as an interaction term with ‘Data type’ to account for potential artificial coordination caused by setup disturbance, which would disproportionately affect shorter watches. Watch duration was modelled as a continuous numerical value. |
| AMax (or SMax) | To account for the upper limit of the number of alternated or synchronised visits we used the variables ‘AMax’ and ‘SMax’ which are the theoretical maximum percentage of provisioning visits that can be alternated/synchronised during a given watch, modelled as a continuous numerical value (mean: 87.5; range: 19.4–98.6). If one carer performed more than half the total visits then some visits exist which cannot be alternated or synchronised due to insufficient visits to alternate or synchronise with, this applies to all values of carer number. This term is used as a proxy for feed rate asymmetry, i.e. the difference between provisioning rates of male and females, used by Bebbington and Hatchwell (2016), but is also applicable for cooperative nests. AMax and SMax must always be the same value for a given watch because synchrony was defined as an alternated feed occurring within 2 minutes of the previous feed. This time restriction can always theoretically be met, so the only remaining restriction on synchrony is whether a feed can be alternated. |
| Brood age | The number of days since recorded hatching (day 0) of chicks at a nest, modelled as integer values (range: 6–16). |
| Hatch date | The number of days after 1st of March each year, modelled as integer values (median: 3rd May; range: 16th April–6th June). |
| Time of day | The number of hours since the beginning of the day on which the provisioning watch was performed, modelled as a numerical value. Included because previous studies on the same population found higher provisioning activity immediately following sunrise (MacColl and Hatchwell 2002, Hatchwell et al. 2004). |
| Sex | Binary factor representing either male or female helpers. |
| Carer status | Factor designating the relationship each carer had to the brood with three categories: breeding female, breeding male, and helper. For our final analysis we did not sub-divide helpers by sex because our investigation on helper coordination ‘(Alt-K’, ‘Sync-K’; see results) found no effect of sex on helpers’ alternation or synchrony (tables 2.5 and 2.6). |
| Kinship with father | Factor representing the pairwise relatedness of helpers to breeding male. Modelled as factors with three levels representing first order kin (r = 0.50), second order kin (r = 0.25) and unrelated individuals (r = 0.00). These levels were selected in accordance with results from previous studies demonstrating kinship of helpers with breeders (Leedale et al. 2018, 2020b). |
| Kinship with mother | Factor representing pairwise relatedness of helper to breeding female. |
| **Non-model terms** | **Description** |
| Percent of AMax (or Percent of SMax) | The overall percentage of visits which could be alternated/synchronised which were alternated or synchronised. These terms was used as the dependent variables in Figures 2.2a,b and 2.3a,b, being the best single metrics for visualising active coordination as they factor in both total feed rate and what proportion of visits could be alternated or synchronised. |

**2.4 Results**

**2.4.1 Carer number**

To test the hypothesis that carers exhibited behaviours resulting in alternated visits, model ‘Alt-C’ compared observed alternation with that expected by chance from null model randomisation. We found that observed alternation was indeed significantly higher than expected by chance, as indicated by the significance of the data type term (*P* < 0.001, Table 2.2). To investigate the effect of other terms on active alternation, we measured their effect on the difference between observed and expected data, i.e. their interaction with data type. Carer number had a positive effect on both expected and observed alternation (Table 2.2), but the interaction term with data type was significant (*P* = 0.024, Table 2.2, Figure 2.2a), indicating that the difference between them, i.e. active alternation, declined as carer number increased. The degree of active alternation was not significantly related to time of day, watch duration, brood size, or provisioning rate (Table 2.2, Figure 2.2b).

To test the hypothesis that carers actively synchronised provisioning visits, we used model ‘Sync-C’ to compare observed and expected synchrony. Just as for alternation, observed synchrony was greater than expected by chance, the data type term being significant (*P* < 0.001, Table 2.3). However, in contrast to our results for alternation, there was no significant interaction between data type and carer number (Table 2.3, Figure 2.3a), indicating that the level of active synchrony was similar at all group sizes. Investigation of the interaction between data type and other predictors of synchrony showed that provisioning rate was the only factor to influence the degree of active synchrony (*P* < 0.001, Table 2.3, Figure 2.3b), the difference between observed and expected synchrony declining with increasing provisioning rate. This result was expected because as provisioning rates increase, the probability that two birds feed within a 2-minute period, even by passive process, inevitably increases. Neither brood size, time of day, nor watch duration was a significant predictor of the level of active synchrony (Table 2.3).

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| Table 2.2. Estimates and *P*-values for fixed effect terms on number of alternated visits per provisioning watch from generalised linear mixed effect model; *N* = 1,590 from 795 watches at 250 nests, significant values in bold. ‘Obs’ is shorthand for data observed directly from field, as opposed to expected data generated from null model. | | | | |
| Parameter | df | Estimate ± SE | F-value | *P*-value |
| **Intercept** | **1** | **2.546 ± 0.014** |  | **<0.001** |
| **Data Type (relative to expected)** | **1** | **Obs: 0.099 ± 0.017** | **38.11** | **<0.001** |
| **Provisioning Rate** | **1** | **0.303 ± 0.010** | **3452.27** | **<0.001** |
| **Brood Size** | **1** | **0.034 ± 0.011** | **22.88** | **<0.001** |
| **Carer Number (relative to 2 carers)** | **3** | **3: 0.135 ± 0.024**  **4: 0.210 ± 0.029**  **5: 0.196 ± 0.050** | **152.88** | **<0.001** |
| **Watch Duration** | **1** | **0.195 ± 0.008** | **1247.49** | **<0.001** |
| **AMax** | **1** | **0.131 ± 0.009** | **209.17** | **<0.001** |
| Brood Age | 1 | 0.000 ± 0.007 | 0.01 | 0.973 |
| Hatch Date | 1 | 0.012 ± 0.008 | 2.21 | 0.126 |
| Time of Day | 1 | -0.016 ± 0.010 | 6.76 | 0.055 |
| Data Type \* Provisioning Rate | 1 | 0.017 ± 0.012 | 0.43 | 0.133 |
| Data Type \* Brood Size | 1 | 0.004 ± 0.014 | 0.02 | 0.798 |
| **Data Type \* Carer Number** | **3** | **Obs, 3: -0.069 ± 0.031**  **Obs, 4: -0.094 ± 0.037**  **Obs, 5: -0.096 ± 0.067** | **2.68** | **0.024** |
| Data Type \* Watch Duration | 1 | 0.015 ± 0.010 | 2.11 | 0.134 |
| Data Type \* Time of Day | 1 | 0.005 ± 0.013 | 0.17 | 0.683 |

A close-up of a graph

Description automatically generated

Figure 2.2. Plots of observed (orange) and expected (purple) percent of maximum alternation achieved by carers versus: (a) the number of carers observed provisioning each nest during a watch; and (b) the total provisioning rate by all carers at a nest during a given watch. Predicted relationships (± 95% CI) are fitted from GLMMs, see Table 2.1. Total *N* = 795 watches on 250 nests for each data type.

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| Table 2.3. Output values for fixed effect terms on number of synchronised visits per provisioning watch from generalised linear mixed effect model, *N* = 1,590 from 795 watches at 250 nests, significant values in bold. | | | | |
| Parameter | df | Estimate ± SE | F-value | *P*-value |
| **Intercept** | **1** | **1.798 ± 0.055** |  | **<0.001** |
| **Data Type (relative to expected)** | **1** | **Obs: 0.245 ± 0.024** | **100.94** | **<0.001** |
| **Provisioning Rate** | **1** | **0.472 ± 0.013** | **3240.41** | **<0.001** |
| **Brood Size** | **1** | **0.064 ± 0.016** | **36.85** | **<0.001** |
| **Carer Number (relative to 2 carers)** | **3** | **3: 0.113 ± 0.034**  **4: 0.221 ± 0.062**  **5: 0.182 ± 0.089** | **44.41** | **<0.001** |
| **Watch Duration** | **1** | **0.200 ± 0.012** | **667.33** | **<0.001** |
| **SMax** | **1** | **0.147 ± 0.013** | **127.52** | **<0.001** |
| Brood Age | 1 | 0.014 ± 0.010 | 1.74 | 0.186 |
| Hatch Date | 1 | 0.013 ± 0.012 | 1.08 | 0.231 |
| Time of Day | 1 | -0.023 ± 0.014 | 1.3 | 0.485 |
| **Data Type \* Provisioning Rate** | **1** | **-0.050 ± 0.015** | **19.79** | **<0.001** |
| Data Type \* Brood Size | 1 | <0.001 ± 0.019 | <0.01 | 0.969 |
| Data Type \* Carer Number | 3 | Obs, 3: -0.030 ± 0.041  Obs, 4: -0.061 ± 0.048  Obs, 5: -0.057 ± 0.085 | 0.46 | 0.574 |
| Data Type \* Watch Duration | 1 | 0.017 ± 0.014 | 1.19 | 0.186 |
| Data Type \* Time of Day | 1 | 0.024 ± 0.018 | 2.11 | 0.146 |

A close-up of a graph

Description automatically generated

Figure 2.3. Plots of observed (orange) and expected (purple) percent of maximum synchrony achieved by carers versus: (a) the number of carers observed provisioning each nest during a watch; and (b) the total provisioning rate by all carers at a nest during a given watch. Predicted relationships (± 95% CI) are fitted from GLMMs, see Table 2.1. Total *N* = 795 watches on 250 nests for each data type.

**2.4.2 Carer status**

To investigate variation in alternation behaviour by birds of different status (breeding male, breeding female, helper) we used model ‘Alt-I’. Carer status appeared to influence the overall level of alternation (*P* = 0.037, Table 2.4), but did not influence the extent of active alternation because the interaction term with data type was non-significant (*P* = 0.975, Table 2.4, Figure 2.4a).

In contrast, in model ‘Sync-I’ the extent of active synchrony was influenced significantly by carer status, as indicated by the interaction term with data type (*P* = 0.024, Table 2.5, Figure 2.5a), with helpers performing the most active synchrony followed by breeding males then breeding females.

The extent of individual active synchrony was also influenced significantly by carer number (*P* < 0.001, Table 2.5), a relationship which was not observed in the collective synchrony model ‘Sync-C’ (*P* = 0.574, Table 2.2). We suspected that this trend may be due to covariances between carer number, individual and total provisioning rate, coupled with load-lightening and the provisioning rate dependence of the null model (*P* < 0.001, Table 2.2, Figure 2.3b). Refitting the model with total provisioning rate and appropriate interaction terms revealed that the effect of carer number on active synchrony was contained within multiple significant 3-way interaction terms which are probably a consequence of load-lightening behaviour and the rate dependence of the synchrony null model (Table 2.2, Figure 2.3b). Importantly, however, the results for the effect of carer status on active synchrony remained qualitatively the same.

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| Table 2.4. Estimates and *P*-values for fixed effect terms on number of alternated visits per individual carer during a watch from generalised linear mixed effect model; *N* = 1,997 samples from 487 unique carers from 795 watches at 250 nests, significant values in bold. | | | | |
| Parameter | df | Estimate ± SE | F-value | *P*-value |
| **Intercept** | **1** | **1.722 ± 0.019** |  | **<0.001** |
| **Data Type (relative to expected)** | **1** | **Obs: 0.056 ± 0.024** | **18.07** | **<0.001** |
| **Carer status (relative to breeding male)** | **2** | **F: 0.030 ± 0.020**  **H: -0.012 ± 0.028** | **49.90** | **0.037** |
| **Individual Provisioning Rate** | **1** | **0.303 ± 0.010** | **2576.93** | **<0.001** |
| **Brood Size** | **1** | **0.045 ± 0.011** | **55.89** | **<0.001** |
| **Carer Number (relative to 2 carers)** | **3** | **3: 0.008 ± 0.026**  **4: 0.027 ± 0.032**  **5: -0.093 ± 0.053** | **31.05** | **0.018** |
| **Watch Duration** | **1** | **0.181 ± 0.008** | **1089.08** | **<0.001** |
| **AMax** | **1** | **0.152 ± 0.009** | **280.17** | **<0.001** |
| **Brood Age** | **1** | **0.024 ± 0.007** | **19.37** | **<0.001** |
| Hatch Date | 1 | 0.015 ± 0.008 | 3.44 | 0.079 |
| **Time of Day** | **1** | **-0.023 ± 0.010** | **15.61** | **0.003** |
| Data Type \* Carer status | 3 | Obs, F: 0.002 ± 0.028  Obs, H: 0.009 ± 0.039 | 0.92 | 0.975 |
| Data Type \* Individual Provisioning Rate | 1 | 0.018 ± 0.012 | 4.38 | 0.137 |
| Data Type \* Brood Size | 1 | 0.007 ± 0.014 | 0.01 | 0.609 |
| Data Type \* Carer Number | 3 | Obs, 3: -0.056 ± 0.033  Obs, 4: -0.078 ± 0.041  Obs, 5: -0.060 ± 0.070 | 1.28 | 0.207 |
| **Data Type \* Watch Duration** | **1** | **0.021 ± 0.010** | **3.93** | **0.044** |
| Data Type \* Time of Day | 1 | 0.005 ± 0.013 | 0.12 | 0.726 |

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Figure 2.4. Boxplots of observed (orange) and expected (purple) percentage of visits alternated by a given individual during a watch versus: (a) the status of a carer; (b) the kinship between a helper and the breeding male; and (c) the kinship between a helper and the breeding female. Total *N* = 408 samples from 130 unique helpers from 273 watches at 95 nests for each data type.

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| Table 2.5. Estimates and *P*-values for fixed effect terms on number of synchronised visits per provisioning individual carer during a watch from generalised linear mixed effect model; *N* = 1,997 samples from 487 unique carers from 795 watches at 250 nests, significant values in bold. | | | | |
| Parameter | df | Estimate ± SE | F-value | *P*-value |
| **Intercept** | **1** | **0.905 ± 0.033** |  | **<0.001** |
| **Data Type (relative to expected)** | **1** | **Obs: 0.301 ± 0.033** | **59.70** | **<0.001** |
| Carer status (relative to breeding male) | 2 | F: 0.059 ± 0.033  H: 0.035 ± 0.042 | 8.89 | 0.210 |
| **Individual Provisioning Rate** | **1** | **0.444 ± 0.014** | **2132.76** | **<0.001** |
| **Brood Size** | **1** | **0.089 ± 0.017** | **72.06** | **<0.001** |
| **Carer Number (relative to 2 carers)** | **3** | **3: 0.097 ± 0.039**  **4: 0.236 ± 0.048**  **5: 0.164 ± 0.075** | **37.97** | **0.019** |
| **Watch Duration** | **1** | **0.180 ± 0.012** | **472.16** | **<0.001** |
| **SMax** | **1** | **0.177 ± 0.015** | **162.39** | **<0.001** |
| **Brood Age** | **1** | **0.071 ± 0.010** | **60.29** | **<0.001** |
| Hatch Date | 1 | 0.011 ± 0.015 | 0.36 | 0.464 |
| **Time of Day** | 1 | -0.052 ± 0.014 | 9.46 | **0.005** |
| **Data Type \* Carer status** | **3** | **Obs, F: -0.079 ± 0.037**  **Obs, H: 0.042 ± 0.051** | **1.56** | **0.024** |
| **Data Type \* Individual Provisioning Rate** | **1** | **-0.084 ± 0.016** | **21.42** | **<0.001** |
| Data Type \* Brood Size | 1 | 0.010 ± 0.019 | 0.11 | 0.602 |
| **Data Type \* Carer Number** | **3** | **Obs, 3: -0.133 ± 0.044**  **Obs, 4: -0.234 ± 0.053**  **Obs, 5: -0.252 ± 0.089** | **7.41** | **<0.001** |
| Data Type \* Watch Duration | 1 | 0.023 ± 0.014 | 1.74 | 0.092 |
| **Data Type \* Time of Day** | **1** | **0.004 ± 0.017** | **5.80** | **0.016** |

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Figure 2.5. Boxplots of observed (orange) and expected (purple) percentage of visits synchronised by a given individual during a watch versus: (a) the status of a carer; (b) the kinship between a helper and the breeding male; and (c) the kinship between a helper and the breeding female. Total *N* = 408 samples from 130 unique helpers from 273 watches at 95 nests for each data type.

**2.4.3 Repeatability of coordination**

Using model ‘Alt-R’ we assessed whether active alternation was consistent within individuals and/or within groups of carers working together at a nest. Active alternation of carers was significantly repeatable within nests (R = 0.145, CI (2.5-97.5%) = 0.010–0.186, *P* < 0.001), but not within individuals (R = 0.000, CI (2.5-97.5%) = 0.000–0.031, *P* = 0.500, Figure 2.6a), indicating that the degree of alternation was a property of social or nest-specific factors. In contrast, model ‘Sync-R’ showed that active synchrony of carers was significantly repeatable within individuals (R = 0.183, CI (2.5–97.5%) = 0.130–0.228, *P* < 0.001), but not within nests (R = 0.000, CI (2.5–97.5%) = 0.000–0.009, *P* = 1.00, Figure 2.6b), indicating that the level of synchrony was a property of individual identity rather than the nest or social environment.

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Figure 2.6. Estimates (R) of the within nest repeatability (Nest ID) and within individual repeatability (Carer ID) for the absolute number of actively (a) alternated and (b) synchronised visits. Estimates calculated from linear mixed effects models (2.5–97.5% CI).

**2.4.4 Helper kinship**

We found no significant effects of helper kinship to the helped breeders on any measures of coordination. Model ‘Alt-K’ investigated variation in alternation behaviour between helpers of varying kinship, but neither the overall level of alternation by helpers nor their degree of active alternation was influenced significantly by their kinship with either the breeding male (Table 2.6, Figure 2.4b) or breeding female (Table 2.6, Figure 2.4c). Similarly, model ‘Sync-K’ showed that neither the overall level of synchrony exhibited by helpers, nor the extent of active synchrony was influenced by kinship with either the breeding male (Table 2.7, Figure 2.5b) or breeding female (Table 2.7, Figure 2.5c).

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| Table 2.6. Estimates and *P*-values for fixed effect terms on number of alternated visits per individual helper during a watch from generalised linear mixed effect model; *N* = 408 samples from 130 unique helpers from 273 watches at 95 nests, significant values in bold. | | | | |
| Parameter | df | Estimate ± SE | F-value | *P*-value |
| **Intercept** | **1** | **1.486 ± 0.159** |  | **<0.001** |
| Data Type (relative to expected) | 1 | Obs: 0.038 ± 0.190 | 0.97 | 0.782 |
| Kinship with Breeding Male (relative to r = 0) | 2 | 0.25: 0.059 ± 0.088  0.5: -0.022 ± 0.057 | 1.47 | 0.837 |
| Kinship with Breeding Female (relative to r = 0) | 2 | 0.25: -0.079 ± 0.141  0.5: 0.012 ± 0.073 | 6.88 | 0.837 |
| Sex (relative to female) |  | M: -0.024 ± 0.057 | 0.04 | 0.728 |
| **Individual Provisioning Rate** | **1** | **0.352 ± 0.022** | **786.89** | **<0.001** |
| Brood Size | 1 | 0.024 ± 0.026 | 0.06 | 0.139 |
| Carer Number | 3 | 3: 0.166 ± 0.147  4: 0.206 ± 0.155  5: 0.069 ± 0.164 | 8.63 | 0.088 |
| **Watch Duration** | **1** | **0.228 ± 0.020** | **390.19** | **<0.001** |
| **AMax** | **1** | **0.070 ± 0.030** | **5.84** | **0.019** |
| Brood Age | 1 | 0.019 ± 0.016 | 1.47 | 0.238 |
| Hatch Date | 1 | 0.033 ± 0.018 | 3.44 | 0.078 |
| Time of Day | 1 | -0.022 ± 0.023 | 3.76 | 0.175 |
| Data Type \* Kinship with Breeding Male | 2 | Obs, 0.25: -0.066 ± 0.123  Obs, 0.5: 0.017 ± 0.075 | 0.22 | 0.818 |
| Data Type \* Kinship with Breeding Female | 2 | Obs, 0.25: 0.039 ± 0.196  Obs, 0.5: -0.017 ± 0.102 | 0.04 | 0.965 |
| Data Type \* Sex | 1 | Obs, M: 0.020 ± 0.080 | 0.16 | 0.804 |
| Data Type \* Individual Provisioning Rate | 1 | 0.025 ± 0.028 | 1.30 | 0.377 |
| Data Type \* Brood Size | 1 | 0.008 ± 0.035 | 0.01 | 0.828 |
| Data Type \* Carer Number | 3 | Obs, 3: -0.065 ± 0.172  Obs, 4: -0.077 ± 0.178  Obs, 5: -0.048 ± 0.191 | 0.07 | 0.972 |
| Data Type \* Watch Duration | 1 | 0.023 ± 0.025 | 0.92 | 0.348 |
| Data Type \* Time of Day | 1 | -0.001 ± 0.032 | 0.00 | 0.984 |

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| Table 2.7. Estimates and *P*-values for fixed effect terms on number of synchronised visits per individual helper during a watch from generalised linear mixed effect model; *N* = 408 samples from 130 unique helpers from 273 watches at 95 nests, significant values in bold. | | | | |
| Parameter | df | Estimate ± SE | F-value | *P*-value |
| **Intercept** | **1** | **0.808 ± 0.229** |  | **<0.001** |
| Data Type (relative to expected) | 1 | Obs: 0.648 ± 0.245 | 25.37 | **<0.001** |
| Kinship with Breeding Male (relative to r = 0) | 2 | 0.25: 0.084 ± 0.128  0.5: 0.029 ± 0.084 | 1.60 | 0.683 |
| Kinship with Breeding Female (relative to r = 0) | 2 | 0.25: 0.208 ± 0.192  0.5: 0.067 ± 0.106 | 1.33 | 0.731 |
| Sex (relative to female) |  | M: -0.036 ± 0.081 | 3.01 | 0.562 |
| **Individual Provisioning Rate** | **1** | **0.432 ± 0.030** | **558.01** | **<0.001** |
| **Brood Size** | **1** | **0.064 ± 0.039** | **4.30** | **0.034** |
| **Carer Number (relative to 2 carers)** | **3** | **3: 0.132 ± 0.211**  **4: 0.285 ± 0.221**  **5: 0.116 ± 0.237** | **5.17** | **0.047** |
| **Watch Duration** | **1** | **0.187 ± 0.029** | **153.70** | **<0.001** |
| **SMax** | **1** | **0.130 ± 0.045** | **8.20** | **0.004** |
| **Brood Age** | **1** | **0.047 ± 0.022** | **5.44** | **0.029** |
| Hatch Date | 1 | 0.033 ± 0.030 | 1.26 | 0.276 |
| **Time of Day** | **1** | **-0.073 ± 0.032** | **7.16** | **0.026** |
| Data Type \* Kinship with Breeding Male | 2 | Obs, 0.25: -0.016 ± 0.158  Obs, 0.5: 0.016 ± 0.097 | 0.01 | 0.982 |
| Data Type \* Kinship with Breeding Female | 2 | Obs, 0.25: -0.180 ± 0.246  Obs, 0.5: -0.122 ± 0.132 | 0.43 | 0.517 |
| Data Type \* Sex | 1 | Obs, M: 0.002 ± 0.100 | 0.50 | 0.982 |
| Data Type \* Individual Provisioning Rate | 1 | -0.050 ± 0.035 | 0.27 | 0.158 |
| Data Type \* Brood Size | 1 | -0.001 ± 0.045 | 0.79 | 0.981 |
| Data Type \* Carer Number | 3 | Obs, 3: -0.409 ± 0.222  Obs, 4: -0.487 ± 0.229  Obs, 5: -0.470 ± 0.244 | 1.73 | 0.190 |
| **Data Type \* Watch Duration** | **1** | **0.063 ± 0.031** | **3.52** | **0.043** |
| Data Type \* Time of Day | 1 | 0.039 ± 0.041 | 0.92 | 0.337 |

**2.5 Discussion**

We found strong evidence for active coordination of care, with both alternation and synchrony being observed more than expected by chance. Active synchrony was detected across the full range of two to five carers (Figure 2.3a), whereas active alternation was detected only in biparental nests and cooperative nests with one helper (Figure 2.2a). Additionally, while breeding males, females, and helpers did not differ in their degree of active alternation (Figure 2.4a), helpers exhibited more active synchrony than breeders, and male breeders showed more active synchrony than female breeders (Figure 2.5a). We also found that the level of active alternation was linked to nest identity (Figure 2.6a), whereas active synchrony was linked to individual carer identity (Figure 2.6b), suggesting that alternation is a plastic behaviour in response to social environment, while synchrony is influenced by both an individual’s identity and current carer status. Finally, contrary to our expectations, the degree of helper coordination was unaffected by their kinship with either breeding bird (Figure 2.4b,c, Figure 2.5b,c).

The null hypothesis of a study seeking to quantify coordination of care is not that there is no apparent coordination, but rather that the observed level of coordination may be wholly explained by passive processes that affect provisioning, such as weather, predation threat, and resource distributions (Schlicht et al. 2016, Ihle et al. 2019a). We used the most conservative randomisation approach (Ihle et al. 2019a), conserving individual refractory periods and hence controlling for much of the coordination that may be explained by passive processes. Our method of data collection and analysis also accounted for potential observer disturbance effects that could enhance apparent coordination. On the other hand, the randomisation process effectively decouples the refractory periods of carers at the same nest, so factors such as weather and predation threat that may impact all carers at the same time remain difficult to control for statistically. However, it can also be argued that highly conservative null models which re-order observed data retain a degree of active coordination that is reflected in refractory periods, thereby underestimating the true level of active coordination. Therefore, we conclude that our results support the case for active coordination of care in long-tailed tits.

The hypothesised function of alternation is that it facilitates conflict resolution between carers because conditional cooperation prevents exploitation by ensuring that carers match changes in one another’s provisioning rates (Johnstone et al. 2014). This enables carers to increase their investment to more closely match the brood’s optimum care level (Trivers 1974) without causing other carers to slacken their effort to increase their individual fitness pay-off. Our finding that active alternation declined as the number of carers increased may indicate a reduced need to monitor the investment of others when care is plentiful, especially as individual carers reduce their own costs by load-lightening when they have helpers (Hatchwell and Russell 1996, Meade et al. 2010b, Adams et al. 2015). This result contrasts with findings from chestnut-crowned babblers, *Pomatostomus ruficeps*, where active alternation was observed across the full range of carer numbers (2–6), using the same null model approach (Savage et al. 2017). This disparity may be due to differences in the ecology or social system of chestnut-crowned babblers and long-tailed tits. Babblers must gather food far from the nest despite not being proficient long-distance fliers, thus incurring substantial provisioning costs (Browning et al. 2012). Therefore, a strict and efficient allocation of effort between carers, with close monitoring, may remain important in this species even in large cooperative groups. In contrast, long-tailed tits are thought to suffer relatively modest costs of parental care (Meade and Hatchwell 2010, Hatchwell et al. 2014), so individual effort may be monitored less closely, resulting in a decline in active alternation with carer number.

Alternatively, the decline in active alternation with carer number may be a consequence of the null model failing to detect active alternation in large groups. In our study, expected alternation approached 90% in 4–5 carer nests, which contrasts with expected synchrony of just 50% or so in larger groups; thus, the scope for detection of active synchrony is greater than it is for active alternation. However, it is unlikely that detectability alone caused our result because Savage et al.’s (2017) study of chestnut-crowned babblers used the same null model approach across a greater range of group sizes (2–6), with expected alternation of >80% at large group sizes, and yet they did not observe the same trend.

We observed no significant difference in active alternation by carers of different status and subsequent analysis revealed that the level of active alternation was highly repeatable within nests rather than within individual carers. These results suggest that that if alternation is adaptive, it is performed by all carers at the nest to their collective benefit, rather than by certain individuals. However, we cannot disentangle whether this is a function of common nest factors or common social environment (Ihle et al. 2019a). For example, some nests may experience regular disturbance by predators that temporarily prevents feeding, causing the feeding cycles of carers to align, thus increasing alternation. Our finding that active alternation was unaffected by carer status could be explained by the interests of breeders and helpers being closely aligned. Long-tailed tit helpers gain only kin-selected benefits from their helping behaviour (Meade and Hatchwell 2010, Hatchwell et al. 2014), and rates of extra-pair paternity and intraspecific brood parasitism are low (Hatchwell et al. 2002) so all carers have a shared interest in raising a related brood. In species where the dynamics of conflict are different the extent of alternation may vary between carers of different status whilst still ultimately providing the adaptive function of conflict resolution (Johnstone et al. 2014, Johnstone and Savage 2019). This may explain why breeders alternate more to ensure the contribution of helpers in chestnut-crowned babblers (Savage et al. 2017) and our contrary finding does not necessarily invalidate conflict resolution as a function of alternation in long-tailed tits.

One proposed function of synchrony is that it facilitates accurate alternation via monitoring of other carers (Mariette and Griffith 2012, 2015, Bebbington and Hatchwell 2016), but there are other adaptive hypotheses for synchrony that do not require alternation *per se*. Synchrony may decrease parental activity at the nest, thereby reducing its conspicuousness and exposure to predators (Raihani et al. 2010, Mariette and Griffith 2012, 2015, Leniowski and Węgrzyn 2018, Khwaja et al. 2019). However, our finding that active synchrony was broadly consistent across group sizes does not support this hypothesis, because in larger groups, where the risk of exposing the nest to a predator may be greater, active synchrony should increase. Alternatively, synchrony may ensure an even distribution of food between chicks by preventing monopolisation (Shen et al. 2010, Mariette and Griffith 2012, 2015). However, contrary to our results, this hypothesis predicts that synchrony would decrease with group size as the increased rate of food delivery reduced the risk of monopolisation. A detailed investigation of the consequences of synchrony for parental activity at the nest, the probability of predation, nestling growth, and survival is beyond the scope of the current study.

Helpers synchronised their nest visits with other carers more than breeders did. One explanation for this result is that helpers synchronise visits to signal their effort to other carers to increase their ‘prestige’ (Zahavi 1977a,b). Most studies have refuted this hypothesis (e.g. McDonald et al. 2008a,b, Raihani et al. 2010, Nomano et al. 2015), but there is some limited empirical support (Doutrelant and Covas 2007, Trapote et al. 2021). For example, in carrion crows, *Corvus corone*, subordinate female helpers overlapped their feeding visits with breeders more than either male helpers or breeders did. This was interpreted as a ‘pay-to-stay’ system where female helpers, which are typically unrelated to breeders (unlike male helpers), signal their effort to remain within the group until they achieve breeding status in their own group (Trapote et al. 2021). Our results appear to support this hypothesis, but we think it is an unlikely explanation for the relatively high synchrony exhibited by long-tailed tit helpers. Helpers are expected to gain direct fitness via signalling when helping is payment of rent for living on the breeders’ territory (Gaston 1978, Kokko et al. 2002, Trapote et al. 2021), or if it increases an individual’s social status or perceived quality among other carers (Zahavi 1977a,b, Lotem et al. 1999). However, studies have yet to detect any direct fitness benefits for helpers from their altruistic care in long-tailed tits (Hatchwell 2016). Therefore, unlike carrion crows, group membership, breeding opportunities, and future direct fitness are not determined by helping behaviour (Napper and Hatchwell 2016, Meade and Hatchwell 2010), so there seems to be no advantage for helpers from signalling their quality to other carers.

We suggest instead that variation in synchrony between carers of different status may be a consequence of group foraging. Collective foraging behaviour may explain synchrony in zebra finches, *Taeniopygia castanotis* (formerly *T. guttata*) (Mariette and Griffith 2012, 2015), where it is thought to reduce predation risk for carers. This hypothesis would not necessarily predict that carers of different status should differ consistently in their degree of synchrony, nor that synchrony would be highly repeatable within individuals, unless also coupled with a defined feeding order. If helpers tend to follow breeders in their visits to the nest, the way in which we measured synchrony means that they would also tend to have a relatively high synchrony score. Apparent following behaviour could result from helpers shadowing breeders or from breeders delaying feeds until helpers are present. In the redirected helping system of long-tailed tits, helpers are likely to be less familiar with the brood and local area than breeders are, so the idea that helpers shadow foraging breeders is plausible. Furthermore, the suggestion that individuals may adopt specific roles, i.e. as leader or follower, when foraging or when visiting nests may also explain why synchrony is individually repeatable. However, more detailed observations of the behavior of individuals as they approach the nest and the sequence in which they do so are needed to investigate these possibilities.

Active coordination by helpers was not influenced significantly by their kinship with the breeders they assisted. This result was unexpected because helper decisions in long-tailed tits, both in who to help and how much to help, are a function of their relatedness to the breeding pair (Russell and Hatchwell 2001, Nam et al. 2010, Leedale et al. 2018, 2020b). Additionally, if alternation functions to resolve conflict between carers, we might expect greater conflict in less related groups, so we anticipated some effect of kinship on coordination. Comparisons with the repeatability results are potentially instructive. The kinship of a helper to breeders is a function of the group, i.e. it is the dyadic relatedness between a helper and a specific male or female breeder, rather than a property of the helper *per se*. We suggested above that the repeatability of alternation within groups could be a function of the social environment (e.g. group composition), which could include kinship. However, the absence of a kinship effect, suggests either that some ecological rather than social factor specific to a nest or group drives the repeatability of alternation, or that a social factor other than kinship (e.g. group familiarity) influences alternation. In contrast, repeatability in synchrony was at the level of individuals rather than groups. Therefore, it is perhaps unsurprising that synchrony of helpers was not predicted by their kinship with breeders, given that this is a property of two or more individuals rather than an individual helper. To our knowledge, this is the first study to explicitly test whether kinship influences coordination, and it would be interesting to explore this question more widely, and especially in species where the interests of helpers and breeders are not so closely aligned.

Several explanations for active alternation and synchrony have linked the two phenomena, with synchrony proposed as an adaptation for ensuring accurate monitoring of other carers, thus enabling alternation (Mariette and Griffith 2012, 2015, Bebbington and Hatchwell 2016). Whilst studies have often found a correlation between alternation and synchrony, several of our findings suggest that alternation and synchrony may, in fact, fulfil separate functions. Firstly, active alternation declined with increasing carer number, whilst active synchrony did not. Secondly, active synchrony varied between carers of different status, whilst active alternation did not. Finally, active alternation was repeatable between watches at the same nest, whilst active synchrony was repeatable between watches of the same individual. The independence of alternation and synchrony is also supported by a study of blue tits, *Cyanistes caeruleus*,which demonstrated that synchrony, but not alternation varied between different habitats (Lejeune et al. 2019). This is compatible with Johnstone et al. (2014)’s theory of conflict resolution for alternation and our suggestions of shadowing for synchrony.

Studies of coordination in parental care are still in their infancy, and much work remains to be done to fully understand its occurrence, function, and the causes of interspecific variation. Careful analysis of provisioning visits is essential to generate appropriate null models against which observed schedules of visits can be compared. In this study, adopting a conservative approach, we have shown that coordination is, to some extent, a function of group size in the cooperative breeding system of long-tailed tits. We have also shown that some measures of coordination vary with social role within groups, but not with the kinship of helpers. In addition, we highlight the need for investigation of the proximate mechanisms by which individuals coordinate care, such as delaying feeding or shadowing others, as well as a need for experimental studies that can isolate and test social and environmental influences that are hard to take account of in observational studies. Finally, despite coordination of care being quite widely demonstrated in nature, the function of these behaviours remains poorly understood.

**2.6 Acknowledgments and data availability**

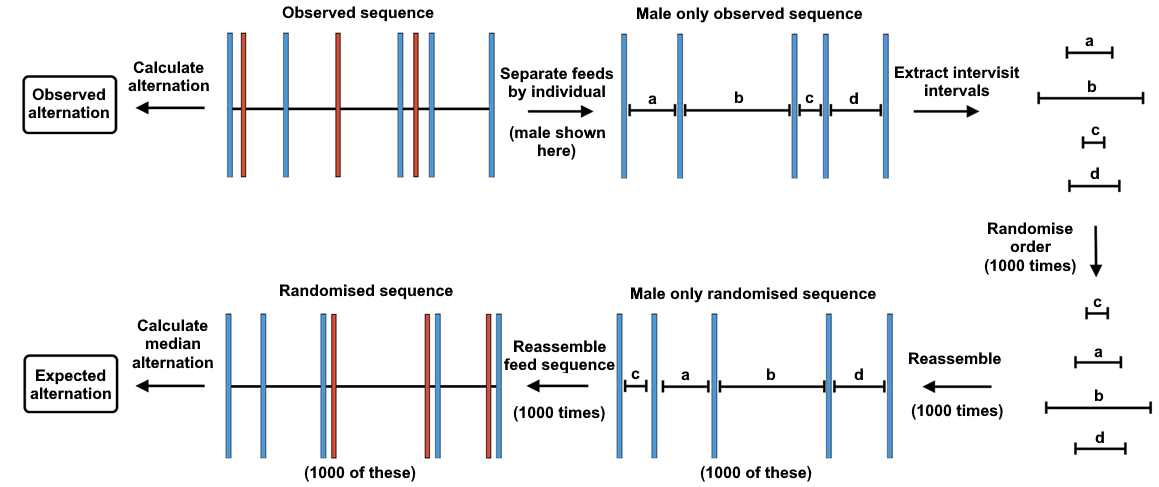
We are grateful to all field researchers who have contributed to the long-tailed tit project, and thank Sheffield City Council, Yorkshire Water, Hallamshire Golf Club, and private landowners of the Rivelin Valley for access to their land. Molecular analyses were conducted at the Natural Environment Research Council (NERC) Biomolecular Analysis Facility at the University of Sheffield, with support from Terry Burke and Deborah Dawson. We also thank James Savage for discussions. This work was supported by the Natural Environment Research Council (NE/S00713X/1 and NE/R001669/1).

Analyses reported in this article can be reproduced using the data provided by Halliwell et al. (2022). https://doi.org/10.5061/dryad.mkkwh712k.

**2.7 Supplementary material**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Table S2.1. Model details, response variables, error distribution, random effects, and fixed effects. | | | | |
| Model name | Response variable | Error distribution | Random effects | Fixed effects |
| Alt-C | Alternated visits (collective) | Poisson | (1|Year) + (1|Nest ID) + (1|Watch ID) + (1|Male ID) + (1|Female ID) + (1|Helper1 ID) + (1|Helper2 ID) + (1|Helper3 ID) + (1|Collective Carer IDs) + (1|Row reference) | Data type\*(Provisioning rate (collective) + Carer number + Watch duration + Brood size, Time of day) + Brood age + Hatch date + AMax |
| Sync-C | Synchronised visits (collective) | Poisson | (1|Year) + (1|Nest ID) + (1|Watch ID) + (1|Male ID) + (1|Female ID) + (1|Helper1 ID) + (1|Helper2 ID) + (1|Helper3 ID) + (1|Collective Carer IDs) + (1|Row reference) | Data type\*(Provisioning rate (collective) + Carer number + Watch duration + Brood size, Time of day) + Brood age + Hatch date + SMax |
| Alt-I | Alternated visits (individual) | Poisson | (1|Year) + (1|Nest ID) + (1|Watch ID) + (1|Carer ID) + (1|Row reference) | Data type\*(Breeding role + Provisioning rate (individual) + Carer number + Watch duration, Brood size + Time of day) + Brood age + Hatch date + AMax |
| Sync-I | Synchronised visits (individual) | Poisson | (1|Year) + (1|Nest ID) + (1|Watch ID) + (1|Carer ID) + (1|Row reference) | Data type\*(Breeding role + Provisioning rate (individual) + Carer number + Watch duration, Brood size + Time of day) + Brood age + Hatch date + SMax |
| Alt-K | Alternated visits (individual) | Poisson | (1|Year) + (1|Nest ID) + (1|Watch ID) + (1|Carer ID) + (1|Row reference) | Data type\*(Sex + Kinship with male + Kinship with female + Provisioning rate (individual) + Carer number + Watch duration + Brood size + Time of day) + Brood age + Hatch date + AMax |
| Sync-K | Synchronised visits (individual) | Poisson | (1|Year) + (1|Nest ID) + (1|Watch ID) + (1|Carer ID) + (1|Row reference) | Data type\*(Sex + Kinship with male + Kinship with female + Provisioning rate (individual) + Carer number + Watch duration + Brood size + Time of day) + Brood age + Hatch date + SMax |
| Alt-R | Active alternated visits (individual) | Normal | (1|Year) + (1|Nest ID) + (1|Carer ID) | Provisioning rate (individual) + Provisioning rate (collective) + Breeding role + Watch duration + Carer number + Brood size + Brood age + Time of Day + AMax |
| Sync-R | Active synchronised visits (individual) | Normal | (1|Year) + (1|Nest ID) + (1|Carer ID) | Provisioning rate (individual) + Provisioning rate (collective) + Breeding role + Watch duration + Carer number + Brood size + Brood age + Time of Day + SMax |

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Table S2.2. Within nest and within individual repeatability estimates for active alternation and synchrony (+CIs) compared between full dataset and subset analysis (subset data omitted individuals only observed provisioning at one nest). Full dataset; *N* = 1,997 samples from 487 unique carers from 795 watches at 250 nests. Subset; *N* = 1,025 samples from 159 unique carers from 599 watches at 185 nests. | | | | |
| Dataset | R | 2.5% CI | 97.5% CI | *P* |
|  | **Alternation** | | | |
| Nest ID repeatability | | | |
| Full dataset | 0.145 | 0.010 | 0.186 | <0.001 |
| Data subset | 0.111 | 0.052 | 0.171 | <0.001 |
|  | Carer ID repeatability | | | |
| Full dataset | 0.000 | 0.000 | 0.031 | 0.500 |
| Data subset | 0.010 | 0.000 | 0.056 | 0.314 |
|  | **Synchrony** | | | |
| Nest ID repeatability | | | |
| Full dataset | 0.000 | 0.009 | 0.029 | 1.000 |
| Data subset | 0.000 | 0.000 | 0.049 | 1.000 |
|  | Carer ID repeatability | | | |
| Full dataset | 0.183 | 0.130 | 0.228 | <0.001 |
| Data subset | 0.157 | 0.091 | 0.224 | <0.001 |

Figure S2.1. Figure illustrating the within-individual, within-watch, inter-visit interval randomisation procedure for calculating alternation (shown) and synchrony (not shown).

**Chapter 3**

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

Chapter published as:

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

**3.1 Abstract**

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, i.e. ‘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 enhances the level of alternation. First, we show that carers who 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. Secondly, we found that the arrival of carers near the nest and their subsequent feeds were tightly synchronised, 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.

**3.2 Introduction**

Parental care is near-ubiquitous among birds, with post-hatching care observed in >98% of species (Cockburn 2006). Parental care enhances the direct fitness of parents by increasing the probability that their offspring survive to breed themselves (Trivers 1974, Godfray 1995, Godfray and Johnstone 2000, Hinde et al. 2010). Additionally, in cooperative breeders, where non-parents help to raise offspring, helpers may accrue direct benefits by increasing their own likelihood of breeding in the future (Zahavi 1977a,b, Kokko et al. 2001, Kokko et al. 2002, Dickinson and Hatchwell 2004) and/or indirect fitness by enhancing 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, e.g. reduced fecundity or immune function (Dijkstra et al. 1990, Gustafsson and Pärt 1990, Nilsson and Svensson 1996, Visser and Lessells 2001). Therefore, in systems of biparental and cooperative care, where benefits are shared but costs are borne individually, carers can maximise 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 (Houston and Davies 1985, Hinde et al. 2010). Despite this conflict, systems of shared care are widespread, being found in ~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 and 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. Whilst this is broadly 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 and 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 maximise brood fitness (Houston and Davies 1985, McNamara et al. 1999, 2003, Lessells and McNamara 2012). Therefore, the threat of exploitation limits the ability of carers to optimise their level of shared care and resulting fitness, unless exploitation can be otherwise prevented (Royle et al. 2002a, 2004, 2006, McNamara et al. 2003). 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, i.e. ‘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 enhance the level of passive alternation (Schlicht et al. 2016, Ihle et al. 2019a, Santema et al. 2019). To account for such effects, studies have compared observed alternation to expected values generated through a variety of null model randomisation and simulation approaches to infer the true level of ‘active’ alternation (e.g. Johnstone et al. 2014, Baldan and Griggio 2019, Khwaja et al. 2019, Ihle et al. 2019b, Halliwell et al. 2022). Whilst many of these found that observed alternation was greater than expected, even when using the most conservative randomisation approach (Johnstone et al. 2014, Savage et al. 2017, Ihle et al. 2019b, Lejeune et al. 2019, Halliwell et al. 2022), 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, their partner waited six times longer to feed again than usual, although this approach can be criticised 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 refined model of Johnstone and Savage (2019) allows 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 (Raihani et al. 2010, Mariette and Griffith 2012, Leniowski and Węgrzyn 2018, Khwaja et al. 2019) and reducing the capacity for more competitive chicks to monopolise food (Shen et al. 2010, Mariette and Griffith 2012, 2015). 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 (Mariette and Griffith 2015, Baldan 2019, Baldan and van Loon 2022). 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 (Mariette and Griffith 2015, Bebbington and Hatchwell 2016, Baldan 2019, Baldan and van Loon 2022). 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 prior study has investigated whether alternation is facilitated by variation in loitering behaviour by carers that is conditional on whether or not 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 and Hatchwell 2016, Halliwell et al. 2022). Halliwell et al. (2022) used a conservative randomisation 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 (Hyp. 1: ‘Loitering facilitates alternation’). We tested two specific predictions of this hypothesis: A – that 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 B – that arriving carers that had been the last to feed a brood would wait until another carer had fed before doing so themselves.

Secondly, 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 (Hyp. 2: ‘Collective arrivals facilitate synchrony’. Here, we predicted: A – that carers would arrive in the vicinity of nests synchronously; and B – that 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 prior 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 synchronise more to signal their effort to gain direct benefits of helping, e.g. 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 (Meade and Hatchwell 2010, Hatchwell 2016), 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 among carers in measures of coordination (Hyp. 3: ‘Status dependent order of visits’). Here, we predicted: A – that breeding females, breeding males and helpers would fill specific positions (e.g. first, middle & last) within sequences of feeds during synchronised bouts; and B – that 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. 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.

**3.3 Methods**

**3.3.1 Study system and data collection**

Field work was conducted in 2020–2021 on a total of 23 breeding pairs of long-tailed tits in an intensively monitored population in the Rivelin Valley, Sheffield, UK (*53°23′N*, *1°34′W*) as part of a long-term study running since 1994. The ~3km2 field site is primarily comprised 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 two days, with daily checks as nests approached incubation and hatching. Nests were typically built <3m from the ground within brambles *Rubus fruticosus*, gorse *Ulex spp.*, rose *Rosa spp.*, holly *Ilex spp.*, or >3m 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 ~15 days (Hatchwell 2016), and all eggs that hatch typically do so within 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 (day ~16), because for ~5 days after hatching nestlings are brooded by their mothers for much of the time and provisioned indirectly by fathers who 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 (2 parents) or cooperatively (2 parents and ≥1 helper). Our dataset included 101 unique watches with 2–6 active carers per watch, with 49% of watches being biparental and 32%, 9%, 7%, and 4% of watches from cooperative nests with 3, 4, 5, and 6 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-minute habituation period to minimise observer disturbance. Watches were typically conducted for 60 minutes 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 minutes; range 41.2–78.3; *N* = 101 watches). We omitted one watch of duration <30 minutes.

The protocol during watches was to record the identity of a carer and time, to the nearest second, they arrived near the nest (within 15m) and then provisioned the brood. Prior to beginning a watch, a video camera was placed ~2m 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 ≥20m 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 CH and the remainder by SJB (13) and MG (15), with distance estimation standardised in joint watches before data collection started.

**3.3.2 Ethical note**

Adult and nestling long-tailed tits were ringed by BJH and SJB 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 post-hatching. 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, 3 females, and 2 unknown). A total of 199 nestlings were ringed from nests used in this study.

Nest monitoring was conducted by non-invasive 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 two 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 two 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 24h. 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 (approx. day 16–18). Provisioning watches necessitated a brief period of nest disturbance (~1 minute) whilst the observer set up a camera on a tripod ~2m from the nest.

**3.3.3 Calculating coordination**

Alternation and synchrony were analysed as the absolute number of alternated and synchronised 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 e.g. A-B-C-A-B-C, simply non-consecutive feeds. A synchronised feed was defined as any alternated feed that occurred within a brief time window of the previous feed, for example, if three feeds occur within quick succession after a gap in provisioning, e.g. A-B-C then feeds B and C are considered synchronised, 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-minutes) and short (30-seconds), a synchronised 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 prior studies of coordination (Bebbington and Hatchwell 2016, Ihle et al. 2019a, Halliwell et al. 2022) 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 utilised this increased resolution to compare the level of active synchrony using a long (2-min) and a short (30-sec) window; a difference between them could indicate whether arrivals or feeds were more or less tightly synchronised than previously shown.

A certain level of passive coordination (alternation and synchrony) is expected by chance (Schlicht et al. 2016, Ihle et al. 2019a, Santema et al. 2019), 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 randomisation. We used a modified version of the within-watch, within-individual intervisit interval randomisation procedure (Figure 3.1) that randomised the times between an individual carer’s feeds within a given watch, i.e. the intervisit intervals (e.g. Johnstone et al. 2014, Savage et al. 2017, Ihle et al. 2019b, Halliwell et al. 2022; Figure 3.1c). Here, we split the intervisit interval into ‘time away’ (mean duration (± SE): 357.6s ± 7.3, *N* = 2010) from and ‘time near’ (loitering) (50.3s ± 1.5, *N* = 2307) the nest (Figure 3.1a). We found no correlation between ‘time away’ and ‘time near’ (Pearson correlation: r100 = 0.137, *P* = 0.171), so we randomised these time periods independently of one another (Figure 3.1b). This approach more precisely defines the length of the refractory period, which is now contained within ‘time away’, thus creating a more biologically realistic approximation of the level of apparent coordination expected by chance. We applied our null model to the observed dataset, generating 1000 randomised 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 randomised 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.

A diagram of different types of data

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Figure 3.1. Demonstration of how (a) an observed sequence of feeds by an individual is randomised by: (b) our modified approach which randomised ‘time away’ and ‘time near’ independently and (c) the approach detailed in Ihle et al. (2019a) which randomised ‘time away’ and ‘time near’ together as fixed blocks.

**Hypothesis 1: Loitering facilitates alternation**

To test predictions of the delayed feeding hypotheses we calculated several metrics of coordination directly from provisioning watches (observed) and the median number from 1000 randomised 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 and waited for another carer to feed before them in the current bout. Secondly, we calculated the mean loitering time for carers when, upon arrival, they were the last carer to feed previously, and 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). Secondly, 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.

Secondly, we quantified the orders in which carers arrived and fed during synchronised bouts. We restricted this investigation to biparental (two carers: M (male) and F (female)) watches and cooperative watches with one helper (three carers: M, F, and H (helper)) which together made up 80% of our watches, because as the number of carers increases, the number of possible orders 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’ synchronised bouts (2-minute window). For a synchronous bout to be isolated it must be separated from the previous bout by at least 2-minutes to avoid one bout influencing another. For example, if a biparental nest has a female-first synchronised feed bout (F-M) followed shortly after by another synchronised 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, i.e. 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 synchronised 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 synchronised 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 synchronised 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 synchronised with one other carer only during isolated synchronised 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 synchronising with another carer, respectively.

**3.3.4 Statistical analysis**

All statistical analysis was performed on R version 4.0.2 (R Core Team 2020). 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 Table 3.1 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 3.1). 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 19/23 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 who feature 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 Table S3.1 (supplementary material). Full outputs, including estimates and *P*-values for all model terms, including covariates are available in Tables S3.2–S3.14.

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| Table 3.1. Details of random and fixed effects applied throughout analyses. | |
| **Random effects** | **Description** |
| 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 were given a unique number corresponding to their row. |
| Carer ID | Unique factor designating carer identity used in individual level analysis. |
| Provisioning rate ratio (FH, MH, and 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** | **Description** |
| 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, in minutes, 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, in hours 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) that a watch was performed on. |
| Hatch date | Integer variable representing the number of days since March 1 each year (median: April 29; range: April 19–June 1). |
| AMax (or SMax) | Continuous numerical variable representing the highest theoretical percentage of visits during a watch which could be alternated (or synchronised). Acts as proxy for provisioning rate disparity between carers, as a visit can only be alternated (or synchronised) if there are sufficient visits by other carers to alternate (or synchronise) with. |
| Data type | Binary factor designating whether data were from field observations (observed) or generated by null model randomisation (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 synchronised visit was from the 2-minute or 30-second synchrony window. |
| Arrival or feed | Binary factor designating whether an arrival or a feed. |
| Carer status | 3-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 | 3-level factor designating the relative position of arrivals or feeds occupied by a carer when all three carers synchronise (first, middle, last). Used in cooperative watches. |
| Association | Binary factor designating the status of the other carer a given carer synchronised with during a synchronised bout, regardless of order. |

**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 dataset by Halliwell et al. (2022). To do so we built a generalised mixed effects model (GLMM) with a Poisson distribution, the key term of interest being ‘Data type’, i.e. 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 generalised linear mixed effects models (GLMMs), as follows.

*Prediction A – 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 a 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 2-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 B – 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’, this interaction term 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 A – 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 seconds of each other and within 2 minutes 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’, ‘Synchrony window’, and their interactions. The interaction terms are informative in different ways. For example, a 2-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 Honest-Significant-Difference post-hoc testing, 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 B – 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 whilst 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 A – 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 2-way interaction of ‘Data type’ and ‘Carer status’, a 3-level factor designating whether an individual was a female, male, or helper (Table 3.1). 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.

Secondly, we investigated the sequences of arrivals and feeds during isolated synchronised 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 synchronised bouts by the parents at biparental nests (F-M & 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 2-way interaction term between ‘Order’ and ‘Arrival or feed’ (i.e. a binary factor indicating whether it was an arrival or feed order) 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 synchronised bouts where all three carers (male, female, helper) fed at cooperative (three carers) nests. Here, we investigated the 3-way interaction term of ‘Carer status’, ‘Arrival or feed’, and ‘Position’, which was a 3-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 B – Preferential associations among carers*. Finally, to test the prediction that carers of a particular status preferentially synchronised with carers of another particular status we built three Poisson-distributed GLMMs. These models investigated the frequency that each carer status (female, male, helper) synchronised with each other carer type during two-carer synchronised 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’.

**3.4 Results**

**3.4.1 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 dataset collected for this study. Observed alternation was significantly greater than expected by chance (GLMM: *P* = 0.041, Table 3.2, Figure 3.2a), as reported previously (Bebbington and Hatchwell 2016, Halliwell et al. 2022). To assess support for the hypothesis that alternation is facilitated by carers delaying their feeding visits if they were last to feed, we tested two predictions.

*Prediction A – 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 non-alternated feed (LMM: *P* = 0.011, Table 3.2, Figure 3.2b).

*Prediction B – 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 3.2, Figure 3.2c). Secondly, 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 3.2, Figure 3.2d). 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.

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| Table 3.2. Models investigating the hypothesis that loitering facilitates alternation. | | | | | |
| Response variable | Fixed effects | Estimates ± SE | df | 𝝌2 | *P* |
| Number of alternated visits per watch | Data type | Observed: 0.062 ± 0.061 | 1,184 | 4.19 | **0.041** |
| *Prediction A – Loiter longer if last to feed* | | | | | |
| Ln(mean loitering time) | Data type \* Last to feed | Observed, Yes: 0.156 ± 0.061 | 1,377 | 6.55 | **0.010** |
| *Prediction B – Loiter to allow alternation* | | | | | |
| Number of visits where cared 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 whilst focal carer loitered | Data type \* Last to feed | Observed, Yes: 0.458 ± 0.155 | 1,377 | 8.70 | **0.003** |

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Figure 3.2. Plots of observed and expected results for: (a) the percent 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 percent of visits where a carer loitered to ensure alternation per watch; and (d) the difference in percent of visits where another carer fed whilst the focal carer loitered, between when the focal carer *was* versus *was* *not* last to feed, per watch. Central emboldened lines represent the median values. Lower and upper boundaries of boxes represent lower and upper quartile values, respectively. Upper and lower boundaries of tails represent maximum observed value within upper fence (3rd quartile + 1.5 \* interquartile range) and minimum observed value within lower fence (1st quartile – 1.5 \* interquartile range), respectively. Points represent outliers (values outside of lower-upper fence range). Total *N* = 101 watches from 23 nests.

**3.4.2 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 A – Carers arrive synchronously*. First, the prediction that carers synchronised 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-minute (Tukey’s HSD: *P* < 0.001, Figure 3.3a) and 30-second synchrony windows (Tukey’s HSD: *P* < 0.001, Figure 3.3a), as was the number of observed synchronous arrivals for both 2-minute (Tukey’s HSD: *P* < 0.001, Figure 3.3b) and 30-second synchrony windows (Tukey’s HSD: *P* < 0.001, Figure 3.3b). There was no significant difference in the level of active synchrony between arrivals and feeds (GLMM: *P* = 0.740, Table 3.3, Figure 3.3). Interestingly, the level of active synchrony was significantly greater for the 30-second window than the 2-minute window (GLMM: *P* < 0.001, Table 3.3, Figure 3.3), suggesting that both arrivals and feeds were more tightly synchronised than previously thought. Furthermore, this disparity in active synchrony between the 2-minute and 30-second windows did not differ significantly between arrivals and feeds (GLMM: *P* = 0.321, Table 3.3, Figure 3.3), indicating that arrivals and feeds were equally tightly synchronised.

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| Table 3.3. Models investigating the hypothesis that collective arrivals facilitate synchrony. | | | | | |
| Response variable | Fixed effects | Estimates ± SE | df | 𝝌2 | *P* |
| *Prediction A – Carers arrive synchronously* | | | | | |
| Number of synchronised arrivals and feed per watch | Data type \* Synchrony window \* Feed or arrival | Observed, Feed, 2-minutes: -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-minutes: 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 B – Carers feed while another loiters* | | | | | |
| Number of visits, per watch, where focal carer fed whilst another loitered | Data type | Observed: 0.588 ± 0.116 | 1,181 | 39.93 | **<0.001** |

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Figure 3.3. Plots of observed and expected percent of maximum theoretical: (a) feed and (b) arrival synchrony achieved per watch for 2-minute and 30-second synchrony windows. Central emboldened lines represent the median values. Lower and upper boundaries of boxes represent lower and upper quartile values, respectively. Upper and lower boundaries of tails represent maximum observed value within upper fence (3rd quartile + 1.5 \* interquartile range) and minimum observed value within lower fence (1st quartile – 1.5 \* interquartile range), respectively. Points represent outliers (values outside of lower-upper fence range). Total *N* = 101 watches from 23 nests per figure.

Synchronous arrival would also result in carers having overlapped loitering periods, so we tested the prediction that there would be significantly more arrivals back to the nest when another carer was present, than expected by chance. This prediction was supported (GLMM: *P* < 0.001, Table 3.3, Figure 3.4a), showing that synchronous arrivals caused carers to actively overlap in their loitering periods.

*Prediction B – Carers feed while another loiters*. Finally, we found support for the prediction that carers were more likely to feed whilst another carer was loitering nearby, as the number of instances where this occurred was greater than expected by chance (GLMM: *P* < 0.001, Table 3.3, Figure 3.4b). Together these results suggest that synchronous feeds of nestlings are a consequence of synchronous arrival near the nest, indicative of collective foraging behaviour.

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Figure 3.4. Plots of observed and expected percentage of visits, per watch, where the focal carer: (a) arrived and (b) fed whilst another carer was nearby. Central emboldened lines represent the median values. Lower and upper boundaries of boxes represent lower and upper quartile values, respectively. Upper and lower boundaries of tails represent maximum observed value within upper fence (3rd quartile + 1.5 \* interquartile range) and minimum observed value within lower fence (1st quartile – 1.5 \* interquartile range), respectively. Points represent outliers (values outside of lower-upper fence range). Total *N* = 101 watches of 23 nests.

**3.4.3 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. It was hypothesised 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 A – Carers arrive and feed in consistent sequence*. First, we found support for the prediction that females arrive back 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 3.4, Figure 3.5). 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, Figure 3.6a) and cooperative nests, where females were more likely to arrive in the first position than the last (Tukey’s HSD: *P* = 0.033, Figure 3.6b,). Moreover, helpers were more likely to arrive in the last position than either the first (Tukey’s HSD: *P* = 0.033, Figure 3.6b,) or middle position (Tukey’s HSD: *P* = 0.006, Figure 3.6b).

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Figure 3.5. 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. Central emboldened lines represent the median values. Lower and upper boundaries of boxes represent lower and upper quartile values, respectively. Upper and lower boundaries of tails represent maximum observed value within upper fence (3rd quartile + 1.5 \* interquartile range) and minimum observed value within lower fence (1st quartile – 1.5 \* interquartile range), respectively. Points represent outliers (values outside of lower-upper fence range). Total *N* = 289 individual samples from 101 watches of 65 individuals at 23 nests.

In contrast, there was no support for the prediction that females also fed first during synchronised bouts. At biparental nests, the order of arrivals was significantly different from the orders of feeds (GLMM: *P* = 0.019, Table 3.4, Figure 3.6a,c), but neither males nor females were more likely to feed first (Tukey’s HSD: *P* = 0.251, Figure 3.6c). At cooperative nests, the order of arrivals was not significantly different from the orders of feeds (GLMM: *P* = 0.123, Table 3.4, Figure 3.6b,d), and the only difference between carer statuses in likelihood of feeding in a particular position was a non-significant trend for females to feed in the middle position more than helpers (Tukey’s HSD: *P* = 0.061, Figure 3.6d).

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| Table 3.4. Models investigating the hypothesis that carers exhibit status dependent orders of visits. | | | | | |
| Response variable | Fixed effects | Estimates ± SE | df | 𝝌2 | *P* |
| *Prediction A – 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 synchronised 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 synchronised 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 B – Preferential associations among carers* | | | | | |
| Frequency that males synchronised with each other carer, per watch, during cooperative synchronised bouts | Association | MH: -0.936 ± 0.272 | 1,45 | 11.82 | **<0.001** |
| Frequency that helpers synchronised with each other carer, per watch, during cooperative synchronised bouts | Association | MH: -0.163 ± 0.319 | 1,33 | 0.26 | 0.609 |
| Frequency that females synchronised with each other carer, per watch, during cooperative synchronised bouts | Association | FM: 0.814 ± 0.290 | 1,43 | 7.87 | **0.005** |

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Figure 3.6. 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 (3 carers) nests; (c) female and male first feed orders at biparental nests; and (d) each carer’s feed position at cooperative (3 carers) nests. Total *N* = 294 synchronised bouts from 46 watches of 13 nests for (a) and (c), *N* = 82 synchronised bouts from 27 watches of 10 nests for (b) and (d).

*Prediction B – 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 synchronise with females than with helpers (GLMM: *P* < 0.001, Table 3.4), and females were significantly more likely to synchronise with males than with helpers (GLMM: *P* = 0.005, Table 3.4). However, helpers showed no active preference for synchronising with either males or females (GLMM: *P* = 0.576, Table 3.4).

**3.5 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. Secondly, 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. Whilst 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 synchronised together at cooperative nests, but helpers showed no active preference for synchronising with either member of the breeding pair.

**3.5.1 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 (Schlicht et al. 2016, Ihle et al. 2019a, Santema et al. 2019). 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. Whilst 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.

**3.5.2 Hypothesis 2: Collective arrivals facilitate synchrony**

Synchrony of provisioning visits is another characteristic of carer coordination, with several hypothesised functions. Some explanations such as reduced predator exposure (Raihani et al. 2010, Mariette and Griffith 2012, Leniowski and Węgrzyn 2018, Khwaja et al. 2019), prevention of food monopolisation by a fraction of a brood (Shen et al. 2010, Mariette and Griffith 2012, 2015) and signalling effort or quality to other carers (Zahavi 1977a,b, Doutrelant and Covas 2007, Trapote et al. 2021) do not require active alternation *per se*. However, synchrony has also been hypothesised 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 (Mariette and Griffith 2015, Bebbington and Hatchwell 2016, Baldan 2019, Baldan and van Loon 2022). Mariette and Griffith (2015) found that zebra finches, *Taeniopygia castanotis* (formerly *T. guttata*), synchronised attendance at feeding stations as well as at the nest, and proposed that synchronous nest visits result from collective foraging behaviour that was an adaptation to reduce predation risk for carers. Similarly, studies using lightweight radio-transmitters to track the time and location of foraging great tits found that parents coordinated their foraging behaviour in time and space (Baldan 2019, Baldan and van Loon 2022). Furthermore, several other species found to synchronise nest visits also forage collectively (e.g. Doutrelant and 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 and Hatchwell 2016, Halliwell et al. 2022). This study supports that hypothesis, with carers synchronising both arrivals and feeds. Utilising 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-second synchrony window than the 2-minute, suggesting that visits were even more tightly synchronised 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 and 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 efficiency (Caraco 1981, Beauchamp 1998, 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 (Hatchwell et al. 2001, McGowan et al. 2006, McGowan et al. 2007, Napper and Hatchwell 2016, Ellison et al. 2020). 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. 1999a). 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.

**3.5.3 Hypothesis 3: Status dependent order of visits**

We also hypothesised 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 and 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 and Radhakrishna 2022) that are often females (e.g. Trillmich et al. 2004, Fischhoff et al. 2007, Barelli et al. 2008, Pyritz et al. 2011, 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 and 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 highest active synchrony by helpers and 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 back to 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 over-represented 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). Secondly, 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 synchronise with females most. Interestingly, whilst 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 synchronise visits at cooperative nests it is usually the breeding pair, while helpers more often synchronise 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 non-breeding 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 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 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.

**3.5.4 Synthesis**

Coordination of care is typically investigated by analysing both alternation and synchrony. These behaviours do not necessarily serve the same function (Lejeune et al. 2019, Halliwell et al. 2022), but they are intrinsically linked because synchronised 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 and Hatchwell 2016, Halliwell et al. 2022) by proposing a mechanism for coordination which is consistent with all findings.

Synchronised nest visits may inevitably lead to alternated visits because all feeds within a synchronised 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 synchronised 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 they 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 and 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 at 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 whilst 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.

**3.5.5 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, though evidence for status dependent feed orders remains circumstantial (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. Whilst 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’ effort 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.

**3.6 Acknowledgements and data availability**

We thank Jamie Thompson and Caroline Milsom for their assistance in the field, and Sheffield City Council, Yorkshire Water, Hallamshire Golf Club and private residents/landowners of the Rivelin Valley field site for access to their land. We also thank Samantha Patrick for discussions. This work was supported by the Natural Environment Research Council (NE/S00713X/1 and NE/R001669/1).

Analysis reported here can be reproduced using the data and code available at https://doi.org/10.5061/dryad.37pvmcvpq.

**3.7 Supplementary material**

**3.7.1 Covariate justifications**

Provisioning rate – 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 which may influence provisioning rate (e.g. brood size, hatch date) to attain a measure of coordination independent of provisioning rate.

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

Watch duration – 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 – included because we expect, based on previous studies, that the provisioning rate increases with the number of live chicks. Therefore, we controlled for brood size to isolate the level of coordination, independent of factors which may modulate provisioning rate.

Watch start time – included because prior research suggests that provisioning rate may change throughout time of day, being greatest in the period immediately following sunrise (MacColl and Hatchwell 2002, Hatchwell et al. 2004).

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

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

AMax (or SMax) – included to account for disparities in provisioning rates between carers which could render coordination 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 aren’t enough other feeds to coordinate with. This term is therefore used as a proxy for provisioning rate asymmetry often use in studies of biparental provisioning systems (Bebbington and Hatchwell 2016), but applicable to a cooperative breeding system. We note that AMax and SMax are always the same value.

**3.7.2 Tables**

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| Table S3.1. 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 dist. | No. of watches |
| **Collective loitering period models** | | | | | |
| Number of synchronised 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 whilst 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 |
| **Synchronised 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 feed and arrival | Position \* Feed or arrival \* Carer status | (1|WatchID) + (1|NestID) + (1|CarerID) + (1|Rowref) |  | 27 |
| **Synchrony association analysis** | | | | | |
| Frequency of female synchronising 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 |

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| Table S3.2. Estimates and *P*-values for fixed effects on the number of alternated visits per provisioning watch from GLMM; *N* = 202 from 101 watches at 23 nests, significant values in bold. | | | | |
| Parameter | df | Estimate ± SE | 𝝌2 | *P*-value |
| **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 |

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| Table S3.3. 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 LMM; *N* = 400 from 101 watches at 23 nests, significant values in bold. | | | | |
| Parameter | df | Estimate ± SE | 𝝌2 | *P*-value |
| **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 |

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| Table S3.4. Estimates and *P*-values for fixed effects on the number of visits where carers loitered to ensure alternation per provisioning watch from GLMM; *N* = 202 from 101 watches at 23 nests significant values in bold. | | | | |
| Parameter | df | Estimate ± SE | 𝝌2 | *P*-value |
| **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 |

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| Table S3.5. 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 GLMM; *N* = 400 from 101 watches at 23 nests, significant values in bold. | | | | |
| Parameter | df | Estimate ± SE | 𝝌2 | *P*-value |
| **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 |

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| Table S3.6. Estimates and *P*-values for fixed effects on the number of visits synchronised arrivals and visits at both 2-minute and 30-second synchrony windows, per provisioning watch from GLMM; *N* = 808 from 101 watches at 23 nests, significant values in bold. | | | | |
| Parameter | df | Estimate ± SE | 𝝌2 | *P*-value |
| **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-seconds)** | **1** | **2-minutes: 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-minutes: 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-minutes: -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-minutes: -0.117 ± 0.118 | 0.98 | 0.321 |

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| Table S3.7. Estimates and *P*-values for fixed effects on the number of visits where the focal carer arrived back with another carer loitering per provisioning watch from GLMM; *N* = 202 from 101 watches at 23 nests, significant values in bold. | | | | |
| Parameter | df | Estimate ± SE | 𝝌2 | *P*-value |
| **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**  **4: 0.560 ± 0.213**  **5: 0.749 ± 0.242**  **6: 1.05 ± 0.296** | **13.89** | **0.008** |
| 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  Obs, 4: -0.282 ± 0.210  Obs, 5: -0.378 ± 0.246  Obs, 6: -0.409 ± 0.277 | 4.51 | 0.341 |
| 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 |

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| Table S3.8. 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 GLMM; *N* = 202 from 101 watches at 23 nests, significant values in bold. | | | | |
| Parameter | df | Estimate ± SE | 𝝌2 | *P*-value |
| **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**  **4: 0.507 ± 0.208**  **5: 0.683 ± 0.247**  **6: 0.999 ± 0.302** | **11.39** | **0.023** |
| 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  Obs, 4: -0.243 ± 0.213  Obs, 5: -0.428 ± 0.251  Obs, 6: -0.405 ± 0.281 | 4.63 | 0.328 |
| 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 |

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| Table S3.9. Estimates and *P*-values for fixed effects on the number of visits where the focal carer arrived back with another carer loitering per individual per provisioning watch from GLMM; *N* = 578 from 101 watches at 23 nests, significant values in bold. | | | | |
| Parameter | df | Estimate ± SE | 𝝌2 | *P*-value |
| **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 |

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| Table S3.10. Estimates and *P*-values for fixed effects on the number of each order of synchronised bouts per provisioning watch at biparental nests from GLMM; *N* = 184 from 46 watches at 13 nests, significant values in bold. | | | | |
| Parameter | df | Estimate ± SE | 𝝌2 | *P*-value |
| **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** |

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| Table S3.11. 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 synchronised bouts per provisioning watch at cooperative (three carers) nests from GLMM; *N* = 477 from 27 watches at 10 nests, significant values in bold. | | | | |
| Parameter | df | Estimate ± SE | 𝝌2 | *P*-value |
| **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 |

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| Table S3.12. Estimates and *P*-values for fixed effects on the number of times each breeding male synchronised visits with females and helpers per provisioning watch at cooperative (three carers) nests from GLMM; *N* = 54 from 27 watches of 10 males at 10 nests, significant values in bold. | | | | |
| Parameter | df | Estimate ± SE | 𝝌2 | *P*-value |
| **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 |

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| Table S3.13. Estimates and *P*-values for fixed effects on the number of times each helper synchronised visits with females and males per provisioning watch at cooperative (three carers) nests from GLMM; *N* = 42 from 21 watches of 9 helpers at 9 nests, significant values in bold. | | | | |
| Parameter | df | Estimate ± SE | 𝝌2 | *P*-value |
| 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 |

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| Table S3.14. Estimates and *P*-values for fixed effects on the number of times each breeding female synchronised 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, significant values in bold. | | | | |
| Parameter | df | Estimate ± SE | 𝝌2 | *P*-value |
| **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 |

**Chapter 4**

**Experimental variation of perceived predation risk does not affect coordination of parental care in long-tailed tits**

Chapter published as:

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

**4.1 Abstract**

To maximise fitness, parents should optimise their investment in each breeding attempt. When there are multiple carers, the optimal strategy may also depend on the relative timing of their investment, with coordination of care hypothesised to maximise its efficiency and reduce predation risk. The aim of this study was to test the hypothesis that carers coordinate provisioning as an antipredator measure that reduces the time that a brood’s location is advertised to predators (‘predation hypothesis’). We presented predatory and non-predatory model birds to provisioning long-tailed tit, *Aegithalos caudatus*,parents and helpers, predicting that coordination would increase, and carer activity near the nest would decrease following predator presentation, relative to controls. First, carers reduced provisioning rates and took longer to resume provisioning following the predator presentation. Second, contrary to predictions, we found no significant change in any metric of coordination following predator presentations, relative to controls. Moreover, following predator presentation carers spent more time near the nest, resulting in greater near-nest activity compared to controls. In conclusion, although provisioning long-tailed tits are sensitive to perceived predation risk, our findings do not support the prediction of the predation hypothesis that carers adjust coordination behaviour in response to that threat.

**4.2 Introduction**

Parental care is any action taken by an individual to directly improve the fitness of their offspring (Trivers 1974, Godfray 1995). However, providing care is costly, so parents must trade-off current investment against potential future productivity and optimise their investment in each breeding attempt to maximise their lifetime reproductive success (Clutton-Brock 1991, Stearns 1992). When offspring are cared for by multiple individuals, this optimisation process must also consider the care provided by others (Houston and Davies 1985, McNamara et al. 1999, 2003, Lessells and McNamara 2012). In such systems, the relative timing of carers’ investment may also influence their fitness pay-offs, with groups of coordinated carers hypothesised to receive greater net benefits than carers behaving independently (e.g*.* Raihani et al. 2010, Shen et al. 2010, Johnstone et al. 2014). For example, strict coordination of care is essential in many pelagic seabirds that have long foraging trips during which their partner must remain at the nest to incubate eggs, brood chicks, and deter predators (Schreiber and Burger 2002, Patrick et al. 2020, McCully et al. 2022). Similar coordination strategies are observed in many terrestrial birds with biparental incubation (Thomson et al. 1998, Al-Rashidi et al. 2010, Boucaud et al. 2016), and pairs exhibiting greater incubation coordination experience greater reproductive success (Spoon et al. 2006).

Another form of parental coordination, based on conditional cooperation between carers, i.e*.* taking-turns to deliver food to offspring (hereafter ‘alternation’), has been hypothesised to facilitate conflict resolution between ultimately selfish individuals (Johnstone et al. 2014, Savage et al. 2017, Johnstone and Savage 2019). By alternating provisioning visits, carers ensure that any individual’s attempt to gain advantage by reducing investment is matched by a similar reduction by the other carer(s), thus preventing would-be defectors from benefiting from the disproportionate effort of others. This enables all carers to more closely achieve their optimal level of care without risking exploitation (Royle et al. 2002a, McNamara et al. 2003) and may explain why some species matched experimental increases in their partner’s provisioning rate (Hinde 2006, Meade et al. 2011). However, alternation requires a mechanism by which carers can reliably monitor the investment of others in real-time, particularly if carers forage solitarily (e.g. Savage et al. 2017). Synchronous provisioning, another form of coordination, is hypothesised to provide this function (Mariette and Griffith 2015, Bebbington and Hatchwell 2016, Baldan 2019, Baldan and van Loon 2022).

Synchronous nest visits have been reported in several biparental (e.g*.* Doutrelant and Covas 2007, Lee et al. 2010, Mariette and Griffith 2012, 2015, Leniowski and Węgrzyn 2018, Khwaja et al. 2019, Lejeune et al. 2019) and cooperatively breeding (e.g. Raihani et al. 2010, Shen et al. 2010, Bebbington and Hatchwell 2016, Koenig and Walters 2016, Halliwell et al. 2022) bird species. However, to synchronise provisioning, carers may have to delay the delivery of resources while they wait for another carer to arrive (Ruckstuhl 1999, Dostalkova and Spinka 2007). Therefore, it must provide an adaptive function that confers fitness benefits which outweigh the potential costs. Provisioning synchrony and alternation co-occur in some species (Koenig and Walters 2016, Baldan and Griggio 2019, Ihle et al. 2019b, Baldan and Quyang 2020) and are sometimes correlated (Bebbington and Hatchwell 2016, Leniowski and Wegryzn 2018), supporting the contention that synchrony facilitates alternation. However, synchronous provisioning is also hypothesised to have several other potential functions. Synchrony may allow carers to signal effort to conspecifics, either to advertise quality (Zahavi 1977a,b, Doutrelant and Covas 2007) or maintain group membership (Gaston 1978, Kokko et al. 2002, Trapote et al. 2021). Synchrony may also increase parity in resource partitioning between offspring. For example, if a brood is provisioned twice in quick succession, the chick fed first may be satiated or still processing the food when the second feed is delivered, and thus synchrony may limit the ability of more competitive chicks to monopolise resources (Shen et al. 2010, Mariette and Griffith 2012, 2015). Alternatively, synchrony could result from group foraging (Forbes 1993), which may increase foraging efficiency by allowing carers who are less experienced or familiar with the area to use cues from others to inform their foraging decisions, and/or reduce the risk of carers being preyed upon when foraging (Beauchamp 1998, Lee et al. 2010, van Rooij and Griffith 2013, Mariette and Griffith 2015, Baldan and van Loon 2022).

Synchrony has also been hypothesised to reduce brood predation risk (‘predation hypothesis’). By provisioning a brood together, carers can reduce the number of discrete feeding events (Skutch 1949), activity near the nest (Martin et al. 2000, Bebbington and Hatchwell 2016, Leniowski and Węgrzyn 2018), and/or begging call duration (Haskell 1994, Briskie et al. 1999), all of which may advertise the nest location to predators. Several studies have linked provisioning synchrony to reduced activity near a nest (Bebbington and Hatchwell 2016, Leniowski and Węgrzyn 2018) and increased brood survival (Raihani et al. 2010, Leniowski and Węgrzyn 2018), but to ourknowledge, only one has yet identified a link between synchrony and predation risk. In a multispecies study, Khwaja et al. (2019) found that New Zealand bellbirds, *Anthornis melanura*, from predator-free island populations synchronised provisioning visits less than mainland populations which historically experienced brood predation. However, in 24 other such intraspecific comparisons, many did not provision synchronously, and in those that did, synchrony did not vary consistently with predation risk (Khwaja et al. 2019).

In this study, we investigated the predation hypothesis in a population of long-tailed tits, *Aegithalos caudatus*, a passerine bird that may provision offspring biparentally, or cooperatively when pairs are helped by failed breeders (Glen and Perrins 1988, Hatchwell et al. 2004). Helping is a kin-selected behaviour and helpers receive no direct fitness benefits from their cooperative investment, so all carers share a common interest in brood survival (Hatchwell et al. 2014). Long-tailed tits coordinate their provisioning via alternation and synchrony, with observed coordination exceeding levels expected by chance (Bebbington and Hatchwell 2016, Halliwell et al. 2022), and they behave in a manner that actively enhances their level of coordination (Halliwell et al. 2023a). Long-tailed tits experience very high rates of nest predation, with 72% of nests failing due to depredation of the eggs or nestlings (Hatchwell et al. 2013), usually by corvids e.g. Eurasian jay, *Garrulus glandarius*. So, we conducted an experiment to test whether coordination (i.e. alternation and synchrony) is adjusted in response to elevated predation risk. Specific objectives were: first, to determine whether model predator presentation disturbed the provisioning behaviour of long-tailed tits, predicting that carers would reduce provisioning during periods of acutely elevated perceived predation risk. Secondly, we tested whether increasing perceived predation risk caused an increase in subsequent coordination behaviours, predicting that carers would increase coordination and reduce total time spent near the nest in watches following predator presentation. We also predicted that any adjustment of coordination and nest activity in response to the predator threat would diminish with time following removal of the model predator.

**4.3 Methods**

**4.3.1 Study system and general field protocol**

Data were collected during the breeding seasons (March–June) of 2021 and 2022 from a population of long-tailed tits in a ~3km2 field site in the Rivelin Valley, Sheffield, UK (*53°23′N*, *1°34′W*). Nests were located by following adult birds during nest building, and once located, were monitored at 1–3 day intervals to record lay dates and the start of incubation, with daily checks to record hatch date within 24h. Brood size was recorded on day 11 (d11) after hatching (d0) when chicks were ringed. Long-tailed tits typically build their nests in low vegetation (<3m), but sometimes also in tree forks (>3m). Our experimental protocol required model presentation within 2m of the nest, so we conducted experiments only on nests within reach of an observer (<3m) (*N* = 22). Whilst this restricts our investigation to a subset of potential nest locations, with slightly lower predation risk than average, predation by corvids occurs at a high rate across the full range of nest heights and in all areas of the field site (Hatchwell et al. 1999b, Higgot 2019), so pairs with low nests should still be sensitive to predator threats. All birds in our study were individually identifiable after being ringed with a British Trust for Ornithology ring and a unique combination of two colour rings either as nestlings in our field site or during nest building if immigrants. In total, 21 breeding females, 20 breeding males, and 11 helpers (10 males, 1 female) were observed at 22 nests. Three (5.8%) of 52 carers were subjected to our experiment twice in successive years resulting in a small degree of pseudoreplication. However, in all cases these birds had different partners in the two years, and our analyses were primarily focused on the property of groups (i.e. coordination) rather than that of individuals. Therefore, we believe that any disproportionate effect of this small number of individuals is likely to be minimal. Furthermore, the birds in our field site must regularly encounter predators throughout the year so we believe that brief exposure to a model bird is unlikely to influence their response to the same models 12 months later. Overall, 68% of broods were provisioned biparentally in our sample, with the remainder provisioned cooperatively by parents plus one (23%), or three (9%) alloparental helpers. It was not possible to record data blind because our study involved focal animals in the field.

**4.3.2 Experimental protocol**

Long-tailed tits provision their brood in the nest from hatching (d0) until failure or fledging (d16–18). Breeding females brood the chicks until around d5, during which time males provide most food, but from d6 onwards brooding ceases and carers provision chicks directly. We conducted experiments on d8–10 at 22 nests (d8: *N* = 12; d9: *N* = 6; d10: *N* = 4) in April–May 2021 and 2022. At each nest, we performed an experiment comprising a series of provisioning watches with intermittent periods of model presentation (Figure 4.1). First, an observer (CH) set up a wooden pole (1.2m tall) for model presentations and a video camera on a tripod ~2m from the nest to record the time, to the nearest second, that each carer fed the brood, before retreating to an observation position ≥20m from the nest. The first watch was a control provisioning period of 1h which commenced upon the first feed observed after an initial 10-minute acclimation period. The observer recorded the time, to the nearest second, that a carer arrived within 15m of the nest, so that the time between arrival and feeding, termed the ‘loitering period’, could be calculated. If two or more carers arrived simultaneously, they were recorded as arriving at the same time, but the observer noted the order in which they were identified. Some arrivals did not result in feeds (4.69%, *N* = 1,561) so were omitted from our final analysis. In addition, some arrivals (4.03%, *N* = 1,491) were missed, in which case the time of arrival was assumed to be the time first seen on camera; the longer a carer loitered the lower the chance that their arrival was missed, so we reasoned that missed arrivals would typically occur with short loitering periods. Watches were performed for one hour after the first observed feed, and watch duration was calculated as the time between first arrival and final feed.

Following the control period, the observer fixed the first taxidermic model atop the pole before retreating to the same observation position. The model was either a non-predatory (rock dove, *Columba livia*) or predatory (Eurasian jay) bird; jays commonly depredate long-tailed tit eggs and chicks, but not adults. The first model was presented for ~15 minutes (dove mean (±SE): 15 mins 19s ± 6s, *N* = 22; jay mean (±SE): 15 mins 22s ± 8s, *N* = 22), while the observer and video camera recorded arrival and feed times to the nearest second. Although we did not systematically quantify other behaviours during this period, carers usually responded to the jay by intensely alarm-calling and mobbing the model before retreating from the nest area. In contrast, during the dove presentation, carers alarm-called less and rarely mobbed the model, often resuming provisioning within 2 minutes of the presentation. After 15 minutes the observer retrieved and concealed the model before returning to the same observation position to perform another 1h provisioning watch. The observer then repeated the presentation procedure and subsequent observation period for the other model. All watches at a focal nest were performed on the same day, back-to-back, with minimal breaks between watch periods and the next model presentation. Each experiment typically lasted 4–5h. The order of model presentations was stratified to minimise confounding order effects in model treatment (dove first: *N* = 10 trials; jay first: *N* = 12 trials). Nevertheless, our experimental design resulted in a potential order effect because the control period necessarily preceded the model presentations to avoid any impact of model presentations on the non-presentation control period. To assess the impact of this, we analysed the effect of watch order (including non-presentation controls) on each of our investigated metrics, finding no significant effect of watch order, nor any change in significance of the key terms with or without the inclusion of the watch order term (Table S4.1). Therefore, final analyses reported in the paper did not include presentation order.

Due to resource constraints, we presented the same predatory and non-predatory models at each nest, so the responses of each group to our treatment were not truly independent as they responded to the same individual models, introducing a degree of potential pseudoreplication (Milinski 1997). Therefore, we cannot rule out the possibility that carers’ responses were influenced by the unique individual characteristics of our chosen models as well as differences between the predatory and non-predatory species overall; though, we believe that this effect should be very small when presenting taxidermic models. Further, our protocol is in line with similar studies presenting the same model(s) to different subjects (e.g. Giles and Huntingford 1984, Ghalambor and Martin 2000, 2002, Peluc et al. 2008). Therefore, we think it is safe to assume that our predatory and non-predatory models were a fair representation of the predation threat exhibited by jays and doves.

A picture containing text, bird

Description automatically generated

Figure 4.1. Illustration of the experimental protocol and models used: rock dove, *Columba livia*, (left) and Eurasian jay, *Garrulus glandarius*, (right). Treatment model illustrations by S. C. Anderson.

**4.3.3 Calculating coordination**

**Effect of experimental treatments on provisioning behaviour**

To establish whether model presentations disturbed regular provisioning behaviour, we first calculated the time between the removal of each model (dove or jay) and the first feed by any carer during the subsequent watch, termed the ‘Lag time’ (Figure 4.1). Secondly, we calculated the ‘Number of feeds’ by all carers during control watches, during model presentation periods (dove or jay present) and in watches following model removal (post-dove and post-jay). This was analysed as the total number of feeds per watch, which functioned as a measure of provisioning rate when watch duration was included in the model.

**Does predation threat increase coordination?**

To test the prediction that carers increase their coordination in response to elevated predation risk, we calculated provisioning and coordination metrics by all carers during control watches and post-dove and post-jay watches, as follows. ‘Alternation’ – the number of alternated feeds, defined as the number of feeds that occurred following the feed of another carer, i.e*.* non-consecutive feeds (e.g*.* A-B-A-C-B) (median = 16, range = 3–37, *N* = 66 watches at 22 nests). ‘Arrival synchrony’ – the number of synchronised arrivals, defined as the number of arrivals that occurred within a time window of 2 minutes following an arrival by another carer (median = 10, range = 1–30, *N* = 66). ‘Feed synchrony’ – the number of synchronised feeds, defined as the number of feeds that occurred within a 2-minute time window of a feed by another carer (median = 10, range = 1–30, *N* = 66). Previous studies of long-tailed tits found that levels of synchrony between 1-, 2-, and 3-min window lengths were highly correlated (rp > 0.94; Halliwell et al. 2022) and studies of long-tailed tits and other species with comparable provisioning rates found qualitatively similar results for different synchrony windows (Mariette and Griffith 2015, Bebbington and Hatchwell 2016, Ihle et al. 2019a, Halliwell et al. 2022), with 2 minutes being most widely used. Therefore, 2 minutes was chosen to ensure that our methods were consistent and comparable with previous studies of coordination in long-tailed tits. ‘Present upon arrival’ – the number of feeds where the focal carer arrived back within 15m of the nest with another carer loitering nearby (median = 6, range = 0–24, *N* = 66). ‘Present upon feed’ – the number of feeds where the focal carer fed whilst another carer loitered nearby (median = 5, range = 0–24, *N* = 66). ‘Loitering time’ – the mean loitering period duration by all carers who provisioned the brood during a watch (mean (±SE) = 45.8s ± 3.8s, *N* = 66) and ‘Duration of time with carer(s) nearby’ – the total time during each watch where one or more carers loitered within 15m of a nest (mean (±SE) = 11 mins 54s ± 36s, *N* = 66); when watch duration was included as a covariate this measure functioned as an analysis of the proportion of a watch where at least one carer was loitering nearby.

To further test the dynamics of any potential response to predation threats, we compared several metrics of carer behaviour between sub-sections of control watches and post-dove and post-jay watches, each split into thirds by watch duration (mean third duration (±SE) = 18 mins 47s ± 8s, *N* = 198); response variables were: ‘Number of feeds’ (provisioning rate), ‘Loitering time’, and the levels of each coordination metric (‘Arrival synchrony’, ‘Present upon arrival’, ‘Present upon feed’, ‘Feed synchrony’, ‘Alternation’). This analysis attempted to determine the time frame on which carers adjusted their provisioning behaviour in response to elevated predation risk.

**4.3.4 Statistical analysis**

All statistical analyses were performed in R version 4.2.1 (R Core Team 2022). All models were built using lme4 (Bates et al. 2015) and *P*-values extracted using lmerTest (Kuznetsova et al. 2017). Where appropriate, we used the package emmeans (Lenth et al. 2019) to perform post-hoc testing. Figures were produced using the packages ggplot2 (Wickham 2016), cowplot (Wilke 2020) and ggsignif (Ahlmann-Eltze and Patil 2021). Our general approach to analyses was to use full mixed effects models with all biologically relevant fixed and random effects. To confirm that our findings were not influenced by overparameterisation of these models, we also conducted analyses of the same dataset using stepwise elimination of non-significant terms and an information theoretic (AIC) approach, but results were very consistent between these methods (see supplementary material, Table S4.3). Therefore, here we present only the results of full mixed effect models.

**Effect of experimental treatments on provisioning behaviour**

To determine whether model presentation treatments affected provisioning behaviour, we first built a normally distributed linear mixed effects model (LMM) to compare the lag time between model removal and the first subsequent feed for dove and jay treatments. The response variable was log-transformed ‘Lag time’ because the assumption of normality was met only when the response variable was appropriately transformed. This model’s term of interest was ‘Treatment’ (post-dove or post-jay), with the fixed effects covariates as follows. ‘Provisioning rate’ – the total number of feeds by all carers per hour in the watch following model removal (in this case: mean (±SE) = 25.09 feeds/h ± 1.33, range = 7.94–46.42, *N* = 44). ‘Carer number’ – the number of unique carers which provisioned during each watch following model removal (in this case: 2: 70.5%, 3: 20.5%, 4: 2.3%, and 5: 6.8%; *N* = 44). ‘Brood size’ – the number of live chicks recorded in the nest on d11 (median = 9, range = 2–11, *N* = 22). ‘Watch start time’ – the time of day each experiment started (mean = 08:30 BST, range = 07:20–12:40, *N* = 22). ‘Brood age’ – the number of days since hatching upon which a watch was performed (d8: *N* = 12; d9: *N* = 6; d10: *N* = 4). Finally, ‘Hatch date’ – the number of days since March 1 of each year on which each brood hatched (median = April 30, range = April 19–May 29, *N* = 22). Random effects were ‘Year’ and ‘Nest ID’ – a unique identifier for each nest. Detailed descriptions of all fixed and random effects are available in Table S4.2 (supplementary material). Secondly, we built a Poisson-distributed generalised linear mixed effects model (GLMM) to compare provisioning rates during control watches, model presentations, and watches following model removal (post-dove and post-jay). The response variable was ‘Number of feeds’ and the term of interest was ‘Treatment’ (control, dove present, jay present, post-dove, or post-jay) with fixed effect covariates as follows: ‘Carer number’ – for provisioning watches, this was the number of carers that provisioned during each watch (in this case: 2: 69.7%, 3: 21.2%, 4: 3.0%, and 5: 6.1%; *N* = 66); for model presentation periods, this was the maximum number of carers observed provisioning the nest during the experiment (2: 68.2%, 3: 22.7%, 4: 0.0%, and 5: 9.1%; *N* = 22), ‘Watch duration’ – the time, in minutes, between first arrival and last feed of each watch (including display periods: mean (±SE) = 41 mins 18s ± 125s, *N* = 110), ‘Brood size’, ‘Watch start time’, ‘Brood age’ and ‘Hatch date’, as above. Random effects were ‘Year’, ‘Nest ID’, and ‘Rowref’, which was an observation level random effect providing a unique identifier for each provisioning watch; included throughout to account for overdispersion in Poisson-distributed models.

**Does predation threat increase coordination?**

To test the prediction that carers increased coordination in response to a perceived predation threat, we first produced a series of Poisson-distributed GLMMs to compare coordination metrics between control watches and watches following model presentations. The response variables were as follows: ‘Arrival synchrony’, ‘Present upon arrival’, ‘Present upon feed’, ‘Feed synchrony’, and ‘Alternation’, as described above, with ‘Treatment’ (control, post-dove, or post-jay) being the term of interest in each model. Fixed effect covariates for these models were: ‘Provisioning rate’ (in this case: mean (±SE) = 22.94 feeds/h ± 1.06, range = 7.94–46.42, *N* = 66), ‘Carer number’, ‘Watch duration’ (in this case: mean (±SE) = 58 mins 36s ± 48s, *N* = 66), ‘Brood size’, ‘Watch start time’, ‘Brood age’, ‘Hatch date’, and ‘Maximum possible alternation’ – a variable that reflects the disparity in provisioning rate within groups of carers, e.g. if two carers feed at the same rate, all feeds (except the first) are potentially alternated, but if one carer feeds more than all others combined there exist several feeds which cannot be alternated (mean (±SE) = 87.80% ± 1.34%). Therefore, this variable represents the percentage of visits performed during a watch which could theoretically be alternated (or synchronised) given the relative number of feeds by all carers during that watch (see Table S4.2 for further details). Random effects were ‘Year’, ‘Nest ID’, and ‘Rowref’.

Secondly, to test whether treatment influenced loitering times and consequently the total time that carers were nearby the nest, we built two normally distributed LMMs. The response variables were log-transformed ‘Loitering time’, and ‘Duration of time with carer(s) nearby’, with the term of interest being ‘Treatment’ (control, post-dove, or post-jay). Fixed effect covariates were: ‘Provisioning rate’, ‘Carer number’, ‘Watch duration’, ‘Brood size’, ‘Watch start time’, ‘Brood age’, and ‘Hatch date’. Additionally, to further investigate the time during a watch with carer(s) nearby we re-ran the original model with mean loitering time included as a covariate to account for the effect of potentially different loitering times during different watches; we report both model outputs. Random effects were ‘Year’, ‘Nest ID’, and ‘Rowref’.

As the final test of this hypothesis, we used a series of Poisson-distributed GLMMs to compare ‘Provisioning rate’ and coordination metrics between successive sections (1st, 2nd, and 3rd) of control watches and watches following model removal. The response variables were: ‘Number of feeds’, ‘Arrival synchrony’, ‘Present upon arrival’, ‘Present upon feed’, ‘Feed synchrony’, ‘Alternation’, and ‘Loitering time’, with the terms of interest being ‘Section’ and its interaction term with ‘Treatment’, which measures whether watches exposed to different treatments varied in their subsequent coordination through time. Fixed effect covariates were: ‘Provisioning rate’, ‘Carer number’, ‘Watch duration’, ‘Brood size’, ‘Watch start time’, ‘Brood age’, ‘Hatch date’, and ‘Maximum possible alternation’ (except the provisioning rate and loitering time models), which was calculated for each individual section of the watch, i.e. ‘Maximum possible alternation’ for 1st, 2nd, and 3rd sections separately. Random effects were ‘Year’, ‘Nest ID’, ‘Rowref’, and ‘Watch ID’ – a unique identifier for each watch from which a section was sampled.

**4.4 Results**

**4.4.1 Effect of experimental treatments on provisioning rates**

Presentation of a model predator had the anticipated effect of disturbing provisioning behaviour. First, the time between removal of the models and the first subsequent feed by any carer was significantly longer after the jay presentation than after the dove (LMM: *P* < 0.001, Table 4.1, Figure 4.2a). Second, there were significant differences in provisioning rates for the two treatments during model presentation periods and following model removal (LMM: *P* < 0.001, Table 4.1, Figure 4.2b). Overall, only 5.8% (3/52) of carers fed during presentation of the jay, whereas 51.9% (27/52) fed during dove presentation. Thus, provisioning rate was significantly lower during the jay presentation than during the dove presentation (Tukey’s HSD: *P* < 0.001), which in turn was significantly lower than provisioning rate during the preceding control period (Tukey’s HSD: *P* < 0.001). Interestingly, post-jay provisioning rate was significantly higher than post-dove (Tukey’s HSD: *P* < 0.001), which in turn was higher than during control watches (Tukey’s HSD: *P* < 0.001). These results show that the jay presentation had the anticipated negative effect on provisioning behaviour relative to the dove, and provisioning rates during subsequent watches suggest that there was some compensation for reduced provisioning during model presentations, especially following presentation of the jay (Figure 4.2b).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Table 4.1. Effect of experimental treatment on provisioning behaviour of long-tailed tits. Fixed effect of interest was ‘Treatment’. Significant values (P < 0.05) in bold. | | | | |
| Response variable | Estimates ± SE | df | 𝝌2 | *P* |
| *Lag time to feed* | | | | |
| Log (lag time) | post-jay: 0.897 ± 0.271 | 1 | 10.950 | **<0.001** |
| *Provisioning rate* | | | | |
| Number of feeds | dove presentation: -1.497 ± 0.309  jay presentation: - 4.182 ± 0.636  post-dove: 0.226 ± 0.081  post-jay: 0.360 ± 0.081 | 4 | 66.817 | **<0.001** |

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Figure 4.2. (a) The lag time (in minutes) between model removal and the first feed during the subsequent watch for the dove (*N* = 22) and jay (*N* = 22) treatments. (b) Provisioning rate (feeds per hour) when dove or jay were present, during control watches and watches following model presentation (post-dove and post-jay) (*N* = 22 watches per treatment). Central emboldened lines are median values. Lower and upper boundaries of boxes are lower and upper quartile values, respectively. Upper and lower boundaries of tails are maximum and minimum observed values within upper (3rd quartile + 1.5 \* interquartile range) and lower fence (1st quartile – 1.5 \* interquartile range), respectively. Points are outliers (values outside of fence range). Significance indicators from Tukey’s HSD post-hoc analysis: \*\*\* = *P* < 0.001.

**4.4.2 Does predation threat increase coordination?**

To investigate whether a model predator affected coordination, we compared coordination levels in control watches and watches following experimental treatments. We found no significant difference between control, dove, and jay treatments in any metric of coordination: arrival synchrony (GLMM: *P* = 0.888, Table 4.2, Figure 4.3a), loitering period overlap (Present upon arrival GLMM: *P* = 0.252, Table 4.2; Present upon feed GLMM: *P* = 0.229, Table 4.2, Figure 4.3b), feed synchrony (GLMM: *P* = 0.965, Table 2, Figure 4.3c), or alternation (GLMM: *P* = 0.641, Table 4.2, Figure 4.3d). We note that Figures 4.3a and 4.3b appear to show less synchrony during control watches, although the models did not identify such an effect (Table 4.2). This is because the level of synchrony inevitably increases with provisioning rate which was higher following model presentation (Figure 4.2). The models control for this effect, but the figures do not.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Table 4.2. Effect of experimental treatment on levels of coordination in subsequent watches. Fixed effect of interest was ‘Treatment’. | | | | |
| Response variable | Estimates ± SE | df | 𝝌2 | *P* |
| *Arrival synchrony* | | | | |
| Number of synchronised arrivals | post-dove: 0.036 ± 0.107  post-jay: 0.057 ± 0.117 | 2 | 0.238 | 0.888 |
| *Present upon arrival* | | | | |
| Number visits where the focal carer arrived back with another carer loitering | post-dove: 0.168 ± 0.134  post-jay: 0.241 ± 0.146 | 2 | 2.759 | 0.252 |
| *Present upon feed* | | | | |
| Number visits where focal carer fed whilst another loitered | post-dove: 0.174 ± 0.134  post-jay: 0.249 ± 0.147 | 2 | 2.945 | 0.229 |
| *Feed synchrony* | | | | |
| Number of synchronised feeds | post-dove: 0.026 ± 0.105  post-jay: 0.028 ± 0.115 | 2 | 0.072 | 0.965 |
| *Alternation* | | | | |
| Number of alternated feeds | post-dove: 0.047 ± 0.083  post-jay: -0.021 ± 0.092 | 2 | 0.889 | 0.641 |

Chart, box and whisker chart

Description automatically generated

Figure 4.3. Percentages of: (a) arrivals synchronised, (b) feeds where the focal carer fed with another carer nearby, (c) feeds synchronised, and (d) feeds alternated, in control watches and watches following model presentation (post-dove and post-jay) (*N* = 22 watches per treatment). Central emboldened lines are median values. Lower and upper boundaries of boxes are lower and upper quartile values, respectively. Upper and lower boundaries of tails are maximum and minimum observed values within upper (3rd quartile + 1.5 \* interquartile range) and lower fence (1st quartile – 1.5 \* interquartile range), respectively. Points are outliers (values outside of fence range). Significance indicators from Tukey’s HSD post-hoc analysis: N.S. = *P* > 0.05.

To examine whether perceived predation threat affected loitering behaviour, we first compared loitering times during control watches and watches following model presentations. The mean duration of loitering periods differed significantly between treatments (LMM: *P* = 0.006, Table 4.3, Figure 4.4a), being significantly longer in post-jay watches than post-dove (Tukey’s HSD: *P* = 0.013). In contrast, there was no significant difference in mean loitering times during control watches and watches post-dove (Tukey’s HSD: *P* = 0.105) or post-jay (Tukey’s HSD: *P* = 0.732). We then tested whether an increase in perceived predation threat reduced parental activity near nests. The time that one or more carers was present near the nest differed significantly between treatments (LMM: *P* = 0.009, Table 4.3, Figure 4.4b), but contrary to expectations, post-jay watches had a higher carer presence than post-dove watches (Tukey’s HSD: *P* = 0.022). This result appears to be a direct consequence of the increased time that carers spent loitering near the nest following the jay treatment rather than a change in loitering period overlap, because when mean loitering time was included in the model, this variable (LMM: *P* < 0.001, Table 4.3), rather than treatment (LMM: *P* = 0.067, Table 4.3) predicted the time that one or more carers spent near the nest.

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| Table 4.3. Effect of experimental treatment on loitering behaviour in subsequent watches. Significant values (*P* < 0.05) in bold. | | | | | |
| Response variable | Fixed effects | Estimates ± SE | df | 𝝌2 | *P* |
| *Loitering time* | | | | | |
| Log(mean loitering time) | Treatment | post-dove: -0.222 ± 0.105  post-jay: 0.090 ± 0.116 | 2 | 10.130 | **0.006** |
| *Carer(s) nearby (without mean loitering time)* | | | | | |
| Duration of time where a carer(s) was nearby | Treatment | post-dove: -2.604 ± 1.154  post-jay: 0.572 ± 1.267 | 2 | 9.416 | **0.009** |
| *Carer(s) nearby (with mean loitering time)* | | | | | |
| Duration of time where a carer(s) was nearby | Treatment | post-dove: -0.248 ± 0.705  post-jay: 1.257 ± 0.737 | 2 | 5.395 | 0.067 |
| Mean loitering time | 4.011 ± 0.388 | 1 | 106.711 | **<0.001** |

Chart, diagram, box and whisker chart

Description automatically generated

Figure 4.4. (a) Log-transformed mean loitering times, and (b) percentage of a watch where at least one carer was loitering nearby, for control watches and watches following model presentation (post-dove and post-jay) (*N* = 22 watches per treatment). Central emboldened lines are median values. Lower and upper boundaries of boxes are lower and upper quartile values, respectively. Upper and lower boundaries of tails are maximum and minimum observed values within upper (3rd quartile + 1.5 \* interquartile range) and lower fence (1st quartile – 1.5 \* interquartile range), respectively. Points are outliers (values outside of fence range). Significance indicators from Tukey’s HSD post-hoc analysis: N.S. = *P* > 0.05, \* = 0.05 ≥ *P* > 0.01.

To further understand the dynamics of carers’ adjustments to their provisioning behaviour in response to predators, we investigated whether provisioning rate, coordination, and loitering times varied through watches when split into three sections. Firstly, provisioning rate generally increased through watches (LMM: *P* = 0.002, Table 4.4, Figure 4.5a), although this effect did not differ between treatments as evidenced by the absence of a significant interaction term between section and treatment (LMM: *P* = 0.234, Table 4.4). Secondly, there was no significant difference between sections in the levels of arrival synchrony (GLMM: *P* = 0.143, Table 4.4), loitering period overlap (Present upon feed GLMM: *P* = 0.953, Table 4.4; Present upon arrival GLMM: *P* = 0.855, Table 4.4) or feed synchrony (GLMM: *P* = 0.158, Table 4.4, Figure 4.5b). However, there was a significant difference in alternation between sections (GLMM: *P* = 0.037, Table 4.4, Figure 4.5c), but with no effect of treatment (GLMM: *P* = 0.999, Table 4.4). Contrary to the prediction of the predation hypothesis, alternation was significantly lower in the first third of a watch (Tukey’s HSD: 1st–2nd, *P* = 0.033) suggesting that disturbance associated with camera set up and model presentation may have inhibited coordination for a brief time. Finally, mean loitering time was significantly influenced by the interaction of watch type and section (LMM: *P* = 0.042, Table 4.4, Figure 4.5a), meaning that the variation in loitering time between sections (1st, 2nd, or 3rd) of a watch depended on whether it was a control, post-dove, or post-jay watch. This effect was seemingly driven by the fact that in both control and post-jay watches, loitering times were significantly longer in the first third (Tukey’s HSD: 1st–2nd Control, *P* = 0.013; 1st–3rd Control, P < 0.001; 1st–2nd jay, *P* < 0.001; 1st–3rd jay, P < 0.001), whereas in post-dove watches there was no difference between thirds (Tukey’s HSD: 1st–2nd, *P* = 0.862; 1st–3rd, *P* = 0.838). These results suggest that initial set up of the experiment may have induced a brief change in provisioning behaviour, though to a lesser extent than the predator presentation.

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| Table 4.4. Effect of experimental treatment on provisioning rate, levels of coordination and loitering duration between sub-sections of watches split into thirds. Significant values (*P* < 0.05) in bold. | | | | | |
| Response Variable | Fixed effects | Estimates ± SE | df | 𝝌2 | *P* |
| *Provisioning rate* | | | | | |
| Number of feeds | Section | 2nd: 0.113 ± 0.131  3rd: 0.390 ± 0.124 | 2 | 12.926 | **0.002** |
|  | Treatment \* section | post-dove, 2nd: -0.199 ± 0.172  post-dove 3rd: -0.333 ± 0.164  post-jay, 2nd: 0.032 ± 0.167  post-jay 3rd: -0.151 ± 0.160 | 4 | 5.572 | 0.234 |
| *Arrival synchrony* |  |  |  |  |  |
| Number of synchronised arrivals | Section | 2nd: 0.235 ± 0.215  3rd: 0.147 ± 0.204 | 2 | 3.889 | 0.143 |
|  | Treatment \* section | post-dove, 2nd: -0.090 ± 0.270  post-dove, 3rd: -0.155 ± 0.257  post-jay, 2nd: -0.043 ± 0.260  post-jay, 3rd: -0.090 ± 0.249 | 4 | 0.373 | 0.985 |
| *Present upon arrival* |  |  |  |  |  |
| Number visits where the focal carer arrived back with another carer loitering | Section | 2nd: -0.168 ± 0.268  3rd: -0.009 ± 0.242 | 2 | 0.314 | 0.855 |
|  | Treatment \* section | post-dove, 2nd: 0.201 ± 0.336  post-dove, 3rd: -0.017 ± 0.307  post-jay, 2nd: 0.296 ± 0.328  post-jay, 3rd: 0.192 ± 0.300 | 4 | 1.319 | 0.858 |
| *Present upon feed* |  |  |  |  |  |
| Number visits where focal carer fed whilst another loitered | Section | 2nd: -0.275 ± 0.267  3rd: -0.116 ± 0.239 | 2 | 0.096 | 0.953 |
|  | Treatment \* section | post-dove, 2nd: 0.304 ± 0.334  post-dove, 3rd: 0.092 ± 0.305  post-jay, 2nd: 0.424 ± 0.327  post-jay, 3rd: 0.291 ± 0.298 | 4 | 2.045 | 0.727 |
| *Feed synchrony* | | | | | |
| Number of synchronised feeds | Section | 2nd: 0.106 ± 0.207  3rd: 0.039 ± 0.195 | 2 | 3.690 | 0.158 |
|  | Treatment \* section | post-dove, 2nd: 0.092 ± 0.263  post-dove, 3rd: 0.031 ± 0.249  post-jay, 2nd: 0.058 ± 0.252  post-jay, 3rd: -0.060 ± 0.241 | 4 | 0.417 | 0.981 |
| *Alternation* | | | | | |
| Number of alternated feeds | Section | 2nd: 0.215 ± 0.161  3rd: 0.123 ± 0.155 | 2 | 6.601 | **0.037** |
|  | Treatment \* section | post-dove, 2nd: -0.035 ± 0.206  post-dove, 3rd: -0.064 ± 0.198  post-jay, 2nd: -0.012 ± 0.201  post-jay, 3rd: -0.027 ± 0.195 | 4 | 0.111 | 0.999 |
| *Loitering time* | | | | | |
| Log(mean loitering time) | Section | 2nd: -0.462 ± 0.128  3rd: -0.666 ± 0.132 | 2 | 49.817 | **<0.001** |
|  | Treatment \* section | post-dove, 2nd: 0.269 ± 0.183  post-dove, 3rd: 0.469 ± 0.183  post-jay, 2nd: -0.123 ± 0.181  post-jay, 3rd: -0.009 ± 0.181 | 4 | 9.882 | **0.042** |

Chart, box and whisker chart

Description automatically generated

Figure 4.5. (a) Provisioning rate (feeds per hour), (b) percentage of feeds synchronised, (c) percentage of feeds alternated, and (d) log-transformed mean loitering time between thirds (1st blue, 2nd orange and 3rd green) of control watches and watches following model presentation (post-dove and post-jay) (*N* = 22 watches per treatment). Central emboldened lines are median values. Lower and upper boundaries of boxes are lower and upper quartile values, respectively. Upper and lower boundaries of tails are maximum and minimum observed values within upper (3rd quartile + 1.5 \* interquartile range) and lower fence (1st quartile – 1.5 \* interquartile range), respectively. Points are outliers (values outside of fence range).

**4.5 Discussion**

In this study, we presented a model predator (jay) and non-predator (dove) near the nests of provisioning long-tailed tits to test whether carers actively increased their behavioural coordination in response to elevated predator threat. Almost all carers completely ceased provisioning during predator presentation and took significantly longer to resume feeding following removal of the predator than the non-predator (Figure 4.2), suggesting an acute antipredator adjustment in provisioning behaviour. However, contrary to expectations, carers did not increase coordination in response to predator treatment, relative to the control period or non-predator treatment (Figure 4.3). Furthermore, the proportion of time that at least one carer was present near the nest was higher following the predator than the non-predator treatment (Figure 4.4b) because of longer loitering periods following the predator treatment (Figure 4.4a). Surprisingly, rates of alternation decreased in the first period of a watch (Figure 4.5c), suggesting that disturbance may interrupt patterns of coordination even for control watches. Overall, we found no support for the prediction that carers would increase coordination in response to elevated perceived predation risk.

Previous studies have demonstrated that more synchronous pairs exhibited lower activity near the nest per provisioning visit (Bebbington and Hatchwell 2016, Leniowski and Wegryzn 2018) and suffered lower rates of brood failure (Raihani et al. 2010, Leniowski and Wegryzn 2018). Circumstantial evidence in support of the predation hypothesis was also reported in New Zealand bellbirds (Khwaja et al. 2019). However, to our knowledge no prior study has experimentally manipulated perceived predation risk to directly test whether parents adjust their coordination of care in response. Therefore, our aim was to experimentally test the hypothesis that carers coordinate provisioning visits as an antipredator measure to reduce carer activity near the nest, thus limiting the time that the nest location is advertised to predators. We anticipated that the presentation of a model predator close to nests would elevate carers’ perception of predation risk, and that coordination would be elevated in watches following predator presentation before declining with time since model presentation. However, despite the high rate of nest predation experienced by long-tailed tits (72%; Hatchwell et al. 2013) and a clear response to the model jay, carers did not increase their synchrony, or any associated metric of coordination. While we found no evidence of facultative adjustment of coordination in response to an elevated predation risk, this does not necessarily mean that synchrony has no function in reducing predation risk. Long-tailed tits may experience a near constant risk of predation and their coordination of care (Halliwell et al. 2022, 2023a) may be an evolved response to that threat. Therefore, it would be interesting to investigate whether broods fed by better coordinated groups of carers are more likely to survive than those provisioned by poorly coordinated carers.

Our conclusion that long-tailed tits did not adjust coordination as an antipredator strategy contrasts with our finding on provisioning rates. There was an almost complete cessation of provisioning during presentation of a model predator and for a period following its removal. This response shows that our manipulation had the anticipated effect on perceived predation risk and is similar to previous studies reporting reduced provisioning rates in response to predator threats (Lima and Dill 1990, Peluc et al. 2008, Ghalambor et al. 2013, Dorset et al. 2017). We anticipated that carer activity near the nest would decrease during watches following predator treatment. However, once feeding resumed, provisioning rates were elevated following the predator treatment, an effect we attribute to compensation for the prolonged period (~25 mins) when provisioning ceased. This result is consistent with a previous study of this species that found higher provisioning rates in response to experimental increases in perceived brood demand (Meade et al. 2011). We also found that the duration of loitering periods was longer following the predator than the non-predator presentation, presumably because carers were more risk averse or vigilant when close to the nest, as reported in house wrens, *Troglodytes aedon* (Dorset et al. 2017). Higher provisioning rates and longer loitering periods led to at least one carer being present near the nest for longer following presentation of the predator than the non-predator. This result was contrary to the prediction that carers would respond to elevated predation risk by reducing activity near the nest, mediated by an increase in coordination (Raihani et al. 2010, Bebbington and Hatchwell 2016, Leniowski and Węgrzyn 2018).

One explanation for these results is that rather than reduce their time near the nest in response to a predator, carers instead are more cautious about provisioning the brood. If being witnessed provisioning compromises brood safety more than simply being witnessed near the nest, then carers may increase vigilance rather than adjusting coordination. Ultimately, this depends on whether nest locations are typically revealed by provisioning visits directly (Skutch 1949) or by activity near the nest (Martin et al. 2000) and associated offspring begging (Haskell 1994, Briskie et al. 1999). Which of these is the dominant driver of nest advertisement is unknown in long-tailed tits. Alternatively, the longer loitering periods following the predator treatment could reflect an increased attentiveness for potential nest defence (Montgomerie and Weatherhead 1988, Kleindorfer et al. 2005). The small size of long-tailed tits relative to predators (long-tailed tit 7–8 g vs Eurasian Jay 140–180 g; Snow et al. 1998) means they are incapable of physically deterring corvids. However, carers may still be able to distract predators as a last resort, and they often approached the model predator closely, mobbing it with frequent alarm-calls. Such behaviour could function as an instruction to the chicks to stop begging (Greig-Smith 1980, Knight and Temple 1986) and the prolonged loitering periods following predator presentation could, therefore, result from parents instructing chicks to stop begging following predator presentation. However, we know little about vocal communication between parents and nestlings in this species, so this explanation is speculative.

In addition to testing the predator hypothesis for parental coordination, our results are potentially informative about the utility of randomisation approaches that test whether coordination occurs more than expected by chance. Several studies have used randomisation approaches to demonstrate higher than expected levels of alternation and synchrony (e.g. Johnstone et al. 2014, Savage et al. 2017; Halliwell et al. 2022). However, alternative explanations have been suggested (Schlicht et al. 2016, Ihle et al. 2019a, Santema et al. 2019), specifically, that a common response by all carers to acute (e.g*.* predator disturbance) or chronic changes (e.g. weather) may cause temporal autocorrelation between carers’ intervisit intervals. Randomisation of these temporally autocorrelated intervisit intervals may therefore underestimate expected coordination (Schlicht et al. 2016, Ihle et al. 2019a; Santema et al. 2019) and hence increase the probability that observed coordination will appear higher than expected. Our results appear to corroborate this critique given that 94% (49/52) of carers ceased provisioning during model predator presentation. However, we also note that alternation was lowest immediately following a period of disturbance, suggesting that long-tailed tits are best able to coordinate their care when undisturbed for long periods. Furthermore, alternation was also lowest in the first third during control watches, suggesting that the disturbance caused by observers may also disrupt coordination. Thus, the extent of behavioural coordination may be underestimated even if no predator is encountered during a watch. Therefore, whilst we agree that acute and chronic changes in conditions during provisioning watches may cause underestimation of apparent coordination by randomisation approaches (Schlicht et al. 2016, Ihle et al. 2019a, Santema et al. 2019), we also highlight that any disturbance may likewise limit the scope for detecting behavioural coordination. We suggest that this possibility should be considered when quantifying coordination from observational data.

In conclusion, our results did not support the hypothesis that carers coordinate provisioning to reduce predation risk, as we found no change in coordination following predator treatment, relative to controls. Nevertheless, we cannot rule out the hypothesis that synchrony is an adaptation to reduce brood predation, as carers may perform a fixed level of coordination which is not adjusted in response to variable predation risk. Whilst carers responded to predator treatment by ceasing provisioning, surprisingly alternation decreased in the period immediately following disturbance, suggesting that disturbance temporarily interrupted provisioning coordination. We detected some limited response to predator threat as carers increased their loitering time in the period immediately following predator treatment, which we suggest may be caused by increased risk aversion or vigilance following predator exposure. Finally, we suggest that further investigation into the link between coordination and brood survival is necessary to fully examine the brood predation hypothesis for coordinated care.

**4.6 Acknowledgements and data availability**

We thank Caroline Milsom, Marion Germain, and Jamie Thompson for their assistance with field work, and Yorkshire Water, Hallamshire Golf Club, Sheffield City Council and the private residents and landowners within the field site for access to their land. We also thank the reviewers and editors who handled this manuscript for their rigorous and constructive feedback, and SC Anderson for their illustrations of our treatment models. This work was supported by the Natural Environment Research Council (NE/S00713X/1 and NE/R001669/1).

The datasets generated during and/or analysed during the current study are available in the Dyrad repository, https://doi.org/10.5061/dryad.cc2fqz69z.

**4.7 Ethics approval**

During nest building, laying and incubation each nest was checked every 1–3 days, with daily checks approaching laying, incubation, and hatching. Whenever possible nests were sampled non-intrusively, *e.g.* incubation confirmed by observing females’ attendance at the nest. However, to record precise hatch dates, after 12 days of incubation, nests were checked daily for hatching by feeling gently within the nest, a practice that has been performed on this population for 29 years. Nestlings and adult immigrants were ringed by BJH and SJB under British Trust for Ornithology (BTO) licence with two colour rings (size code: XF) on one leg and a metal BTO ring (size code: XF) on the other. When ringing nestlings, to minimise time chicks spent out of the nest and to ensure that carers did not return to an empty nest, half the brood was ringed at a time. During ringing, 5–20µl of blood was taken by brachial venepuncture under UK Home Office licence (Project Licence PP5912664; Personal Licence (BJH) IE73AE8C8) for genotyping and sex determination. During sampling, nestlings were stored in an insulated bird-bag and remained warm and dry throughout. In total, 183 nestlings were ringed from nests sampled for this study. When ringing adult immigrants, mist-nests were watched continuously, and birds were extracted and processed immediately upon capture. In total, 21 breeding females, 20 breeding males, and 11 helpers (10 males, 1 female) were observed in this study. Our experimental procedure necessitated some observer disturbance when setting up the camera and presenting models, however, we recorded no events of brood abandonment during or following our experiment. All applicable international, national, and institutional guidelines for the use of animals were followed and all regulated procedures were approved by the Animal Welfare and Ethical Review Body at the University of Sheffield.

**4.8 Supplementary material**

**4.8.1 Methods**

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| Table S4.1. *P-*values for watch order and treatment *with* and *without* the inclusion of watch order within the model. Significant values (*P* < 0.05) in bold. | | | |
| Response variable | Watch order *P-*value | Treatment *P-*value *without* watch order | Treatment P-value *with* watch order |
| Lag time | 0.266 | **<0.001** | **<0.001** |
| Provisioning rate | 0.276 | **<0.001** | **<0.001** |
| Synchronised feeds | 0.775 | 0.965 | 0.992 |
| Synchronised arrivals | 0.956 | 0.888 | 0.917 |
| Present upon feed | 0.670 | 0.229 | 0.223 |
| Present upon arrival | 0.696 | 0.252 | 0.249 |
| Alternated feeds | 0.533 | 0.641 | 0.621 |
| Loitering time | 0.959 | **0.006** | **0.007** |
| Carer(s) nearby | 0.895 | **0.009** | **0.010** |

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| Table S4.2. Details of all terms of interest, fixed effect covariates and random effects used throughout analysis | |
| **Terms of interest** | **Description** |
| Treatment | Factor denoting which treatment each watch received. In most cases this was a 3-level factor (control watches, watches following dove presentation, and watches following jay presentation). For comparison of provisioning rates this factor also included watches during the presentation periods of models (dove presentation period, and jay presentation period). |
| Section | Factor denoting whether a given sub-section of a watch was the first, middle or last third. Additionally, the interaction of section and treatment informed whether the relationship between sections depended on the type of treatment. |
| **Fixed effect covariates** | **Description** |
| Carer number | Ordinal factor denoting the number of carers observed provisioning during a given watch (5>4>3>2). Because often no carers fed during presentation periods, for these watches, carer number was taken as greatest number of carers which provisioned at another watch during the same experiment. 2: 69.7%, 3: 21.2%, 4: 3.0%, and 5: 6.1%. |
| Watch duration | Continuous numerical variable denoting the time, in minutes, between first arrival and last feed of each watch. Mean (±SE): 58 mins 36s ± 48s, *N* = 66. |
| Watch start time | Continuous numerical variable denoting the time of day that each experiment was started. Mean: 08:30am; range: 7:20am–12:40pm. |
| Brood age | Integer numerical variable denoting the number of days since first recording hatching on which each experiment was performed. Day 8: *N* = 12; Day 9: *N* = 6; Day 10: *N* = 4. |
| Brood size | Integer numerical variable denoting the number of live chicks present on d11. Median: 9; range 2–11. |
| Hatch date | Integer numerical variable denoting the number of days since March 1 each year that each nest hatched. Median: April 30; range: April 19–May 29. |
| Provisioning rate | Continuous numerical variable denoting the collective hourly provisioning rate of all carers observed provisioning during a given watch. Mean (±SE): 22.94 ± 1.06 feeds/h; range: 7.94–46.42 feeds/h. |
| Maximum possible alternation | Continuous numerical variable denoting the percentage feeds during each watch which can theoretically be alternated (and thus synchronised). For example, if more than half of the feeds during a given watch are performed by one carer then there are insufficient feeds by other carers with which to alternate. This term is used as a proxy for provisioning rate parity, generalised to conform with scenarios with >2 carers. Mean (±SE): 87.80 ± 1.34%; range: 57.14–97.67%. For analysis of different sections of watches, we calculated maximum possible alternation for each specific section for use as a response variable and a covariate in other analysis. |
| Mean loitering time | The mean loitering period duration for all carers during a given watch, used as a covariate only in analysis of total time that a carer(s) was loitering nearby at their nest during each watch. Modelled as a continuous numerical variable. Mean (±SE): 45.8s ± 3.8s. |
| **Random effects** | **Description** |
| Year | Factor denoting the year from which the data were collected. Used ubiquitously throughout analyses. Modelled as a factor. |
| Nest ID | Factor denoting the unique identity of each nest. Used ubiquitously throughout analyses. |
| Watch ID | Factor denoting the unique identity of each provisioning watch. Used only when watches were split into thirds. |
| Rowref | The observation level random effect, used to account for overdispersion in Poisson distributed models. |

**Checking for overparameterisation**

When investigating the effect of treatment, it is important to include biologically relevant covariates that could influence coordination behaviour. Therefore, we built covariate inclusive full models from which we tested directly whether our terms of interest were significant. This approach was used in previous studies of coordination of care (e.g. Ihle et al. 2019a, Halliwell et al. 2022, Halliwell et al. 2023a), however, these studies used larger sample sizes than we have here. So, to investigate whether our results were influenced by overparameterisation we also analysed our data using two further approaches. The first reduced the number of parameters within the models by performing stepwise elimination of the largest *P*-value terms until only key and significant terms remained. In most cases, this considerably reduced the number of terms included in the final model, addressing potential concerns about overparamterisation. We note that all key results from this analysis were qualitatively the same as from the full model approach. The second used an information theoretic (AIC) approach to produce several best fitting models (within 2 AIC scores of the top model) from the full set of terms using the package MuMIn (Bartoń 2022). As we test specific predictions using an a priori hypothesis framework, we believe that *P*-values are the most appropriate analytical approach, however this approach is useful to test whether results are influenced by overparameterisation. In 18/23 models, findings from our *P*-value approaches were fully corroborated by this AIC approach (i.e. key term present/absent from all best fitting models when *P*-values were significant/not significant, respectively). In 4/23 cases, results were partially corroborated between these approaches (i.e. key terms present in some of the best fitting models), and in only one case did the results of these approaches differ. We conclude that our key results are not influenced by overparameterisation, so we present our findings from the covariate inclusive full model approach in the main text. Details and key results from these approaches are available in table S4.3.

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| Table S4.3. Comparison of results using different analytical approaches. The first approach used all biologically relevant covariates to build a full model and extracts *P*-values from this model directly (covariate inclusive full model). The second approach used stepwise elimination of covariate terms on the full model until a minimum adequate model (MAM) remained containing only the terms of interest and significant terms (stepwise elimination approach). The third used an information theoretic approach to generate best fitting models; all models which were within 2 AIC scores of the top model were considered the best fitting models (AIC approach). Significant values (*P* < 0.05 or included in best fitting models) in bold. | | | | | |
| Model term | *P* from full model | *P* from stepwise elimination MAM | Fixed effects present in MAM (df) | Term present in best fitting AIC models | Corroborated between approaches? |
| *Lag time to feed model* | | | | |  |
| Treatment | **<0.001** | **<0.001** | 1 (3 df) | **Yes (1/1)** | Yes |
| *Provisioning rate model* | | | | |  |
| Treatment | **<0.001** | **<0.001** | 3 (7 df) | **Yes (5/5)** | Yes |
| *Arrival synchrony model* | | | | |  |
| Treatment | 0.888 | 0.785 | 3 (9 df) | No (0/10) | Yes |
| *Present upon arrival model* | | | | |  |
| Treatment | 0.252 | 0.197 | 5 (11 df) | No (0/4) | Yes |
| *Present upon feed model* | | | | |  |
| Treatment | 0.229 | 0.177 | 5 (11 df) | No (0/4) | Yes |
| *Feed synchrony model* | | | | |  |
| Treatment | 0.965 | 0.758 | 3 (9 df) | No (0/3) | Yes |
| *Alternation model* | | | | |  |
| Treatment | 0.641 | 0.588 | 4 (8 df) | No (0/4) | Yes |
| *Loitering time model* | | | | |  |
| Treatment | **0.006** | **0.009** | 3 (6 df) | **Yes (1/2)** | Mixed |
| *Carer(s) nearby model (without mean loitering time)* | | | | |  |
| Treatment | **0.009** | **0.012** | 4 (7 df) | **Yes (5/5)** | Yes |
| *Carer(s) nearby model (with mean loitering time)* | | | | |  |
| Treatment | 0.067 | 0.073 | 5 (8 df) | **Yes (7/7)** | Mixed |
| *Provisioning rate model (thirds)* | | | | |  |
| Section | **0.002** | **0.001** | 5 (10 df) | **Yes (5/5)** | Yes |
| Treatment \* section | 0.234 | 0.233 | 6 (14 df) | No (0/5) | Yes |
| *Arrival synchrony model (thirds)* | | | | |  |
| Section | 0.143 | 0.119 | 3 (8 df) | **Yes (2/6)** | Mixed |
| Treatment \* section | 0.985 | 0.988 | 5 (14 df) | No (0/6) |  |
| *Present upon arrival model (thirds)* | | | | |  |
| Section | 0.855 | 0.896 | 4 (9 df) | No (0/6) | Yes |
| Treatment \* section | 0.858 | 0.867 | 6 (17 df) | No (0/6) | Yes |
| *Present upon feed model (thirds)* | | | | |  |
| Section | 0.953 | 0.975 | 4 (11 df) | No (0/7) | Yes |
| Treatment \* section | 0.727 | 0.733 | 6 (17 df) | No (0/7) | Yes |
| *Feed synchrony model (thirds)* | | | | |  |
| Section | 0.158 | 0.153 | 3 (8 df) | **Yes (3/9)** | Mixed |
| Treatment \* section | 0.981 | 0.989 | 5 (14 df) | No (0/9) | Yes |
| *Alternation model (thirds)* | | | | |  |
| Section | **0.037** | **0.035** | 3 (8 df) | **Yes (10/10)** | Yes |
| Treatment \* section | 0.999 | 0.998 | 5 (14 df) | No (0/10) | Yes |
| *Loitering time (thirds)* | | | | |  |
| Section | **<0.001** | **<0.001** | 6 (15 df) | **Yes (2/2)** | Yes |
| Treatment \*section | **0.042** | **0.044** | 6 (15 df) | No (0/2) | No |

**Estimating expected coordination**

In prior investigations of coordination of care, researchers have quantified a level of ‘active’ coordination by comparing observed levels of coordination to those expected by chance using randomisation and simulation approaches. The purpose of this was to account for a certain level of apparent coordination expected by pure random chance. Studies have highlighted how factors such as changing weather and refractory periods can induce different levels of expected coordination, so when determining if carers coordinate their care, it has been essential to compare observed levels of coordination to those expected by chance. In this study, where appropriate, we compared observed coordination to levels expected by chance using a null model randomisation approach developed in Halliwell et al. (2023a) which independently randomises each carers times near the nest (loitering periods) and time away from the nest within a watch to create 1000 randomised sequences per watch, the expected levels of each coordination metric are the median values, per watch, from these 1000 randomised sequences. The term ‘Data type’ is a binary factor used to distinguish observed levels of collected directly from field observation from expected levels generated by the randomisation approach. Comparing observed levels of coordination to those expected by chance allows for: i) quantification of whether coordination occurs more than expected by chance, i.e. active coordination, by investigating the effect of ‘Data type’ directly, and ii) comparison of the levels of active coordination between different treatments by investigating the effect of the interaction of ‘Data type’ and ‘Treatment’. This latter approach differs from a direct comparison of observed coordination between treatments because it accounts for any potential increase in coordination caused by a standardisation of provisioning behaviours. For example, if a group of carers provision independently (i.e. no coordination) and have highly variable and inconsistent intervisit intervals the level of both observed and expected coordination will be low, however if these uncoordinated carers have consistent and similar intervisit intervals the levels of both observed and expected coordination will be high (Johnstone et al. 2014, Ihle et al. 2019a). Therefore, a direct comparison of levels of observed coordination would equate a standardisation of intervisit intervals with an increase in coordination, while the comparison between observed and expected coordination would not. If carers coordinate their provisioning by actively arriving and feeding together (synchrony) but have high intervisit interval variation, e.g. due to stochastic variation in foraging time, then observed coordination will be high but expected levels will be low. Whilst we consider both mechanisms of increasing coordination theoretically possible and the distinction between them informative, we believe that an increase in coordination mediated by standardisation of length of intervisit intervals only is highly unlikely. We consider a true and direct increase in provisioning coordination in response to predator treatment the most likely mechanism by which alternation, synchrony etc. would increase. In this case an increase in both observed coordination and ‘active’ coordination (observed minus expected) would be found following predator presentation, which would be reflected in the results of both the direct comparison of observed coordination approach (as in main text) and a comparison of the levels of ‘active’ coordination between treatments (see below). To test this, we compared observed coordination between treatments directly (main text) and compared the deviation from expectation, i.e. active coordination (see below).

We compared the observed and expected levels of each coordination metric (‘Arrival synchrony’, ‘Present upon arrival’, ‘Present upon feed’, ‘Feed synchrony’ and ‘Alternation’) and the proportion of each watch where a carer(s) was present in the nearby area between control watches and watches following each treatment (dove and jay). Here we used ‘Data type’ directly to compare observed levels to those expected by chance and the interaction of ‘Treatment’ and ‘Data type’ to compare differences in deviation from expected between watches following each treatment.

**4.8.2 Results**

**Full model outputs from the main text**

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| Table S4.3. Estimates and *P-*values for fixed effects (terms of interest and covariates) from analysis of the lag time between model (dove and jay) removal and first feed of the following watch. *N* = 44 from 22 nests. Significant values (*P* < 0.05) in bold. Corresponding summary table in the main text: Table 4.1. | | | | |
| Parameter | Estimates ± SE | df | 𝝌2 | *P* |
| Intercept | -6.075 ± 0.212 |  |  |  |
| Treatment | post-jay: 0.897 ± 0.271 | 1 | 10.950 | **<0.001** |
| Provisioning rate | 0.263 ± 0.162 | 1 | 2.643 | 0.104 |
| Carer number | 3: 0.435 ± 0.360  4: -1.884 ± 0.884  5: -0.076 ± 0.563 | 3 | 6.195 | 0.103 |
| Brood size | -0.262 ± 0.164 | 1 | 2.544 | 0.111 |
| Watch start time | -0.324 ± 0.173 | 1 | 3.513 | 0.061 |
| Brood age | 0.023 ± 0.154 | 1 | 0.022 | 0.882 |
| Hatch date | 0.243 ± 0.185 | 1 | 1.736 | 0.188 |

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| Table S4.4. Estimates and *P-*values for the fixed effects (terms of interest and covariates) from analysis of the provisioning rate during control watches, during and following each model presentation period (dove and jay). *N* = 110 watches from 22 nests. Significant values (*P* < 0.05) in bold. Corresponding summary table in the main text: Table 4.1. Note: to account for the fact that during several presentation periods no carers fed, for this analysis carer number was considered the total number of carers observed at a nest rather than the number which fed during each specific watch. | | | | |
| Parameter | Estimates ± SE | df | 𝝌2 | *P* |
| Intercept | 1.067 ± 0.228 |  |  |  |
| Treatment | dove presentation: -1.497 ± 0.309  jay presentation: -4.182 ± 0.636  post-dove: 0.226 ± 0.081  post-jay: 0.360 ± 0.081 | 4 | 66.817 | **<0.001** |
| Carer number | 3: 0.006 ± 0.106  5: 0.094 ± 0.156 | 2 | 0.360 | 0.835 |
| Watch duration | 0.395 ± 0.135 | 1 | 7.044 | **0.008** |
| Brood size | 0.102 ± 0.507 | 1 | 4.040 | **0.044** |
| Watch start time | 0.104 ± 0.055 | 1 | 3.539 | 0.060 |
| Brood age | 0.030 ± 0.049 | 1 | 0.379 | 0.538 |
| Hatch date | -0.199 ± 0.058 | 1 | 11.755 | **0.001** |

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| Table S4.5. Estimates and *P*-values for the fixed effects (terms of interest and covariates) from analysis of the number of synchronised arrivals during control watches and watches following each model presentation (dove and jay). *N* = 66 watches from 22 nests. Significant values (*P* < 0.05) in bold. Corresponding summary table in the main text: Table 4.2. | | | | |
| Parameter | Estimates ± SE | df | 𝝌2 | *P* |
| Intercept | 2.158 ± 0.089 |  |  |  |
| Treatment | post-dove: 0.036 ± 0.107  post-jay: 0.057 ± 0.117 | 2 | 0.238 | 0.238 |
| Provisioning rate | 0.458 ± 0.049 | 1 | 87.110 | **<0.001** |
| Carer number | 3: 0.119 ± 0.109  4: -0.028 ± 0.271  5: 0.299 ± 0.166 | 3 | 3.896 | 0.273 |
| Watch duration | 0.060 ± 0.054 | 1 | 1.239 | 0.266 |
| Brood size | 0.004 ± 0.054 | 1 | 0.007 | 0.935 |
| Watch start time | 0.020 ± 0.060 | 1 | 0.107 | 0.744 |
| Brood age | 0.015 ± 0.046 | 1 | 0.107 | 0.743 |
| Hatch date | -0.079 ± 0.061 | 1 | 1.651 | 0.199 |
| Maximum possible alt. | 0.074 ± 0.054 | 1 | 1.902 | 0.168 |

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| Table S4.6. Estimates and *P*-values for the fixed effects (terms of interest and covariates) from analysis of the number of instances where a carer arrived with another carer present loitering nearby during control watches and watches following each model presentation (dove and jay). *N* = 66 watches from 22 nests. Significant values (*P* < 0.05) in bold. Corresponding summary table in the main text: Table 4.2. | | | | |
| Parameter | Estimates ± SE | df | 𝝌2 | *P* |
| Intercept | 1.580 ± 0.114 |  |  |  |
| Treatment | post-dove: 0.168 ± 0.134  post-jay: 0.241 ± 0.146 | 2 | 2.759 | 0.252 |
| Provisioning rate | 0.266 ± 0.062 | 1 | 18.311 | **<0.001** |
| Carer number | 3: 0.296 ± 0.132  4: 0.054 ± 0.296  5: 0.511 ± 0.190 | 3 | 10.066 | **0.018** |
| Watch duration | 0.127 ± 0.064 | 1 | 3.965 | **0.046** |
| Brood size | -0.025 ± 0.064 | 1 | 0.147 | 0.701 |
| Watch start time | -0.069 ± 0.070 | 1 | 0.972 | 0.324 |
| Brood age | 0.040 ± 0.059 | 1 | 0.473 | 0.492 |
| Hatch date | 0.030 ± 0.074 | 1 | 0.166 | 0.684 |
| Maximum possible alt. | 0.157 ± 0.071 | 1 | 4.872 | **0.027** |

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| Table S4.7. Estimates and *P-*values for the fixed effects (terms of interest and covariates) from analysis of the number of instances where a carer fed whilst another carer loitered nearby during control watches and watches following each model presentation (dove and jay). *N* = 66 watches from 22 nests. Significant values (*P* < 0.05) in bold. Corresponding summary table in the main text: Table 4.2. | | | | |
| Parameter | Estimates ± SE | df | 𝝌2 | *P* |
| Intercept | 1.574 ± 0.114 |  |  |  |
| Treatment | post-dove: 0.174 ± 0.134  post-jay: 0.249 ± 0.147 | 2 | 2.945 | 0.229 |
| Provisioning rate | 0.266 ± 0.062 | 1 | 18.309 | **<0.001** |
| Carer number | 3: 0.296 ± 0.132  4: -0.025 ± 0.305  5: 0.510 ± 0.190 | 3 | 10.354 | **0.016** |
| Watch duration | 0.132 ± 0.064 | 1 | 4.266 | **0.039** |
| Brood size | -0.024 ± 0.064 | 1 | 0.145 | 0.703 |
| Watch start time | -0.069 ± 0.070 | 1 | 0.966 | 0.326 |
| Brood age | 0.040 ± 0.059 | 1 | 0.468 | 0.494 |
| Hatch date | 0.031 ± 0.074 | 1 | 0.179 | 0.672 |
| Maximum possible alt. | 0.157 ± 0.071 | 1 | 4.870 | **0.027** |

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| Table S4.8. Estimates and *P*-values for the fixed effects (terms of interest and covariates) from analysis of the number of synchronised feeds during control watches and watches following each model presentation (dove and jay). *N* = 66 watches from 22 nests. Significant values (*P* < 0.05) in bold. Corresponding summary table in the main text: Table 4.2. | | | | |
| Parameter | Estimates ± SE | df | 𝝌2 | *P* |
| Intercept | 2.213 ± 0.087 |  |  |  |
| Treatment | post-dove: 0.026 ± 0.105  post-jay: 0.028 ± 0.115 | 2 | 0.072 | 0.965 |
| Provisioning rate | 0.465 ± 0.048 | 1 | 92.883 | **<0.001** |
| Carer number | 3: 0.127 ± 0.106  4: 0.030 ± 0.257  5: 0.236 ± 0.163 | 3 | 2.897 | 0.408 |
| Watch duration | 0.084 ± 0.052 | 1 | 2.556 | 0.110 |
| Brood size | -0.032 ± 0.051 | 1 | 0.402 | 0.526 |
| Watch start time | -0.011 ± 0.059 | 1 | 0.032 | 0.858 |
| Brood age | 0.016 ± 0.045 | 1 | 0.119 | 0.730 |
| Hatch date | -0.057 ± 0.060 | 1 | 0.891 | 0.345 |
| Maximum possible alt. | 0.070 ± 0.053 | 1 | 1.782 | 0.182 |

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| Table S4.9. Estimates and *P-*values for the fixed effects (terms of interest and covariates) from analysis of the number of alternated feeds during control watches and watches following each model presentation (dove and jay). *N* = 66 watches from 22 nests. Significant values (*P* < 0.05) in bold. Corresponding summary table in the main text: Table 4.2. | | | | |
| Parameter | Estimates ± SE | df | 𝝌2 | *P* |
| Intercept | 2.691 ± 0.069 |  |  |  |
| Treatment | post-dove: 0.047 ± 0.083  post-jay: -0.021 ± 0.092 | 2 | 0.889 | 0.641 |
| Provisioning rate | 0.391 ± 0.040 | 1 | 97.781 | **<0.001** |
| Carer number | 3: 0.072 ± 0.087  4: 0.208 ± 0.187  5: 0.146 ± 0.133 | 3 | 2.369 | 0.500 |
| Watch duration | 0.095 ± 0.041 | 1 | 5.455 | **0.020** |
| Brood size | -0.038 ± 0.040 | 1 | 0.891 | 0.345 |
| Watch start time | -0.005 ± 0.047 | 1 | 0.013 | 0.909 |
| Brood age | 0.028 ± 0.036 | 1 | 0.598 | 0.439 |
| Hatch date | -0.062 ± 0.048 | 1 | 1.667 | 0.197 |
| Maximum possible alt. | 0.081 ± 0.042 | 1 | 3.815 | 0.051 |

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| Table S4.10. Estimates and *P-*values for the fixed effects (terms of interest and covariates) from analysis of the log-transformed mean loitering period duration during control watches and watches following each model presentation (dove and jay). *N* = 66 watches from 22 nests. Significant values (*P* < 0.05) in bold. Corresponding summary table in the main text: Table 4.3. | | | | |
| Parameter | Estimates ± SE | df | 𝝌2 | *P* |
| Intercept | -7.726 ± 0.087 |  |  |  |
| Treatment | post-dove: -0.222 ± 0.105  post-jay: 0.090 ± 0.116 | 2 | 10.130 | **0.006** |
| Provisioning rate | -0.289 ± 0.057 | 1 | 25.498 | **<0.001** |
| Carer number | 3: 0.325 ± 0.121  4: -0.019 ± 0.264  5: 0.283 ± 0.204 | 3 | 8.826 | **0.032** |
| Watch duration | 0.147 ± 0.046 | 1 | 10.410 | **0.001** |
| Brood size | -0.143 ± 0.057 | 1 | 6.269 | **0.012** |
| Watch start time | -0.121 ± 0.060 | 1 | 4.087 | **0.043** |
| Brood age | -0.062 ± 0.054 | 1 | 1.299 | 0.253 |
| Hatch date | 0.050 ± 0.066 | 1 | 0.587 | 0.444 |

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| Table S4.11. Estimates and *P-*values for the fixed effects (terms of interest and covariates) from analysis of the duration of time that a carer(s) was loitering nearby (without mean loitering time) during control watches and watches following each model presentation (dove and jay). *N* = 66 watches from 22 nests. Significant values (*P* < 0.05) in bold. Corresponding summary table in the main text: Table 4.3. | | | | |
| Parameter | Estimates ± SE | df | 𝝌2 | *P* |
| Intercept | 12.347 ± 0.911 |  |  |  |
| Treatment | post-dove: -2.604 ± 1.154  post-jay: 0.572 ± 1.267 | 2 | 9.416 | **0.009** |
| Provisioning rate | 0.226 ± 0.604 | 1 | 0.140 | 0.709 |
| Carer number | 3: 1.269 ± 1.205  4: -2.435 ± 2.698  5: 0.699 ± 2.056 | 3 | 2.176 | 0.537 |
| Watch duration | 3.266 ± 0.484 | 1 | 45.496 | **<0.001** |
| Brood size | -1.295 ± 0.568 | 1 | 5.197 | **0.023** |
| Watch start time | -0.621 ± 0.596 | 1 | 1.085 | 0.298 |
| Brood age | -0.193 ± 0.535 | 1 | 0.130 | 0.719 |
| Hatch date | -0.067 ± 0.658 | 1 | 0.011 | 0.918 |

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| Table S4.12. Estimates and *P-*values for the fixed effects (terms of interest and covariates) from analysis of the duration of time that a carer(s) was loitering nearby (with mean loitering time) during control watches and watches following each model presentation (dove and jay). *N* = 66 watches from 22 nests. Significant values (*P* < 0.05) in bold. Corresponding summary table in the main text: Table 4.3. | | | | |
| Parameter | Estimates ± SE | df | 𝝌2 | *P* |
| Intercept | 11.936 ± 0.534 |  |  |  |
| Mean loitering time | 4.011 ± 0.388 | 1 | 106.711 | **<0.001** |
| Treatment | post-dove: -0.248 ± 0.705  post-jay: 1.257 ± 0.737 | 2 | 5.395 | 0.067 |
| Provisioning rate | 1.974 ± 0.392 | 1 | 25.39 | **<0.001** |
| Carer number | 3: -1.432 ± 0.761  4: -0.688 ± 1.596  5: -0.672 ± 1.222 | 3 | 3.809 | 0.283 |
| Watch duration | 1.814 ± 0.315 | 1 | 33.068 | **<0.001** |
| Brood size | -0.306 ± 0.350 | 1 | 0.763 | 0.382 |
| Watch start time | 0.796 ± 0.379 | 1 | 4.409 | **0.036** |
| Brood age | 0.537 ± 0.325 | 1 | 2.731 | 0.098 |
| Hatch date | -0.942 ± 0.398 | 1 | 5.589 | **0.018** |

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| Table S4.13. Estimates and *P-*values for the fixed effects (terms of interest and covariates) from analysis of provisioning rate during sections of control watches and watches following each model presentation (dove and jay) split into equal duration thirds by duration. *N* = 66 watches of 22 nests. Significant values (*P* < 0.05) in bold. Corresponding summary table in the main text: Table 4.4. | | | | |
| Parameter | Estimates ± SE | df | 𝝌2 | *P* |
| Intercept | 1.577 ± 0.108 |  |  |  |
| Treatment | post-dove: 0.404 ± 0.131  post-jay: 0.408 ± 0.131 | 2 | 19.462 | **<0.001** |
| Section | 2nd: 0.113 ± 0.131  3rd: 0.390 ± 0.124 | 2 | 12.926 | **0.002** |
| Carer number | 3: 0.004 ± 0.107  4: -0.086 ± 0.230  5: 0.133 ± 0.174 | 3 | 0.871 | 0.833 |
| Watch duration | 0.111 ± 0.040 | 1 | 7.588 | **0.006** |
| Brood size | 0.125 ± 0.050 | 1 | 6.302 | **0.012** |
| Watch start time | 0.102 ± 0.055 | 1 | 3.471 | 0.062 |
| Brood age | 0.046 ± 0.047 | 1 | 0.951 | 0.330 |
| Hatch date | -0.174 ± 0.057 | 1 | 9.298 | **0.002** |
| Treatment \* section | post-dove, 2nd: -0.199 ± 0.172  post-dove 3rd: -0.333 ± 0.164  post-jay, 2nd: 0.032 ± 0.167  post-jay 3rd: -0.151 ± 0.160 | 4 | 5.572 | 0.234 |
| Table S4.14. Estimates and *P-*values for the fixed effects (terms of interest and covariates) from analysis of the number of synchronised arrivals during sections of control watches and watches following each model presentation (dove and jay) split into equal duration thirds by duration. *N* = 66 watches of 22 nests. Significant values (*P* < 0.05) in bold. Corresponding summary table in the main text: Table 4.4. | | | | |
| Parameter | Estimates ± SE | df | 𝝌2 | *P* |
| Intercept | 0.837 ± 0.168 |  |  |  |
| Treatment | post-dove: 0.123 ± 0.204  post-jay: 0.061 ± 0.211 | 2 | 0.103 | 0.950 |
| Section | 2nd: 0.235 ± 0.215  3rd: 0.147 ± 0.204 | 2 | 3.889 | 0.143 |
| Provisioning rate | 0.505 ± 0.052 | 1 | 94.454 | **<0.001** |
| Carer number | 3: 0.039 ± 0.103  4: -0.025 ± 0.268  5: 0.314 ± 0.158 | 3 | 4.080 | 0.253 |
| Watch duration | 0.018 ± 0.054 | 1 | 0.108 | 0.742 |
| Brood size | 0.007 ± 0.053 | 1 | 0.017 | 0.895 |
| Watch start time | 0.015 ± 0.060 | 1 | 0.059 | 0.809 |
| Brood age | -0.010 ± 0.046 | 1 | 0.051 | 0.822 |
| Hatch date | -0.073 ± 0.060 | 1 | 1.472 | 0.225 |
| Maximum possible alt. | 0.325 ± 0.077 | 1 | 18.010 | **<0.001** |
| Treatment \* section | post-dove, 2nd: -0.090 ± 0.270  post-dove, 3rd: -0.155 ± 0.257  post-jay, 2nd: -0.043 ± 0.260  post-jay, 3rd: -0.090 ± 0.249 | 4 | 0.373 | 0.985 |

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| Table S4.15. Estimates and *P-*values for the fixed effects (terms of interest and covariates) from analysis of the number of instances where a carer arrived with another carer present loitering nearby during sections of control watches and watches following each model presentation (dove and jay) split into equal duration thirds by duration. *N* = 66 watches of 22 nests. Significant values (*P* < 0.05) in bold. Corresponding summary table in the main text: Table 4.4. | | | | |
| Parameter | Estimates ± SE | df | 𝝌2 | *P* |
| Intercept | 0.465 ± 0.192 |  |  |  |
| Treatment | post-dove: 0.054 ± 0.237  post-jay: 0.003 ± 0.247 | 2 | 1.595 | 0.451 |
| Section | 2nd: -0.168 ± 0.268  3rd: -0.009 ± 0.242 | 2 | 0.314 | 0.855 |
| Provisioning rate | 0.245 ± 0.071 | 2 | 12.064 | **0.001** |
| Carer number | 3: 0.258 ± 0.125  4: 0.021 ± 0.292  5: 0.493 ± 0.178 | 3 | 10.696 | **0.013** |
| Watch duration | 0.072 ± 0.065 | 1 | 1.226 | 0.268 |
| Brood size | -0.021 ± 0.065 | 1 | 0.114 | 0.736 |
| Watch start time | -0.092 ± 0.070 | 1 | 1.711 | 0.191 |
| Brood age | 0.009 ± 0.058 | 1 | 0.878 | 0.878 |
| Hatch date | 0.077 ± 0.072 | 1 | 0.289 | 0.289 |
| Maximum possible alt. | 0.543 ± 0.108 | 1 | 25.157 | **<0.001** |
| Treatment \* section | post-dove, 2nd: 0.201 ± 0.336  post-dove, 3rd: -0.017 ± 0.307  post-jay, 2nd: 0.296 ± 0.328  post-jay, 3rd: 0.192 ± 0.300 | 4 | 1.319 | 0.858 |

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| Table S4.16. Estimates and *P-*values for the fixed effects (terms of interest and covariates) from analysis of the number of instances where a carer fed whilst another carer loitered nearby during sections of control watches and watches following each model presentation (dove and jay) split into equal duration thirds by duration. *N* = 66 watches of 22 nests. Significant values (*P* < 0.05) in bold. Corresponding summary table in the main text: Table 4.4. | | | | |
| Parameter | Estimates ± SE | df | 𝝌2 | *P* |
| Intercept | 0.539 ± 0.186 |  |  |  |
| Treatment | post-dove: -0.009 ± 0.232  post-jay: -0.066 ± 0.242 | 2 | 1.759 | 0.415 |
| Section | 2nd: -0.275 ± 0.267  3rd: -0.116 ± 0.239 | 2 | 0.096 | 0.953 |
| Provisioning rate | 0.257 ± 0.070 | 1 | 13.330 | **<0.001** |
| Carer number | 3: 0.264 ± 0.125  4: -0.046 ± 0.301  5: 0.506 ± 0.178 | 3 | 11.530 | **0.009** |
| Watch duration | 0.079 ± 0.065 | 1 | 1.466 | 0.226 |
| Brood size | -0.023 ± 0.063 | 1 | 0.136 | 0.712 |
| Watch start time | -0.091 ± 0.070 | 1 | 1.680 | 0.195 |
| Brood age | 0.008 ± 0.058 | 1 | 0.017 | 0.896 |
| Hatch date | 0.074 ± 0.072 | 1 | 1.067 | 0.302 |
| Maximum possible alt. | 0.508 ± 0.106 | 1 | 22.968 | **<0.001** |
| Treatment \* section | post-dove, 2nd: 0.304 ± 0.334  post-dove, 3rd: 0.092 ± 0.305  post-jay, 2nd: 0.424 ± 0.327  post-jay, 3rd: 0.291 ± 0.298 | 4 | 2.045 | 0.727 |

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| Table S417. Estimates and *P-*values for the fixed effects (terms of interest and covariates) from analysis of the number of synchronised feeds during sections of control watches and watches following each model presentation (dove and jay) split into equal duration thirds by duration. *N* = 66 watches of 22 nests. Significant values (*P* < 0.05) in bold. Corresponding summary table in the main text: Table 4.4. | | | | |
| Parameter | Estimates ± SE | df | 𝝌2 | *P* |
| Intercept | 0.978 ± 0.158 |  |  |  |
| Treatment | post-dove: -0.024 ± 0.197  post-jay: -0.030 ± 0.201 | 2 | 0.323 | 0.851 |
| Section | 2nd: 0.106 ± 0.207  3rd: 0.039 ± 0.195 | 2 | 3.690 | 0.158 |
| Provisioning rate | 0.526 ± 0.051 | 1 | 106.356 | **<0.001** |
| Carer number | 3: 0.049 ± 0.102  4: 0.047 ± 0.254  5: 0.250 ± 0.155 | 3 | 2.669 | 0.446 |
| Watch duration | 0.040 ± 0.053 | 1 | 0.584 | 0.444 |
| Brood size | -0.036 ± 0.050 | 1 | 0.526 | 0.469 |
| Watch start time | -0.018 ± 0.059 | 1 | 0.088 | 0.766 |
| Brood age | -0.036 ± 0.050 | 1 | 0.042 | 0.838 |
| Hatch date | -0.051 ± 0.059 | 1 | 0.759 | 0.384 |
| Maximum possible alt. | 0.321 ± 0.075 | 1 | 18.449 | **<0.001** |
| Treatment \* section | post-dove, 2nd: 0.092 ± 0.263  post-dove, 3rd: 0.031 ± 0.249  post-jay, 2nd: 0.058 ± 0.252  post-jay, 3rd: -0.060 ± 0.241 | 4 | 0.417 | 0.981 |

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| --- | --- | --- | --- | --- |
| Table S4.18. Estimates and *P-*values for the fixed effects (terms of interest and covariates) from analysis of the number of alternated feeds during sections of control watches and watches following each model presentation (dove and jay) split into equal duration thirds by duration. *N* = 66 watches of 22 nests. Significant values (*P* < 0.05) in bold. Corresponding summary table in the main text: Table 4.4. | | | | |
| Parameter | Estimates ± SE | df | 𝝌2 | P |
| Intercept | 1.407 ± 0.126 |  |  |  |
| Treatment | post-dove: 0.088 ± 0.156  post-jay: -0.022 ± 0.162 | 2 | 1.446 | 0.485 |
| Section | 2nd: 0.215 ± 0.161  3rd: 0.123 ± 0.155 | 2 | 6.601 | **0.037** |
| Provisioning rate | 0.405 ± 0.042 | 1 | 92.051 | **<0.001** |
| Carer number | 3: 0.023 ± 0.082  4: 0.198 ± 0.184  5: 0.161 ± 0.127 | 3 | 2.464 | 0.482 |
| Watch duration | 0.050 ± 0.041 | 1 | 1.519 | 0.218 |
| Brood size | -0.027 ± 0.040 | 1 | 0.452 | 0.501 |
| Watch start time | -0.011 ± 0.047 | 1 | 0.057 | 0.811 |
| Brood age | 0.007 ± 0.036 | 1 | 0.033 | 0.855 |
| Hatch date | -0.055 ± 0.047 | 1 | 1.369 | 0.242 |
| Maximum possible alt. | 0.298 ± 0.058 | 1 | 26.472 | **<0.001** |
| Treatment \* section | post-dove, 2nd: -0.035 ± 0.206  post-dove, 3rd: -0.064 ± 0.198  post-jay, 2nd: -0.012 ± 0.201  post-jay, 3rd: -0.027 ± 0.195 | 4 | 0.111 | 0.999 |

|  |  |  |  |  |
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| Table S4.19. Estimates and *P-*values for the fixed effects (terms of interest and covariates) from analysis of the log-transformed mean loitering period duration during sections of control watches and watches following each model presentation (dove and jay) split into equal duration thirds by duration. *N* = 66 watches of 22 nests. Significant values (*P* < 0.05) in bold. Corresponding summary table in the main text: Table 4.4. | | | | |
| Parameter | Estimates ± SE | df | 𝝌2 | P |
| Intercept | -7.339 ± 0.114 |  |  |  |
| Treatment | post-dove: -0.500 ± 0.150  post-jay: 0.062 ± 0.151 | 2 | 8.904 | **0.012** |
| Section | 2nd: -0.462 ± 0.128  3rd: -0.666 ± 0.132 | 2 | 49.817 | **<0.001** |
| Provisioning rate | -0.244 ± 0.043 | 1 | 33.170 | **<0.001** |
| Carer number | 3: 0.331 ± 0.120  4: 0.052 ± 0.263  5: 0.241 ± 0.202 | 3 | 8.707 | **0.033** |
| Watch duration | 0.100 ± 0.046 | 1 | 4.782 | **0.029** |
| Brood size | -0.165 ± 0.054 | 1 | 9.363 | **0.002** |
| Watch start time | -0.115 ± 0.058 | 1 | 3.957 | **0.047** |
| Brood age | -0.038 ± 0.053 | 1 | 0.524 | 0.469 |
| Hatch date | 0.082 ± 0.062 | 1 | 1.744 | 0.187 |
| Treatment \* section | post-dove, 2nd: 0.269 ± 0.183  post-dove, 3rd: 0.469 ± 0.183  post-jay, 2nd: -0.123 ± 0.181  post-jay, 3rd: -0.009 ± 0.181 | 4 | 9.882 | **0.042** |

**Observed minus expected coordination**

To investigate the effect of perceived predation threat on coordination we first compared the levels of active coordination (observed minus expected by chance) between control watches, watches following dove and watches following jay display; using the interaction of treatment and data type to compare differences in active coordination between treatments. Most metrics of coordination occurred more than expected by chance; including feed synchrony (GLMM: *P* < 0.001, Table S4.20, Figure S4.1a), arrival synchrony (GLMM: *P* < 0.001, Table S4.20), overlap of loitering periods (Present upon feed GLMM: *P* < 0.001, Table S4.20, Figure S4.1b; Present upon arrival GLMM: P < 0.001), but not alternation (GLMM: *P* = 0.109, Table S4.20, Figure S4.1c). Most importantly, we did not find that levels of active coordination (observed minus expected) or carer presence varied between different model presentations (Table S4.20, Figure S4.1).

Comparing observed proportions of time a carer(s) was loitering near the nest to those expected by chance we found that overall, observed watches had lower carer presence than expected by chance (LMM: *P* < 0.001, Table S4.20, Figure S4.1d). Though there was no difference between treatments in this disparity, as evidenced by the interaction term of treatment and data type (LMM: *P* = 0.092, Table S4.20, Figure S4.1d). We conclude that the results of our analysis comparing ‘active’ coordination between treatments are redundant with our primary analysis comparing observed coordination between treatments directly, dismissing the idea that coordination increased via standardisation of intervisit interval duration, thus report only the latter within the main text.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Table S4.20. Effect of experimental treatment on observed and expected coordination and the observed and expected time that a carer(s) was nearby the nest. Significant values (*P* < 0.05) in bold. | | | | | |
| Response Variable | Fixed effects | Estimates ± SE | df | 𝝌2 | *P* |
| *Synchronised feeds* | | | | | |
| Number of synchronised feeds | Treatment \* data type | observed, post-dove: 0.024 ± 0.155  observed: post-jay: 0.070 ± 0.163 | 2 | 0.208 | 0.901 |
| Data type | observed: 0.220 ± 0.147 | 1 | 15.988 | **<0.001** |
| Treatment | post-dove: 0.026 ± 0.105  post-jay: 0.028 ± 0.115 | 2 | 0.072 | 0.965 |
| *Synchronised arrivals* | | | | | |
| Number of synchronised arrivals | Treatment \* data type | observed, post-dove: -0.014 ± 0.156  observed, post-jay: 0.042 ± 0.164 | 2 | 0.179 | 0.914 |
| Data type | observed: 0.168 ± 0.148 | 1 | 10.52 | **<0.001** |
| Treatment | post-dove: 0.036 ± 0.107  post-jay: 0.057 ± 0.117 | 2 | 0.238 | 0.888 |
| *Present upon feed* | | | | | |
| Number visits where focal carer fed whilst another loitered | Treatment \* data type | observed, post-dove: 0.306 ± 0.227  observed, post-jay: 0.143 ± 0.234 | 2 | 1.905 | 0.386 |
| Data type | observed: 0.470 ± 0.201 | 1 | 71.457 | **<0.001** |
| Treatment | post-dove: 0.174 ± 0.134  post-jay: 0.249 ± 0.147 | 2 | 2.945 | 0.229 |
| *Present upon arrival* | | | | | |
| Number visits where the focal carer arrived back with another carer loitering | Treatment \* data type | observed, post-dove: 0.287 ± 0.226  observed, post-jay: 0.134 ± 0.234 | 2 | 1.690 | 0.430 |
| Data type | observed: 0.489 ± 0.200 | 1 | 71.310 | **<0.001** |
| Treatment | post-dove: 0.168 ± 0.134  post-jay: 0.241 ± 0.146 | 2 | 2.759 | 0.252 |
| *Alternated feeds* | | | | | |
| Number of alternated feeds | Treatment \* data type | observed, post-dove: 0.048 ± 0.116  observed, post-jay: 0.029 ± 0.123 | 2 | 0.171 | 0.918 |
| Data type | observed: 0.005 ± 0.106 | 1 | 2.563 | 0.109 |
| Treatment | post-dove: 0.047 ± 0.083  post-jay: -0.021 ± 0.092 | 2 | 0.889 | 0.641 |
| *Carer(s) nearby* |  |  |  |  |  |
| Duration of time when a carer(s) was nearby | Treatment \* data type | observed, post-dove: -0.220 ± 0.502  observed, post-jay: -1.088 ± 0.543 | 2 | 4.769 | 0.092 |
| Data type | observed: -1.874 ± 0.471 | 1 | 72.059 | **<0.001** |
| Treatment | post-dove: -2.604 ± 1.154  post-jay: 0.572 ± 1.267 | 2 | 9.416 | **0.009** |

Chart, box and whisker chart

Description automatically generated

Figure S4.1. Observed and expected percentages of: (a) feeds synchronised, (b) feeds where the focal carer fed with another carer nearby, (c) feeds alternated, and (d) a watch where at least one carer was loitering nearby, for control watches and watches following each treatment (post-dove and post-jay). *N* = 22 watches per treatment.

**Chapter 5**

**Consequences of coordination of care support the hypotheses that alternation facilitates conflict resolution and synchrony reduces brood predation risk**

**5.1 Abstract**

Parental care is costly to carers, so when raising shared offspring carers are in conflict over relative investment, which could lead to sub-optimal investment unless resolved. Conditional cooperation is hypothesised to resolve this conflict, with coordinated provisioning (i.e. alternating visits) predicted to enable carers to mutually increase their investment without being exploited. However, despite much empirical attention, evidence in support of this hypothesis is rare. Most attempted to demonstrate that alternation occurs more than expected by chance, but critics highlight that this could also be plausibly explained by changing environmental conditions, and no study has yet demonstrated any definitive benefits to offspring fitness or post-fledging survival. Additionally, the relative costs and benefits of parental care to offspring may also depend on the relative timing of visits, with another form of coordinated provisioning in which carers feed together (i.e. synchrony) hypothesised to optimise these payoffs; though, support for an adaptive function is mixed. In this study, we used long-term (1994–2022) provisioning watch and reproductive success data from long-tailed tits, *Aegithalos caudatus*, to test the predictions of three hypotheses for coordinated provisioning. First, the conditional cooperation hypothesis (Hypothesis 1), finding that alternation scores corresponded with increased provisioning and more local recruitment of offspring from cooperative groups, though this was not mediated by a change in offspring mass at the midpoint of development. Second, that carers synchronised provisioning visits to facilitate efficient distribution of resources among a brood (Hypothesis 2). This hypothesis was not supported, as synchrony scores did not significantly influence offspring mass or intrabrood mass variation. Finally, that synchrony reduces the risk of brood predation by limiting the chance that a brood’s location is advertised to predators (Hypothesis 3). We found support for this hypothesis as synchronous provisioning was associated with prolonged nest survival and reduced brood predation.

**5.2 Introduction**

Parental care increases the survival chances and fitness of offspring, which benefits parents by increasing their genetic contribution to future generations (Trivers 1974, Godfray 1995, Godfray and Johnstone 2000, Hinde et al. 2010). However, parental care is costly to carers as it must be drawn from a finite pool of resources (Clutton-Brock 1991, Stearns 1992). Therefore, cooperating carers should be selected to maximise their partner’s contribution to shared offspring, relative to their own, thus saving their own residual investment for future reproduction (Stearns 1989). This leads to conflict between carers (Trivers 1972), incentivising reduced investment, which can be costly to offspring (Parker 1985, Royle et al. 2002a, McNamara et al. 2003). Despite this, systems of shared parental care are found throughout the animal kingdom and are particularly prevalent in birds (~90% of species; Cockburn 2006).

Several game-theoretic approaches have modelled how this conflict could be mitigated or resolved. These models allowed for carers to enter into partnerships with either a fixed level of investment, which reaches a stable equilibrium over evolutionary time (i.e. sealed bid) (Houston and Davies 1985), or a flexible amount of investment which is negotiated with their partner(s) in behavioural time (McNamara et al. 1999, 2003, Lessells and McNamara 2012). These models predict that carers provision at stable rates below the brood’s optimum level, so each carer would benefit from mutually increased investment (Johnstone et al. 2014). However, carers cannot do this because, to prevent exploitation, each carer is expected to respond to changes in their partner’s investment with incomplete compensation. Whilst this prediction is broadly supported by empirical studies (Harrison et al. 2009), others have refuted this prediction by showing that carers instead matched changes in their partner’s investment (e.g. Hinde 2006, Meade et al. 2011, Enns and Williams 2022).

To address this, Johnstone et al. (2014) proposed a model for shared parental investment based on coordinated provisioning where continued cooperation is conditional upon observing one’s partner provision the brood (i.e. conditional cooperation). This ensures fair investment because each carer refuses to feed until their partner has taken their turn, resulting in a perfectly alternating pattern of feeds. In this model, carers can mutually increase their investment to more closely match the brood’s optimum but must follow unrealistically strict turn-taking rules, with cooperation breaking down when a carer misses their partner’s visit, as they both believe it is the other’s turn to feed. Additionally, this model offers no explanation for empirical studies finding compensatory investment (Harrison et al. 2009). Conditional cooperation also applies to cooperative breeders when alloparental helpers have a genetic stake in the offspring, and thus stand to benefit from success of the brood (Hamilton 1964). In this case, conditional cooperation may limit the extent to which parents can reduce their investment in response to help (Crick 1992, Hatchwell 1999), enabling helpers to augment the productivity of the group, and thus their own payoffs, rather than simply replacing the parents’ investment (Savage et al. 2017).

The conditional cooperation model was later expanded to accommodate imperfect monitoring, time dependent costs and benefits, shared costs of care, as well as asymmetries in monitoring and payoffs between carers (Johnstone and Savage 2019). This facilitated stable imperfect alternation and recovered the prediction of incomplete compensation when carers experience asymmetric costs, although carers must still reliably monitor the nest visits of their partner(s). This model predicts that when carers differ in their monitoring accuracy, the more observant carer invests less and thus receives greater net payoffs, thus selecting for reliable monitoring (Johnstone and Savage 2019). Another form of provisioning coordination has been hypothesised to facilitate this monitoring; namely, synchrony of provisioning visits (i.e. feeding the brood together).

Synchronous provisioning co-occurs with alternation in several species (Koenig and Walters 2016, Baldan and Griggio 2019, Ihle et al. 2019a, Baldan and Quyang 2020) and they are often correlated (Bebbington and Hatchwell 2016, Leniowski and Węgrzyn 2018). However, there is evidence that alternation and synchrony may have separate functions (Lejeune et al. 2019, Halliwell et al. 2022). Furthermore, synchrony is hypothesised to confer several adaptive functions which do not require alternation *per se*. Synchrony may: (i) reduce the time that a brood’s location is advertised to predators when provisioning (predation hypothesis; Sargent 1993, Raihani et al. 2010, Mariette and Griffith 2012, van Rooij and Griffith 2013, Leniowski and Węgrzyn 2018, Khwaja et al. 2019), (ii) facilitate efficient allocation of resources among the brood by preventing certain chicks from monopolising investment (Shen et al. 2010, Mariette and Griffith 2012, 2015, Lejeune et al. 2019), (iii) enable carers to signal their investment to others, either to demonstrate their quality as a parent (prestige hypothesis; Zahavi 1977a,b, Doutrelant and Covas 2007) or to pay for group membership (pay-to-stay hypothesis; Gaston 1978, Kokko et al. 2002, Trapote et al. 2021). Alternatively, nest visit synchrony may confer no direct benefits, but could instead be a consequence of behaviours that do, such as collective or group foraging, which could increase foraging efficiency and/or reduce the risk of carer predation (Beauchamp 1998, Lee et al. 2010, Sorato et al. 2012, van Rooij and Griffith 2013, Mariette and Griffith 2015, Baldan and van Loon 2022). None of these hypotheses are mutually exclusive, so coordination of care may have multiple functions in the same species.

Many empirical studies have sought to identify patterns of alternation and synchrony from analysis of sequences of provisioning visits (review: Savage and Hinde 2019, Savage et al. 2020).However, some alternation and synchrony are expected to occur by chance even if carers do not actively coordinate (Schlicht et al. 2016, Ihle et al. 2019a, Santema et al. 2019), so various null model randomisation and simulation approaches have been used to show that observed coordination was greater than expected in both biparental (Johnstone et al. 2014, Bebbington and Hatchwell 2016, Lejeune et al. 2019; but see Enns and Williams 2022) and cooperatively breeding species (Koenig and Walters 2016, Savage et al. 2017, Halliwell et al. 2022; but see Khwaja et al. 2017). Nevertheless, critics argue that these approaches do not fully capture expected coordination because they fail to account for temporal autocorrelation in provisioning rates due to shared environmental effects (e.g. changing weather or predator nearby) (Schlicht et al. 2016, Ihle et al. 2019a, Sanetma et al. 2019; but see Johnstone et al. 2016, Halliwell et al. 2023b). This phenomenon can result in high levels of apparent coordination even in groups of uncoordinated carers because their provisioning rates are adjusted in the same direction at the same time.Therefore, it appears unlikely that behavioural coordination can be confirmed simply by comparing observed levels to those expected by chance.

More compelling evidence of coordination would be the demonstration that carers perform condition dependent behaviours resulting in coordinated provisioning.Studies have shown that a carer’s return rate following their own feed was slower than when following the feed of another carer (Johnstone et al. 2014, Savage et al. 2017, Griffioen et al. 2021). However, these results could be plausibly explained by a high degree of temporal autocorrelation in provisioning rates (Schlicht et al. 2016, Santema et al. 2019). A condition dependent behaviour that facilitates alternation has also been reported in long-tailed tits, *Aegithalos caudatus*, with carers loitering near the nest for longer and being more likely to let another carer feed before them if feeding immediately would have resulted in a non-alternated feed (Halliwell et al. 2023a). Similarly, in other species, active synchrony occurs when carers actively wait for others before returning to the nest area (Raihani et al. 2010) or feeding the brood (Doutrelant and Covas 2007).

Although several studies have investigated links between coordination and offspring condition and/or survival, evidence that alternation facilitates conflict resolution between carers, to the benefit of their offspring, is rare. Notably, Burdick and Siefferman (2020) identified a positive link between alternation and offspring growth in eastern bluebirds, *Sialia sialis*. However, most studies found no effect of alternation on offspring condition (Bebbington and Hatchwell 2016, Iserbyt et al. 2017, Griffioen et al. 2019a) or survival (Iserbyt et al. 2017), and Ihle et al. (2019b) even found a negative relationship between alternation and offspring survival in house sparrows, *Passer domesticus*. More convincing support has been found for other functions of coordinated provisioning. For example, Shen et al. (2010) found that food was more evenly distributed among offspring during large-party provisioning bouts in Taiwan yuhinas, *Yuhina brunneiceps*, supporting the hypothesis that synchrony increases resource distribution parity among offspring. In the zebra finch, *Taeniopygia castanotis* (formerly *T. guttata*), Mariette and Griffith (2015) reported a positive relationship between foraging synchrony and offspring mass (but not feeding synchrony), and mixed support for the hypothesis that synchrony increases food distribution parity. Similarly, in blue tits, *Cyanistes caeruleus*, Lejeune et al. (2019) found a positive relationship between offspring mass and synchrony and lower intrabrood mass variation with greater alternation. In support of the predation hypothesis, previous studies found that synchronous provisioning reduced the total time that carers were active around a nest potentially advertising its location to predators (Bebbington and Hatchwell 2016, Leniowski and Węgrzyn 2018) and reduced brood predation risk (Raihani et al. 2010, Leniowski and Węgrzyn 2018). However, many of these studies either did not explicitly test any specific hypothesis (e.g. van Rooij and Griffith 2013, Lejeune et al. 2019), or restricted their investigation to a single hypothesis for either alternation (e.g. Griffioen et al. 2019a) or synchrony (e.g. Shen et al. 2010, Mariette and Griffith 2015). This constrains these studies by limiting the scope of their investigation to only one aspect of a broader system with potentially interconnected functions of coordinated provisioning.

In this study, we tested several hypotheses for coordinated provisioning in the long-tailed tit, a short-lived passerine bird with a facultative cooperative breeding system in which failed breeders may redirect their investment to help raise broods of other pairs to whom they are typically related (Glen and Perrins 1988, Nam et al. 2010, Leedale et al. 2020b). Thus, broods may be raised biparentally (2 parents only) or cooperatively (2 parents plus 1–8 helpers). Helpers gain indirect fitness benefits by increasing the provisioning rate and recruitment of related offspring (MacColl and Hatchwell 2002, 2003, McGowan et al. 2003, Hatchwell et al. 2004, 2014), and reducing the reproductive costs of related breeders (Meade and Hatchwell 2010). In contrast, helpers derive no direct fitness benefits from their cooperative behaviour; helper extrapair paternity and intraspecific brood parasitism are negligible (Hatchwell et al. 2002), and their future fitness is not improved by helping others (McGowan et al. 2007, Meade and Hatchwell 2010, Hatchwell et al. 2014).

We developed an *a priori* hypothesis-prediction framework to investigate three hypotheses for coordinated provisioning that are applicable to the breeding system of long-tailed tits. First, we tested the hypothesis that alternation facilitates conflict resolution between carers over shared investment (Hypothesis 1). Long-tailed tits experience high annual mortality (Meade et al. 2010b) and divorce rates (Hatchwell et al. 2000), so associations between carers are short-lived and the scope for conflict is high. Furthermore, long-tailed tits alternate and synchronise their provisioning visits more than expected by chance (Bebbington and Hatchwell 2016, Halliwell et al. 2022) and actively delay feeding to facilitate alternation (Halliwell et al. 2023a), making them an excellent candidate for testing this hypothesis. We predicted that greater alternation would result in higher provisioning rates (Prediction 1a), heavier chicks (Prediction 1b), and recruitment of more offspring (Prediction 1c). Second, we tested the hypothesis that synchrony facilitates more even resource distribution among offspring (Hypothesis 2). Their large brood size (median = 9) and remarkably low rates of chick starvation (0.2% daily; Hatchwell et al. 2004) mean that long-tailed tits are potential candidates for this hypothesis. We predicted that more synchronous provisioning would result in greater overall chick mass (Prediction 2a), lower intrabrood mass variation (Prediction 2b), and recruitment of more offspring (Prediction 2c). Note that, due to their low rate of starvation, it is unlikely that coordination would influence fledging success in long-tailed tits; nonetheless we also investigated the effects of alternation and synchrony on the proportion of a brood to successfully fledge and present our findings in the supplementary material (section: ‘Fledging success’). Finally, we tested the hypothesis that synchrony reduces the risk of advertising a brood’s location to predators (Hypothesis 3). Long-tailed tits experience considerable brood predation (~75% of nests; Hatchwell et al. 2013), and synchronous provisioning reduced the total time that carers were active near the nest (Bebbington and Hatchwell 2016). Whilst they did not increase synchrony in response to temporary experimental elevation of predation risk (Halliwell et al. 2023b), it is still possible that synchrony over the course of the nestling period reduces predation risk. Therefore, long-tailed tits are a good candidate for testing this hypothesis. We predicted that more synchronous provisioning results in lower rates of brood predation (Prediction 3a) and prolonged brood survival (Prediction 3b). It should be noted that we did not test the hypothesis that synchrony facilitates signalling of investment by helpers because the absence of direct fitness benefits for helpers in this system means that the pay-to-stay and prestige hypotheses (both of which require signalling of effort) do not apply.

**5.3 Methods**

**5.3.1 Study system and general field protocol**

All data were collected during the breeding seasons (March–June) of 1994–2022 as part of a long-term project intensively monitoring a wild population of long-tailed tits in a ~3km2 field site in the Rivelin Valley, Sheffield, UK *(53°23′N*, *1°34′W)*. From February of each year, nests were located by following adult birds building nests, which they do so mostly in low-lying (<3m) shrubs (e.g. brambles *Rubus fruticosus*, rose *Rosa spp*., holly *Ilex spp*.,or gorse *Ulex spp*.), but sometimes also >3m from the ground in forks of tree branches. Once located, nests were monitored regularly throughout their development, typically at 1–3 day intervals but with daily checks when nests approached incubation, hatching, and fledging. Incubation starts once the clutch is complete, lasts ~15 days, and all eggs that hatch do so within 24h of the first. Once hatched (day 0), chicks are regularly brooded by the mother for up to 5 days while the father delivers prey items (e.g. flies, spiders, caterpillars), often passing food to the chicks via the brooding mother. Helpers may join a group at any point between hatching (d0) and fledging (d16–18), and because the number of failed breeders increases through the season, helping is more common later in offspring development. Long-tailed tits lose 71.9% of all clutches and broods to predation (Hatchwell et al. 2013), typically by corvids (e.g. Eurasian jay *Garrulus glandarius*) and mammals (e.g. stoat *Mustela erminea*). Predation events are usually complete (i.e. all eggs/chicks dead or missing) but in a few cases broods may be partially predated (3.86% of successful nests; 9/233). Partial predation was usually identified by damage to the exterior of the nest and confirmed by inspection of the brood.

**5.3.2 Biometric sampling**

Where possible, clutch size (median = 10; range 4–12; *N* = 293) was recorded once incubation had begun. Brood size (median = 9; range 1–11; *N* = 275) was recorded on d11 when nestlings were ringed, as follows. Half the brood was removed from the nest and placed within an insulated bird-bag. Each chick was then ringed under British Trust for Ornithology (BTO) licence with a unique combination of colour rings (size code: XF) on one leg and a metal BTO ring on the other, weighed to the nearest 0.1g with digital scales (mean = 7.4g ± 0.0142 SE; *N* = 1970), and their tarsus length measured to the nearest 0.1mm with a calliper (mean = 18.3mm ± 0.0188 SE; *N* = 1970). These chicks were then returned to the nest and the process repeated with the other half of the brood. This ensured that carers never returned to an empty nest and limited the time chicks were out of the nest. We also usually took 5–20µl of blood by brachial venepuncture (under UK Home Office licence) of broods for genetic sex determination of nestlings using the *P2*–*P8* sex-typing primers (Griffiths et al. 1998). Because clutch and/or brood size were included as covariates in all analyses, we only used nests where these metrics could be sampled, biasing our sample in favour of low-lying nests in shrubs and against nests high in trees. Overall, the weight and sex of every chick from a given brood was known in 77.7% (185/238) of nests. Sex determination of adults was performed using a combination of genetic and observational approaches. Only females incubate eggs and brood chicks, which allows their sex, and the sex of their partner, to be inferred. Where genetic and observational sex determination conflicted (0.39%; 6/1533), priority was given to observation.

The population is open and each year about 40% of all breeding birds were immigrants to our field site. Unringed birds were captured in mist-nets, ringed, and processed as described for nestlings, with wing cord to the nearest 1mm also recorded. Each season ~95% of breeders and helpers in the study population were individually marked. Since the establishment of the long-term project in 1994, a total of 1531 unique adult birds have been observed attempting to breed (i.e. building a nest) within the field site. Our sample included only individuals that were recorded provisioning chicks from d6 onwards in a watch which met our criteria (see below), so 37.6% (576/1531) of these individuals were present in this analysis. Specifically, our sample contained 239 unique breeding females, 227 unique breeding males, and 110 unique individuals that were only recorded provisioning when helping others. Additionally, 61 of these breeders (mostly males) were also observed helping at another nest within our sample of provisioning watches.

**5.3.3 Calculating coordination**

Provisioning watches (hereafter ‘watches’) were typically performed from d2 post-hatching every other day until either failure or fledging (d16–18), so most watches took place on even brood ages (95.0% of watches; 849/894), although watches from odd days were still included. Because females brood for ~5 days post-hatching, during this time the types of provisioning coordination we investigate here are not possible. Therefore, analysis was restricted to watches done from d6 onwards when both parents provision the brood regularly (median = d10; range d6–18; *N* = 894). Most carers were individually identifiable by their unique combination of colour rings. If an unringed carer provisioned during a watch (4.36% of watches; 39/894) we assumed all feeds were by the same unringed individual. Any watches at nests where we observed >1 unringed birds simultaneously were not used in our analyses.

The provisioning watch protocol was consistent throughout the study. After a habituation period of ~10 min, watches typically lasted one hour but were sometimes shorter when curtailed by inclement weather (minimum duration = 30 mins); when a carer provisioned the brood its identity and time was recorded to the nearest minute, either by direct observation through binoculars (15–25m away) or video camera (1–5m away) for later review. The length of watches used in this study was defined by the time between the first and last feed in a watch (mean = 54 mins 1 second ± 25 seconds SE; range = 30–117 mins; *N* = 894). We excluded any watch where the identity of a single feed was not known because this could potentially impact levels of coordination. Any watches at nests subjected to an experiment (e.g. brood swap or predator presentation) that were conducted during or after the manipulation were excluded from analyses. Watches where hatch date was not precisely known were also excluded. Watches were conducted between 04:00 and 19:30, with 89.4% of watches starting between 06:00 and 14:00.

For each watch the total number of feeds, alternated feeds, and synchronised feeds by all carers was calculated. An alternated feed was defined as any that occurred following a feed by another carer (median = 15; range 1–68; *N* = 894), meaning that at cooperative nests alternation did not necessarily require a repeated consistent pattern of feeds (e.g. A-B-C-A-B-C), just non-consecutive feeds (e.g. A-B-A-C-B-A). A synchronised feed was defined as any non-consecutive feed that occurred within 2 minutes of the prior feed (median = 8; range 0–55; *N* = 894), therefore all synchronised feeds were also necessarily alternated. This 2-minute synchrony window was chosen in accordance with prior studies which found that rates of synchrony using different window lengths were highly correlated (rp > 0.94; Halliwell et al. 2022) and key results were qualitatively the same using different time windows (Mariette and Griffith 2015, Bebbington and Hatchwell 2016, Ihle et al. 2019a, Halliwell et al. 2022). By these definitions of alternation and synchrony, at watches where one carer performed the majority of feeds there were a number of feeds which could not be alternated or synchronised. Therefore, for each watch we calculated a percent value of ‘Maximum possible coordination’ (mean = 87.4% ± 0.414 SE; *N* = 894), which functions as a proxy for the level of provisioning rate asymmetry between carers.

For each watch, certain levels of inherent apparent alternation and synchrony are expected by random chance (Schlicht et al. 2016, Ihle et al. 2019a, Santema et al. 2019). To control for this, a null model randomisation approach was used to estimate the level of apparent coordination expected by chance (e.g. Johnstone et al. 2014, Ihle et al. 2019a,b, Halliwell et al. 2022). The null model randomised the order of each carer’s intervisit intervals within a watch, then combined all carers’ sequences to produce a new randomised feed sequence. This procedure was applied to each watch to generate 1000 randomised sequences of feeds by all carers per watch and the median number of alternated and synchronised feeds was considered the level of apparent coordination expected by chance for that watch; thus, each watch receives its own values of expected alternation and synchrony. This approach was found to be the most conservative null model for estimating expected apparent coordination (Ihle et al. 2019a), likely because it conserved refractory periods (i.e. minimum time to prey capture). The difference between observed and expected coordination in each watch is termed ‘active’ coordination. Observed and expected alternation (and synchrony) were later used to generate measures of how much each group of carers deviated from their expected alternation or synchrony in each watch; termed ‘Active alternation score’ (mean = 0.0663 ± 0.00499 SE; *N* = 894) and ‘Active synchrony score’ (mean = 0.206 ± 0.00884 SE; *N* = 894), respectively. Active alternation scores were calculated from log(observed alternated feeds + 0.5) – log(expected alternated feeds + 0.5), and synchrony scores likewise. We added 0.5 to each value to avoid taking the log of zero.

**5.3.4 Local recruitment**

Successful recruitment of fledglings into the local breeding population was determined by whether an individual was recorded attempting to breed in the field site in subsequent years. Long-tailed tits exhibit female-biased dispersal (Sharp et al. 2008, 2011), so ~25% of male, but only ~10% of female fledglings recruit locally. Dispersal could not be distinguished from mortality, so the recruitment rate of male fledglings is a more accurate metric of successful recruitment into a breeding population (Hatchwell et al. 2014). Therefore, we used resighting data of ringed fledglings attempting to breed in subsequent years to estimate the number of males from each brood that were recruited locally (median = 1; range = 0–5; *N* = 170) and were not recruited locally (median = 3; range = 0–7; *N* = 170). These data were later used to model the proportion of male chicks from each brood which were locally recruited (mean = 0.241 ± 0.0212 SE; *N* = 170), which was our primary metric of each brood’s recruitment success.

**5.3.5 Statistical analysis**

All statistical analysis was performed on R version 4.2.3 (R Core Team 2023). Models were built using lme4 (Bates et al. 2015), coxme (Therneau 2022), and analysed with lmerTest (Kuznetsova et al. 2017). Figures were produced using ggplot2 (Wickham 2016), survminer (Kassambara et al. 2021), and cowplot (Wilke 2020). After omitting watches that did not meet our criteria, we had a sample of 871 watches at 275 nests (**full sample**), however a slightly larger sample was also later used specifically for predation analysis which included watches from nests that were predated prior to ringing on d11, so brood size was assumed to equal clutch size (N = 894 watches at 293 nests; **predation sample**). Testing the predictions of our hypotheses often required analysis of specific subsets of these data, e.g. only watches conducted prior to biometric assessment on d11 were used to analyse the effects of coordination on chick mass. Details of data subsets used for each analysis are described where appropriate and a full diagram of all data subsets is available in the supplementary material (Figure S5.1).

**Quantifying coordination**

When investigating the influence of alternation and synchrony on reproductive success we used ‘Active alternation score’ and ‘Active synchrony score’, respectively. Alternation and synchrony are intrinsically linked because for a feed to be synchronised, by definition, it must also be alternated, so they are often positively correlated (Bebbington and Hatchwell 2016, Leniowski and Węgrzyn 2018). Therefore, we analysed alternation and synchrony scores in separate models. Furthermore, these scores alone do not adequately quantify the true level of coordination unless appropriate covariates are controlled for. For example, Halliwell et al. (2022) found that the difference between observed and expected alternation declined with increasing numbers of helpers; an effect probably caused by a disproportionate increase in expected alternation when there are more carers to alternate with. Similarly, the difference between observed and expected synchrony declined with increasing provisioning rate because more feeds inevitably fall within the synchrony window by chance at high provisioning rates. Therefore, whenever we investigated the effect of ‘Active alternation score’ on reproductive success we also included its 2-way interaction with ‘Helped during watch?’ – a binary factor indicating whether a brood was fed by a pair or a pair plus helper(s) in each watch, as a covariate. Likewise, for synchrony analyses we included ‘Active synchrony score’ and its interaction with ‘Provisioning rate’ – a continuous numerical variable denoting the number of feeds performed per hour by all carers during a given watch (mean = 23.8 feeds/h ± 0.320 SE; *N* = 894), as covariates. These interaction terms are themselves informative; for example, ‘Active synchrony score’ alone informs whether synchrony influences reproductive success independently of other variables, whilst the interaction of ‘Active synchrony score’ and ‘Provisioning rate’ informs whether the direction and/or strength of the effect of synchrony on a given trait varies with the provisioning rate of the group.

Variation in the provisioning rates of carers during each watch may influence the ability of the null model randomisation approach to detect active coordination. For example, if all carers provision at perfectly consistent rates (i.e. zero intervisit interval variation) then randomising the order of intervisit intervals does not change the order of feeds in the sequence. Therefore, despite very high rates of observed alternation, the level of expected alternation (and synchrony) will necessarily equal the observed, resulting in low active coordination scores. However, watches where all carers provision at consistent rates may still be coordinated even if the null model cannot detect it. In fact, the conflict resolution hypothesis (hypothesis 1) predicts that if alternation effectively resolves conflict between carers, then all carers would consistently provision at their optimal rate, which could result in low provisioning rate variation. Critically, if components of reproductive success are regressed against ‘Active alternation score’ without adequately controlling for this effect, counterintuitive results could give the false impression that alternation negatively influences traits it is predicted to improve. Therefore, the level of provisioning rate variation by all carers during each watch must be quantified and its effect on the ability of the null model to detect ‘active’ coordination investigated. If the level of provisioning rate variation within a watch significantly influences the relative levels of observed and expected coordination, as we anticipate, then this effect must be controlled for in subsequent analyses investigating the effect of coordination of components of reproductive success. So, we built two Poisson-distributed generalised linear mixed effects models (GLMMs) with the number of alternated (and synchronised) feeds per watch as response variables (‘Number of alternated feeds’ and ‘Number of synchronised feeds’, respectively).

The first GLMM compared observed and expected alternation in each watch from our **full sample** of watches (N = 871 watches at 275 nests). Our explanatory terms of interest were ‘Data type’ – a binary factor denoting whether data were taken directly from field observation (observed) or generated by null model intervisit interval randomisation (expected), ‘IVI SD’ – a continuous numerical variable denoting the provisioning rate variation by all carers during a given watch (Mean = 0.583 ± 0.00738 SE; *N* = 871), and their interaction term. ‘IVI SD’ was calculated as follows; for each watch, we calculated the standard deviation of the time between each feeding visit (i.e. the intervisit interval) for each carer, which we then divided by their mean intervisit interval duration during that watch to generate a mean-adjusted measure of provisioning rate variation for each individual. We then averaged these values across all carers active during the watch to calculate the overall mean value of provisioning rate variation per watch. Additional fixed effect covariates were as follows. ‘Helped during watch?’ – see above for definition. ‘Brood size’ – an integer numerical variable denoting the number of live chicks recorded at a nest on d11 post-hatching, modelled as both linear and quadratic terms. ‘Watch duration’ – a continuous numerical variable denoting the time, in minutes, between the first and last recorded feeds by any carer during a given watch; included here because as watch duration increases the total number of feeds, and thus coordinated feeds, inherently increases. ‘Watch start time’ – a continuous numerical variable denoting the time at which each watch started (mean = 9:54am ± 5 mins SE; *N* = 871). ‘Maximum possible coordination’ – a continuous numerical variable denoting the highest theoretical percentage of feeds which could be alternated (or synchronised) during a given watch; this functions as a proxy for provisioning rate disparity between carers. ‘Hatch date’ – an integer numerical variable denoting the number of days after March 1 that a brood hatched (Median = May 3; range April 16–June 6; *N* = 275), modelled as both linear and quadratic terms. ‘Brood age’ – an integer numerical variable denoting the number of days between hatching and when a watch was performed; and ‘Provisioning rate’, as described above. We also included the interaction term of ‘Data type’ and ‘Helped during watch?’ to account for fundamental increases in expected alternation at helped nests. Random effects were as follows: ‘Year’ – a factor denoting the year in which a watch was performed. ‘Nest ID’ – a factor denoting the identity of a nest which was watched. ‘Watch ID’ – a factor denoting the identity of each provisioning watch, used when comparing observed and expected coordination from the same watch. ‘Pair ID’ – a factor denoting the unique combination of parents at a given nest. ‘Female ID’ – a factor denoting the unique identity of each biological mother at a given nest. ‘Male ID’ – a factor denoting the unique identity of each biological father at a given nest. ‘Rowref’ – an observation level random effect used to account for overdispersion in Poisson-distributed models. Fitting this model revealed that the difference between observed and expected alternation (i.e. active alternation) increased significantly with provisioning rate variation, as evidenced by the interaction of ‘Data type’ and ‘IVI SD’ (GLMM: *P* < 0.001, table S5.1, figure S5.2a).

We repeated this analysis using the number of synchronised feeds as the response variable. The model structure was the same as for alternation except that it also included the interaction of ‘Data type’ and ‘Provisioning rate’ to account for the inevitable increase in expected synchrony as provisioning rate increases (Halliwell et al. 2022), but it did not include the interaction of ‘Data type’ and ‘Helped during watch?’. Just as with alternation, active synchrony increased significantly with provisioning rate variation (GLMM: *P* < 0.001, table S5.2, figure S5.2b). This means that the ability of the null model to detect active coordination increased with provisioning rate variation. Therefore, to control for this statistical effect, whenever we investigated the effect of ‘Active alternation score’ or ‘Active synchrony score’ on reproductive success, we also included their interaction with ‘IVI SD’ as a covariate throughout.

**Hypothesis 1: Alternation facilitates conflict resolution**

To test the hypothesis that alternation of provisioning visits facilitates conflict resolution, thus allowing carers to increase their investment closer to the brood’s optimum without the risk of exploitation, we built a series of (G)LMMs to test three predictions of this hypothesis, as follows.

*Prediction 1a: Alternation increases provisioning rate.*

We used a normally distributed linear mixed effects model (LMM) to investigate the relationship between alternation and provisioning rate in the **full sample** of watches (N = 871 watches at 275 nests). The response variable was the log-transformed ‘Provisioning rate’ per watch and the explanatory terms of interest were ‘Active alternation score’ and its interaction with ‘Helped during watch?’, which informs whether the relationship between alternation and provisioning rate varies between biparental and cooperative nests. Additional fixed effect covariates were ‘Brood size’ (linear and quadratic), ‘Watch duration’, which was included to account for potential variation in provisioning rate caused by observer disturbance which could disproportionately influence shorter watches, ‘Watch start time’, ‘Maximum possible coordination’, ‘Hatch date’ (linear and quadratic), ‘Brood age’, ‘IVI SD’, and its interaction with ‘Active alternation score’. Random effects were ‘Year’, ‘Nest ID’, ‘Pair ID’, ‘Female ID’, and ‘Male ID’.

*Prediction 1b: Alternation increases chick mass.*

To test this prediction, we fitted a normally distributed LMM to investigate the relationship between alternation and chick mass using a subset of watches taken prior to biometric assessment (d11) from nests where all chicks’ biometrics and sexes were known (**Chick mass sample sex known**; *N* = 360 watches at 185 nests containing 1533 chicks). The response variable was each individual chick’s mass on d11 (‘Chick mass’). Because several watches were usually performed prior to biometric assessment, certain metrics were summed (e.g. watch duration) or averaged across all watches performed at the nest. For some metrics, we took the mean value from all watches performed at the nest (e.g. watch start time, maximum possible coordination, brood age, IVI SD), whilst at others we took aggregate values by summing metrics taken over all watches then dividing by the relevant metric (e.g. active alternation score, active synchrony score, provisioning rate). For example, aggregate alternation scores were calculated from: log(total observed alternated feeds + 0.5) + log(total expected alternated feeds + 0.5), and provisioning rate was the total number of feeds/total duration of watches. We used this aggregate approach to quantify coordination scores, rather than mean values from all watches (as in Ihle et al. 2019b), because if a nest had a short duration and/or low provisioning rate during some watches, but a long duration and/or high provisioning rate during others, then taking mean values would give disproportionate weight to coordination scores from short and/or low provisioning rate watches. However, the aggregate approach gives appropriate weight to watches based on duration and provisioning rate, which we believe makes it the more accurate measure of the overall coordination performed at a nest. Furthermore, aggregate and mean coordination scores were highly correlated (Alternation: rs = 0.968, *P* < 0.001; Synchrony: rs = 0.925, *P* < 0.001, *N* = 220). We also used aggregate provisioning rate as a covariate throughout; again noting that aggregate and mean provisioning rates were also highly correlated (rs = 0.998, *P* < 0.001, *N* = 220). Watches were usually performed every other day, however, some watches were missed due to inclement weather or excluded as they did not meet our criteria. This could skew results based on the age at which watches performed, so to account for this we included ‘Mean brood age’ of all watches performed at each nest as a covariate throughout.

Explanatory terms of interest were ‘Aggregate active alternation score’ and its interaction with ‘Nest helped?’ – a binary factor denoting whether a nest was provisioned by more than two carers during any watch within the range of watches analysed. Additional fixed effect covariates were as follows. ‘Brood size’ (linear and quadratic). ‘Mean watch start time’. ‘Mean maximum possible coordination’. ‘Hatch date’ (linear and quadratic). ‘Mean brood age’. ‘Aggregate provisioning rate’. ‘Tarsus length’ (linear and quadratic) – a continuous numerical variable denoting the length (in mm) of a given chick’s tarsus (as in MacColl and Hatchwell 2004, Ihle et al. 2019b). ‘Brood sex ratio’ – continuous numerical variable denoting the ratio of female:male chicks within a given brood (mean = 0.511 ± 0.0124 SE; *N* = 185), included to account for differences in chick mass between broods of different sexual composition. ‘Chick sex’ – a binary factor denoting whether a chick was male or female, and its interaction with ‘Brood sex ratio’ to account for potential density dependent effects of being an over or underrepresented sex within the brood, ‘Mean IVI SD’, and its interaction with ‘Aggregate active alternation score’. Random effects were ‘Year’, ‘Nest ID’, ‘Pair ID’, ‘Female ID’, and ‘Male ID’.

*Prediction 1c: Alternation increases recruitment rate.*

To test the final prediction of this hypothesis, we built a binomially distributed GLMM to investigate the relationship between active alternation score and the proportion of male offspring from a brood which were recruited into the local breeding population using a subset of watches from nests which fledged where all chick sexes were known (**Recruit sample**; *N* = 574 watches at 170 nests containing 719 male chicks). The response variable was a two-column variable (number of males recruited, number of males not recruited), which functions as a measure of proportion recruited (mean = 0.241 ± 0.0212 SE; *N* = 170). Explanatory terms of interest were ‘Aggregate active alternation score’ and its interaction with ‘Nest helped?’. Additional fixed effect covariates were ‘Brood size’ (linear and quadratic), ‘Mean watch start time’, ‘Mean maximum possible coordination’, ‘Hatch date’ (linear and quadratic), ‘Brood sex ratio’, ‘Mean brood age’, ‘Aggregate provisioning rate’, ‘Mean IVI SD’, and its interaction with ‘Aggregate active alternation score’. Random effects were ‘Year’, ‘Pair ID’, ‘Female ID’, and ‘Male ID’.

Because the interaction of ‘Active alternation score’ and ‘Nest helped?’ was significant, we repeated this analysis on a subset of the **recruit sample** containing only biparental (2 carers) watches (N = 331 watches at 101 nests containing 420 male chicks) and then a subset containing only cooperative (>2 carers) watches (N = 243 watches at 69 nests containing 299 male chicks). The model structures were the same as above minus the ‘Nest helped?’ term and the cooperative model also included ‘(mean) carer number’ – continuous numerical variable denoting the mean number of carers observed provisioning a brood during all watches of a given nest (mean = 3.21 ± 0.0798 SE; *N* = 69, cooperative nests only) and its interaction with ‘Aggregate active alternation score’ as covariates.

**Hypothesis 2: Synchrony increases resource distribution parity**

To test the hypothesis that synchrony of provisioning visits facilitates greater resource distribution parity between chicks within a brood, we fitted a series of (G)LMMs to test three predictions of this hypothesis. There was an outlier data point for ‘Active synchrony score’ where at one watch carers performed no synchronised feeds despite being expected to perform three. This was the only watch performed at that nest, so this outlier remained statistically influential even when using aggregate values from all watches taken at a nest. For all synchrony analyses we ran models both with and without this nest, in most cases we found no qualitative difference in any of our terms (supplementary material tables S5.10, S5.11, S5.13, S5.15, and S5.17). However, where results differ, we present model outputs both with and without this outlier, and for all other models we present outputs including this watch but exclude it from relevant figures to avoid blank space between this outlier and the rest of our data.

*Prediction 2a: Synchrony increases chick mass.*

To test whether synchronous feeds were associated with greater chick mass, we built a normally distributed LMM using the same structure as for prediction 1b but with ‘Aggregate active synchrony score’ instead of alternation and the interaction of ‘Aggregate active synchrony score’ and ‘Aggregate provisioning rate’ as an additional fixed effect of interest. This model was applied to the same data subset as alternation (**Chick mass sample sex known**; *N* = 360 watches at 185 nests containing 1533 chicks).

*Prediction 2b: Synchrony reduces intrabrood mass variation.*

To test the prediction that synchronous provisioning reduces variance in chick mass, we used a normally distributed LMM to investigate the relationship between active synchrony score and the within-brood standard deviation in chick mass. This analysis was conducted on a subset of watches recorded prior to biometric assessment (d11) from nests where all chicks’ biometrics and sexes were known (**Chick mass sample sex known**; *N* = 360 watches at 185 nests containing 1533 chicks). The response variable was the log-transformed standard deviation of chick mass within a brood (‘Intrabrood mass SD’, mean = 0.380 ± 0.0133 SE; *N* = 185). Explanatory terms of interest were ‘Aggregate active synchrony score’ and its interaction with ‘Aggregate provisioning rate’, which informed whether the impact of synchrony on intrabrood mass variation varied with provisioning rate. Additional fixed effect covariates were as follows: ‘Brood size’ (linear and quadratic), ‘Mean watch start time’, ‘Mean maximum possible coordination’, ‘Hatch date’ (linear and quadratic), ‘Mean brood age’, ‘Brood sex ratio’, ‘Aggregate provisioning rate’, ‘Nest helped?’, its interaction with ‘Aggregate active synchrony score’, ‘Mean IVI SD’, and its interaction with ‘Aggregate active synchrony score’. Random effects were ‘Year’, ‘Pair ID’, ‘Female ID’, and ‘Male ID’. The term ‘Brood sex ratio’ was not significant in this model, so we repeated the analysis without this term on a larger sample where chick sexes were not necessarily known (**Chick mass sample**; *N* = 466 watches at 238 nests containing 1970 chicks). We report this model’s outputs in our final analysis.

*Prediction 2c: Synchrony increases recruitment rate.*

To test the final prediction of this hypothesis, we built a binomially distributed GLMM using the same structure as prediction 1c but with ‘Aggregate active synchrony score’ instead of alternation and the interaction of ‘Aggregate active synchrony score’ and ‘Aggregate provisioning rate’ as an additional fixed effect of interest. This model used the same data subset as alternation (**Recruit sample**; *N* = 574 watches at 170 nests containing 719 male chicks). The effect of alternation on male recruitment differed between biparental and cooperative nests, so we also repeated the synchrony analysis on subsets of the **recruit sample** thatcontained either biparental watches only (N = 331 watches at 101 nests containing 420 male chicks) or cooperative watches only (N = 243 watches at 69 nests containing 299 male chicks). The model structures were the same as before minus the ‘Nest helped?’ term and the cooperative model also included ‘(mean) carer number’ and its interaction with ‘Aggregate active synchrony score’ as covariates.

**Hypothesis 3: Synchrony reduces brood predation risk**

To test the hypothesis that synchrony reduces the risk of brood predation, we built two models investigating the effect of synchrony on the likelihood and relative timing of brood predation. Brood size was recorded on day 11, so for this analysis nests predated pre-d11 were assumed to have a brood size equal to clutch size. We excluded any watches taken after partial predation events, resulting in a sample size of *N* = 894 watches at 293 nests used specifically for the predation risk analysis (**Predation sample**).

*Prediction 3a: Predated nests are provisioned less synchronously.*

When comparing synchrony in watches from nests that were predated with those from nests that fledged, it is important to consider potential sample biases. Nests that fledged inevitably have more watches from older broods (Mean brood age = 10.5d for fledged nests *vs.* 8.5d for predated nests; *N* = 894), so if active synchrony scores change with brood age (e.g. due to more helpers later in development) this could confound our results on predation risk. For example, if active synchrony increases with brood age, then fledged nests could appear more synchronous than predated nests. However, the correlation between ‘Active synchrony score’ and ‘Brood age’ (rp = -0.10) was weakly negative, so our analysis was conservative because this effect would tend to mask any potential effect of synchrony to reduce predation risk. To limit this effect, ‘Mean brood age’ from all watches at a given nest was included as a covariate throughout the predation risk analysis.

To test this prediction, we used a binomially distributed GLMM to evaluate whether predation risk varied with synchrony score. The response variable was whether a brood was predated (1) or fledged without predation (0). Explanatory terms of interest were ‘Aggregate active synchrony score’ and its interaction with ‘Aggregate provisioning rate’, which informs whether the impact of synchrony on predation risk varies with provisioning rate. Additional fixed effect covariates were as follows: ‘Brood size’ (linear and quadratic), ‘Mean watch start time’, ‘Maximum possible coordination’, ‘Hatch date’ (linear and quadratic), ‘Mean brood age’, ‘Nest helped?’, ‘Mean IVI SD’, and its interaction with ‘Aggregate active synchrony score’. ‘Year’, ‘Pair ID’, ‘Female ID’, and ‘Male ID’ were included as random effects.

*Prediction 3b: More synchronous nests survive longer.*

The second prediction of this hypothesis was that high levels of synchrony would prolong brood survival. We estimated how time to predation or fledging varied with synchrony score using a Cox proportional hazard mixed model (CPHMM) (Therneau 2022). The response variable was a two-column variable (number of days until event, whether event was fledging or predation). The data were treated as right censored with all fledged broods defined as age 18. Explanatory terms of interest were ‘Aggregate active synchrony score’ and its interaction with ‘Aggregate provisioning rate’, which informs whether the impact of synchrony on time to predation varies with provisioning rate. Model structures, covariates, and random effects were the same as for prediction 3a.

**5.4 Results**

**5.4.1 Hypothesis 1: Alternation facilitates conflict resolution**

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Table 5.1. Effect of active alternation score and associated interaction terms on provisioning rate at each watch as well as offspring condition and reproductive success at each nest. Significant values (*P* < 0.05) in bold. | | | | | |
| Response variable | Term of interest | Estimates ± SE | df | 𝝌2 | *P* |
| **Prediction 1a: Alternation increases provisioning rate** | | | | | |
| Log(provisioning rate) | Active alternation score | 0.033 ± 0.012 | 1,871 | 9.74 | **0.002** |
| Active alternation score \* Helped during watch? | Yes: 0.048 ± 0.029 | 1,871 | 2.78 | 0.096 |
| **Prediction 1b: Alternation increases chick mass.** | | | | | |
| Chick mass | Active alternation score | -0.036 ± 0.031 | 1,1533 | 1.14 | 0.285 |
| Active alternation score \* Nest helped? | Yes: 0.103 ± 0.078 | 1,1533 | 1.73 | 0.188 |
| **Prediction 1c: Alternation increases recruitment rate** | | | | | |
| *All nests* | | | | | |
| Proportion of males recruited | Active alternation score | -0.340 ± 0.202 | 1,170 | 0.58 | 0.445 |
| Active alternation score \* Nest helped? | Yes: 0.929 ± 0.402 | 1,170 | 5.36 | **0.021** |
| *Biparental nests only* | | | | | |
| Proportion of males recruited | Active alternation score | -0.401 ± 0.245 | 1,101 | 2.37 | 0.123 |
| *Cooperative nests only* | | | | | |
| Proportion of males recruited | Active alternation score | 0.800 ± 0.293 | 1,69 | 9.09 | **0.003** |

*Prediction 1a: Alternation increases provisioning rate.*

To test whether alternation facilitates conflict resolution between carers we investigated the effect of several key terms on provisioning rate. As predicted, we found a significant positive effect of ‘Active alternation score’ on provisioning rate (LMM: *P* = 0.002, table 5.1, figure 5.1a). This effect did not differ significantly between biparental and cooperative breeding groups, as evidenced by its interaction with ‘Helped during watch?’ (LMM: *P* = 0.096, table 5.1). There were also significant positive effects of ‘Maximum possible coordination’ (LMM: *P* < 0.001, supplementary material table S5.3), ‘Brood size (linear)’ (LMM: *P* = 0.020, table S5.3), and ‘Helped during watch?’ (LMM: *P* = 0.017, table S5.3) on provisioning rate, showing that the presence of helpers increased the total food delivered to broods, as reported in previous analyses (e.g. MacColl and Hatchwell 2003, Hatchwell et al. 2014). Furthermore, we found significant negative effects of ‘Watch duration’ (*P* = 0.015, table S5.3) and ‘Watch start time’ (LMM: *P* < 0.001, table S5.3), while all other terms were not significant (supplementary material).

*Prediction 1b: Alternation increases chick mass.*

The second prediction of the conflict resolution hypothesis, that alternation increased nestling mass, was not supported (LMM: *P* = 0.285, table 5.1, figure 5.1b). As expected, larger chicks were heavier, chick mass increasing with tarsus length then plateauing at large values, as shown by the significant quadratic effect of ‘Tarsus length’ (LMM: *P* < 0.001, table S5.4). Additionally, male offspring were significantly larger than female offspring (LMM: *P* < 0.001, table S5.4). Surprisingly, we found no significant effect of any other terms on chick mass (table S5.4), including whether a nest was helped (*P* = 0.535), conflicting with previous studies of long-tailed tits (MacColl and Hatchwell 2002, Hatchwell et al. 2004).

*Prediction 1c: Alternation increases recruitment rate.*

There was a significant effect of the interaction of ‘Aggregate alternation score’ and ‘Nest helped?’ on the recruitment of male fledglings from a sample of biparental and cooperative nests (GLMM: *P* = 0.021, table 5.1, figure 5.1c). This suggests that there was a positive effect of alternation on male recruitment rate when broods were helped, but not when they were fed by parents alone. Additionally, there was a significant positive effect of ‘Maximum possible coordination’ (GLMM: *P* = 0.046, table 5.1), so male recruitment rate increased with provisioning rate parity between carers. No other term was significant within this model (table S5.5).

Analysing recruitment at biparental (2 carers) nests identified no significant effect of any investigated terms (table S5.6). In contrast, analysis of cooperative (>2 carers) nests revealed significant positive effects of ‘Active alternation score’ (GLMM: *P* = 0.003, table 5.1, figure 5.1c) and ‘Carer number’ (GLMM: *P* = 0.021, table S5.7) on male recruitment rate. Meaning that at cooperative nests greater alternation and more helpers both independently increased offspring recruitment rate (as found in McGowan et al. 2003, Hatchwell et al. 2004, 2014). All other terms were not significant (tables S5.9), including ‘Maximum possible coordination’ which, despite being marginally significant in the overall model (see above), was not significant in either biparental (GLMM: *P* = 0.057, table S5.6) or cooperative (GLMM: *P* = 0.630, table S5.7) specific models.

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Figure 5.1. (a) Provisioning rate (feeds/hour) versus active alternation score per watch from the full sample of watches (N = 871 watches at 275 nests). (b) Chick mass (in grams) at d11 vs aggregate active alternation score per nest from a subsample of watches taken prior to weighing where all chick sexes were known (N = 360 watches at 185 nests containing 1533 chicks). (c) Proportion of male offspring recruited into the local breeding population versus the aggregate active alternation score at biparental (blue; *N* = 331 watches at 101 nests containing 420 male chicks) and cooperative nests (orange; *N* = 243 watches at 69 nests containing 299 male chicks) which fledged and all chick sexes were known. Data points were translucent, so overlapping data points results in darker shades. Predicted relationships (± 95% CI) are fitted from GLMMs, see table 5.1.

**5.4.2 Hypothesis 2: Synchrony increases resource distribution parity**

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Table 5.2. Effect of active synchrony score and associated interaction terms on offspring condition and reproductive success at each nest. Significant values (*P* < 0.05) in bold. | | | | | |
| Response variable | Term of interest | Estimates ± SE | df | 𝝌2 | *P* |
| **Prediction 2a: Synchrony increases chick mass** | | | | | |
| Chick mass | Active synchrony score | -0.010 ± 0.032 | 1,1533 | 0.096 | 0.757 |
| Active synchrony score \* Provisioning rate | -0.021 ± 0.030 | 1,1533 | 0.47 | 0.494 |
| **Prediction 2b: Synchrony reduces intrabrood mass variation** | | | | | |
| Log(intrabrood mass SD) | Active synchrony score | 0.021 ± 0.036 | 1,238 | 0.0015 | 0.969 |
| Active synchrony score \* Provisioning rate | 0.026 ± 0.034 | 1,238 | 0.60 | 0.437 |
| **Prediction 2c: Synchrony increases recruitment rate** | | | | | |
| *All watches* | | | | | |
| Proportion of males recruited | Active synchrony score | 0.278 ± 0.251 | 1,170 | 0.044 | 0.833 |
| Active synchrony score \* Provisioning rate | 0.334 ± 0.219 | 1,170 | 2.33 | 0.127 |
| *Biparental nests only* | | | | | |
| Proportion of males recruited | Active synchrony score | 0.268 ± 0.336 | 1,101 | 0.00 | 0.993 |
| Active synchrony score \* Provisioning rate | 0.399 ± 0.315 | 1,101 | 1.60 | 0.206 |
| *Cooperative nests only* | | | | | |
| Proportion of males recruited | Active synchrony score | 0.683 ± 0.311 | 1,69 | 1.18 | 0.277 |
| Active synchrony score \* Provisioning rate | 0.717 ± 0.320 | 1,69 | 5.02 | **0.025** |

*Prediction 2a: Synchrony increases chick mass.*

To test the hypothesis that synchrony increases resource distribution parity between offspring, first we investigated the effect of synchrony and other key terms on chick mass. We found no significant effect of ‘Active synchrony score’ (LMM: *P* = 0.757, table 5.2, figure 5.2a) or its interaction with ‘Provisioning rate’ on chick mass (LMM: *P* = 0.494, table 5.2). However, this model corroborated our earlier findings that ‘Chick sex’, ‘Hatch date’, and ‘Tarsus length’ had significant effects on chick mass, while all other terms were not significant (table S5.9).

*Prediction 2b: Synchrony reduces intrabrood mass variation.*

We found no significant effect of ‘Active synchrony score’ (LMM: *P* = 0.969, table 5.2, figure 5.2b) or its interaction with ‘Provisioning rate’ (LMM: *P* = 0.437, table 5.2) on intrabrood mass variation. The only significant term in the model was a quadratic effect of ‘Hatch date’ (LMM: *P* = 0.036, table S5.10), with offspring mass variation at d11 peaking in the middle of the breeding season.

*Prediction 2c: Synchrony increases recruitment rate.*

Analysis of male recruitment rate at biparental and cooperative nests together revealed no significant effect of ‘Active synchrony score’ (GLMM: *P* = 0.833, table 5.2), its interaction with ‘Provisioning rate’ (GLMM: *P* = 0.127, table 5.2) or any other terms (supplementary material). However, when we restricted analysis to cooperative nests there was a significant effect of the interaction of ‘Active synchrony score’ and ‘Provisioning rate’ (GLMM: *P* = 0.025, table 5.2, figure 5.2c) on male recruitment rate, indicating that the strength of the positive relationship between synchrony and recruitment at cooperative nests increased with provisioning rate. Furthermore, this analysis corroborated our earlier finding that male recruitment rate increased with the number of carers at cooperative nests (GLMM: *P* = 0.013, table S5.12). No other terms significantly influenced male recruitment rate at cooperative or biparental nests (table S5.13).

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Figure 5.2. (a) Chick mass (in grams) at day 11 vs aggregate active synchrony score per nest from a subsample of watches taken prior to weighing where all chick sexes were known (N = 359 watches at 184 nests containing 1524 chicks). (b) Standard deviation in intrabrood chick mass versus aggregate active synchrony score per nest from a subsample of watches taken prior to weighing (N = 465 watches at 237 nests containing 1961 chicks). For graphical clarity, figures (a) and (b) are presented without outlier data points from a single watch where the active synchrony score was < -1.8. (c) Proportion of male offspring recruited into the local breeding population versus the aggregate active synchrony score at low (green; *N* = 68 watches at 23 nests), medium (orange; *N* = 82 watches at 23 nests) and high (blue; *N* = 93 watches at 23 nests) provisioning rate nests which fledged and all chick sexes were known. Data points were translucent, so overlapping data points results in darker shades. Predicted relationships (± 95% CI) are fitted from GLMMs, see table 5.2.

**5.4.3 Hypothesis 3: Synchrony reduces brood predation risk**

*Prediction 3a: Predated nests are provisioned less synchronously.*

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Table 5.3. Effect of active synchrony score and associated interaction terms on the probability of brood predation, applied to the dataset with and without the inclusion of the outlier where ‘Active synchrony score’ was < -1.8. The response variable was the binary factor denoting whether a brood fledged without predation (0) or was predated (1). *N* = 894 watches at 293 nests. Significant values (*P* < 0.05) in bold. Df = 1, 293 for each variable (outlier included) and 1, 292 (outlier excluded). | | | | |
| Parameter | Estimates ± SE | 𝝌2 | *P* | *P* (excluding outlier) |
| Intercept | -1.889 ± 0.432 |  |  |  |
| Active synchrony score | -0.375 ± 0.248 | 0.058 | 0.809 | 0.875 |
| IVI SD | -0.077 ± 0.185 | 0.22 | 0.638 | 0.666 |
| Nest helped? | Yes: -0.059 ± 0.434 | 0.018 | 0.892 | 0.838 |
| Brood size | -1.099 ± 0.870 | 1.60 | 0.206 | 0.212 |
| Brood size2 | 1.370 ± 0.873 | 2.46 | 0.117 | 0.116 |
| Watch start time | -0.047 ± 0.181 | 0.068 | 0.795 | 0.852 |
| Maximum possible coordination | 0.276 ± 0.219 | 1.59 | 0.207 | 0.202 |
| Hatch date | -0.718 ± 1.751 | 0.17 | 0.682 | 0.706 |
| Hatch date2 | 0.680 ± 1.732 | 0.15 | 0.695 | 0.719 |
| Brood age | -1.230 ± 0.293 | 19.66 | **<0.001** | **<0.001** |
| Provisioning rate | -0.425 ± 0.284 | 0.19 | 0.659 | 0.735 |
| Active synchrony score \* IVI SD | -0.391 ± 0.163 | 5.75 | **0.017** | 0.135 |
| Active synchrony score \* Provisioning rate | -0.630 ± 0.272 | 5.35 | **0.021** | **0.012** |

There was a significant effect of the interaction of ‘Active synchrony score’ and ‘Provisioning rate’ on the probability that a brood was predated (GLMM: *P* = 0.021, table 5.3, figure 5.3). This result was driven primarily by synchrony decreasing the risk of predation when provisioning rate was medium-high (Figure 5.3). Additionally, the interaction of ‘Active synchrony score’ and ‘IVI SD’ was significant when the outlier data point was included (GLMM: *P* = 0.017, table 5.3), but not when it was omitted (GLMM: *P* = 0.135, table 5.3, table S5.14). This effect is difficult to interpret biologically but suggests that the effect of synchrony to reduce predation risk is stronger when provisioning rates are more variable. In addition, brood age (GLMM: *P* < 0.001, table 5.3) had a significant negative relationship with predation risk; this result is trivial because longer surviving broods are inevitably watched at older ages under our observation protocol. No other biologically relevant terms had any significant effect on brood predation rate (Table 5.3). **A diagram of different colors and lines

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Figure 5.3. Probability of brood predation versus aggregate active synchrony scores from all watches taken prior to predation and all watches from nests which fledged without predation which exhibited low (green; *N* = 265 watches at 97 nests), medium (orange; *N* = 312 watches at 98 nests) and high (blue; *N* = 345 watches at 97 nests) provisioning rate. For graphical clarity, the figure is presented without outlier data points from a single watch where the active synchrony score was < -1.8. Data points were translucent, so overlapping data points results in darker shades. Predicted relationships (± 95% CI) are fitted from the GLMM, see table 5.3.

*Prediction 3b: More synchronous nests survive longer.*

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Table 5.4. Effect of active synchrony score and associated interaction terms on the risk of brood predation over time, applied to the dataset with and without the inclusion of the outlier where ‘Active synchrony score’ was < -1.8. The response variable was a two-column variable denoting whether a nest was predated and the number of days to each predation or fledging event. Regression coefficient (*b*) represents the proportional change in risk of predation for each variable. For example, *b* = 0 means the term has no effect of predation risk while *b* > 0 denotes an increased risk of predation as the variable increases. *N* = 894 watches at 293 nests. Significant values (*P* < 0.05) in bold. Df = 1, 293 for each variable (outlier included) and 1, 292 (outlier excluded). | | | | | |
| Parameter | *b* ± SE | *z* | 𝝌2 | *P* | *P* (excluding outlier) |
| Active synchrony score | -0.404 ± 0.197 | -2.06 | <0.001 | 0.981 | 0.569 |
| IVI SD | 0.033 ± 0.148 | 0.23 | 0.002 | 0.967 | 0.915 |
| Nest helped? | Yes: -0.224 ± 0.345 | -0.65 | 0.42 | 0.516 | 0.519 |
| Brood size | -0.966 ± 0.688 | -1.40 | 1.97 | 0.161 | 0.149 |
| Brood size2 | 1.332 ± 0.665 | 2.00 | 4.01 | **0.045** | **0.037** |
| Watch start time | -0.141 ± 0.147 | -0.96 | 0.92 | 0.338 | 0.374 |
| Maximum possible coordination | 0.265 ± 0.181 | 1.47 | 2.15 | 0.142 | 0.144 |
| Hatch date | 0.184 ± 1.269 | -0.15 | 0.021 | 0.884 | 0.969 |
| Hatch date2 | 0.313 ± 1.247 | 0.25 | 0.063 | 0.802 | 0.880 |
| Brood age | -1.156 ± 0.185 | -6.26 | 39.23 | **<0.001** | **<0.001** |
| Provisioning rate | -0.430 ± 0.230 | -1.87 | 0.71 | 0.400 | 0.476 |
| Active synchrony score \* IVI SD | -0.331 ± 0.128 | -2.59 | 6.73 | **0.010** | 0.154 |
| Active synchrony score \* Provisioning rate | -0.544 ± 0.206 | -2.64 | 6.97 | **0.008** | **0.002** |

Survival analysis revealed a significant effect of the interaction of ‘Active synchrony score’ and ‘Provisioning rate’ on brood survival time (CPHMM: *b* = -0.544, *P* = 0.008, table 5.4, figure 5.4a); the effect of synchrony to prolong nest survival being strongest when provisioning rate was high. This corroborates our earlier finding that synchrony increased brood survival at medium-high provisioning rates. Just as for the predation risk analysis, the interaction of ‘Active synchrony score’ and ‘IVI SD’ was significant when the outlier was included (CPHMM: *b* = -0.331, *P* = 0.010, table 5.4), but not when it was omitted (CPHMM: *b* = -0.173, *P* = 0.154, table 5.4, table S5.15). This would mean that the effect of synchrony to prolong nest survival is more prominent when provisioning rates are more variable. However, this result must again be treated with caution. There was also a significant quadratic effect of brood size on survival (CPHMM: linear *b* = -0.966, quadratic *b* = 1.332, *P* = 0.045, table 5.4, figure 5.4b), with the largest broods typically being predated sooner. As expected, brood age (CPHMM: *b* = -1.156, *P* < 0.001, table 5.4) had a significant effect on survival time because the longer a nest survived, the age at which watches were performed increases. All other terms showed no significant effect on survival time (table 5.4).

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Figure 5.4. Cumulative probability of brood survival versus brood age for (a) nests above average (mean) aggregate provisioning rate and above average (mean) aggregate active synchrony scores (blue; *N* = 151 watches at 38 nests), above average aggregate provisioning rate and below average aggregate active synchrony score (orange; *N* = 339 watches at 98 nests), below average aggregate provisioning rate and above average aggregate active synchrony score (green; *N* = 238 watches at 97 nests) and below average aggregate provisioning rate and below average aggregate active synchrony score (purple; *N* = 166 watches at 60 nests), and (b) nests with equal to or above average (median) brood size (blue; *N* = 482 watches at 159 nests) and nests with below average brood size (orange; *N* = 412 watches at 134 nests).

**5.5 Discussion**

In this study, we used an *a priori* hypothesis-prediction framework to investigate support for three hypotheses for coordinated provisioning in long-tailed tits. First, we found some support for the hypothesis that carers alternate visits to facilitate conflict resolution (i.e. conditional cooperation), because higher active alternation scores were associated with higher total provisioning rate and an increased likelihood that offspring provisioned by cooperative groups (≥ 1 helper) would recruit into the local breeding population. However, higher levels of alternation were not associated with greater offspring mass on day 11 of their development. Second, whilst synchronous provisioning increased offspring recruitment at medium-high provisioning rate cooperative groups, we found no support for the hypothesis that synchronous provisioning improves resource distribution parity among offspring because there was no effect of synchrony on offspring mass or intrabrood mass variation. Finally, our results support the predation hypothesis because at medium-high provisioning rates synchronous provisioning was associated with prolonged brood survival and decreased the likelihood of brood predation. Viewed together, our results suggest that large groups of hard-working, highly coordinated carers experienced the best reproductive outcomes because their offspring were less susceptible to predation and were more likely to recruit into the local breeding population.

Our study broadly corroborated the results of previous long-tailed tit studies, finding that overall provisioning rate increased with brood age and size, decreased throughout the day (as in MacColl and Hatchwell 2003), and was higher in cooperative nests (MacColl and Hatchwell 2003, Hatchwell et al. 2004). Likewise, we found that larger cooperative groups had more offspring recruit locally (MacColl and Hatchwell 2002, McGowan et al. 2003, Hatchwell et al. 2004, 2014) and were not more susceptible to predation than biparental groups (Hatchwell et al. 2004). However, in contrast to previous studies, we detected no effect of helpers or provisioning rate on nestling mass at d11 (c.f. MacColl and Hatchwell 2002, Hatchwell et al. 2004), suggesting that improved nestling condition may not be the primary mechanism by which helpers enhance productivity. There could be several reasons for this. Firstly, we used a larger sample size (185 vs 93 and 129 broods, respectively), which was collected from a single population, whereas Hatchwell et al. (2004) used data from three populations; one of which had a much higher rate of helping than ours (mean helpers per nest; 1.66 vs 3.90), suggesting meaningful differences in breeding ecology that may have also affected nestling mass. Second, helpers may join a nest at any stage of the nestling period, and in many cases do so only shortly before biometric assessment at d11 (mean carer number: D6 = 2.34; D8 = 2.48; D10 = 2.58; D12 = 2.63; D14 = 2.64; D16 = 2.69; *N* = 849). In such instances, there is very little opportunity for additional carers to have a substantial effect on nestling mass. Third, we used different model structures with additional covariates such as active alternation score, provisioning rate parity (‘Maximum possible coordination’), and temporal variation (‘IVI SD’), which all covary with helper number, so may absorb some of the variation previously attributed to helpers. However, by controlling for these effects, we were able to detect several meaningful consequences of coordinated provisioning that are consistent with previous studies of long-tailed tits. For example, we corroborated Bebbington and Hatchwell’s (2016) findings that alternation was positively correlated with provisioning rate but did not influence chick mass, and our result that synchrony reduced predation risk at medium-high provisioning rate nests is consistent with their findings that synchrony reduced near-nest activity and that alternation was negatively correlated with brood failure.

A challenge when investigating the consequences of coordination is accurately quantifying the true levels of behavioural alternation and synchrony performed. Our coordination scores were calculated from the difference between observed and expected coordination (i.e. active coordination), estimated using the most conservative null model approach (Ihle et al. 2019a). The nature of the null model means that these coordination scores are also influenced by other aspects of provisioning such as the number of carers (alternation), overall provisioning rate (synchrony), and temporal provisioning rate variation (both; see figure S5.2), so these effects must be controlled for. This is particularly problematic because the conflict resolution hypothesis (Hypothesis 1) predicts that alternation enables carers to mutually raise their provisioning rate to more closely match the brood’s optimum, which may also result in more consistent provisioning rates. Therefore, more well-coordinated groups may, counterintuitively, have lower coordination scores unless this effect is controlled for. This may explain why Ihle et al. (2019b) found a negative relationship between active alternation score and fledging success in house sparrows, as this may instead result from greater fledging success in broods raised by more consistent carers.

**5.5.1 Hypothesis 1: Alternation facilitates conflict resolution**

Since its conception (Johnstone et al. 2014), the conditional cooperation model for provisioning has received much empirical attention, with many studies testing whether observed levels of alternation were greater than expected by chance (e.g. Ihle et al. 2019a, Lejeune et al. 2019), and/or whether return rate following others’ feeds was faster than following one’s own feed (Johnstone et al. 2014, Savage et al. 2017, Griffioen et al. 2021; but see Enns and Williams 2022). However, these results could also be plausibly explained by uncoordinated carers responding mutually to shared environmental factors (Schlicht et al. 2016, Ihle et al. 2019a, Santema et al. 2019; but see Johnstone et al. 2016). Halliwell et al. (2023a) later demonstrated that long-tailed tit carers actively delayed feeding to facilitate alternation, a behaviour which cannot be explained by common environmental factors. However, whilst prior studies demonstrated that alternation score was positively correlated with provisioning rate (Bebbington and Hatchwell 2016) and chick mass gain (Burdick and Siefferman 2020), no study had identified a positive link between alternation and offspring survival. We corroborated the link between alternation and provisioning rate, and found that overall provisioning rate increased with group provisioning rate parity, suggesting that collective investment was higher when conflict between carers was effectively mitigated. Crucially, we also found that in cooperative groups, alternation scores were positively associated with offspring recruitment rate, an important component of fitness in this species (MacColl and Hatchwell 2004). We believe that this is currently the best evidence that coordination of care, and specifically turn-taking, is an adaptive behaviour that mitigates conflict among carers. However, it is important to note that our study is correlational so we cannot claim a causal relationship between alternation and offspring survival.

Although alternation scores increased provisioning and recruitment rates, we found no effect on offspring mass or fledging success (see supplementary material). Long-tailed tits experience extremely low rates of offspring starvation (0.2% daily; Hatchwell et al. 2004), so unless predated, nearly all chicks fledge (98.5%). Therefore, it is unsurprising that we detected no effect of alternation on fledging success given that this represents an extremely small component of reproductive failure. However, it was surprising that active alternation scores did not influence chick mass given that larger chicks are more likely to recruit locally (MacColl and Hatchwell 2002, Hatchwell et al. 2004). The is probably because offspring mass analysis only used watches prior to biometric assessment (i.e. d6–11), whereas our provisioning rate and recruitment analyses utilised the full range of watches (i.e. d6–16); if the benefits to offspring of alternation primarily occur after d11 then our analysis might not detect this effect. Therefore, it is possible that alternation increases offspring mass gain, as was found in eastern bluebirds (Burdick and Siefferman 2020), but we lacked the data resolution necessary to test this prediction.

**5.5.2 Hypothesis 2: Synchrony increases resource distribution parity**

The hypothesis that synchronous provisioning facilitates efficient food distribution among the brood has received empirical support in several bird species. Coordinated provisioning, in one form or another, increases parity in resource partitioning among a brood (Shen et al. 2010, Mariette and Griffith 2015) and reduces intrabrood mass variation (Lejeune et al. 2019). Why carers coordinate care is likely determined by a combination of their life history traits, ecology, and associated selection pressures. For example, many seabirds temporally coordinate their foraging bouts such that the times between feeding bouts are as short and consistent as possible, thus reducing the risk of offspring starvation (Congdon et al. 2005, Tyson et al. 2017, Wojczulanis-Jakubas et al. 2018). Coordination in these seabirds is constrained by long foraging times and potential starvation of their single chick. In contrast, many other bird species may be selected to mitigate the detrimental effects of intrabrood conflict (e.g. partial brood starvation) by temporally clustering visits (i.e. synchrony). Long-tailed tits have large (median = 9), synchronously hatching broods, so may be expected to suffer high rates of brood reduction and thus intrabrood competition. However, they instead experience extremely low rates of offspring starvation (0.2% daily; Hatchwell et al. 2004); perhaps because optimal parental provisioning effectively limits intrabrood conflict between offspring, e.g. via synchrony. Therefore, it was surprising that we detected no effect of provisioning synchrony on offspring mass or intrabrood mass variation. Although, as discussed, our measures of offspring mass and intrabrood mass variation only used watches from d6–11, so it is possible that synchrony influenced brood mass dynamics after this stage. If so, we would expect the effect of synchrony to increase offspring fitness to be strongest when resources are scarce, e.g. large broods and/or low provisioning rate. However, we found no effect of brood size on chick mass, intrabrood variation, or recruitment rate, and the effect of synchrony to increase recruitment rate was, in fact, stronger at higher provisioning rates. So, although long-tailed tits possess many of the prerequisites for this hypothesis, we found no support for its predictions in our sample of breeding attempts. To investigate this hypothesis further, it would be interesting to experimentally vary temporal food distribution to the chicks and/or investigate the effect of synchrony on chick mass gain over several days.

**5.5.3 Hypothesis 3: Synchrony reduces brood predation risk**

Long-tailed tits also possess many of the prerequisites for the predation hypothesis. They have a short breeding season and although they may build multiple nests, they only attempt to raise one brood per year, despite losing most to predation (72%; Hatchwell et al. 2013). As a result, only a minority of birds achieve any direct fitness (MacColl and Hatchwell 2004), so there should be strong selection for strategies to reduce brood predation, e.g. synchronous provisioning. Bebbington and Hatchwell (2016) found that synchronous provisioning reduced the total time that long-tailed tit carers spent near the nest when provisioning, which can advertise a nest’s location to predators (Skutch 1949, Martin et al. 2000). However, in a previous test of this hypothesis, long-tailed tits did not respond to experimental predator presentation by increasing provisioning coordination (Halliwell et al. 2023b). Here, we found that in broods provisioned at medium-high rates, synchrony was associated with reduced brood predation and prolonged brood survival. Our finding that the effect of synchrony to reduce predation risk increases with provisioning rate makes intuitive sense because as the number of nest visits increases, so does the chance that the brood’s location is advertised to predators. Additionally, we found a significant quadratic effect of brood size on nest survival time, suggesting that the largest broods suffer increased predation risk, which was likely due to increased conspicuousness via begging (Haskell 1994, Briskie et al. 1999). Decreased predation risk was the only significant benefit we detected of coordination for offspring raised biparentally and supports the findings of other studies linking parental coordination to reduced predation risk (Raihani et al. 2010, Bebbington and Hatchwell 2016, Leniowski and Węgrzyn 2018). Viewed together with the findings of a previous experiment (Halliwell et al. 2023b), our results suggest that synchronous provisioning is an antipredator strategy that is performed continuously and at a fixed rate rather than dynamically adjusted in response to changes in perceived predation risk.

**5.5.4 Synthesis**

Long-tailed tits are an excellent model species for investigating coordination of care because their unusual breeding system, life history traits, and ecology impose selection pressures that could select for the evolution of coordination for several independent reasons, whilst ruling out others (e.g. pay-to-stay or prestige). Unlike most cooperative breeders, long-tailed tit helpers are failed breeders, not retained offspring (Kokko et al. 2001, Griesser et al. 2017), so the scope for territory or individual quality effects to covary with group size is extremely limited (Hatchwell 2016). Therefore, any effect of helper number, or its interactions with coordination scores, on offspring fitness is likely to represent a causal effect. However, alternation and synchrony are inherently linked, and one or both may be influenced by other factors such as the number of carers, overall provisioning rate, and temporal provisioning rate variation. This can make identifying the behaviours underpinning coordination and their consequences difficult, so to understand why carers coordinate provisioning, these results should be interpreted inclusively with previous studies of long-tailed tits and coordination of care.

Long-tailed tits exhibit greater than expected levels of synchrony and alternation of provisioning (Bebbington and Hatchwell 2016, Halliwell et al. 2022). Detailed observations of provisioning behaviour by Halliwell et al. (2023a) subsequently showed that synchronous provisioning was facilitated by collective arrivals, and that alternation was facilitated by carers actively delaying feeding if it was not their turn to feed. These findings suggest that alternation and synchrony result from two distinct behaviours. Our results are compatible with this notion and suggest that coordination may serve two independent functions. Firstly, alternation facilitates conflict resolution between carers (Johnstone et al. 2014), particularly in cooperative groups where the potential for conflict is greater (Savage et al. 2017), because higher alternation scores corresponded with faster overall provisioning and higher recruitment rates of offspring from cooperative nests. Previous studies identified offspring condition at fledging as a key component of group productivity that is augmented by helpers (MacColl and Hatchwell 2002, McGowan et al. 2003, Hatchwell et al. 2004, 2014), and our results suggest that conditional cooperation (i.e. alternation) may play an important role enabling helpers to augment the productivity of a group. Although it should be noted that we did not detect any effect of alternation on offspring mass at the midpoint of their development. Secondly, although a previous experimental study found that synchrony was not sensitive to changes in local predation risk (Halliwell et al. 2023b), here we found that more synchronous provisioning was associated with reduced predation risk and prolonged brood survival. In long-tailed tits, collective foraging has been suggested as a mechanism by which synchrony is facilitated, with carers tending to arrive back together, as well as feed together, during synchronised bouts (Halliwell et al. 2023a). Our results are compatible with this idea because collective foraging may facilitate synchronous provisioning, and the associated reduction in time that a brood’s location is advertised to predators (e.g. via offspring begging), while minimising the time carers spend waiting for others. This could explain why more synchronous groups and smaller broods, which are presumably quieter, experienced reduced predation risk. Thus, our results support the notion that alternation and synchrony may co-occur while having independent functions, with coordination broadly facilitated by collective foraging and synchronous returns to the nest, while loitering periods prior to feeding are used to monitor other’s effort and negotiate whose turn it is to feed, thereby preventing exploitation by ensuring that each carer contributes fairly.

Quantifying an empirical effect of collective foraging on group productivity via coordination is challenging because synchrony is fundamentally linked to provisioning rate. However, one can imagine conceptually how collective foraging might aid with conflict resolution between carers. For example, breeders benefit from an extra carer(s) delivering food during their synchronised bouts, while helpers can benefit from augmenting a group’s provisioning rate simply by following others. This reduces the need for helpers to independently gather information about local resource distribution or brood demand and prevents breeders from unilaterally reducing their investment in response to help. Therefore, collective foraging, and associated coordination, could enable helpers to augment the overall productivity of a group without risking disproportionate investment (i.e. exploitation), which might explain why coordination only increased offspring recruitment rates in cooperative groups. Thus, there is support for the role of collective foraging in facilitating efficient provisioning, although the consequences are not limited to foraging behaviours away from the nest because synchronous provisioning reduced brood predation risk at medium-high provisioning rates, probably mediated directly by a reduction in near-nest activity and associated offspring begging (Skutch 1949, Martin et al. 2000, Bebbington and Hatchwell 2016).

**5.5.5 Conclusion**

To our knowledge, this is the first study to demonstrate that coordinated provisioning confers benefits to offspring post-fledging and joins the short list of studies finding that coordination of care reduces brood predation risk (Raihani et al. 2010, Leniowski and Węgrzyn 2018). We found support for the conditional cooperation hypothesis because higher active alternation scores and greater provisioning rate parity corresponded with higher overall provisioning rate and increased recruitment of offspring raised by cooperative groups. Additionally, our results support the predation hypothesis because in medium-high provisioning rate groups, higher active synchrony scores corresponded with less brood predation and prolonged brood survival. However, we found no support for the hypothesis that synchrony facilitates resource distribution parity among offspring because neither offspring mass, nor intrabrood mass variation, were influenced by active synchrony score. Together, these results support the notion that alternation and synchrony co-occur while having independent functions and are consistent with the idea that coordination in long-tailed tits is partly facilitated by collective foraging away from the nest and partly by periods of negotiation prior to provisioning (i.e. loitering periods). Although, questions remain over the precise mechanism by which coordination promotes increased recruitment. Finally, we highlight how each species’ unique ecology and life history shapes their adaptive coordination behaviour(s).

**5.6 Acknowledgements**

We thank all researchers and field technicians who contributed to data collection and Sheffield City Council, Yorkshire Water, Hallamshire Golf Club, and the private residents and landowners of the Rivelin Valley for use of their land. This work was supported by the Natural Environment Research Council (NE/S00713X/1 and NE/R001669/1).

**5.7 Supplementary material**

**5.7.1 Tables**

**Full sample** – all watches with brood size and hatch date known, watch duration ≥ 30 mins, carer number ≥ 2, excluding nests which failed for unknown reasons or were partially predated pre-d6

871 watches

275 nests

**Chick mass sample** – subset of full sample with all chicks masses and tarsus lengths known. Watches pre-d12 only.

466 watches

238 nests

1970 chicks

**Chick mass sample sex known** – subset of chick mass sample, but where all chick sexes were known.

360 watches

185 nests

1533 chicks

**Fledged number sample sex known** – subset of full sample where nests fledged, all chick sexes were known and the number of fledglings was known.

574 watches

170 nests

1334 chicks

**Recruit sample** – subset of full sample where nests fledged and all chick sexes known.

574 watches

170 nests

719 male chicks

**Recruit sample (biparental only)**

331 watches

101 nests

420 male chicks

**Recruit sample (cooperative only)**

243 watches

69 nests

299 male chicks

**Predation sample** – substitute clutch size for brood size for nests predated pre-d11 and omit watches taken after partial predation events.

894 watches

293 nests

**Fledged number** – subset of full sample where nests fledged and the number of fledglings was known.

756 watches

220 nests

1690 chicks

Figure S5.1. Diagram illustrating different subsets of the full data sample used throughout each analysis.

A collage of different colored lines

Description automatically generated with medium confidence

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| Table S5.1. Estimates and *P*-values for fixed effects from analysis of the number of observed (directly from field observation) and expected (generated by null model) alternated feeds. The response variable was the number of alternated feeds per watch. *N* = 871 watches at 275 nests (**full sample**). Significant values (*P* < 0.05) in bold. Df = 1,871 for each variable. | | | |
| Parameter | Estimates ± SE | 𝝌2 | *P* |
| Intercept | 2.547 ± 0.013 |  |  |
| Data type | Observed: 0.097 ± 0.017 | 41.03 | **<0.001** |
| IVI SD | -0.080 ± 0.009 | 42.56 | **<0.001** |
| Helped during watch? | Yes: 0.140 ± 0.020 | 57.62 | **<0.001** |
| Brood size | 0.062 ± 0.037 | 2.82 | 0.093 |
| Brood size2 | -0.031 ± 0.036 | 0.74 | 0.390 |
| Watch duration | 0.187 ± 0.006 | 961.34 | **<0.001** |
| Watch start time | -0.016 ± 0.007 | 6.35 | **0.012** |
| Maximum possible coordination | 0.142 ± 0.009 | 249.35 | **<0.001** |
| Hatch date | -0.014 ± 0.069 | 0.040 | 0.841 |
| Hatch date2 | 0.020 ± 0.070 | 0.085 | 0.771 |
| Brood age | 0.007 ± 0.007 | 1.11 | 0.293 |
| Provisioning rate | 0.330 ± 0.007 | 2207.88 | **<0.001** |
| Data type \* IVI SD | 0.067 ± 0.012 | 31.07 | **<0.001** |
| Data type \* Helped during watch? | Cooperative: -0.048 ± 0.024 | 3.90 | **0.048** |

Figure S5.2. Percentage of observed (orange) and expected (blue): (a) alternated feeds versus the level of mean-adjusted within watch standard deviation in intervisit interval duration (i.e. provisioning rate variation) per watch from the full sample of watches (N = 871 watches at 275 nests), and (b) synchronised feeds versus the level of provisioning rate variation per watch from the full sample of watches (N = 871 watches at 275 nests). Predicted relationships (± 95% CI) are fitted from GLMMs, see tables S5.1 and S5.2.

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| Table S5.2. Estimates and *P-*values for fixed effects from analysis of the number of observed (directly from field observation) and expected (generated by null model) synchronised feeds. The response variable was the number of synchronised feeds per watch. *N* = 871 watches at 275 nests (**full sample**). Significant values (*P* < 0.05) in bold. Df = 1,871 for each variable. | | | |
| Parameter | Estimates ± SE | 𝝌2 | *P* |
| Intercept | 1.833 ± 0.018 |  |  |
| Data type | Observed: 0.224 ± 0.018 | 136.12 | **<0.001** |
| IVI SD | -0.035 ± 0.013 | 0.31 | 0.581 |
| Helped during watch? | Yes: 0.137 ± 0.022 | 37.14 | **<0.001** |
| Brood size | 0.095 ± 0.057 | 2.72 | 0.099 |
| Brood size2 | -0.034 ± 0.055 | 0.39 | 0.531 |
| Watch duration | 0.177 ± 0.009 | 420.20 | **<0.001** |
| Watch start time | -0.018 ± 0.009 | 3.72 | 0.054 |
| Maximum possible coordination | 0.156 ± 0.013 | 141.70 | **<0.001** |
| Hatch date | 0.032 ± 0.106 | 0.09 | 0.764 |
| Hatch date2 | -0.029 ± 0.106 | 0.07 | 0.787 |
| Brood age | 0.022 ± 0.010 | 4.95 | **0.026** |
| Provisioning rate | 0.491 ± 0.012 | 2080.84 | **<0.001** |
| Data type \* IVI SD | 0.071 ± 0.016 | 20.27 | **<0.001** |
| Data type \* Provisioning rate | -0.070 ± 0.013 | 28.36 | **<0.001** |

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| Table S5.3. Estimates and *P-*values for fixed effects from analysis of the effect of alternation on provisioning rate. The response variable was the log-transformed hourly provisioning rate at each watch. *N* = 871 watches at 275 nests (**full sample**). Significant values (*P* < 0.05) in bold. Df = 1,871 for each variable. Corresponding summary table in main text: Table 5.1a. | | | |
| Parameter | Estimates ± SE | 𝝌2 | *P* |
| Intercept | 3.076 ± 0.030 |  |  |
| Active alternation score | 0.032 ± 0.012 | 9.74 | **0.002** |
| IVI SD | 0.006 ± 0.012 | 0.0088 | 0.925 |
| Helped during watch? | Yes: 0.078 ± 0.030 | 5.73 | **0.017** |
| Brood size | 0.162 ± 0.069 | 5.44 | **0.020** |
| Brood size2 | -0.041 ± 0.070 | 0.34 | 0.560 |
| Watch duration | -0.028 ± 0.011 | 5.95 | **0.015** |
| Watch start time | -0.041 ± 0.011 | 14.32 | **<0.001** |
| Maximum possible coordination | 0.067 ± 0.012 | 33.25 | **<0.001** |
| Hatch date | -0.031 ± 0.146 | 0.044 | 0.834 |
| Hatch date2 | -0.010 ± 0.144 | 0.0049 | 0.944 |
| Brood age | 0.138 ± 0.010 | 209.04 | **<0.001** |
| Active alternation score \* IVI SD | -0.013 ± 0.008 | 2.57 | 0.109 |
| Active alternation score \* Helped during watch? | Cooperative: 0.048 ± 0.029 | 2.78 | 0.096 |

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| Table S5.4. Estimates and *P-*values for fixed effects from analysis of the effect of alternation on chick mass. The response variable was the mass of each chick at day 11. *N* = 1533 chicks from 360 watches at 185 nests (**Chick mass sample sex known**). Significant values (*P* < 0.05) in bold. Df = 1,1533 for each variable. Corresponding summary table in main text: Table 5.1b. | | | |
| Parameter | Estimates ± SE | 𝝌2 | *P* |
| Intercept | 7.391 ± 0.039 |  |  |
| Active alternation score (aggregate) | -0.036 ± 0.031 | 1.14 | 0.285 |
| IVI SD (mean) | 0.019 ± 0.029 | 1.39 | 0.238 |
| Nest helped? | Yes: 0.007 ± 0.065 | 0.38 | 0.535 |
| Brood size | 0.029 ± 0.146 | 0.039 | 0.844 |
| Brood size2 | -0.045 ± 0.150 | 0.089 | 0.766 |
| Watch start time (mean) | 0.031 ± 0.025 | 1.58 | 0.208 |
| Maximum possible coordination (mean) | 0.039 ± 0.027 | 2.01 | 0.156 |
| Hatch date | 0.231 ± 0.251 | 0.85 | 0.357 |
| Hatch date2 | -0.169 ± 0.248 | 0.47 | 0.495 |
| Brood age (mean) | 0.034 ± 0.025 | 1.90 | 0.168 |
| Chick sex | Male: 0.147 ± 0.017 | 74.55 | **<0.001** |
| Brood sex ratio | -0.014 ± 0.026 | 0.0012 | 0.973 |
| Tarsus length | 1.426 ± 0.257 | 30.72 | **<0.001** |
| Tarsus length2 | -0.990 ± 0.258 | 14.75 | **<0.001** |
| Provisioning rate (aggregate) | -0.024 ± 0.028 | 0.75 | 0.388 |
| Active alternation score (aggregate) \* IVI SD | -0.035 ± 0.024 | 2.04 | 0.154 |
| Active alternation score (aggregate) \* Nest helped? | Yes: 0.103 ± 0.078 | 1.73 | 0.188 |
| Chick sex \* Brood sex ratio | Male: 0.029 ± 0.019 | 2.41 | 0.120 |

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| Table S5.5. Estimates and *P-*values for fixed effects from analysis of the effect of alternation on male recruitment rate at biparental and cooperative nests. The response variable was the two-column variable representing the number of male chicks which recruited and did not recruit from each nest; this functioned as an analysis of the proportion of chicks recruited. *N* = 719 male chicks from 574 watches at 170 nests (**Recruit sample**). Significant values (*P* < 0.05) in bold. Df = 1,170 for each variable. Corresponding summary table in main text: Table 5.1c. | | | |
| Parameter | Estimates ± SE | 𝝌2 | *P* |
| Intercept | -1.177 ± 0.248 |  |  |
| Active alternation score (aggregate) | -0.340 ± 0.202 | 0.582 | 0.445 |
| IVI SD (mean) | 0.053 ± 0.169 | 0.076 | 0.783 |
| Nest helped? | Yes: -0.162 ± 0.322 | 0.76 | 0.383 |
| Brood size | 1.647 ± 0.129 | 2.13 | 0.144 |
| Brood size2 | -1.552 ± 1.055 | 2.16 | 0.141 |
| Watch start time (mean) | 0.048 ± 0.138 | 0.12 | 0.730 |
| Maximum possible coordination (mean) | 0.375 ± 0.188 | 3.97 | **0.046** |
| Hatch date | 1.002 ± 1.448 | 0.48 | 0.489 |
| Hatch date2 | -1.087 ± 1.453 | 0.56 | 0.454 |
| Brood age (mean) | 0.032 ± 0.150 | 0.045 | 0.831 |
| Brood sex ratio | 0.128 ± 0.145 | 0.78 | 0.376 |
| Provisioning rate (aggregate) | 0.050 ± 0.170 | 0.087 | 0.768 |
| Active alternation score (aggregate) \* IVI SD | -0.022 ± 0.137 | 0.025 | 0.875 |
| Active alternation score (aggregate) \* Nest helped? | Yes: 0.929 ± 0.402 | 5.36 | **0.021** |

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| Table S5.6. Estimates and *P-*values for fixed effects from analysis of the effect of alternation on male recruitment rate at biparental nests. The response variable was the two-column variable representing the number of male chicks which recruited and did not recruit from each nest; this functioned as an analysis of the proportion of chicks recruited. *N* = 420 male chicks from 331 watches at 101 nests (**Recruit sample (biparental only)**). Significant values (*P* < 0.05) in bold. Df = 1,101 for each variable. Corresponding summary table in main text: Table 5.1c. | | | |
| Parameter | Estimates ± SE | 𝝌2 | *P* |
| Intercept | -1.295 ± 0.267 |  |  |
| Active alternation score (aggregate) | -0.401 ± 0.245 | 2.37 | 0.123 |
| IVI SD (mean) | 0.128 ± 0.233 | 0.089 | 0.766 |
| Brood size | 1.156 ± 1.463 | 0.294 | 0.294 |
| Brood size2 | -1.591 ± 1.418 | 0.262 | 0.262 |
| Watch start time (mean) | 0.281 ± 0.176 | 2.55 | 0.110 |
| Maximum possible coordination (mean) | 0.428 ± 0.225 | 3.63 | 0.057 |
| Hatch date | -0.734 ± 2.084 | 0.12 | 0.725 |
| Hatch date2 | 0.490 ± 2.101 | 0.054 | 0.816 |
| Brood age (mean) | -0.041 ± 0.197 | 0.044 | 0.834 |
| Brood sex ratio | 0.160 ± 0.186 | 0.75 | 0.388 |
| Provisioning rate (aggregate) | 0.086 ± 0.219 | 0.16 | 0.693 |
| Active alternation score (aggregate) \* IVI SD | -0.133 ± 0.186 | 0.51 | 0.475 |

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| Table S5.7. Estimates and *P-*values for fixed effects from analysis of the effect of alternation on male recruitment rate at cooperative nests. The response variable was the two-column variable representing the number of male chicks which recruited and did not recruit from each nest; this functioned as an analysis of the proportion of chicks recruited. *N* = 299 male chicks from 243 watches at 69 nests (**Recruit sample (cooperative only)**). Significant values (*P* < 0.05) in bold. Df = 1,69 for each variable. Corresponding summary table in main text: Table 5.1c. | | | |
| Parameter | Estimates ± SE | 𝝌2 | *P* |
| Intercept | -1.521 ± 0.277 |  |  |
| Active alternation score (aggregate) | 0.800 ± 0.293 | 9.09 | **0.003** |
| IVI SD (mean) | -0.295 ± 0.242 | 1.94 | 0.164 |
| Carer number (mean) | 0.554 ± 0.252 | 5.31 | **0.021** |
| Brood size | 1.370 ± 1.911 | 0.51 | 0.473 |
| Brood size2 | -1.009 ± 1.695 | 0.35 | 0.552 |
| Watch start time (mean) | -0.180 ± 0.218 | 0.68 | 0.410 |
| Maximum possible coordination (mean) | -0.130 ± 0.271 | 0.23 | 0.630 |
| Hatch date | 5.559 ± 2.478 | 5.03 | **0.025** |
| Hatch date2 | -5.252 ± 2.468 | 4.53 | **0.033** |
| Brood age (mean) | 0.016 ± 0.235 | 0.0046 | 0.946 |
| Brood sex ratio | 0.201 ± 0.227 | 0.79 | 0.374 |
| Provisioning rate (aggregate) | 0.123 ± 0.250 | 0.24 | 0.622 |
| Active alternation score (aggregate) \* IVI SD | -0.028 ± 0.279 | 0.010 | 0.920 |
| Active alternation score (aggregate) \* Carer number (mean) | -0.083 ± 0.288 | 0.083 | 0.774 |

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| Table S5.8. Estimates and *P-*values for fixed effects from analysis of the effect of synchrony on chick mass, applied to the dataset with and without the inclusion of the outlier where ‘Active synchrony score’ was < -1.8. The response variable was the mass of each chick at day 11. *N* = 1533 chicks from 360 watches at 185 nests (**Chick mass sample sex known**). Significant values (*P* < 0.05) in bold. Df = 1,1533 for each variable (outlier included) and 1,1524 (outlier excluded). Corresponding summary table in main text: Table 5.2a. | | | | |
| Parameter | Estimates ± SE | 𝝌2 | *P* (including outlier) | *P* (excluding outlier) |
| Intercept | 7.362 ± 0.040 |  |  |  |
| Active synchrony score (aggregate) | -0.010 ± 0.032 | 0.096 | 0.757 | 0.797 |
| IVI SD (mean) | -0.042 ± 0.027 | 2.87 | 0.090 | 0.101 |
| Nest helped? | Yes: -0.014 ± 0.062 | 0.21 | 0.650 | 0.669 |
| Brood size | -0.104 ± 0.150 | 0.48 | 0.488 | 0.513 |
| Brood size2 | 0.021 ± 0.155 | 0.18 | 0.895 | 0.919 |
| Watch start time (mean) | 0.034 ± 0.025 | 1.80 | 0.180 | 0.184 |
| Maximum possible coordination (mean) | 0.034 ± 0.028 | 1.51 | 0.219 | 0.219 |
| Hatch date | 0.151 ± 0.265 | 0.32 | 0.569 | 0.557 |
| Hatch date2 | -0.087 ± 0.263 | 0.11 | 0.739 | 0.726 |
| Brood age (mean) | 0.035 ± 0.025 | 1.89 | 0.169 | 0.167 |
| Chick sex | Male: 0.147 ± 0.017 | 74.51 | **<0.001** | **<0.001** |
| Brood sex ratio | -0.026 ± 0.026 | 0.18 | 0.670 | 0.647 |
| Tarsus length | 1.418 ± 0.017 | 30.37 | **<0.001** | **<0.001** |
| Tarsus length2 | -0.983 ± 0.258 | 14.53 | **<0.001** | **<0.001** |
| Provisioning rate (aggregate) | -0.011 ± 0.031 | 0.019 | 0.891 | 0.884 |
| Active synchrony score (aggregate) \* IVI SD | -0.015 ± 0.024 | 0.523 | 0.523 | 0.771 |
| Active synchrony score (aggregate) \* Provisioning rate | -0.021 ± 0.030 | 0.494 | 0.494 | 0.480 |
| Active synchrony score (aggregate) \* Nest helped? | Yes: 0.084 ± 0.080 | 0.295 | 0.295 | 0.299 |
| Chick sex \* Brood sex ratio | Male: 0.030 ± 0.019 | 0.103 | 0.103 | 0.097 |

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| Table S5.9. Estimates and *P-*values for fixed effects from analysis of the effect of synchrony on intrabrood chick mass variation, applied to the dataset with and without the inclusion of the outlier where ‘Active synchrony score’ was < -1.8. The response variable was the log-transformed intrabrood standard deviation in chick mass. of each chick at day 11 *N* = 1533 chicks from 360 watches at 185 nests (**Chick mass sample sex known**). Significant values (*P* < 0.05) in bold. Df = 1,1533 for each variable (outlier included) and 1,1524 (outlier excluded). | | | | |
| Parameter | Estimates ± SE | 𝝌2 | *P* (including outlier) | *P* (excluding outlier) |
| Intercept | -1.077 ± 0.045 |  |  |  |
| Active synchrony score (aggregate) | 0.037 ± 0.042 | 0.048 | 0.826 | 0.815 |
| IVI SD (mean) | -0.021 ± 0.034 | 0.051 | 0.821 | 0.742 |
| Nest helped? | Yes: 0.045 ± 0.080 | 0.32 | 0.569 | 0.551 |
| Brood size | 0.307 ± 0.215 | 2.05 | 0.152 | 0.163 |
| Brood size2 | -0.257 ± 0.212 | 1.47 | 0.226 | 0.237 |
| Watch start time (mean) | -0.019 ± 0.033 | 0.33 | 0.563 | 0.564 |
| Maximum possible coordination (mean) | -0.027 ± 0.036 | 0.59 | 0.443 | 0.452 |
| Hatch date | -0.451 ± 0.337 | 1.79 | 0.181 | 0.181 |
| Hatch date2 | -0.257 ± 0.212 | 2.61 | 0.106 | 0.107 |
| Brood age (mean) | -0.043 ± 0.034 | 1.63 | 0.202 | 0.197 |
| Brood sex ratio | -0.001 ± 0.032 | 0.0009 | 0.976 | 0.988 |
| Provisioning rate (aggregate) | 0.017 ± 0.040 | 0.094 | 0.760 | 0.728 |
| Active synchrony score (aggregate) \* IVI SD | 0.070 ± 0.031 | 5.21 | **0.022** | 0.153 |
| Active synchrony score (aggregate) \* Provisioning rate | 0.090 ± 0.041 | 4.87 | **0.027** | **0.031** |
| Active synchrony score (aggregate) \* Nest helped | Yes: 0.003 ± 0.108 | 0.0006 | 0.981 | 0.981 |

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| Table S5.10. Estimates and *P-*values for fixed effects from analysis of the effect of synchrony on intrabrood chick mass variation. The response variable was the log-transformed intrabrood standard deviation in chick mass. *N* = 1970 chicks from 466 watches at 238 nests (**Chick mass sample**). Significant values (*P* < 0.05) in bold. Df = 1,1970 for each variable. Corresponding summary table in main text: Table 5.2b. | | | |
| Parameter | Estimates ± SE | 𝝌2 | *P* |
| Intercept | -1.061 ± 0.037 |  |  |
| Active synchrony score (aggregate) | 0.021 ± 0.036 | 0.0015 | 0.969 |
| IVI SD (mean) | -0.008 ± 0.030 | <0.001 | 0.978 |
| Nest helped? | Yes: 0.012 ± 0.067 | 0.061 | 0.805 |
| Brood size | 0.012 ± 0.165 | 0.0053 | 0.942 |
| Brood size2 | 0.040 ± 0.164 | 0.060 | 0.807 |
| Watch start time (mean) | -0.015 ± 0.028 | 0.28 | 0.596 |
| Maximum possible coordination (mean) | -0.034 ± 0.030 | 1.23 | 0.268 |
| Hatch date | -0.478 ± 0.275 | 3.03 | 0.082 |
| Hatch date2 | 0.576 ± 0.274 | 4.41 | **0.036** |
| Brood age (mean) | -0.042 ± 0.280 | 2.26 | 0.133 |
| Provisioning rate (aggregate) | -0.004 ± 0.035 | 0.20 | 0.656 |
| Active synchrony score (aggregate) \* IVI SD | 0.033 ± 0.027 | 1.57 | 0.210 |
| Active synchrony score (aggregate) \* Provisioning rate | 0.026 ± 0.034 | 0.60 | 0.437 |
| Active synchrony score (aggregate) \* Nest helped? | Yes: -0.026 ± 0.088 | 0.085 | 0.770 |

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| Table S5.11. Estimates and *P-*values for fixed effects from analysis of the effect of synchrony on male recruitment rate at biparental and cooperative nests, applied to the dataset with and without the inclusion of the outlier where ‘Active synchrony score’ was < -1.8. The response variable was the two-column variable representing the number of male chicks which recruited and did not recruit from each nest; this functioned as an analysis of the proportion of chicks recruited. *N* = 719 male chicks from 574 watches at 170 nests (**Recruit sample**). Significant values (*P* < 0.05) in bold. Df = 1,170 for each variable (outlier included) and 1, 169 (outlier excluded). Corresponding summary table in main text: Table 5.2c. | | | | |
| Parameter | Estimates ± SE | 𝝌2 | *P* (including outlier) | *P* (excluding outlier) |
| Intercept | -1.263 ± 0.240 |  |  |  |
| Active synchrony score (aggregate) | 0.278 ± 0.251 | 0.044 | 0.833 | 0.919 |
| IVI SD (mean) | -0.091 ± 0.145 | 0.26 | 0.608 | 0.607 |
| Nest helped? | Yes: -0.165 ± 0.313 | 0.25 | 0.619 | 0.590 |
| Brood size | 1.171 ± 1.074 | 1.19 | 0.276 | 0.260 |
| Brood size2 | -1.193 ± 1.009 | 1.40 | 0.237 | 0.222 |
| Watch start time (mean) | 0.024 ± 0.136 | 0.031 | 0.861 | 0.837 |
| Maximum possible coordination (mean) | 0.239 ± 0.180 | 1.77 | 0.184 | 0.181 |
| Hatch date | 0.507 ± 1.461 | 0.12 | 0.729 | 0.670 |
| Hatch date2 | -0.691 ± 1.464 | 0.22 | 0.637 | 0.585 |
| Brood age (mean) | 0.050 ± 0.151 | 0.11 | 0.739 | 0.680 |
| Brood sex ratio | 0.176 ± 0.147 | 1.43 | 0.231 | 0.259 |
| Provisioning rate (aggregate) | 0.160 ± 0.181 | 0.32 | 0.575 | 0.607 |
| Active synchrony score (aggregate) \* IVI SD | 0.088 ± 0.148 | 0.35 | 0.553 | 0.434 |
| Active synchrony score (aggregate) \* Provisioning rate | 0.334 ± 0.219 | 2.33 | 0.127 | 0.149 |
| Active alternation score (aggregate) \* Nest helped? | Yes: -0.116 ± 0.493 | 0.056 | 0.814 | 0.997 |

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| Table S5.12. Estimates and *P-*values for fixed effects from analysis of the effect of synchrony on male recruitment rate at cooperative nests. The response variable was the two-column variable representing the number of male chicks which recruited and did not recruit from each nest; this functioned as an analysis of the proportion of chicks recruited. *N* = 299 male chicks from 243 watches at 69 nests (**Recruit sample (cooperative only)**). Significant values (*P* < 0.05) in bold. Df = 1,69 for each variable. Corresponding summary table in main text: Table 5.2c. | | | |
| Parameter | Estimates ± SE | 𝝌2 | *P* |
| Intercept | -1.141 ± 0.258 |  |  |
| Active synchrony score (aggregate) | 0.683 ± 0.311 | 1.18 | 0.277 |
| IVI SD (mean) | -0.161 ± 0.195 | 0.69 | 0.407 |
| Carer number (mean) | 0.578 ± 0.234 | 6.11 | **0.013** |
| Brood size | 0.657 ± 1.510 | 0.19 | 0.664 |
| Brood size2 | -0.597 ± 1.356 | 0.19 | 0.660 |
| Watch start time (mean) | -0.215 ± 0.200 | 1.15 | 0.284 |
| Maximum possible coordination (mean) | -0.293 ± 0.242 | 1.46 | 0.226 |
| Hatch date | 4.783 ± 2.465 | 3.77 | 0.052 |
| Hatch date2 | -4.907 ± 2.523 | 3.78 | 0.052 |
| Brood age (mean) | -0.017 ± 0.210 | 0.0066 | 0.935 |
| Brood sex ratio | 0.099 ± 0.224 | 0.20 | 0.658 |
| Provisioning rate (aggregate) | 0.614 ± 0.267 | 1.79 | 0.181 |
| Active synchrony score (aggregate) \* IVI SD | -0.025 ± 0.253 | 0.0097 | 0.921 |
| Active synchrony score (aggregate) \* Provisioning rate | 0.717 ± 0.320 | 5.02 | **0.025** |
| Active synchrony score (aggregate) \* Carer number (mean) | -0.010 ± 0.205 | 0.0023 | 0.962 |

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| Table S5.13. Estimates and *P-*values for fixed effects from analysis of the effect of synchrony on male recruitment rate at biparental nests, applied to the dataset with and without the inclusion of the outlier where ‘Active synchrony score’ was < -1.8. The response variable was the two-column variable representing the number of male chicks which recruited and did not recruit from each nest; this functioned as an analysis of the proportion of chicks recruited. *N* = 420 male chicks from 331 watches at 101 nests (**Recruit sample (biparental only)**). Significant values (*P* < 0.05) in bold. Df = 1,101 for each variable (outlier included) and 1, 100 (outlier excluded). Corresponding summary table in main text: Table 5.2c. | | | | |
| Parameter | Estimates ± SE | 𝝌2 | *P* (including outlier) | *P* (excluding outlier) |
| Intercept | -1.314 ± 0.271 |  |  |  |
| Active synchrony score (aggregate) | 0.268 ± 0.336 | <0.001 | 0.993 | 0.711 |
| IVI SD (mean) | -0.207 ± 0.187 | 1.02 | 0.312 | 0.327 |
| Brood size | 1.686 ± 1.485 | 1.29 | 0.256 | 0.220 |
| Brood size2 | -1.834 ± 1.433 | 1.64 | 0.201 | 0.171 |
| Watch start time (mean) | 0.267 ± 0.176 | 2.30 | 0.130 | 0.127 |
| Maximum possible coordination (mean) | 0.340 ± 0.217 | 2.45 | 0.117 | 0.116 |
| Hatch date | -1.827 ± 2.087 | 0.77 | 0.381 | 0.455 |
| Hatch date2 | 1.492 ± 2.097 | 0.51 | 0.477 | 0.554 |
| Brood age (mean) | 0.044 ± 0.204 | 0.047 | 0.829 | 0.754 |
| Brood sex ratio | 0.245 ± 0.192 | 1.62 | 0.203 | 0.282 |
| Provisioning rate (aggregate) | 0.109 ± 0.230 | 0.11 | 0.744 | 0.818 |
| Active synchrony score (aggregate) \* IVI SD | 0.102 ± 0.216 | 0.23 | 0.635 | 0.472 |
| Active synchrony score (aggregate) \* Provisioning rate | 0.399 ± 0.315 | 1.60 | 0.206 | 0.223 |

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| Table S5.14. Effect of active synchrony score and associated interaction terms on the probability of brood predation, applied to the dataset without the outlier where synchrony was <-1.8. The response variable was the binary factor denoting whether a brood fledged without predation (0) or was predated (1). *N* = 893 watches at 292 nests. Significant values (*P* < 0.05) in bold. Df = 1,292 for each variable. | | | |
| Parameter | Estimates ± SE | 𝝌2 | *P* |
| Intercept | -1.980 ± 0.454 |  |  |
| Active synchrony score (aggregate) | -0.566 ± 0.311 | 0.025 | 0.875 |
| IVI SD (mean) | -0.084 ± 0.185 | 0.19 | 0.666 |
| Nest helped? | Yes: -0.090 ± 0.441 | 0.042 | 0.838 |
| Brood size | -1.098 ± 0.880 | 1.56 | 0.212 |
| Brood size2 | 1.393 ± 0.885 | 2.48 | 0.116 |
| Watch start time (mean) | -0.034 ± 0.184 | 0.035 | 0.852 |
| Maximum possible coordination (mean) | 0.281 ± 0.220 | 1.63 | 0.202 |
| Hatch date | -0.669 ± 1.772 | 0.14 | 0.706 |
| Hatch date2 | 0.631 ± 1.755 | 0.13 | 0.719 |
| Brood age (mean) | -1.271 ± 0.295 | 18.52 | **<0.001** |
| Provisioning rate (aggregate) | -0.575 ± 0.319 | 0.11 | 0.735 |
| Active synchrony score (aggregate) \* IVI SD | -0.233 ± 0.156 | 2.24 | 0.135 |
| Active synchrony score (aggregate) \* Provisioning rate | -0.662 ± 0.265 | 6.25 | **0.012** |

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| Table S5.15. Effect of active synchrony score and associated interaction terms the risk of brood predation over time, applied to the dataset without the inclusion of the outlier where ‘Active synchrony score’ was < -1.8. The response variable was a two-column variable denoting whether a nest was predated and the number of days to each predation or fledging event. Regression coefficient (*b*) represents the proportional change in risk of predation for each variable. For example, *b* = 0 means the term has no effect of predation risk while *b* > 0 denotes an increased risk of predation as the variable increases. Significant values (*P* < 0.05) in bold. Df = 1,292 for each variable. | | | | |
| Parameter | *b* ± SE | *z* | 𝝌2 | P |
| Active synchrony score | -0.590 ± 0.231 | -2.55 | 0.32 | 0.569 |
| IVI SD | 0.000 ± 0.149 | 0.00 | 0.012 | 0.915 |
| Nest helped? | Yes: -0.227 ± 0.352 | -0.65 | 0.42 | 0.519 |
| Brood size | -1.001 ± 0.693 | -1.44 | 2.09 | 0.149 |
| Brood size2 | 1.402 ± 0.672 | 2.09 | 4.36 | **0.037** |
| Watch start time | -0.132 ± 0.148 | -0.89 | 0.79 | 0.374 |
| Maximum possible coordination | 0.263 ± 0.189 | 1.46 | 2.14 | 0.144 |
| Hatch date | -0.050 ± 1.293 | -0.04 | 0.0015 | 0.969 |
| Hatch date2 | 0.192 ± 1.273 | 0.15 | 0.023 | 0.880 |
| Brood age | -1.127 ± 0.186 | -6.07 | 36.85 | **<0.001** |
| Provisioning rate | -0.576 ± 0.253 | -2.27 | 0.51 | 0.476 |
| Active synchrony score \* IVI SD | -0.173 ± 0.121 | -1.43 | 2.03 | 0.154 |
| Active synchrony score \* Provisioning rate | -0.581 ± 0.192 | -3.02 | 9.15 | **0.002** |

**5.7.2 Fledging success**

**Methods**

Nests were checked daily as broods approached fledging (d16–18). If a nest was empty and there were no signs of damage, the number of fledglings was assumed equal to the brood size at d11. If one or more dead chicks remained in the nest this number was subtracted from the number of successful fledglings. When a nest was damaged, suggesting brood predation, the number of fledglings was confirmed by locating the fledged brood. Using this approach, we recorded the number of chicks which successfully fledged (median = 9; range 1–12; *N* = 220) and failed to fledge (median = 0, range 0–5; *N* = 220), then calculated the proportion of the brood which successfully fledged from each successful nest (mean = 0.985 ± 0.00587 SE; *N* = 220).

Despite large brood sizes (median = 9), long-tailed tits experience extremely low rates of chick starvation (0.2% daily starvation rate per chick; Hatchwell et al. 2004), so it is unlikely there will be any systematic effect of coordination on the proportion of chicks fledged from broods aside from via predation. Nonetheless, we built a binomially distributed GLMM to investigate the relationship between active alternation score and the proportion of a brood which successfully fledged initially using a subset of watches from nests which fledged without partial depredation where the number of fledglings and the sex of each chick was known (**Fledged number sample sex known**; *N* = 574 watches at 170 nests containing 1334 chicks). The response variable was a two-column variable (number fledged, number not fledged), which functions as a measure of proportion fledged (Mean = 0.987 ± 0.00538 SE; *N* = 170). Explanatory terms of interest were ‘Aggregate active alternation score’ and its interaction with ‘Nest helped?’. Additional fixed effect covariates were ‘Brood size’ (linear and quadratic), ‘Mean watch start time’, ‘Mean maximum possible coordination’, ‘Hatch date’ (linear and quadratic), ‘Mean brood age’, ‘Brood sex ratio’, ‘Aggregate provisioning rate’, ‘Mean IVI SD’, and its interaction with ‘Aggregate active alternation score’. Random effects were ‘Year’, ‘Pair ID’, ‘Female ID’, and ‘Male ID’. The term ‘Brood sex ratio’ was ultimately found not to be significant in the model, so we fitted another model without this term on a larger sample of watches where all chick sexes were not necessarily known (**Fledged number sample**; *N* = 756 watches at 220 nests containing 1690 chicks). We report this model’s outputs in our final analysis.

To examine whether synchronous feeding visits were associated with higher fledging success, we fitted a binomially distributed GLMM with the same structure as for alternation but with ‘Aggregate active synchrony score’ instead of alternation and the interaction of ‘Aggregate active synchrony score’ and ‘Aggregate provisioning rate’ as an additional fixed effect of interest. The term ‘Brood sex ratio’ did not influence fledging success significantly, so the model was applied to the same data subset as alternation where chick sexes weren’t necessarily known (**Fledged number sample**; *N* = 756 watches at 220 nests containing 1690 chicks).

**Results**

*Alternation*

Offspring starvation is rare in long-tailed tits and accounts for a very small component of reproductive failure, so we considered it unlikely that provisioning coordination would systematically influence partial brood failure in non-predated nests. Unsurprisingly, we found no significant effect of ‘Active alternation score’ (GLMM: *P* = 0.230, table S5.17, figure S5.3a) or any other biologically relevant term on the proportion of a brood which successfully fledged (table S5.17).

*Synchrony*

As expected, we found no significant effect of ‘Active synchrony score’ (GLMM: *P* = 0.913, table S5.19, figure S5.3b) or its interaction with ‘Provisioning rate’ (GLMM: *P* = 0.456, table S5.19). No other biologically relevant terms significantly influenced fledging success (supplementary material table S5.19), corroborating our earlier findings from the alternation model.

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| Table S5.16. Estimates and *P-*values for fixed effects from analysis of the effect of alternation on fledging success. The response variable was the two-column variable representing the number of chicks which fledged and did not fledge from each nest; this functioned as an analysis of the proportion of chicks which fledged. *N* = 1334 chicks from 574 watches at 170 nests (**Fledged number sample sex known**). Significant values (*P* < 0.05) in bold. Df = 1,170 for each variable. | | | |
| Parameter | Estimates ± SE | 𝝌2 | *P* |
| Intercept | 11.627 ± 6.661 |  |  |
| Active alternation score (aggregate) | 0.179 ± 1.050 | 0.0066 | 0.935 |
| IVI SD (mean) | 0.949 ± 0.905 | 1.00 | 0.318 |
| Nest helped? | Yes: 4.257 ± 6.639 | 0.45 | 0.504 |
| Brood size | -2.080 ± 4.165 | 0.25 | 0.618 |
| Brood size2 | 1.963 ± 4.449 | 0.19 | 0.659 |
| Watch start time (mean) | 0.377 ± 0.607 | 0.39 | 0.535 |
| Maximum possible coordination (mean) | -0.126 ± 0.654 | 0.037 | 0.847 |
| Hatch date | -13.344 ± 21.927 | 0.37 | 0.543 |
| Hatch date2 | 13.282 ± 22.593 | 0.35 | 0.557 |
| Brood age (mean) | 1.115 ± 1.085 | 1.06 | 0.304 |
| Brood sex ratio | 0.163 ± 0.870 | 0.035 | 0.851 |
| Provisioning rate (aggregate) | 0.627 ± 1.239 | 0.26 | 0.613 |
| Active alternation score (aggregate) \* IVI SD | 0.454 ± 1.007 | 0.20 | 0.652 |
| Active alternation score (aggregate) \* Nest helped? | Yes: 1.724 ± 4.905 | 0.12 | 0.725 |

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| Table S5.17. Estimates and *P-*values for fixed effects from analysis of the effect of alternation on fledging success. The response variable was the two-column variable representing the number of chicks which fledged and did not fledge from each nest; this functioned as an analysis of the proportion of chicks which fledged.  *N* = 1690 chicks from 756 watches at 220 nests (**Fledged number sample**). Significant values (*P* < 0.05) in bold. Df = 1,220 for each variable. Corresponding summary table in main text: Table 5.1c. | | | |
| Parameter | Estimates ± SE | 𝝌2 | *P* |
| Intercept | 16.045 ± 5.564 |  |  |
| Active alternation score (aggregate) | 0.240 ± 0.863 | 1.44 | 0.230 |
| IVI SD (mean) | 1.196 ± 0.949 | 1.65 | 0.198 |
| Nest helped? | Yes: 1.380 ± 2.364 | 1.20 | 0.273 |
| Brood size | -3.659 ± 3.858 | 0.90 | 0.343 |
| Brood size2 | 2.962 ± 3.906 | 0.58 | 0.448 |
| Watch start time (mean) | 0.588 ± 0.498 | 1.40 | 0.237 |
| Maximum possible coordination (mean) | -0.412 ± 0.614 | 0.45 | 0.502 |
| Hatch date | -27.461 ± 17.291 | 2.52 | 0.112 |
| Hatch date2 | 26.907 ± 17.587 | 2.34 | 0.126 |
| Brood age (mean) | 2.028 ± 0.963 | 4.43 | **0.035** |
| Provisioning rate (aggregate) | 1.033 ± 1.193 | 0.75 | 0.387 |
| Active alternation score (aggregate) \* IVI SD | 0.425 ± 0.731 | 0.34 | 0.561 |
| Active alternation score (aggregate) \* Nest helped? | Yes: -3.306 ± 2.134 | 2.40 | 0.121 |

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| Table S5.18. Estimates and *P-*values for fixed effects from analysis of the effect of synchrony on fledging success, applied to the dataset with and without the inclusion of the outlier where ‘Active synchrony score’ was < -1.8. The response variable was the two-column variable representing the number of chicks which fledged and did not fledge from each nest; this functioned as an analysis of the proportion of chicks which fledged. *N* = 1334 chicks from 574 watches at 170 nests (**Fledged number sample sex known**). Significant values (*P* < 0.05) in bold. Df = 1,170 for each variable (outlier included) and 1,169 (outlier excluded). | | | | |
| Parameter | Estimates ± SE | 𝝌2 | *P* (including outlier) | *P* (excluding outlier) |
| Intercept | 17.175 ± 16.268 |  |  |  |
| Active synchrony score (aggregate) | 2.830 ± 6.546 | 0.012 | 0.913 | 0.562 |
| IVI SD (mean) | 1.147 ± 1.444 | 0.44 | 0.509 | 0.284 |
| Nest helped? | Yes: 2.878 ± 3.660 | 0.62 | 0.431 | 0.547 |
| Brood size | -3.753 ± 5.817 | 0.42 | 0.519 | 0.351 |
| Brood size2 | 3.303 ± 5.491 | 0.36 | 0.548 | 0.418 |
| Watch start time (mean) | 0.804 ± 1.374 | 0.34 | 0.559 | 0.391 |
| Maximum possible coordination (mean) | -0.312 ± 0.792 | 0.16 | 0.693 | 0.898 |
| Hatch date | -31.952 ± 47.758 | 0.45 | 0.504 | 0.213 |
| Hatch date2 | 32.348 ± 49.205 | 0.43 | 0.511 | 0.231 |
| Brood age (mean) | 1.823 ± 2.355 | 0.60 | 0.439 | 0.229 |
| Brood sex ratio | 0.368 ± 1.097 | 0.11 | 0.737 | 0.519 |
| Provisioning rate (aggregate) | 1.953 ± 3.689 | 0.18 | 0.669 | 0.580 |
| Active synchrony score (aggregate) \* IVI SD | 1.465 ± 3.314 | 0.20 | 0.659 | 0.966 |
| Active synchrony score (aggregate) \* Provisioning rate | 1.540 ± 4.136 | 0.14 | 0.710 | 0.240 |
| Active synchrony score (aggregate) \* Nest helped? | Yes: 2.308 ± 9.911 | 0.054 | 0.816 | 0.852 |

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| Table S5.19. Estimates and *P-*values for fixed effects from analysis of the effect of synchrony on fledging success. The response variable was the two-column variable representing the number of chicks which fledged and did not fledge from each nest; this functioned as an analysis of the proportion of chicks which fledged. *N* = 1690 chicks from 756 watches at 220 nests (**Fledged number sample**). Significant values (*P* < 0.05) in bold. Df = 1,220 for each variable. Corresponding summary table in main text: Table 5.2c. | | | |
| Parameter | Estimates ± SE | 𝝌2 | *P* |
| Intercept | 15.112 ± 4.844 |  |  |
| Active synchrony score (aggregate) | 0.944 ± 1.243 | 0.012 | 0.913 |
| IVI SD (mean) | 0.988 ± 0.923 | 1.24 | 0.266 |
| Nest helped? | Yes: 5.817 ± 3.315 | 1.07 | 0.300 |
| Brood size | -1.155 ± 4.637 | 0.65 | 0.803 |
| Brood size2 | 0.277 ± 4.686 | 0.0035 | 0.953 |
| Watch start time (mean) | 0.378 ± 0.469 | 0.65 | 0.421 |
| Maximum possible coordination (mean) | -0.600 ± 0.581 | 1.07 | 0.302 |
| Hatch date | -12.616 ± 9.983 | 1.60 | 0.206 |
| Hatch date2 | 10.518 ± 9.267 | 1.29 | 0.256 |
| Brood age (mean) | 2.173 ± 1.010 | 4.63 | 0.315 |
| Provisioning rate (aggregate) | 1.027 ± 1.161 | 0.39 | 0.534 |
| Active synchrony score (aggregate) \* IVI SD | 0.606 ± 0.769 | 0.62 | 0.431 |
| Active synchrony score (aggregate) \* Provisioning rate | 1.095 ± 1.468 | 0.46 | 0.456 |
| Active synchrony score (aggregate) \* Nest helped? | Yes: -4.618 ± 3.258 | 2.01 | 0.156 |

*A comparison of a graph

Description automatically generated with medium confidence*

Figure S5.3. Proportion of a brood which fledged versus aggregate active (a) alternation score and (b) synchrony score per nest from a subsample of nests which fledged without any recorded predation (N = 756 watches at 2022 nests containing 1690 chicks). Data points were translucent, so overlapping data points results in darker shades. Predicted relationships (± 95% CI) are fitted from GLMMs, see tables S5.17 (a) and S5.19 (b)).

**6. General discussion**

**6.1 Introduction**

Parental care is beneficial to offspring (Trivers 1974, Godfray 1995, Hinde et al. 2010), but costly to carers (Clutton-Brock 1991, Stearns 1992), so unless lifelong monogamous breeders, carers are in conflict over their relative investment in shared broods (Trivers 1972, Westneat and Sargent 1996). This conflict, and the associated threat of exploitation, could lead to carers delivering sub-optimal investment to their offspring (Royle et al. 2002a, McNamara et al. 2003). To resolve this conflict, carers may engage in conditional cooperation when provisioning, with each carer monitoring the nest visits of others and adjusting their provisioning behaviour accordingly, leading to a form of coordinated provisioning where carers take turns feeding the offspring (i.e. alternation; Johnstone et al. 2014). This is hypothesised to prevent potential exploitation and enable carers to more closely achieve their optimal level of investment.

In cooperative breeders, where helpers assist with raising relatives’ offspring, conditional cooperation may limit the extent to which breeders can reduce investment in response to help (Savage et al. 2017). Crucially, this enables helpers to augment the productivity of a relative’s breeding attempt, rather than simply replacing their investment. Additionally, parental care may confer risk to offspring, such as advertising a brood’s location to predators (Skutch 1949, Martin et al. 2000), and the relative timing of provisioning may also influence the benefits of investment; so, when multiple carers raise the same brood, coordinated provisioning may enable carers to achieve a higher benefit-to-cost ratio from their investment. Carers are hypothesised to coordinate provisioning via synchrony (i.e. feeding together) to reduce the risk of predation (Sargent 1993), increase efficiency of resource distribution (Shen et al. 2010), and/or to signal their contribution to others. The latter case, in which helpers signal their effort either to retain group membership (pay-to-stay; Gaston 1978, Kokko et al. 2002) or to signal their quality to potential mates (prestige; Zahavi 1977a,b), only applies when helpers derive direct benefits from others observing their investment. In this thesis, I studied the provisioning behaviour of facultative cooperatively breeding long-tailed tits, *Aegithalos caudatus*, which are thought to derive only indirect fitness benefits of helping (Hatchwell 2016); so, the signalling hypothesis is not applicable, and I instead focus my investigation on the other hypotheses for coordination of care.

Despite much empirical attention, no study had yet demonstrated conclusive evidence of conditional cooperation in provisioning birds, as many of the findings that seemingly support this hypothesis could be plausibly explained by passive processes (Schlicht et al. 2016, Ihle et al. 2019a, Santema et al. 2019). Furthermore, support for the adaptive functions of synchrony is mixed, with some demonstrating that synchronous provisioning reduced the risk of offspring predation (e.g. Raihani et al. 2010, Leniowski and Węgrzyn 2018), and others finding that it may reduce the costs of sibling-sibling competition (e.g. Shen et al. 2010, Mariette and Griffith 2012, 2015). However, many studies have failed to support these hypotheses (e.g. van Rooij and Griffith 2013, Ihle et al. 2019b), suggesting that the function of coordinated provisioning differs between species. Additionally, nest visit synchrony may serve no specific function for broods, but may instead result from other adaptive behaviours, such as collective foraging. In this thesis, I investigated provisioning coordination in long-tailed tits; particularly whether, how, and why carers alternate and/or synchronise their provisioning. Using this framework, I examined support for several mutually compatible hypothesised functions of coordination and sought to identify the proximate mechanisms by which coordination may be facilitated.

**6.2 Summary of results**

The first aim of my thesis was to determine whether carers provisioned in certain patterns, suggesting coordination. So, in chapter 2 I used a long-term database (1994–2019) of provisioning watches to determine whether carers alternated and synchronised more than expected by chance. Carers significantly exceeded their expected level of alternation, but only in groups of two and three carers, as ‘active’ alternation (observed minus expected) decreased with group size. Carers synchronised significantly more than expected by chance across the full range of group sizes (2–5), but the level of active synchrony decreased with group provisioning rate, as more feeds inherently occurred within the synchrony window by chance. Additionally, helpers performed the most active synchrony, followed by breeding males, then females. Because multiple watches were taken at each nest, and there were several instances of carers provisioning at multiple nests within and between years, I was able to quantify the repeatability of coordination; finding that alternation was significantly repeatable within multiple watches of the same nest, while synchrony was repeatable between multiple watches of the same carer across multiple nests. Finally, contrary to expectations, there was no effect of a helper’s relatedness to either breeder on their levels of active alternation or synchrony.

Although carers outperformed their expected alternation and synchrony, due to potential limitations of the null model, this alone was not definitive evidence of true behavioural coordination of care. So, in chapter 3 I designed and applied a novel provisioning watch protocol at 23 long-tailed tit nests. During these watches I recorded the time that each carer arrived in the proximity of nests (15m) and the time they each fed. Further, I increased the resolution of these data by recording time to the nearest second instead of to the minute. Using these detailed observations, I investigated the mechanisms by which alternation and synchrony may be facilitated. Crucially, I found that when a carer arrived back to the nest area having fed the brood last, they waited for longer and were more likely to allow another carer to feed before them, thereby actively avoiding consecutive feeds and ensuring conditional cooperation. I also found that carers synchronised their arrivals as often as they synchronised their feeds, and thus had highly overlapped loitering periods, suggesting that synchronous provisioning was facilitated by collective returns to the nest area. Next, I analysed the order of arrivals and feeds within synchronous bouts for groups of two and three carers, finding that breeding females usually led returns to the nest, followed by males, with helpers returning last. However, this consistent arrival order was not reflected in feed order, possibly due to sample size limitations. Finally, the breeding pair synchronised together more than expected given their provisioning rates, though helpers showed no consistent active preference for synchronising with either breeder.

In chapter 4, I tested whether carers increased synchrony in response to experimentally elevated local predation risk using a predator presentation experiment at 22 long-tailed tit nests during a critical stage of their development. I compared the provisioning dynamics between control watches and watches following presentation of a predatory (Eurasian jay, *Garrulus glandarius*) and non-predatory model bird (rock dove, *Columba livia*). Carers recognised the model predator as a threat, as most birds did not provision during its presentation, and took significantly longer to resume provisioning following the removal of the predator than the non-predator. However, contrary to predictions of the hypothesis that coordination serves to reduce brood predation risk, carers did not increase coordination following predator presentation, but instead increased the time they spent loitering prior to provisioning, thus increasing overall near-nest activity. Interestingly, the levels of alternation were significantly lower in the first section of a watch in all treatments, suggesting that disturbance, such as from model presentation or experimental set up, upset the regular patterns of provisioning and that carers are most able to conditionally cooperate when undisturbed.

The aim of chapter 5 was to investigate the effect of alternation and synchrony on reproductive success, so I tested key predictions of certain hypotheses using long-term provisioning watch and offspring survival data (1994–2022). I used the same null model approach as before to calculate ‘active coordination scores’ for alternation and synchrony at each nest. Testing the conditional cooperation hypothesis, I found that active alternation scores were positively correlated with a group’s overall provisioning rate and the rate of offspring recruitment in cooperative groups, though there was no significant effect on offspring mass or starvation. Testing predictions of the predation hypothesis, I found that at medium-high provisioning rates, higher active synchrony scores were associated with reduced predation and prolonged nest survival. Finally, I found no support for the intrabrood conflict hypothesis, as synchrony had no significant effect of offspring mass, intrabrood mass variation, or offspring starvation.

**6.3 Implications and future direction**

**6.3.1 Conditional cooperation hypothesis**

Conditional cooperation has been proposed as a mechanism by which ultimately selfish individuals can stably and efficiently cooperate to raise shared offspring (Johnstone et al. 2014). Unlike previous uncoordinated negotiation-based models (e.g. McNamara et al. 1999), this hypothesis explains why a number of empirical studies have found that carers matched experimental changes in their partner’s provisioning rate (e.g. Hinde 2006), including long-tailed tits (Meade et al. 2011). A key aim of this thesis was to identify whether carers take turns feeding the brood (i.e. alternation). In chapter 2, I demonstrated that carers alternated more than expected by chance. However, this finding alone is not definitive evidence of conditional cooperation, as highlighted in critiques of empirical evidence for alternation (Schlicht et al. 2016, Ihle et al. 2019a, Santema et al. 2019). Interestingly, the level of active alternation appeared to decrease with group size, with observed alternation being greater than expected only in groups of two and three carers, though the overall level of alternation increased with carer number. Initially, it was not known whether this represented an adaptive reduction in alternation in large groups or resulted from a loss of power by the null model as expected alternation approached saturation (>90%) in large groups. To my knowledge, only one study had previously applied this null model to a cooperative breeder. Savage et al. (2017) found that level of active alternation by chestnut crowned babblers, *Pomatostomus ruficeps*, was greater than expected by chance across the full range of group sizes (2–6), although their level of expected alternation was lower in large groups than ours (80% vs 90%). However, my finding that alternation was associated with increased offspring recruitment only in cooperative groups suggests that conditional cooperation may confer benefits even when observed alternation is not greater than expected by chance. This highlights a limitation of highly conservative null model approaches for identifying coordination and suggests that the reduction in active alternation with group size is probably a result of the null model losing power in large groups.

The conditional cooperation hypothesis predicts that well-coordinated groups should more closely achieve their optimal level of investment, to the benefit of their offspring. My finding that alternation scores were associated with increased provisioning and more offspring recruitment in cooperative groups (chapter 5), an important component of fitness in long-tailed tits (Hatchwell et al. 2014), therefore strongly support this hypothesis. However, given that previous studies of long-tailed tits found positive relationships between provisioning rate and offspring mass (MacColl and Hatchwell 2002), and between offspring mass and recruitment rate (Hatchwell et al. 2004), I had expected that the benefits of conditional cooperation would be mediated by an increase in offspring mass. Therefore, it was surprising that there was no observed effect of alternation on offspring mass at day 11 (chapter 5). This discrepancy could have been caused by different model structures and/or sample compositions, though given that a significant effect of alternation on recruitment success was observed only in cooperative nests, it is also possible that the benefits of conditional cooperation occurred after day 11, when helping was more common. In future, it would be interesting to record offspring mass and size at several points throughout development to investigate the effect of alternation and group size on offspring mass gain to determine the relative importance of coordination and/or helpers at different stages of development.

As discussed, conditional cooperation could facilitate conflict resolution between pairs of breeders and/or between breeders and helpers, as alternation may limit the extent to which breeders can reduce investment in response to help, allowing helpers to augment group productivity (Crick 1992, Hatchwell 1999). Therefore, it is unsurprising that fledglings from well-coordinated groups were more likely to recruit than those from uncoordinated groups. However, it is interesting that conditional cooperation appeared to only benefit offspring raised by cooperative groups (i.e. parents and helpers), especially given the wealth of studies reporting greater than expected alternation in biparental species (e.g. Johnstone et al. 2014, Lejeune et al. 2019) and that alternation corresponded with an increased provisioning rate at biparental nests, here (chapter 5) and previously (Bebbington and Hatchwell 2016). Perhaps this phenomenon is unique to the unusual redirected helping system of long-tailed tits, where cooperative groups of carers have higher productivity than pairs alone. If well-coordinated pairs are more likely to receive help, this would contribute to cooperative groups’ advantage and mask a potential effect of alternation on reproductive success at unhelped nests. Given that conditional cooperation may enable helpers to increase group productivity, and thus their payoffs, rather than just replacing a breeder’s investment, there may be an incentive for helpers to join well-coordinated pairs and groups. In support of this, Sturrock et al. (2022) found that helpers preferred to join groups that were already being helped. Whilst it can be difficult to distinguish the effects of coordination and group size, it would be interesting to test whether helpers show an active preference for joining well-coordinated groups.

I believe the most compelling support for conditional cooperation to date comes from my fine-scale investigation of the mechanisms by which coordination is facilitated (chapter 3). I showed that carers actively waited near the nest for others to feed if it was not their turn to feed, thus ensuring turn-taking and preventing exploitation. Unlike faster return rates following another carer or greater than expected alternation (e.g. Savage et al. 2017, Griffioen et al. 2021), this cannot be plausibly explained by refractory periods or temporal autocorrelation. Thus, I showed for the first time that carers behave in a condition dependent manner that actively facilitates alternation. Along with my findings that alternation benefits offspring fitness, these demonstrate strong empirical support for the conditional cooperation hypothesis in cooperatively breeding long-tailed tits. Given the variety of avian breeding systems, and the substantial interspecies variation in their responses to experimental changes in their partner’s provisioning rates (Harrison et al. 2009), it would be interesting to apply these approaches to other bird species, particularly those that breed in closed populations (e.g. Seychelles warbler, *Acrocephalus sechellensis*; Komdeur and Richardson 2007), as their lifetime reproductive success can be precisely and fully quantified.

Conditional cooperation is hypothesised to resolve conflict between carers; therefore, one would expect alternation to be higher when intercarer conflict was stronger (e.g. shared paternity, variably related helpers). So, it was surprising that there was no effect of helper relatedness on alternation (chapter 2), especially given that helpers’ decisions in who to help and how much to invest are influenced by relatedness to the brood (Nam et al. 2010, Leedale et al. 2020b). However, alternation was significantly repeatable between multiple watches of the same nest, suggesting that it was determined by some feature of the breeding pair or group overall. For example, if a breeding pair is more alert to helpers potentially shirking their duties, they may be more likely to wait near the nest for the helper to feed, so fine-scale investment differences between variably related helpers may have limited power to influence the overall level of alternation. Nonetheless, it would be interesting to investigate the relative level of alternation between differentially invested pairs and/or groups of carers, whether naturally occurring or experimentally induced. For example, when pairs exhibit variation in the share of paternity by the social male (e.g. superb fairywrens, *Malurus cyaneus*; Colombelli-Négrel 2009) or when helpers facultatively co-breed with the dominant pair (e.g. Seychelles warblers).

An important prerequisite for conditional cooperation is that carers reliably observe their partners’ nest visits. Thus, synchronous nest visits have been hypothesised to facilitate alternation, and the two coordination behaviours are often associated (e.g. Bebbington and Hatchwell 2016, Leniowski and Węgrzyn 2018). I found that carers highly synchronised their arrivals resulting in a high level of overlap, and that these shared loitering periods enabled carers to negotiate whose turn it is to feed (chapter 3); supporting the notion that that synchronous nest visits play an important role in facilitating conditional cooperation.

**6.3.2 Predation hypothesis**

Long-tailed tits suffer extremely high rates of nest predation, with 72% of all clutches and broods being lost to predators such as corvids and mustelids (Hatchwell et al. 2013), so there should be a strong selection pressure for behaviours that reduce the risk and/or cost of brood predation. There is some evidence for an antipredator function of synchronous nest visits in birds (Raihani et al. 2010, Leniwoski and Węgrzyn 2018, Khwaja et al. 2019), including long-tailed tits, where synchrony was associated with reduced near-nest activity per food delivered (Bebbington and Hatchwell 2016). Throughout this thesis, I conducted analyses which either explicitly tested the predictions of this hypothesis or allowed for inferences about why carers synchronised their feeds. Carers synchronised their arrivals and feeds more than was expected by chance, the degree of active synchrony was greater than for alternation, and unlike alternation, occurred across the full range of carer numbers (chapters 2 and 3). However, it is still possible that this resulted from shared environmental factors, and simply demonstrating that carers synchronise visits is not definitive evidence of an adaptive function, as it could plausibly result from another adaptive behaviour, such as collective foraging.

In an explicit test of this hypothesis, I found that at medium-high provisioning rates increased synchrony was associated with reduced predation and prolonged brood survival (chapter 5). Unlike conditional cooperation, this benefit was observed in both biparental and cooperative breeding groups and was the only beneficial consequence of coordination at unhelped nests. The fact that this effect was stronger at faster provisioning rates also supports this hypothesis, as more provisioning increases the risk of advertising a nest’s location to predators, and thus the importance of synchrony. However, there are also several key findings from this thesis which question this hypothesis. If synchrony is an antipredator behaviour, one might expect carers to synchronise more when the risk of predation is higher. For example, I found that larger broods were more likely to suffer predation (chapter 5), likely due to their increased conspicuousness from offspring begging, but were not provisioned more synchronously (chapter 2).

Perhaps most surprisingly, in an experimental test of this hypothesis, carers did not adjust their synchrony in response to elevated predation risk, despite making dynamic adjustments to their provisioning rate and loitering behaviour prior to feeding (chapter 4). This suggests that although synchrony confers reduced brood predation risk, carers appear to lack the behavioural flexibility to adjust it in response to predator sightings. There are several potential explanations for this; firstly, long-tailed tits could experience a near-constant brood predation threat, so always aim to maximise their synchrony; however, this offers no explanation for the other dynamic adjustments in provisioning in response to predators. Secondly, carers may vary in their degree of risk aversion, so bolder carers would resume provisioning sooner than timid ones, temporarily limiting the ability of carers to synchronise their nest visits. This idea is supported by the finding that alternation was reduced in the first section of a watch following a period of disturbance (chapter 4), suggesting that disturbances, such as a predator nearby, upset the typical rhythm of coordination. However, the level of synchrony was not significantly reduced in the first section of a watch following disturbance (chapter 4), as would be expected if this were the case. Finally, and most likely, carers may facilitate synchrony by foraging collectively, which could confer additional benefits away from the nest, so there may be no advantage to carers reducing synchrony when predation risk is low. Note that this explanation is still compatible with the notion that nest visit synchrony reduces predation risk (chapter 5).

Collective foraging is also the most parsimonious explanation for several other findings of this thesis, including that carers synchronise arrivals as often as feeding visits, and that helpers, who tend to arrive back last during synchronous bouts, exhibit the most active synchrony. Therefore, whilst my findings support the antipredator function of synchronous provisioning, they also suggest that this behaviour is facilitated by collective foraging, which could also confer another independent function (e.g. increased foraging efficiency or reduced risk of adult predation; Beauchamp 1998, Sorato et al. 2012). Nonetheless, it would be interesting to repeat my chapter 4 experiment: i) with a larger sample, ii) with different models (e.g. mustelid), and iii) on a different species. Additionally, it would be interesting to experimentally manipulate brood size or begging intensity (e.g. via playback) to determine whether carers’ synchrony is truly unresponsive to changes in their perceived brood predation risk. It is possible that carers’ loitering times increased following predator presentation due to increased vigilance, which could reduce predation risk if nest locations are more likely to be advertised by feeding visits directly rather than simply near-nest activity (Skutch 1949), or if carers issue alarm calls instructing chicks to stop begging (Greig-Smith 1980, Knight and Temple 1986), though these explanations are purely speculative.

**6.3.3 Intrabrood conflict hypothesis**

Synchronous provisioning has also been hypothesised to facilitate a more efficient distribution of resources among offspring in a brood. Several studies have found support for this hypothesis, with coordination in one form or another being associated with reduced mass and/or quality variation within a brood (Shen et al. 2010, Lejeune et al. 2019). All organisms are under selection to optimise their own lifetime fitness, even at the expense of their relatives, so if a chick can achieve greater fitness by improving their own condition than they would from indirect kin produced by their sibling, then this ultra selfish behaviour will be favoured (Hamilton 1964). However, parents are usually equally related to each offspring, so should favour a distribution of resources that maximises the total fitness of the brood (Trivers 1974, Godfray 1995). Therefore, if the monopolisation of resources by certain chicks increases the risk of maladaptive brood reduction, then parents may be selected to provision synchronously, as this could limit the ability of competitive chicks to monopolise resources, thereby limiting brood reduction and allowing carers to successfully rear larger broods to fledging.

Long-tailed tits have particularly large, synchronously hatching broods (median 9), and remarkably low rates of offspring starvation (0.2% daily; Hatchwell et al. 2004), suggesting that they may be reducing the costs of intrabrood conflict by provisioning synchronously. If so, I would expect synchrony to be most prominent when this conflict is strongest, such as when broods are large, and groups of carers are small. However, there was no observable effect of brood or group size on active synchrony (chapter 2). Additionally, in an explicit test of this hypothesis there was no significant effect of synchrony on offspring mass, intrabrood mass variation, or offspring starvation rate (chapter 5), so this hypothesis was not supported in this species. There was a significant positive relationship between synchrony and offspring recruitment at medium-high provisioning rate cooperative groups; though, this was likely the result of other factors such as collective foraging rather than a direct result of mitigated intrabrood conflict. To further test this hypothesis, it could be informative to experimentally vary intrabrood conflict, either by manipulating brood size or food distribution among offspring and record its effect on offspring starvation, mass, and intrabrood mass variation.

**6.3.4 Synthesis**

It is clear from the wealth of empirical studies of coordination of care that different bird species vary in how and why they coordinate their provisioning, and that coordination is shaped by their breeding systems, environments, and associated selection pressures. For example, subordinate female carrion crows, *Corvus corone*,who help others to pay for group membership, actively synchronised their visits with dominant breeders (Trapote et al. 2021), while long-tailed tits, seeking to avoid costly overinvestment, synchronised their arrivals and used the time near the nest to negotiate fair investment via turn-taking (chapter 3). Given that the largest barrier to long-tailed tit reproductive success is brood predation (MacColl and Hatchwell 2004), it is unsurprising that their coordination centred around reducing the risk of brood predation and enabling productive redirected investment by helpers whose own nests were destroyed.

It can be difficult to disentangle alternation and synchrony, especially as synchrony is hypothesised to facilitate alternation (Bebbington and Hatchwell 2016). Nevertheless, in this thesis I have identified several functions of coordinated provisioning, with alternation playing an important role in conflict resolution and synchrony limiting the risk of advertising a brood’s location to predators, in addition to facilitating accurate monitoring for alternation. The most parsimonious explanation for these findings is that coordination of care is largely facilitated by collective foraging. For example, arrivals to the nest area were synchronised as often as feeding visits themselves, allowing for a high degree of loitering period overlap which carers used to negotiate accurate turn-taking. While females generally led returns to the nest in both biparental and cooperative groups (chapter 3). Breeding females are typically the most well-informed about brood demand and, along with the breeding male, have more experience foraging near the nest than helpers, so it makes sense that they lead foraging trips. Further, there is some evidence that females lead coordinated foraging trips in great tits, *Parus major* (Baldan 2019). If this arrival order were also reflected in feed order it could explain why helpers exhibited the highest levels of active synchrony (chapter 2) as, by the definition of synchrony used in this thesis, the first feed within a bout was not necessarily considered synchronous, but all subsequent feeds were. Analysis of a small sample of synchronised bouts did not identify a significant conserved feed order (chapter 3), but the finding that helpers performed the most active synchrony came from a large sample of 795 provisioning watches (chapter 2), whereas the feed order analysis was performed on just 73 watches (chapter 3). Applying this analysis to a larger sample of watches may reveal a significant conserved feed order. Alternatively, the higher levels of synchrony by helpers could be a consequence of helpers being more likely to take part in large-party synchronous bouts, whereas the breeding pair maybe more often participate in small-party bouts (i.e. a pair) as they preferentially synchronise together in cooperative groups (chapter 3). If carers do not feed in a conserved order, then during isolated synchronous bouts each has a 50% chance of performing a synchronised feed as part of a pair, a 66.7% chance in a trio, 75% in a quartet, and so on. If helpers are more likely to participate in large party bouts, as suggested by chapter 3, then on average they will appear more synchronous.

Synchronous provisioning with a conserved feed order inherently leads to alternation of provisioning visits, so could facilitate conditional cooperation without the need for carers to keep track of who was last to feed. Whilst this could explain a certain degree of active alternation, particularly in large groups, it cannot explain why carers actively wait near the nest for another carer to feed before them if it was not their turn to feed. Thus, conditional cooperation in long-tailed tits appears to be driven by collective foraging, with imperfections that may arise during provisioning being corrected by fine-scale adjustments during synchronous bouts. This idea is also compatible with the theory that synchronous provisioning is an antipredator behaviour, though the order in which carers feed should not affect the likelihood of advertising a brood’s location to predators; in fact, time spent negotiating whose turn it is to feed could result in more near-nest activity and thus increased predation risk (Skutch 1949, Martin et al. 2000). Therefore, carers may face a trade-off between the benefits of conditional cooperation (i.e. increased productivity) and synchrony (i.e. reduced predation risk). Alternation and synchrony seem to confer mutually compatible benefits and are both at least partly facilitated by collective foraging. My results suggest that large groups of highly coordinated carers experienced the best reproductive outcomes, as their offspring: i) received more (allo)parental investment, ii) were less susceptible to predation, and iii) were more likely to recruit into the local breeding population.

I suggest that future studies of coordinated care should broaden their focus to investigate the behaviours of carers away from the nest (e.g. collective foraging), and their role in facilitating optimal parental investment via provisioning (e.g. Baldan and van Loon 2022). For example, it would be interesting to use radio-tracking, or some other means, to quantify the degree of spatio-temporal proximity and group cohesion by foraging carers, and its role in facilitating coordinated provisioning. Additionally, it would be interesting to investigate foraging dynamics in flocks to determine whether carers form coordinated sub-groups and selectively breed with compatible partners (Schuett et al. 2011), and/or whether carers also coordinate nest building, as this may be a useful mechanism by which pairs build trust and cohesion prior to the critical provisioning stage (Royle et al. 2010).

**6.4 Conclusion**

In conclusion, the results of my thesis support the hypothesis that conditional cooperation facilitates conflict resolution between groups of cooperative long-tailed tits, with greater alternation associated with increased productivity, and carers actively delaying feeding near the nest to facilitate turn-taking. In addition to facilitating conditional cooperation, nest visit synchrony also reduces the risk of brood predation in both pairs and groups of carers, though carers did not dynamically adjust their synchrony in response to elevated predation risk. This may be because collective foraging also confers other benefits, such as increased foraging efficiency or reduced carer predation risk, although identification of these is beyond the scope of my thesis. In future, I suggest that researchers focus their attention on the consequences of coordination, and potentially coordinated behaviours away from the nest (e.g. collective foraging) and outwith the typical provisioning periods (e.g. nest building) to further understand the nature of coordinated parental investment.

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