# The Costs and Benefits of Coordination During Provisioning in Eurasian Blue Tits, *Cyanistes caeruleus*

By

Rosie Irwin Holbrey

This thesis is submitted for the degree of MSc by Research

November 2021

Supervised by Dr Ian Hartley

Lancaster Environment Centre

Lancaster University

# Abstract

Sexual conflict over parental investment in offspring occurs in species with biparental care due to the shared benefits but individual costs of care, such that the optimum level of investment for an individual is less than that of its partner. Sexual conflict can result in costs for offspring, but a recent theoretical model suggests that parents might reduce such costs via conditional cooperation in the form of turn-taking (alternation) during provisioning. Various empirical studies have found evidence supporting this model. In addition, provisioning synchrony is thought to be related to alternation, perhaps facilitating alternation by enabling partner monitoring. Whether these behaviours are adaptive is not yet fully understood, with studies calling for more research into the fitness consequences of these behaviours. As a result, this thesis explored potential costs and benefits for alternation and synchrony in blue tits, *Cyanistes caeruleus*, using 6 years of breeding and provisioning data. This study is the first to find evidence for benefits of alternation, finding that alternation predicts indicators of reproductive success. In addition, alternation was found to be predicted by brood size. Finally, this study found evidence for sex-specific costs of alternation, finding increased mortality in females that showed high alternation, while this trend did not occur males. These results provide novel insights into the costs and benefits of alternation, an important step in understanding whether this behaviour is adaptive.

# Table of Contents

# Acknowledgements

Firstly, I would like to thank Dr Ian Hartley for his supervision, advice and support throughout this project. I would also like to thank the members of the CEEDS use-R group for their help and support on my journey to learn how to program in R - they made the journey much easier. Thanks to Dr James Savage for advice on methods and coding for this project. Finally, I thank my partner Dave for his limitless support and encouragement throughout my degrees.

# Author’s Declaration

I declare that this thesis is my own work and has not been submitted in substantially the same form for the award of a higher degree elsewhere.

Word count: 15349

# Introduction: Sex Differences, Conflict and Patterns in Parental Care

## Introduction

Parental care refers to parental traits that enhance the fitness of a parent's offspring (Clutton-Brock, 1991; Royle *et al.*, 2012). Patterns of parental care vary widely between species - Cockburn (2006) specified 6 distinct modes of care: cooperative breeding, biparental care, female-only care, male-only care, brood parasitism and geothermal incubation. Parents provide care for offspring in diverse ways – from selecting an ideal site to lay eggs (Refsnider and Janzen, 2010), to providing food (Clutton-Brock, 1991; Royle *et al.*, 2012), to defending offspring from predators (Lima, 2009) and more. The study of parental care is vital to many other fields of research, given that parental care influences a wide range of phenomena including sexual selection, life-history evolution, sociality, conflict, genetics and phenotypic plasticity (Royle *et al.*, 2012). Much parental care research aims to understand how sex differences in providing care arise (Trivers, 1972; Kokko and Jennions, 2008; Alonzo, 2010; Kokko and Jennions, 2012), how sexual conflict arises and is resolved (Trivers, 1972; Houston and Davies, 1985; McNamara *et al.*, 1999; Lessells, 2012) and what patterns of care arise as a result (Clutton-Brock, 1991; McNamara *et al.*, 1999; Reynolds *et al.*, 2002; Johnstone *et al.*, 2014).

Over the past 60 years, parental care has become central in evolutionary biology research (Royle *et al.*, 2012). This topic has become so well-established in ecology and evolution due to a number of key innovations, as explained by Royle *et al*. (2012): Hamilton (1964) incorporated the idea of kin selection to evolutionary ideas, Lack (1968) highlighted the relationship between ecology, life-history and parental care patterns of organisms, Wilson (1971) recognised that certain ecological condition can favour the evolution of parental care, Trivers (1972) connected parental care, parental investment and sexual selection, and Maynard Smith (1977) pioneered using evolutionary game theory to study the evolution of parental care and family conflicts. Trivers in particular generated a wave of research on sexual selection and parental investment (Royle *et al.*, 2012). Since Clutton-Brock's widely cited book on parental care (Clutton-Brock, 1991), parental care research has become a focal topic in behavioural and evolutionary biology, with many key advances and concepts coming into fruition in the past 30 years (Royle *et al.*, 2012).

This literature review will explore the major findings and gaps in research of parental care. This will cover the extensive research around the evolution of sex differences in parental care, highlighting some of the diverse factors that lead to sex differences and different modes of care. Additionally, the key theories surrounding sexual conflict and its resolution will be investigated, plus the mixed empirical evidence for these. This review will then explore recent theories and research into coordinated behaviours during parental care, which are receiving growing attention as a useful behavioural strategy for increasing offspring fitness and decreasing the costs of sexual conflict. Finally, this review will highlight the key research gaps in current studies and provide an outline of plans for future research, which will be conducted in the subsequent chapters of this thesis.

## Sex Differences in Parental Care

Across taxa, there are sex differences in behaviour where females are more likely to provide care for offspring and males are more likely to compete for mates. Much research has centred around studying how this asymmetry evolves and what it means for the life history of males and females. Early research suggested that there is a direct link between gamete investment and care, as females initially invest more in their gametes than males, so are more likely to provide care (Trivers, 1972). This suggests that there is a direct link between anisogamy and which sex provides care. However, it has since been shown that past investment does not directly drive sex differences in future investment – i.e. females should not continue to invest highly in offspring just because they have already done so (Dawkins and Carlisle, 1976; Kokko and Jennions, 2008). Anisogamy alone does not lead to sex role divergence, but increases the likelihood of this occurring when other factors come into play (Kokko and Jennions, 2008). Recent theoretical research supports the view that anisogamy favours a higher probability of females developing parental care and males investing in reproductive competition (Fromhage and Jennions, 2016; Lehtonen *et al.*, 2016; Clutton-Brock, 2017). Anisogamy is a driving force in sex role divergence, but other factors must be in play for such divergence to occur.

Sex differences in the costs and benefits of care influence sex role divergence. For example, the certainty of parentage may differ between the sexes, which influences the benefits of caring for each sex and thus which sex is more likely to provide care or desert offspring. Extra-pair paternity is common, particularly in birds, so a male may only father a portion of the brood. Theoretically, females have a higher certainty of parentage than males, so females have higher potential benefits of caring for that brood (Queller, 1997; Kokko and Jennions, 2012). However, Alonzo (2010) notes that empirical evidence for a positive relationship between certainty of paternity and paternal care is mixed, with some studies having found this relationship (Møller and Birkhead, 1993; Sheldon and Ellegren, 1998; Møller and Cuervo, 2000; Hunt and Simmons, 2002; DiSciullo *et al.*, 2019) and others finding no relationship (Peterson *et al.*, 2001; Dickinson, 2003; Sakaluk and Müller, 2008). Additionally, a negative relationship has been found in beetles (Hopwood *et al.*, 2015) and wrasses (Alonzo and Heckman, 2010). Poor assumptions may explain the mixed evidence for this relationship, such as assuming that males have information about certainty of paternity, or that there is a trade-off between paternal investment in the current brood vs investment in future broods (Westneat and Sargent, 1996; Alonzo, 2010; Schrader *et al.*, 2020). The relationship between confidence of paternity and paternal care is in fact rather complex (Alonzo and Klug, 2012).

Assuming that males may decrease care in response to decreased paternity, researchers have been surprised that females mate multiple times if it might reduce paternal care (Alonzo, 2010). Extra-pair copulations (EPCs) may occur if females gain indirect benefits from remating that outweigh the cost of losing paternal care (Birkhead and Møller, 1996; Gowaty, 1996). There may be little need for male care – extrapair paternity has been found to be more frequent in bird species where males have a minor role in care (Møller, 2000). Females may also have EPCs to insure against infertile mates (Wetton and Parkin, 1991; Sheldon, 1994) or unattractive partners (Birkhead and Møller, 1992). Alonzo (2010) also suggests that males may not necessarily decrease their parental effort when there is extra-pair paternity, given the mixed evidence for this.

The proportion of each sex in the population is also an important factor in sex differences in parental care. The proportion of each sex is expressed in various ways in the literature: the adult sex ratio (ASR) refers to the proportion of adult males in the adult population, but the operational sex ratio (OSR) refers to the ratio of sexually available males to females (Emlen and Oring, 1977). Much study has gone into understanding the influence of sex ratios on reproductive behaviour, mainly focusing on the OSR (McNamara *et al.*, 2000; Kokko and Jennions, 2008; Székely *et al.*, 2014). Only recently have the differences between the ASR and OSR been teased apart - while intrinsically linked, the ASR and OSR can have different effects on sex role evolution (Kokko and Jennions, 2008). The OSR, for example, varies much more than the ASR because males and females shift between states of being sexually active and sexually unavailable (time-in and time-out) (Clutton-Brock and Parker, 1992; Alonzo, 2010).

Each sex is more likely to be polygamous when the ASR is biased towards the opposite sex – males are more likely to be polygamous when the ASR is female-biased, and vice-versa (Liker *et al.*, 2013; Liker *et al.*, 2014). Many models have shown that greater male care is favoured when the OSR is male-biased, and the same pattern occurs for females (Houston and McNamara, 2002; Kokko and Jennions, 2008). A biased OSR can result in frequency-dependent selection for increased parental investment in the sex facing stronger competition for mates (i.e., the most common sex), as it becomes more beneficial to care for current offspring when the chances of remating are low, due to fewer available mates (Queller, 1997; Kokko and Jennions, 2008). However, there is mixed evidence for increased care from the more common sex – experimental manipulation of sex ratios in cichlid fish, *Herotilapia multispinosa,* found that males were more likely to abandon their mates when the sex ratio was female-biased, but females did not abandon mates, regardless of the sex ratio (Keenleyside, 1983). In zebra finches, *Taeniopygia guttata*, males increased parental care under a male-biased sex ratio more than under female-biased sex ratio, but female care behaviour did not change in response to the sex ratio (Burley and Calkins, 1999). However, the predicted pattern has been observed in shorebirds (Liker *et al.*, 2013).

Sex differences in care can also arise as a result of one sex being subject to stronger sexual selection, such that they can re-mate faster, so it is more costly to provide care than to remate (Trivers, 1972; Queller, 1997; Kokko and Jennions, 2008). The higher variance in male mating success compared to female success increases the costs of providing care (Queller, 1997). This, along with potential costs of mixed paternity in the brood, favours less male care (Queller, 1997; Klug *et al.*, 2012). However, as previously mentioned, the relationship between male care and paternity is complex and evidence is mixed (Alonzo, 2010). Additionally, male-only care has been found in various species with high extra-pair paternity and high variation in male mating success (Brennan and Hyseni, 2008; Farmer and Alonzo, 2008; Brennan, 2010). This could be explained by female mate choice – if females bias mating efforts towards caring males, this inter-sexual selection may favour male care (Alonzo, 2012).

Sex differences in care arise due to a wide range of factors, some of which are yet to be fully understood. Anisogamy was once thought to directly drive sex differences in reproductive behaviour, but this has since been disproven (Kokko and Jennions, 2008). While anisogamy is a driving force, other factors must be involved for sex roles to diverge. These factors include the costs and benefits of caring vs remating, certainty of parentage, adult and operational sex ratios, sexual competition and mate choice. There are complex interactions between these factors that influence the evolution of sex roles and different care patterns. There is mixed evidence for some of these factors, such that the extent of their influence on sex roles is yet to be understood and will require further research. Factors influencing sex differences can also interact with sexual conflict, as a result of divergent interests between males and females. Understanding the causes and consequences of sexual conflict is also vital for understand patterns of parental care.

## Sexual Conflict

Sexual conflict is broadly defined as “a conflict between the evolutionary interests of individuals of the two sexes” (Parker, 1979). Sexual conflict can occur in two main ways: (i) when the optimal value of a trait differs between the sexes (Chapman *et al.*, 2003) and (ii) when there is conflict over the outcome of a male-female interaction (Rice and Holland, 1997). It can occur over any aspect of reproduction, such as whether to mate, to provide care to offspring, or how much to invest in offspring (Lessells, 2012). Parental investment is defined as “any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence of reproductive success) at the cost of the parent's ability to invest in other offspring” (Trivers, 1972). Sexual conflict over parental investment arises because the benefits of investment are shared, but each parent pays the cost of their own contribution, so a parent’s optimum level of investment is less than that of its partner, which results in sexual conflict (Trivers, 1972; Lessells, 2012). The extent of sexual conflict can be measured as the difference between the two optimum values of the trait under conflict, referred to as the “battleground” (Godfray, 1995), or by how far each sex’s fitness is below the trait’s optimum value, referred to as the “conflict load” (Lessells, 2006).

Research on sexual conflict primarily focuses on what the evolutionary outcome of sexual conflict is, i.e., how conflict is “resolved”. This may occur by (i) evolving traits that allow manipulation of traits under conflict, or, more commonly, (ii) by coevolving parental investment by each sex to a point where changing behaviour does not increase the fitness of either sex (Lessells, 2012). Parents may manipulate their partner’s investment by exploiting signalling systems (Haig, 2004; Müller *et al.*, 2007), by sabotaging their partner’s attempts to remate (Hansson *et al.*, 1997) or by deceiving their partner into providing more parental care than themself (Balshine-Earn and Earn, 1997). While manipulation can occur, most cases of sexual conflict resolution do not involve manipulation (Lessells, 2012). Instead, it is more common for parental investment in each sex to coevolve, so each parent controls its own parental investment and not their partner’s (Lessells, 2012). Game theoretical modelling has been heavily relied on to understand this process, as these models explore how the fitness outcome of a parent’s reproductive attempt depends on their partner.

The first key model to address conflict resolution in biparental care was from Houston and Davies (1985), who presented a ‘sealed bid’ model of care. This model assumed a fixed level of investment from each parent which is not altered in response to their partner's investment in behavioural time. They suggested that biparental care is a stable strategy when changes in the effort of one parent select for incomplete compensation of effort by its partner over *evolutionary* time (Houston and Davies, 1985). McNamara *et al.* (1999) expanded upon this idea, developing a model where parents negotiate levels of care in *behavioural* time. This model predicted that parents are responsive to changes in their partner's effort, but will only partially compensate for such changes (McNamara *et al.*, 1999). This partial compensation would force parents to reduce investment below optimum levels for offspring fitness (Houston and Davies, 1985; McNamara *et al.*, 1999; Lessells and McNamara, 2012), resulting in fitness costs for offspring, which has been supported by empirical study (Royle *et al.*, 2002; Royle *et al.*, 2010).

The majority of empirical studies support this theory of partial compensation, which was found to be the mean response to reduced partner effort in a meta-analysis of empirical studies, focusing on birds (Harrison *et al.*, 2009). However, other studies have found this response to be highly variable (Johnstone and Hinde, 2006; Harrison *et al.*, 2009), varying from full compensation (Paredes *et al.*, 2005), to matching compensation (Slagsvold and Lifjeld, 1988; Schwagmeyer *et al.*, 2002), to none at all (Hinde, 2006; Meade *et al.*, 2011). Models of conflict resolution are criticised for failing to consider the multidimensionality of parental care, thus ignoring many key components (Houston *et al.*, 2005; Iserbyt *et al.*, 2017). Given the variation in the results of empirical studies, it is evident that sexual conflict and its resolution occur in more varied ways than are currently explained by widely accepted models in the literature.

## Coordinated Behaviours for Parental Care – Alternation and Synchrony

Models to date suggest that the evolutionarily stable outcome of sexual conflict is for parents to only partially compensate for reduced partner investment, leading to a reduction in parental investment below optimum levels for offspring fitness, causing a loss of offspring fitness (McNamara *et al.*, 1999; Royle *et al.*, 2002; Royle *et al.*, 2010; Lessells and McNamara, 2012). Recently, Johnstone *et al.* (2014) proposed a game-theoretical model where parents reduce such costs of sexual conflict via conditional cooperation in the form of turn-taking (alternation). By alternating provisioning visits to the nest, perhaps refusing to provision until their partner has done so, this system may ensure equal investment from each partner, reducing fitness costs for offspring. Previous models presented parental care as a continuous variable, but this model suggests that parental care may be delivered as repeated discrete "visits" (Johnstone *et al.*, 2014). The model shows that if parents can monitor each other's visits, selection may favour a strategy where parents refuse to visit the nest until their partner has done so. This would result in strict turn-taking in nest visits.

Many empirical studies have found evidence supporting this model by Johnstone *et al*. (2014), including studies of both biparental (Iserbyt *et al.*, 2017; Leniowski and Węgrzyn, 2018; Iserbyt *et al.*, 2019) and cooperatively breeding species (Bebbington and Hatchwell, 2016; Savage *et al.*, 2017). All of these studies found that alternation occurs significantly more than is expected by chance. Leniowski and Węgrzyn (2018) found that alternation significantly increased with parental synchronisation in blackcaps, showing that these processes are linked. Bebbington and Hatchwell (2016) found that parental alternation increased the provisioning rate and reduced the predation rate in long-tailed tits. Savage *et al*. (2017) found significant alternation in care groups of chestnut-crowned babblers, with evidence that turn-taking was due to both passive and active alternation. However, some of the predictions of the model by Johnstone *et al*. (2014) were not supported by these studies. For example, while these studies found a significant tendency for alternation, strict turn-taking was not found in any of the studies. This prediction of strict turn-taking was made based on the unrealistic assumption that partners can accurately monitor each other's visit rate (Johnstone and Savage, 2019). Johnstone and Savage (2019) later improved the model to be more realistic and flexible on patterns of turn-taking, taking into account variation in both the accuracy of partner monitoring and the costs and benefits of care.

Behavioural compatibility and coordination between mates has recently been shown to be important for reproductive fitness (Spoon *et al.*, 2006; Schuett *et al.*, 2011; Mariette and Griffith, 2012; Mainwaring and Griffith, 2013). High nest visit synchrony, which is thought to function to reduce nest predation by reducing the frequency of nest visits (Fontaine and Martin, 2006; Raihani *et al.*, 2010), has been observed in various bird species, including zebra finches (Mariette and Griffith, 2012), long-tailed finches (Van Rooij and Griffith, 2013) and blackcaps (Leniowski and Węgrzyn, 2018). Bebbington and Hatchwell (2016) highlighted that recent research has identified 3 key functions of synchronous nest visits: (i) to signal provisioning information (Doutrelant and Covas, 2007), (ii) to reduce the risk of predation by reducing the amount of activity at the nest (Martin *et al.*, 2000; Raihani *et al.*, 2010), and (iii) to enhance provisioning and hence reproductive success (Mariette and Griffith, 2012). Synchronising nest visits may also reduce sexual conflict and associated fitness costs for offspring by allowing partners to monitor each other's investment and respond accordingly (Johnstone and Hinde, 2006; Mariette and Griffith, 2012; Bebbington and Hatchwell, 2016). Leniowski and Węgrzyn

(2018) found that alternation of provisioning visits was positively related to parental synchrony, suggesting that synchrony may function to enable partners to monitor each other's visit rate to allow effective turn-taking (Bebbington and Hatchwell, 2016).

As parental coordination is being increasingly considered in parental care literature, some studies are investigating what factors may influence such behaviours. For example, Iserbyt *et al.* (2017) found that sex-specific task specialisation during the early stages of reproduction constrains the degree of parental alternation. Alternation increases as task specialisation decreases as the nestlings develop better endothermic capacity (Iserbyt *et al.*, 2017). A recent study by Lejeune *et al.* (2019) found that nest visits were more synchronous in edge habitats than interior woodland, and more synchronous at high elevation on cold and wet days (Lejeune *et al.*, 2019). Pairs alternated more and fed more frequently at lower altitudes, with a 23% reduction in alternation for every 100m increase in altitude. They also found a positive relationship between nest visit synchrony and nestling mass in woodland habitats, suggesting that coordination can mitigate the costs of sexual conflict for offspring (Lejeune *et al.*, 2019). Another study by Iserbyt *et al.* (2019) created disturbance by catching and releasing a parent, creating a 2-hour absence by one parent, and investigated how coordinated behaviour changed in response. They found that parents quickly resumed nest visits and continued alternating at the same rate as before the disturbance, suggesting that such coordinated behaviour is resilient against environmental disturbance (Iserbyt *et al.*, 2019). These studies demonstrate that coordinated parental behaviour is variable depending on a range of factors, but can be resilient in the face of disturbances.

While the theory of conditional cooperation seems promising as a conflict resolution strategy, some studies have pointed out that patterns of alternation may be due to processes other than active turn-taking (Baldan *et al.*, 2019; Ihle *et al.*, 2019a; Santema *et al.*, 2019). Temporal environmental variation can cause the provisioning rates of both parents to change at the same time so that their inter-visit interval (IVI) is matched (Schlicht *et al.*, 2016; Baldan *et al.*, 2019). A study by Baldan *et al.* (2019) suggests that temporal environmental variation accounts for around a fifth of observed alternation in great tits. These studies conclude that conditional cooperation has not yet been fully supported by existing studies, given that observed alternation may be due to other interacting effects (Baldan *et al.*, 2019; Ihle *et al.*, 2019a), but admit that it may be nearly impossible to account for all factors (Santema *et al.*, 2019). So far, there is little evidence for any fitness benefits of coordination (Ihle *et al.*, 2019a) – the only evidence so far is a reduced predation risk with synchronous nest visits (Raihani *et al.*, 2010). It has therefore been suggested that future study explores the fitness consequences of coordination (Ihle *et al.*, 2019a). It has also been suggested that more manipulation experiments should be carried out (Griffioen *et al.*, 2019a; Santema *et al.*, 2019) and studies should explore relationships between pair or brood characteristics and coordinated behaviours (Ihle *et al.*, 2019a).

## Conclusions

Differences in sex roles during reproduction were once thought to be directly driven by anisogamy, however recent advancements have shown that sex differences are influenced by complex interactions between a wide range of factors including the cost-benefit trade-offs of caring and remating, certainty of parentage, the ASR and OSR, sexual competition and mate choice. Anisogamy does have an important role in sex role divergence, however its role is indirect. Empirical evidence is mixed for some of the key factors involved in sex differences, thus more research is required to fully understand their importance. Differences in the evolutionary interests of males and females can result in sexual conflict, particularly over parental investment. It is most beneficial for a parent to invest less than their partner due to the shared benefits but individual costs of parental care, which results in conflict over investment. Theoretical research has relied heavily on game-theoretical modelling to understand how such sexual conflict is resolved. Models to date predict that parents will incompletely compensate for a reduction in their mate's effort, such that total parental investment is below optimum levels for offspring fitness and offspring may suffer a fitness cost. However, there is mixed empirical evidence for incomplete compensation.

A recent model proposed that parents might mitigate this cost by conditional cooperation in the form of turn-taking. This model suggests that parental care is delivered in discrete "visits" and parents will alternate nest visits so that their investment is equal. Empirical studies have found supporting evidence for this theory, but questions remain about whether observed alternation is due to active turn-taking or other passive processes. The importance of coordinated behaviour such as alternation and synchronisation has recently become a focal topic of research, with studies finding that these behaviours occur more than expected by chance. Studies are beginning to investigate how these behaviours are affected by environmental factors and disturbance. This new avenue of research presents exciting new opportunities to investigate fine-scale behavioural mechanisms involved in resolving sexual conflict.

## Future Research

While many studies support that parental alternation occurs more than expected by chance, the phenomenon of conditional cooperation is yet to be fully supported (Baldan *et al.*, 2019; Ihle *et al.*, 2019a; Santema *et al.*, 2019). Ihle *et al*. (2019a) call for studies to explore the potential fitness consequences of coordination for both parents and offspring (Iserbyt *et al.*, 2017; Ihle *et al.*, 2019a) as it may be that parents, not offspring, bear the costs of sexual conflict (Barta *et al.*, 2014; Iserbyt *et al.*, 2017). Ihle *et al*. (2019a) also call for investigation into the potential relationships between pair or brood characteristics and coordinated parental behaviour. They suggest that this further research will help us to better understand the adaptive significance of coordinated behaviour (Ihle *et al.*, 2019a). This thesis will therefore investigate these suggested research avenues to fill the gaps in this field.

Taking this into account, the key questions that this study aims to investigate are: (i) what are the fitness consequences of coordination behaviours for parents and offspring? And (ii) what relationships are there between pair/brood characteristics and coordinated parental behaviour? The specific coordination behaviours investigated in this study are alternation and synchrony. The next chapter of this thesis will investigate the relationships between alternation and synchrony and indicators of reproductive success such as nestling mass, brood size on day 14 and number of fledglings (Chapter 1). This chapter will focus on finding potential benefits for alternation and synchrony, investigating relationships with brood characteristics. This chapter will also investigate whether alternation and synchrony occur more than expected by chance. The following chapter (Chapter 2) will investigate potential costs and benefits of alternation and synchrony, specifically looking at relationships with pair divorce and likelihood of mortality. There is evidence that increased parental effort results in decreased survival in male parents, but not female parents (Santos and Nakagawa, 2012). If better coordination occurs due to increased parental effort, it may be interesting to identify whether this pattern occurs.

Given the demand for more research into the fitness consequences of coordination behaviours such as alternation and synchrony (Ihle *et al.*, 2019a), this research hopes to provide novel insights into the costs and benefits of these behaviours. Only a handful of studies have been published in this area to date, thus this study will add to the growing body of evidence for coordinated behaviours with an aim to bolster the understanding of such behaviours. In addition, only one previous study has investigated the relationships of alternation and synchrony with divorce (Ihle *et al.*, 2019b), thus this study may add to current understanding of such relationships. This study will use 6 years of breeding and provisioning data from a population of blue tits, *Cyanistes caeruleus*, living in woodland surrounding Lancaster University. One average, 75 nest boxes are occupied per year. As a result, the dataset used for this study is larger than many previous studies on alternation and synchrony, which will be beneficial to produce reliable and accurate results.

# Chapter 1 – Alternating Parental Provisioning Visits Increases Reproductive Success in Blue Tits (*Cyanistes caeruleus*)

## Abstract

Species with biparental care face sexual conflict over parental investment in offspring due to the shared benefits but individual costs of care, such that the optimum level of investment for an individual is less than that of its partner. This conflict can result in costs for offspring, but a recent theoretical model suggests that parents may reduce the costs of sexual conflict via conditional cooperation in the form of turn-taking (alternation) during provisioning, and various empirical studies have found evidence supporting this model. In addition, provisioning synchrony is thought to be related to alternation, perhaps playing a role in partner monitoring. This study investigated alternation and synchrony of nest provisioning visits in blue tits, *Cyanistes caeruleus*, using 6 years of breeding data. Alternation and synchrony were found to occur more than expected by chance. This study explored whether alternation and synchrony predict indicators of reproductive success, finding that that brood size on day 14 was predicted by alternation, providing evidence for fitness benefits of alternation. Neither alternation nor synchrony were significantly related to mean chick mass and number of fledglings. This study also found that brood size on day 14 predicted alternation, suggesting that parents may respond to the number of nestlings to make decisions about investment in alternation. This study finds previously undiscovered relationships between brood size and alternation, presenting the first evidence for fitness benefits of alternation, an important step in understanding whether this behaviour is adaptive.

## Introduction

When caring for offspring, parents face a trade-off between investment in the current reproductive attempt and the costs of such investment for future reproduction (Williams, 1966; Stearns, 1989). In addition to this, species with biparental care face sexual conflict over parental investment in offspring. This occurs due to the benefits of investment being shared, while each individual pays the cost of their own contribution, such that the optimum level of investment for an individual is less than that of their partner (Trivers, 1972; Lessells, 2012). Much research over the past 50 years has centred on trying to understand the resolution of sexual conflict, mainly through game-theoretical models. Early models proposed that each parent has a fixed level of investment which does not change in response to their partner’s investment in behavioural time (Houston and Davies, 1985). This model suggested that biparental care is only a stable strategy when changes in a parent’s investment select for incomplete compensation by its partner over evolutionary time (Houston and Davies, 1985). Further models have since built upon this, suggesting that parents partially compensate for their partner’s effort in behavioural time (McNamara *et al.*, 1999). Partial compensation is expected to result in parental investment that is below the optimum level for offspring fitness (Houston and Davies, 1985; McNamara *et al.*, 1999; Lessells and McNamara, 2012), which results in fitness costs for offspring, as supported by empirical studies (Royle *et al.*, 2002; Royle *et al.*, 2010).

Partial compensation is generally supported by empirical studies (Harrison *et al.*, 2009), but is not found in all species. Some studies have found partial compensation to be highly variable (Johnstone and Hinde, 2006; Harrison *et al.*, 2009), varying from full compensation (Paredes *et al.*, 2005), to matching compensation (Slagsvold and Lifjeld, 1988; Schwagmeyer *et al.*, 2002), to no compensation at all (Hinde, 2006; Meade *et al.*, 2011). Given that partial compensation is not fully supported, there may be more to sexual conflict resolution than is considered by these models. A recent theoretical model by Johnstone *et al*. (2014) suggested that parents may reduce the costs of sexual conflict via conditional cooperation, in the form of turn-taking. By alternating provisioning visits to the nest, perhaps refusing to provision young until their partner has done so, carers could ensure equal investment from their partner (Johnstone *et al.*, 2014). Various empirical studies have since tested and found evidence supporting this theory, both in cooperative (Bebbington and Hatchwell, 2016; Savage *et al.*, 2017) and biparental breeding systems (Iserbyt *et al.*, 2017; Leniowski and Węgrzyn, 2018; Iserbyt *et al.*, 2019). This model and associated studies show that, with some level of partner monitoring involved, selection may favour a strategy where parents refuse to provision young at the nest until their partner has done so, resulting in alternation of provisioning visits.

In addition to studies on alternation, some have also investigated the importance of synchrony on reproductive fitness. High nest visit synchrony has been observed in various bird species (Mariette and Griffith, 2012; Van Rooij and Griffith, 2013; Leniowski and Węgrzyn, 2018) and is thought to function to reduce nest predation by reducing the number of visits to the nest (Fontaine and Martin, 2006; Raihani *et al.*, 2010). In addition to reducing nest predation, synchrony is thought to facilitate signalling of provisioning information between carers (Doutrelant and Covas, 2007) and optimise provisioning and reproductive success (Mariette and Griffith, 2012). Studies which investigate both alternation and synchrony have found the two to be positively associated with one another (Bebbington and Hatchwell, 2016; Leniowski and Węgrzyn, 2018), suggesting that synchrony may enable carers to monitor each other to facilitate effective alternation.

While conditional cooperation seems to be a promising conflict resolution strategy, some studies have suggested that observed patterns of alternation may be due to factors other than active turn-taking (Baldan *et al.*, 2019; Ihle *et al.*, 2019a; Santema *et al.*, 2019). For example, temporal environmental variation can cause the provisioning rates of carers to change at the same time, so that their inter-visit intervals (IVI) are matched (Schlicht *et al.*, 2016; Baldan *et al.*, 2019). This can be caused by such a wide range of factors that it may be near-impossible to account for all of them (Ihle *et al.*, 2019a; Santema *et al.*, 2019). As a result of such interacting effects, these studies suggest that conditional cooperation is yet to be fully supported by existing studies, but that it may be difficult to account for all interacting effects (Baldan *et al.*, 2019; Ihle *et al.*, 2019a). A key gap in coordination studies to date is the lack of evidence for fitness benefits of coordination, with reduced predation risk with synchronous nest visits being the only evidence so far (Raihani *et al.*, 2010; Ihle *et al.*, 2019a). Further exploration of the fitness consequences of coordination has been recommended, in addition to more studies on the relationships between pair or brood characteristics and coordinated behaviours such as alternation and synchrony (Ihle *et al.*, 2019a).

With these recommendations in mind, this study will investigate potential fitness consequences of alternation and synchrony during nest provisioning in blue tits, *Cyanistes caeruleus*, using 6 years of breeding and provisioning data. This study will investigate whether alternation and synchrony occur more than expected by chance and assess the relationship between alternation and synchrony. The potential reproductive benefits of alternation and synchrony will also be explored by investigating relationships between these behaviours and brood size, number of fledglings and nestling mass. Finally, this study will explore potential predictors of alternation and synchrony.

## Methods

This study used breeding and provisioning data from blue tits breeding in nest boxes in deciduous woodland around Lancaster University, Lancashire, U.K., from 2016 to 2021. On average, 75 nest boxes were occupied by blue tits each year. Nest boxes were visited every 5 days during April to record first egg date and clutch size, then every day during May to record hatch date and hatch success (the number of eggs hatched). When nestlings were 10-12 days old, the nest box was video recorded for one hour. The entry and exit times of adults visiting the nest box were recorded, as well as the adults' sex and whether a faecal sac was removed. Observations where a nest was being provisioned by only a single male or female were removed from the dataset so that the analyses were only inclusive of provisioning pairs. Nestlings were weighed (± 0.1g electronic balance) and counted at 14 days old after hatching. The number of fledglings at each nest was also counted.

## Quantifying Alternation

Pair alternation was quantified as the proportion of alternated visits, using the equation $A = F/(t-1)$, where $F$ is the number of times one parent visited after the other and $t$ is the total number of nest visits. To assess whether alternation occurred more than expected by chance, observed alternation was compared with "expected" alternation values generated from simulated observations based on the observed data.

The following process was used to generate expected alternation values. The inter-visit intervals (IVIs) of the male and female provisioning visits at each nest were extracted from the provisioning data. For each nest, the associated IVIs were randomly sampled without replacement until all male and female IVIs associated with the nest had been sampled. This was repeated 1000 times per nest. For each random sample, the cumulative totals of the sampled male and female IVIs were made separately, then combined to create a simulated observation as a series of visit times plus the sex associated with each visit (similar to Bebbington and Hatchwell, 2016). Alternation was calculated for each simulated observation, resulting in 1000 expected alternation values per nest. This method sampled the IVIs in the observed ratio of male and female visits at each nest, resulting in expected alternation values that take this ratio into account. To calculate whether observed alternation differed from expected, a t-test was used to determine whether observed alternation was different than expected by chance, comparing all observed with all expected values. In addition, the percentage of nests with observed alternation above the upper 95% confidence interval of expected alternation values associated with that nest was also calculated.

## Quantifying Synchrony

Kernel density estimation is a data smoothing technique typically used to visualise the distribution of data and estimate the probability density function of a variable. This works by placing a 'kernel', a non-negative function, at each datapoint along the x axis (the red dashed curves, figure 1). In this study, a normal (gaussian) kernel is used. These kernels are summed to produce the kernel density estimate (blue line, figure 1). The "smoothness" of this line is determined by the bandwidth of the kernels. Bandwidth is a "free parameter", thus the optimal bandwidth for a kernel density estimate (KDE) must be estimated. If the bandwidth is too small, the KDE may be undersmoothed, but if too high the KDE may be oversmoothed.

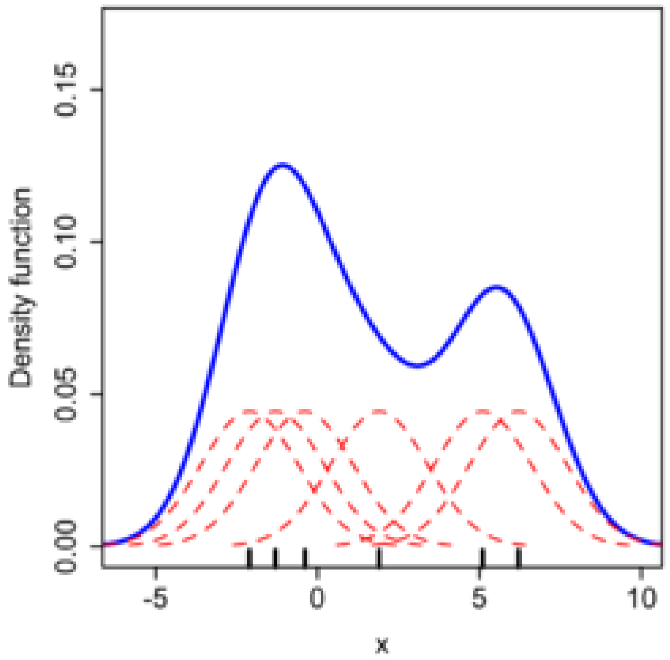

**Figure 1.** Graphical representation of how kernel density estimates are calculated. Sourced from en.wikipedia.org/wiki/Kernel_density_estimation.

To quantify the synchronicity of provisioning blue tit pairs, this study cross-correlated the kernel density estimates of the time series of provisioning visits by male and female blue tits, following methods used by Lejeune *et al*. (2019). This produced a correlation coefficient between -1 and 1 representing the synchronicity of visits to the nest by the provisioning male and female, a "synchrony score". To assess whether synchrony occurred more often than expected by chance, simulated observations were generated by randomising the inter-visit intervals of each parent 1000 times. For each randomisation, cumulative totals of the IVIs were made separately for males and females, then combined and sorted in ascending order to create a simulated watch, similar to Bebbington and Hatchwell's method (Bebbington and Hatchwell, 2016). For each randomisation, a synchrony score was calculated, resulting in 1000 synchrony scores expected by chance based on the pair's provisioning rate and inter-visit interval. The mean and standard deviation of these expected synchrony scores were used to create a z-score for each nest showing whether actual synchrony was more or less than expected by chance, using the following equation: $Z = (x - \mu)/\sigma$, where $x$ is the actual synchrony score, $\mu$ is the mean expected synchrony score and $\sigma$ is the standard deviation of expected synchrony scores. The resulting distribution of z-scores was normally distributed (Shapiro-Wilks test, W = 0.996, *P* = 0.679; Kolmogorov-Smirnoff test, D = 0.0439, *P* = 0.638; Figure 2).

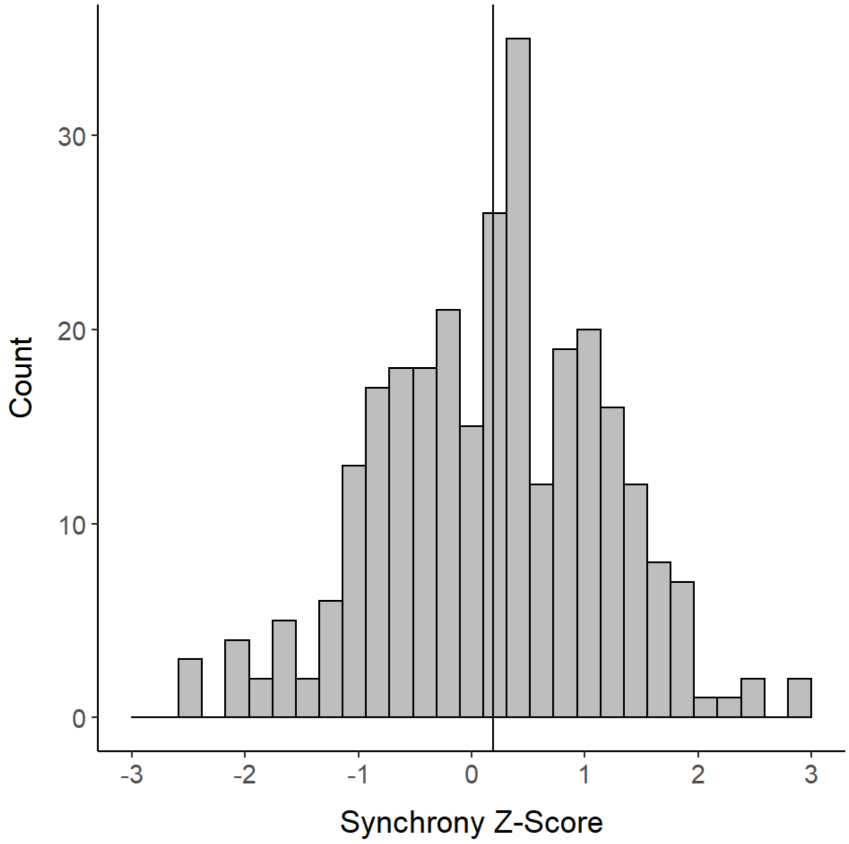

**Figure 2.** Histogram of z-scores calculated using the equation $Z = (x - \mu)/\sigma$, where x is the observed synchrony score, μ is mean expected synchrony score and σ is the standard deviation of expected synchrony scores. The black vertical line represents the mean synchrony z-score of all nests (0.182). Synchrony scores were calculated using cross-correlation of kernel density estimates of the time series of visits by the provisioning male and female the nest. Kernel density estimates were calculated at a bandwidth of 20.

The bandwidth used to calculate kernel density estimates was 20. Too low a bandwidth may not detect synchronicity between carers, but a high bandwidth may detect more synchronicity than actually occurs. The change in mean observed synchrony score with different bandwidths can be seen in figure 3. However, using z-score as an indicator of synchronicity reduces the influence of bandwidth on the results. There was a strong positive correlation between the z-scores calculated using a bandwidth of 20 and those calculated with bandwidths 10-60 (Table 1), showing that, in this study, changing the bandwidth has little influence on the results.

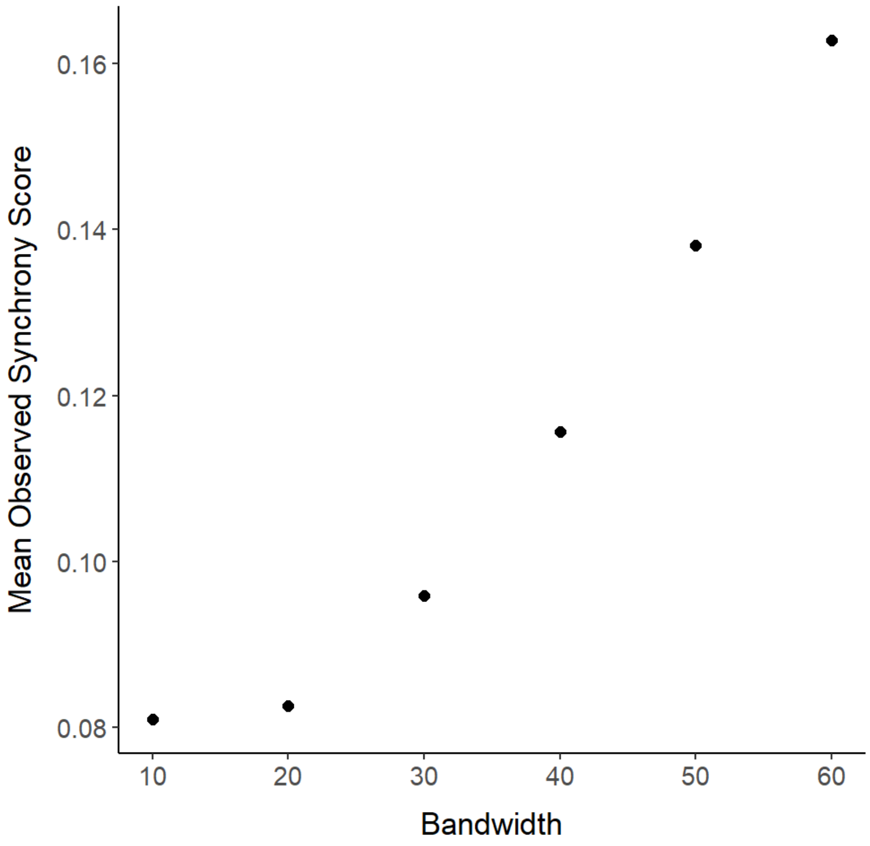

**Figure 3.** Mean observed synchrony score at bandwidths 10-60. Synchrony scores were calculated using cross-correlation of kernel density estimates of the time series of visits by the provisioning male and female the nest. Kernel density estimates were calculated at a bandwidth of 20.

**Table 1.** Pearson's correlation coefficient between synchrony z-scores calculated using kernel density estimation with a bandwidth of 20 and those calculated using bandwidths 10-60.

| **Bandwidth** | Correlation coefficient | P-value |
|---|---|---|
| **10** | 0.853 | <0.001 |
| **20** | 1.000 | <0.001 |
| **30** | 0.952 | <0.001 |
| **40** | 0.876 | <0.001 |
| **50** | 0.816 | <0.001 |
| **60** | 0.765 | <0.001 |

## Statistical Analysis

### Fitness consequences of alternation and synchrony

The effect of alternation and synchrony on reproductive fitness was investigated using a series of generalised linear mixed models (GLMMs). Models were run twice, each with either male or female identity as the random effect. The first GLMM investigated whether alternation predicts brood size on day 14, with brood size on day 14 as a Poisson response variable. Alternation and first egg date were included as fixed effects, with the latter being included to account for variation caused by this variable. Total feeds per hour was originally to be included in the model but was excluded due to its correlation with alternation. A similar model was run with synchrony z-score as a fixed effect in place of alternation. Also using these same fixed effects, the next GLMMs investigated the effect of alternation and synchrony on the number of fledglings, modelling number of fledglings as a Poisson response variable. Clutch size was included as an additional fixed effect in this model.

A linear model was used to investigate the effect of alternation and synchrony on mean nestling mass (mass on day 14). Potential fixed effects included alternation/synchrony, first egg date and total feeds per hour, though total feeds was excluded due to its correlation with alternation and synchrony. This was again run separately for alternation and synchrony.

### Which brood characteristics predict alternation and synchrony?

A linear mixed model (LMM) was used to investigate potential predictors of alternation and synchrony, again run twice, once with male identity as a random effect and again with female identity as a random effect. In the model investigating predictors of alternation, alternation was modelled as a gaussian response. The same was done for the model investigating predictors of synchrony. Potential predictors included first egg date, clutch size, hatch success, brood size on day 14 and total feeds per hour. Due to their correlation with brood size on day 14, clutch size (Pearson's $r = 0.664$, df = 275, $P < 0.001$) and hatch success (Pearson's $r = 0.806$, df = 274, $P < 0.001$) were excluded from the model. Total feeds per hour was highly correlated with alternation and synchrony but was excluded as it masked the effects of other predictors in the model. While first egg date was not a significant predictor, it was included to account for variation caused by this variable.

All statistical analyses were carried out in R Studio, version 4.1.0. All models were reduced using the likelihood ratios test to identify and remove non-significant fixed effects until only significant ($P < 0.05$) or relevant effects remained. Linear mixed models and generalised linear mixed models were performed using the “lme4” package (Bates *et al.*, 2015) and associated results tables were produced using the “broom.mixed” output. Figures were produced using the “ggplot2” package (Wickham, 2009).

## Results

### Alternation and synchrony

Alternation in blue tits was significantly higher than would be expected by chance ($t = 5.44$, $df = 289$, $P < 0.0001$). Observed alternation was higher than the upper 95% expected alternation for that pair in 77.6% of blue tit pairs.

58.4% of pairs had a positive synchrony z-score (mean = 0.182) (Figure 2), indicating that they synchronised more than expected by chance.

A linear regression of alternation predicted by synchrony shows a weak positive association ($P < 0.001$, $R^2 = 0.097$) between alternation and synchrony z-score of provisioning blue tit pairs (Figure 4).

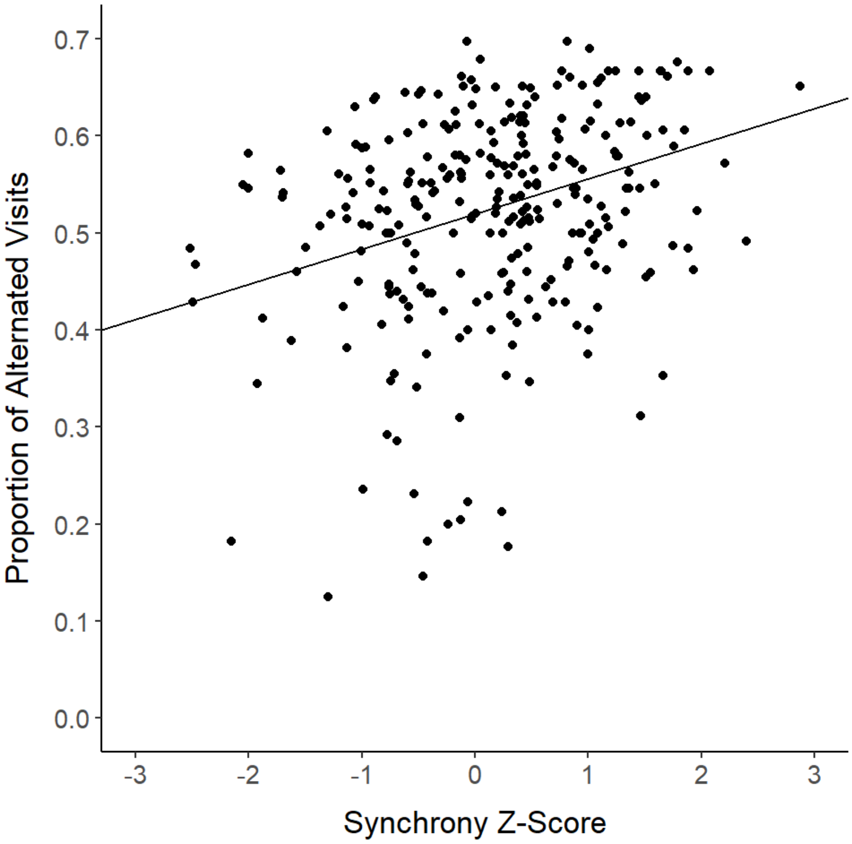

**Figure 4.** Alternation (proportion of alternated visits) against synchrony z-score of provisioning blue tit pairs, with associated regression line.

## Fitness consequences of alternation and synchrony

Brood size on day 14 (mean 7.77 ± 0.12 standard error, SE) was significantly predicted by alternation but not synchrony z-score (Table 2, Table 3). Neither alternation nor synchrony predicted number of fledglings (mean 7.14 ± 0.18 SE) (Table 2, Table 3) nor mean chick mass (Table 4).

**Table 2.** Poisson mixed models to identify whether alternation (proportion of alternated visits) or synchrony z-score predict brood size on day 14 or number of fledglings, with female identity as random effect. Significant (P<0.05) effects are highlighted in bold.

| Effect | Estimate | Standard Error | Statistic | P |
|---|---|---|---|---|
| **a) Does alternation predict brood size on day 14?** | | | | |
| Alternation | 0.392 | 0.180 | 2.184 | **0.029** |
| First egg date | -0.013 | 0.004 | -3.421 | **0.001** |
| **b) Does synchrony predict brood size on day 14?** | | | | |
| Sync Z-score | 0.028 | 0.022 | 1.272 | 0.204 |
| First egg date | -0.015 | 0.004 | -3.940 | **<0.001** |
| **c) Does alternation predict number of fledglings?** | | | | |
| Alternation | 0.245 | 0.228 | 1.071 | 0.284 |
| First egg date | -0.017 | 0.006 | -2.944 | **0.003** |
| Clutch size | 0.078 | 0.018 | 4.404 | **<0.001** |
| **d) Does synchrony predict number of fledglings?** | | | | |
| Sync Z-score | 0.015 | 0.029 | 0.504 | 0.614 |
| First egg date | -0.018 | 0.006 | -3.040 | **0.002** |
| Clutch size | 0.078 | 0.018 | 4.269 | **<0.001** |

**Table 3.** Poisson mixed models to identify whether alternation (proportion of alternated visits) or synchrony z-score predict brood size on day 14 or number of fledglings, with male identity as random effect. Significant (P<0.05) effects are highlighted in bold.

| **Effect** | **Estimate** | **Standard Error** | **Statistic** | **P** |
|---|---|---|---|---|
| **a) Does alternation predict brood size on day 14?** | | | | |
| Alternation | 0.376 | 0.183 | 2.052 | **0.040** |
| First egg date | -0.012 | 0.004 | -3.170 | **0.002** |
| **b) Does synchrony predict brood size on day 14?** | | | | |
| Synchrony Z-score | 0.034 | 0.023 | 1.502 | 0.133 |
| First egg date | -0.014 | 0.004 | -3.663 | **<0.001** |
| **c) Does alternation predict number of fledglings?** | | | | |
| Alternation | 0.238 | 0.231 | 1.032 | 0.302 |
| First egg date | -0.017 | 0.006 | -2.856 | **0.004** |
| Clutch size | 0.077 | 0.018 | 4.336 | **<0.001** |
| **d) Does synchrony predict number of fledglings?** | | | | |
| Synchrony Z-score | 0.020 | 0.029 | 0.670 | 0.503 |
| First egg date | -0.017 | 0.006 | -2.940 | **0.003** |
| Clutch size | 0.078 | 0.019 | 4.195 | **<0.001** |

**Table 4.** Linear models investigating whether alternation (proportion of alternated visits) or synchrony z-score predict mean nestling mass at day 14.

| **Effect** | **Estimate** | **Standard Error** | **Statistic** | **P** |
|---|---|---|---|---|
| **a) Does alternation predict mean nestling mass?** | | | | |
| Alternation | -0.308 | 0.418 | -0.736 | 0.463 |
| First egg date | -0.028 | 0.009 | -2.942 | **0.004** |
| Coefficient of variance | -11.440 | 1.425 | -8.026 | **<0.001** |
| **b) Does synchrony predict mean nestling mass?** | | | | |
| Synchrony Z-score | -0.012 | 0.052 | -0.224 | 0.823 |
| First egg date | -0.025 | 0.009 | -2.670 | **0.008** |
| Coefficient of variance | -11.602 | 1.411 | -8.222 | **<0.001** |

### Which brood characteristics predict alternation and synchrony?

Alternation was significantly predicted by brood size on day 14, with more alternation occurring at larger broods (Figure 5). Brood size on day 14 only predicted synchrony when male identity was used as the random effect, but not when female identity was used (Table 5, Table 6).

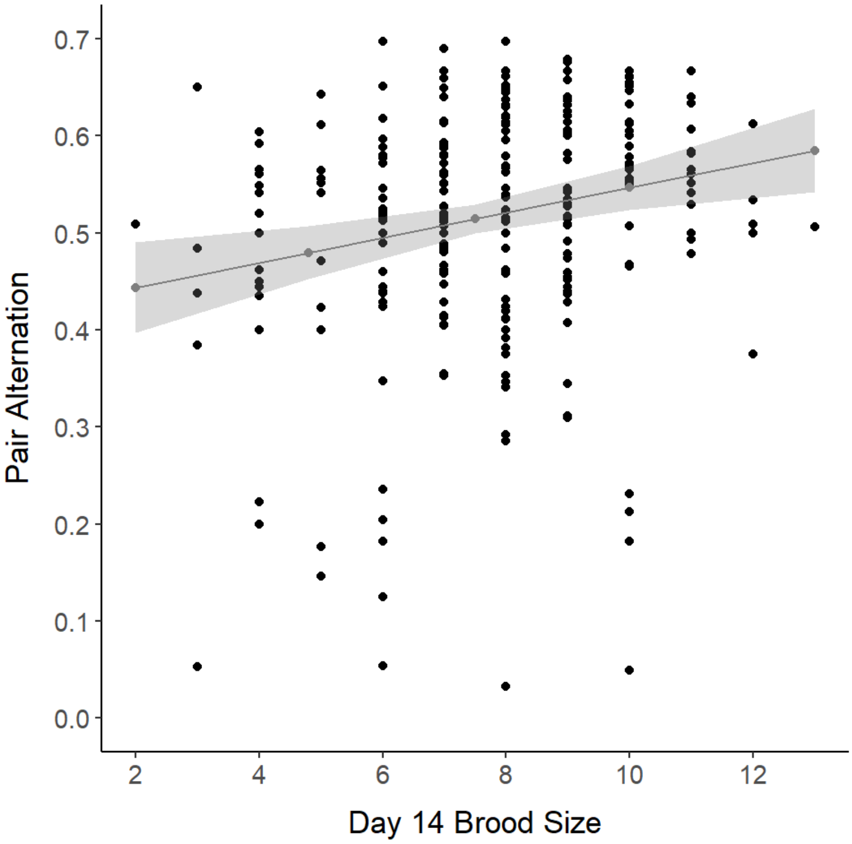

**Figure 5.** Relationship between brood size on day 14 and alternation (proportion of alternated visits). The line shows model estimates for brood size on day 14 (model *a*, table 5) with 95% confidence intervals.

**Table 5.** Linear mixed models to identify predictors of alternation (proportion of alternated visits) and synchrony z-score, with female identity as a random effect. Significant (P<0.05) effects are highlighted in bold.

| Effect | Estimate | Standard Error | Statistic | P |
|---|---|---|---|---|
| **a) Does brood size predict alternation?** | | | | |
| Brood size day 14 | 0.013 | 0.004 | 3.292 | **0.001** |
| First egg date | -0.002 | 0.001 | -1.315 | 0.187 |
| **b) Does brood size predict synchrony?** | | | | |
| Brood size day 14 | 0.059 | 0.032 | 1.881 | 0.060 |
| First egg date | 0.012 | 0.011 | 1.098 | 0.270 |

**Table 6.** Linear mixed models to identify predictors of alternation and synchrony, with male identity as a random effect. Significant (P<0.05) effects are highlighted in bold.

| Effect | Estimate | Standard Error | Statistic | P |
|---|---|---|---|---|
| **a) Does brood size predict alternation?** | | | | |
| Brood size day 14 | 0.012 | 0.004 | 3.094 | **0.002** |
| First egg date | -0.002 | 0.001 | -1.506 | 0.131 |
| **b) Does brood size predict synchrony?** | | | | |
| Brood size day 14 | 0.073 | 0.031 | 2.305 | **0.022** |
| First egg date | 0.011 | 0.011 | 1.035 | 0.299 |

## Discussion

This study investigated alternation and synchrony of provisioning in blue tits, finding a significant positive association between alternation and synchrony (Figure 4). Alternation significantly predicted brood size on day 14 (Table 2, Table 3), with pairs that alternated more often producing larger broods (Figure 5). Neither the number of fledglings nor mean chick mass were predicted by alternation or synchrony (Table 2, Table 3, Table 4). This study also found that alternation was significantly predicted by brood size on day 14 (Table 5, Table 6). After having thoroughly searched the literature, this study appears to be the first to find a relationship between alternation and brood size on day 14, a key finding that suggests a potential fitness benefit of alternation in blue tits.

Observed alternation was higher than the upper 95% expected alternation for that pair in 77.6% of blue tit pairs. This is notably higher than found in other studies which investigated the frequency of pairs that alternate more than expected by chance: in a study by Lejeune *et al*. (2019), 41% of blue tit pairs were found to alternate more than expected by chance. However, this may be due to differences in methodology. 58.4% of pairs in the present study had a positive synchrony z-score, indicating that they synchronised more than expected by chance (Figure 2). This is lower than found by Lejeune *et al*. (2019), where 66% of pairs had a positive z-score for synchrony. Lejeune *et al*. (2019) used the same methods to quantify synchrony and the same study species as used in the present study. These differences could be due to a variety of factors that might influence whether pairs invest in alternation and/or synchrony, such as predation risk (Raihani *et al.*, 2010), habitat and climate (Lejeune *et al.*, 2019). The availability of prey may constrain synchrony - at lower temperatures and high precipitation, caterpillar growth and survival are reduced, resulting in lower availability of food (Ayres, 1993; Tamburini *et al.*, 2013; Schöll *et al.*, 2016). Comparative studies investigating alternation and synchrony in regionally separated sites may therefore be useful to assess the impact of regional differences in climate and habitat on these behaviours.

There was a significant, but weak, positive relationship between alternation and synchrony z-score in provisioning blue tit pairs (Figure 4), as has been found in other studies (Bebbington and Hatchwell, 2016; Leniowski and Węgrzyn, 2018). To successfully alternate with one another, pairs may need to monitor one another's visits, thus some synchronisation in the pair's nest visits is to be expected (Bebbington and Hatchwell, 2016; Johnstone and Savage, 2019). Parents cannot spend all their time monitoring one another so perfect monitoring is unlikely (Johnstone and Savage, 2019), which may explain the weakness of the association between alternation and synchrony

(Figure 4). Synchrony may also function to allow pairs to signal information to one another (Doutrelant and Covas, 2007), which may also facilitate alternation if signalling that they have provisioned at the nest.

This study finds evidence for reproductive benefits of alternation during provisioning. Alternation significantly predicted brood size on day 14, with pairs that alternated more often rearing larger broods (Table 2, Table 3). Given that nestlings tend to fledge at 18-21 days old, brood size on day 14 is a good indicator of reproductive success. Johnstone *et al.*'s (2014) model of alternation predicts that alternation should increase parental investment and thus maximise parental fitness and optimise provisioning rates. The results found in the present study suggest that alternation may indeed increase parental fitness, supporting Johnstone *et al.*'s (2014) theory. Previous studies have investigated the relationship between alternation and brood size but did not find such a relationship (Bebbington and Hatchwell, 2016; Griffioen *et al.*, 2019a; Lejeune *et al.*, 2019), which may be due to these studies having a much smaller sample size than the present study. As a result, studies on larger sample sizes may be needed to find further evidence for reproductive benefits of this behaviour. This relationship is to be expected, given that brood size and provisioning rate are usually positively related (Magrath *et al.*, 2007; Bowers *et al.*, 2014). This finding is the first evidence of potential fitness benefits for alternation - an important step in understanding whether this behaviour is adaptive.

This study also found that brood size on day 14 significantly predicted alternation (Table 5, Table 6), suggesting that blue tit parents respond to brood size to make decisions about investment in alternation. This may also suggest a limitation for the study, if there is a correlation between brood size and alternation, such that it may be difficult to disentangle which variable truly predicts the other. On the one hand, both relationships may exist, such that parents respond to brood size to make decisions about alternating with one another, and parents that are more successful in doing so rear larger broods. On the other hand, alternation may not truly result in larger brood sizes on day 14 if, instead, parents respond to brood size to make decisions about investment in alternation. One way for future studies to better understand this relationship is to identify whether alternation changes when brood size is manipulated. One previous study has done so (Griffioen *et al.*, 2019b) which found that alternation did not change with brood size manipulation, suggesting a fixed agreement about parental investment. If this is so, this supports that the relationship found in the present study may indeed be due to brood size on day 14 being predicted by alternation. Due to the small number of studies investigating these relationships, more study is required to better understand the prevalence of the benefits of this behaviour such as those found in the present study.

Surprisingly, this study found no increase in nestling mass or number of fledglings with alternation (Table 2, Table 3, Table 4). Previous studies also found little improvement of nestling condition with greater alternation and provisioning rate (Bebbington and Hatchwell, 2016; Ihle *et al.*, 2019b). Bebbington and Hatchwell (2016) suggested that the effect of increased provisioning resulting from high alternation may be diluted by high offspring demand for food, resulting in little to no increase in nestling mass from increased provisioning. This has been known to occur in other studies on biparental passerines, particularly in species that produce large broods (Bonneaud *et al.*, 2003; Titulaer *et al.*, 2012). The benefits of alternation may instead present as larger broods rather than increased nestling mass. Additionally, no relationship was found between alternation and number of fledglings, despite a relationship with brood size on day 14 (Table 2, Table 3). Due to much less available data on the number of fledglings (n = 170) than for brood size on day 14 (n = 274), a relationship between pair alternation and number of fledglings may not have been detected.

Given the correlation between alternation and synchrony (Figure 4), it was expected that variables that were significantly related to alternation would also be related to synchrony. However, synchrony did not predict any of the fitness variables investigated. Given that synchrony is known to reduce nest predation (Raihani *et al.*, 2010), it is possible that this behaviour only occurs when perceived predation risk is high. If the predation risk in this study population was low, a relationship between synchrony and the fitness variables investigated in this study is unlikely. While alternation may function to optimise provisioning, synchrony may not. Synchrony is also thought to facilitate partner monitoring to enable alternation (Bebbington and Hatchwell, 2016; Johnstone and Savage, 2019), however, this effect of synchrony on alternation via partner monitoring may be too indirect for a significant relationship with indicators of offspring fitness to occur.

Methods to quantify synchrony are limited in that they often do not account for variability in the synchronicity of nest visits. Particularly in fast-provisioning species such as blue tits, it is difficult to accurately decide what timeframe between one parent’s nest visit and the next parent’s visit is appropriate to accurately define a synchronous event. While the methods used for the present study attempt to account for this issue, the need to define a bandwidth for the kernel density estimation may result in a similar issue of being unable to accurately define the correct “timeframe” to define synchronous visits. This may result in the lack of relationships with synchrony found in the present study. As such, further investigations into possible methods that may improve the way studies define synchrony would be an asset to the field.

This study finds the first known evidence for fitness benefits of alternation, finding that alternation predicts brood size on day 14, suggesting that alternation increases the efficiency of provisioning and increases reproductive fitness. Alternation was also found to be predicted by brood size on day 14, suggesting that parents may respond to brood size to make decisions about alternating. Previous studies have investigated the relationship between alternation and brood size but did not find such a relationship (Bebbington and Hatchwell, 2016; Griffioen *et al.*, 2019a; Lejeune *et al.*, 2019), which may be due to the smaller sample sizes in these studies. Due to this being the first study to find such a result, further study is required to better understand the prevalence of this relationship, particularly in studies with larger sample sizes. In addition, more studies manipulating brood size may provide further insights into the relationship between brood size and alternation. This first evidence of benefits for alternation is an important step in understanding whether alternation is an adaptive behaviour.

# Chapter 2: Sex-Specific Costs of Alternation During Provisioning in Blue Tits, *Cyanistes caeruleus*

## Abstract

Around 90% of bird species form socially monogamous partnerships and provide biparental care to offspring. Within such partnerships, sexual conflict over parental care occurs. A recent theory suggests that the costs of sexual conflict may be reduced via conditional cooperation, where partners may alternate provisioning visits to the nest. Partners may also coordinate provisioning by synchronising provisioning visits, a behaviour thought to reduce nest predation. While studies have found evidence for these coordinated patterns of provisioning, questions remain about whether such behaviours are adaptive due to little evidence for their fitness consequences. This study explores the fitness costs and benefits of these behaviours by investigating the effects of alternation and synchrony on divorce and mortality in blue tits, *Cyanistes caeruleus*, using 6 years of breeding data. High alternation was associated with higher probability of mortality in females, but not males, suggesting sex differences in the costs of this behaviour. No effect of alternation or synchrony on divorce was found, but this remains a useful avenue for research. This study is the first to find costs of alternation in the form of mortality, finding evidence that alternation may be an adaptive strategy, given the costs of this behaviour.

## Introduction

In around 90% of bird species, individuals form socially monogamous partnerships and provide biparental care to offspring (Cockburn, 2006). The length of time that these partnerships are maintained varies widely between species, with some species finding a new social partner every year (e.g., great blue heron, *Ardea herodias*; Simpson *et al.*, 1987), while others stay with their social partner for life (e.g., waved albatross, *Phoebastria irrorata*; Harris, 1973). There is likely a selective pressure to form new partnerships when breeding success is low, but to maintain partnerships that lead to high reproductive success (Culina *et al.*, 2015b). Studies have found that reproductive success increases with length of the pair bond (Van de Pol *et al.*, 2006; Sánchez-Macouzet *et al.*, 2014) while pairs that divorce tend to have lower reproductive success (Dubois and Cézilly, 2002; Culina *et al.*, 2015b). Mate retention is thought to be a favourable strategy due to the costs of changing mates and the reproductive benefits of staying with a familiar partner (Ens *et al.*, 1996; Pampus *et al.*, 2005). While evidence suggests that mate retention leads to increased reproductive success in long-lived species (Fowler, 1995), the advantage of long-term pair bonds in short lived species, such as blue tits, is less clear (Pampus *et al.*, 2005), although this may be due to differences in methodological approaches for studying long-lived and short-lived species (Culina *et al.*, 2015b).

Despite reduced reproductive success when compared to mate retention, divorce tends to lead to increased reproductive success when compared to the previous partnership, with females tending to benefit from divorce more than males (Culina *et al.*, 2015b). Divorce has been observed in 92% of socially monogamous species (Jeschke and Kokko, 2008) and is believed to be an adaptive strategy, being triggered by low breeding success and leading to a positive change in breeding success (Culina *et al.*, 2015b). Two main hypotheses attempt to explain why divorce may be adaptive in birds: (i) the "incompatibility" hypothesis, where the two individuals do not breed together successfully as a pair, and (ii) the "better option" hypothesis, where an individual may increase their reproductive success by leaving their partner for a better partner and/or territory (Ens *et al.*, 1993; Dhondt and Adriaensen, 1994).

Individuals may also seek a new partnership due to the death of their previous partner. Parental care is costly, sometimes resulting in survival costs for carers (Alonso-Alvarez and Velando, 2012). Various manipulation experiments have yielded evidence that parental effort can influence individual mortality. For example, female great tits that were subjected to experimentally enlarged broods showed increased parasitaemia and lower overwinter survival rates (Stjernman *et al.*, 2004). The feathers of collared flycatchers with experimentally enlarged broods showed greater wear than control birds, and the severity of this damage was positively correlated with post-breeding mortality (Merilä and Hemborg, 2000). Additionally, blue tit parents with experimentally enlarged broods showed increased levels of heat shock proteins in their blood, a key indicator of physiological stress (Merino *et al.*, 2006). These studies support the expected trend that individuals investing less parental effort should show greater survival, though definitive evidence for this relationship has generally been inconsistent (Graves, 1991; Roff and Fairbairn, 2007; Santos and Nakagawa, 2012).

Survival costs of parental care may also differ between the sexes. A meta-analysis by Santos and Nakagawa (2012) found that males whose parental effort was experimentally increased were less likely to survive than control males, but this trend did not occur in females. This sex difference in the cost of experimentally increased parental effort may be due to sex differences in perceived brood value (Santos and Nakagawa, 2012). Studies suggest that females are less responsive to changes in brood value than males

(Mock *et al.*, 2005; Nakagawa *et al.*, 2007), which may be explained by females provisioning at a rate that is closer to their maximum possible effort during normal levels of parental demand (Low *et al.*, 2011; Santos and Nakagawa, 2012). As a result, females may not have the capacity to increase their parental effort when demand increases, while males, which often provision at lower rates than females, may have more room to increase parental effort, leading to greater survival costs (Santos and Nakagawa, 2012). Differences in the base level of parental effort provided by each sex could be due to differences in certainty of parentage of the brood (Westneat and Sargent, 1996; Queller, 1997; Kokko and Jennions, 2012).

The outcome of partnerships, whether pairs stay together or divorce, seems to be linked with survival in birds. A study on great tits and blue tits found that pairs that stay together show increased survival compared to those that divorced and found new mates (Culina *et al.*, 2015a). In addition, a study on 158 species found that species with high mortality rates also had high divorce rates (Jeschke and Kokko, 2008). This is to be expected, given the likelihood that a partner does not survive to the next breeding season reduces the likelihood of an individual finding and re-pairing with the same partner (Jeschke and Kokko, 2008). As a result, it may be more beneficial to seek a better mate due to the high availability of un-partnered individuals – supporting the “better option” hypothesis of divorce (Jeschke and Kokko, 2008).

Recent theoretical models of sexual conflict and parental care have investigated the possibility that carers may reduce the costs of sexual conflict via conditional cooperation, in the form of turn-taking (alternation) when delivering resources (Johnstone *et al.*, 2014). Evidence supporting this theory has been found in various empirical studies, in both cooperative (Bebbington and Hatchwell, 2016; Savage *et al.*, 2017) and biparental breeding systems (Iserbyt *et al.*, 2017; Leniowski and Węgrzyn, 2018; Iserbyt *et al.*, 2019). While this may be a promising conflict resolution strategy, some studies point out that observed alternation may not be due to active alternation (Baldan *et al.*, 2019; Ihle *et al.*, 2019a; Santema *et al.*, 2019), but may be a result of temporal environmental variation (Schlicht *et al.*, 2016; Baldan *et al.*, 2019). In addition to alternation, studies have investigated the importance of synchrony during provisioning for reproductive fitness. High nest visit synchrony has been observed in various bird species (Mariette and Griffith, 2012; Van Rooij and Griffith, 2013; Leniowski and Węgrzyn, 2018) and is thought to function to reduce nest predation by reducing the number of visits to the nest (Fontaine and Martin, 2006; Raihani *et al.*, 2010). Provisioning synchrony may also facilitate signalling of information between carers (Doutrelant and Covas, 2007) and optimise provisioning and reproductive success (Mariette and Griffith, 2012).

Recent studies have suggested that further exploration of the fitness consequences of coordination is required to fill key gaps in the research of these behaviours (Ihle *et al.*, 2019a). In particular, the only solid evidence of fitness benefits for these behaviours is a reduced predation risk in pairs that synchronise provisioning visits (Raihani *et al.*, 2010). As a result of demand for such research, this study will investigate the fitness consequences of alternation and synchrony during provisioning, specifically looking at divorce and perceived mortality in blue tits, *Cyanistes caeruleus*. If alternation and synchrony are adaptive provisioning strategies, they should result in higher reproductive success. Evidence for such a trend was found in Chapter 1 of this thesis. Divorce tends to occur following low breeding success, thus it is predicted that pairs which alternate or synchronise more often will stay together while those that alternate or synchronise less often will divorce. Investigating the potential for relationships between mortality and alternation and synchrony will be useful to identify the costs and benefits of these behaviours, an important step in better understanding their adaptive significance.

## Methods

This study used breeding and provisioning data from blue tits breeding in nest boxes in deciduous woodland around Lancaster University, Lancashire, U.K. from 2016 to 2021. On average, 75 nest boxes were occupied by blue tits each year. When nestlings were 10-12 days old, parental nest visits were assessed during a 1 hour video recording taken from the outside of the nest box using a camera on a tripod. The entry and exit times of adults visiting the nest box were recorded, as well as the adult's sex and whether a faecal sac was removed. Nests where a brood was being provisioned by only a single male or female were removed from the dataset so that the analyses were only inclusive of provisioning pairs.

Alternation and synchrony z-score were quantified following the same methods detailed in Chapter 1.

### Statistical Analysis

Two sets of analyses were conducted. The first used a binomial generalised linear mixed model (GLMM) to investigate whether alternation or synchrony predicted whether pairs re-paired with one another the following year or divorced, with divorce treated as a binary response variable (yes or no). This was done separately for male and female parents, to test whether alternation or synchrony in one year influenced repairing with the same or a different partner in the following year. To distinguish true divorce from widowing, pair separation was only labelled as divorce if both individuals had been re-captured the year following their initial breeding attempt but were not partnered with one another. This shows that both individuals were alive and present in the population but changed their breeding partners. Individual identity was included as a random effect in both models. Potential fixed effects included alternation and synchrony (model ran separately for alternation and synchrony), proportion of feeds by the opposite sex, total feeds per hour and age of the opposite sex. Age was a factor grouping birds into two categories: 1-year-old birds, and birds aged 2 or more years old.

The second analysis investigated the effects of alternation and synchrony on mortality. To isolate individuals that apparently died versus those that were known to have survived, individuals that bred at the study site for one year only but were not seen in following years were presumed dead. Those that bred at the site for two or more years were categorised as survivors for comparison. Mortality was modelled as a binary response variable (died/survived) and the model was run separately for males and females. Fixed effects were alternation or synchrony, clutch size, age of the individual, age of their partner and calendar year. Age and year were factors. This was again run separately for alternation and synchrony. The interactions of alternation*age, synchrony*age, and male age * female age were explored but were excluded from the model due to having no significant effect.

## Results

The proportion of alternated visits in blue tit pairs ranged from 0.03 to 0.76. Synchrony z-score ranged from -2.51 to 2.87.

### Divorce

A series of binomial GLMMs showed that pair divorce was not predicted by alternation or synchrony for males or females (Table 7, Table 8). The model presented in table 7 was conducted on 54 male blue tits, 38 of which re-paired with their partner the following year and 16 divorced. The model presented in table 8 was conducted on 48 females, 38 of which re-paired with their partner the following year and 10 divorced.

**Table 7.** Binomial mixed models to identify whether alternation or synchrony predict pair divorce in males, with year as a random effect. Proportion of female feeds, total feeds per hour and female age were included in the model to account for variation caused by these effects. Significant (P<0.05) effects are highlighted in bold.

| **Effect** | **Estimate** | **Standard Error** | **Statistic** | **P** |
|---|---|---|---|---|
| **a) Does alternation predict divorce?** | | | | |
| Proportion alternated visits | -5.012 | 3.363 | -1.490 | 0.136 |
| Proportion of feeds by female | 2.986 | 2.358 | 1.266 | 0.205 |
| Total feeds per hour | 0.009 | 0.027 | 0.314 | 0.754 |
| Female age | -1.373 | 0.794 | -1.730 | 0.084 |
| **b) Does synchrony predict divorce?** | | | | |
| Sync Z-score | 0.287 | 0.388 | 0.738 | 0.460 |
| Proportion of feeds by female | 2.142 | 2.288 | 0.936 | 0.349 |
| Total feeds per hour | -0.004 | 0.027 | -0.156 | 0.876 |
| Female age | -0.997 | 0.774 | -1.288 | 0.198 |

**Table 8.** Binomial mixed models to identify whether alternation or synchrony predict pair divorce in females, with year as a random effect. Proportion of male feeds, total feeds per hour and male age were included in the model to account for variation caused by these effects. Significant (P<0.05) effects are highlighted in bold.

| **Effect** | **Estimate** | **Standard Error** | **Statistic** | **P** |
|---|---|---|---|---|
| **a) Does alternation predict divorce?** | | | | |
| Proportion alternated visits | -5.100 | 3.743 | -1.363 | 0.173 |
| Proportion of feeds by male | -0.672 | 2.371 | -0.283 | 0.777 |
| Total feeds per hour | 0.007 | 0.028 | 0.233 | 0.816 |
| Male age | -0.836 | 0.783 | -1.068 | 0.286 |
| **b) Does synchrony predict divorce?** | | | | |
| Sync Z-score | -0.359 | 0.353 | -1.017 | 0.309 |
| Proportion of feeds by male | -0.647 | 2.522 | -0.257 | 0.797 |
| Total feeds per hour | -0.001 | 0.025 | -0.039 | 0.969 |
| Male age | -0.632 | 0.736 | -0.859 | 0.391 |

## Mortality

The second set of binomial GLMMs found an association between alternation and mortality in female blue tits (Table 10, Figure 7), but not in males (Table 9). Females in pairs with higher alternation were more likely to apparently die between breeding seasons than those in pairs with lower alternation (Figure 6, Figure 7). Pair synchrony did not predict mortality for males or females (Table 9, Table 10). Age and year were significant predictors of mortality in all models (Table 9, Table 10, Figure 8, Figure 9). The models presented in table 9 were conducted on 273 males, 91 of which died and 182 survived for two breeding seasons or more. The models presented in table 10 were conducted on 277 females, 98 of which died and 179 survived for two breeding seasons or more.

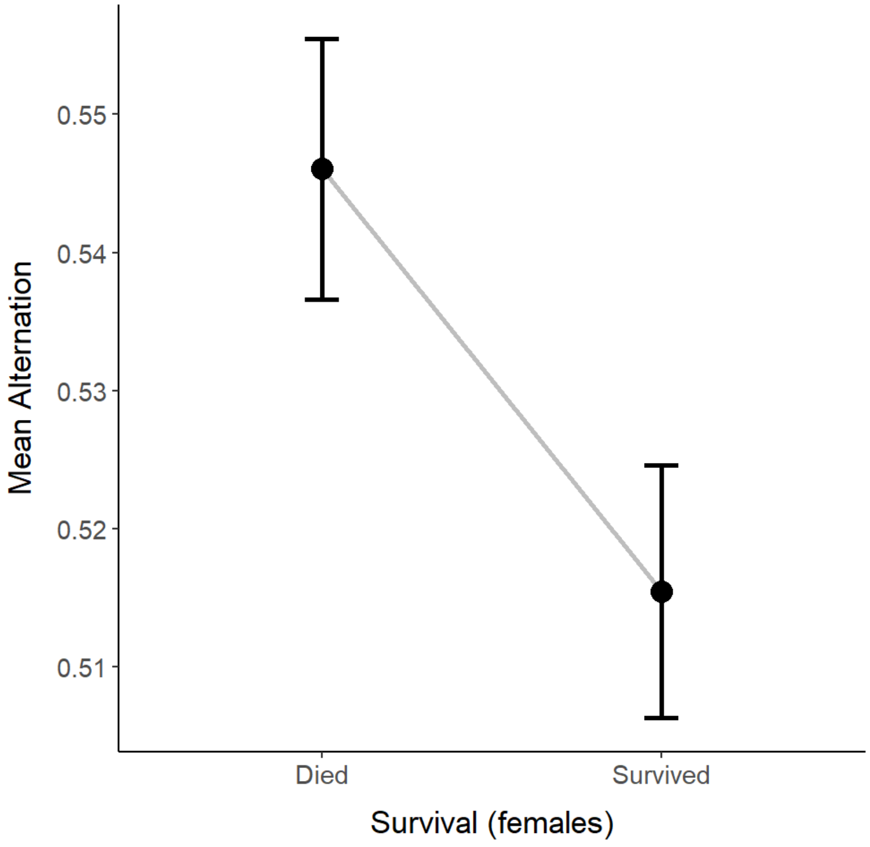

**Figure 6.** Mean ± standard error of pair alternation of female blue tits that died vs those that survived. Pair alternation was measured as the proportion of feeding visits where one parent fed after the other (proportion of alternated visits).

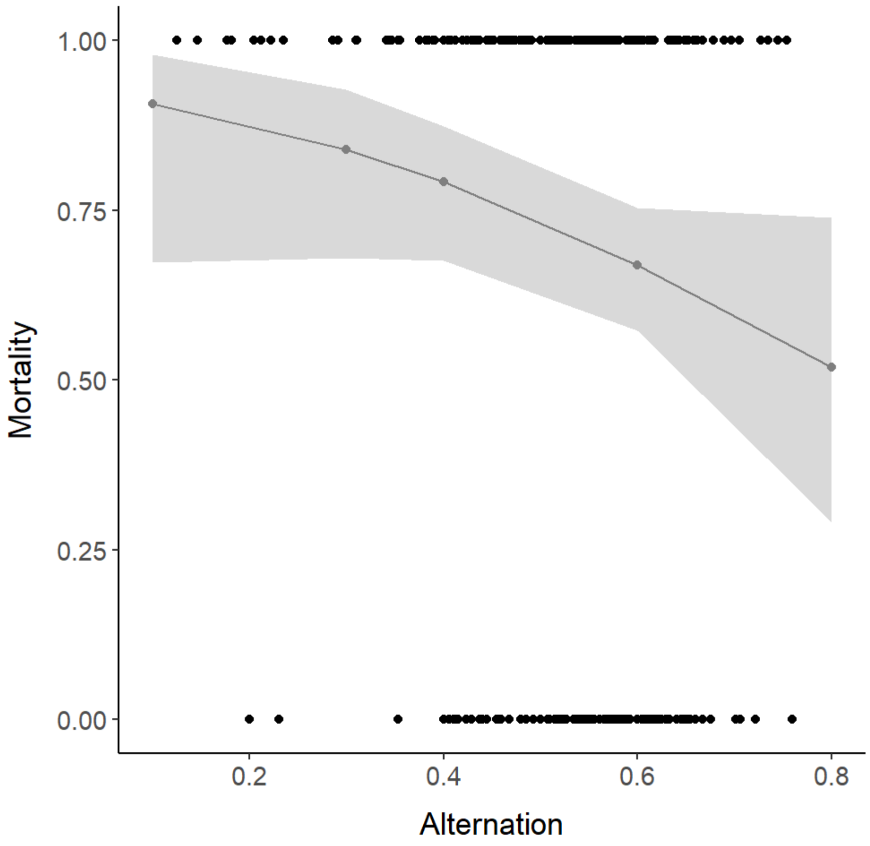

**Figure 7.** Relationship between alternation (proportion of alternated visits) and mortality. The line shows model estimates for alternation (model a, table 10) with 95% confidence intervals.

**Table 9.** Binomial mixed models to identify whether alternation or synchrony predict mortality of male blue tits, with male identity as a random effect. Alternation or synchrony, clutch size, male age, female age and year were included in the model to account for variation caused by these effects. Significant (P<0.05) effects are highlighted in bold.

| **Effect** | **Estimate** | **Standard Error** | **Statistic** | **P** |
|---|---|---|---|---|
| **a) Does alternation predict mortality?** | | | | |
| Proportion alternated visits | 0.828 | 1.782 | 0.465 | 0.642 |
| Clutch size | -0.020 | 0.119 | -0.166 | 0.869 |
| Male age | 2.612 | 0.461 | 5.671 | <**0.001** |
| Female age | 0.630 | 0.374 | 1.684 | 0.092 |
| Year (2017) | 2.074 | 0.627 | 3.305 | **0.001** |
| Year (2018) | 1.599 | 0.591 | 2.707 | **0.007** |
| Year (2019) | 2.210 | 0.624 | 3.544 | **<0.001** |
| Year (2020) | 2.267 | 0.627 | 3.617 | **<0.001** |
| **b) Does synchrony predict mortality?** | | | | |
| Synchrony | 0.019 | 0.181 | 0.106 | 0.916 |
| Clutch size | -0.004 | 0.115 | -0.039 | 0.969 |
| Male age | 2.581 | 0.454 | 5.684 | **<0.001** |
| Female age | 0.640 | 0.374 | 1.711 | 0.087 |
| Year (2017) | 2.092 | 0.626 | 3.342 | **0.001** |
| Year (2018) | 1.602 | 0.591 | 2.711 | **0.007** |
| Year (2019) | 2.188 | 0.622 | 3.515 | **<0.001** |
| Year (2020) | 2.304 | 0.623 | 3.700 | **<0.001** |

**Table 10.** Binomial mixed models to identify whether alternation or synchrony predict mortality of female blue tits, with female identity as a random effect. Alternation or synchrony, clutch size, male age, female age and year were included in the model to account for variation caused by these effects. Significant (P<0.05) effects are highlighted in bold.

| Effect | Estimate | Standard Error | Statistic | P |
|---|---|---|---|---|
| **a) Does alternation predict mortality?** | | | | |
| Proportion alternated visits | -3.148 | 1.756 | -1.792 | 0.073 |
| Clutch size | 0.010 | 0.111 | 0.092 | 0.926 |
| Male age | 0.524 | 0.369 | 1.421 | 0.155 |
| Female age | 1.938 | 0.391 | 4.956 | **<0.001** |
| Year (2017) | 2.021 | 0.593 | 3.409 | **0.001** |
| Year (2018) | 0.911 | 0.515 | 1.771 | 0.076 |
| Year (2019) | 2.107 | 0.579 | 3.641 | **<0.001** |
| Year (2020) | 1.761 | 0.563 | 3.129 | **0.002** |
| **b) Does synchrony predict mortality?** | | | | |
| Synchrony | -0.162 | 0.171 | -0.944 | 0.345 |
| Clutch size | -0.041 | 0.108 | -0.383 | 0.701 |
| Male age | 0.624 | 0.363 | 1.718 | 0.086 |
| Female age | 1.857 | 0.382 | 4.868 | **<0.001** |
| Year (2017) | 1.917 | 0.581 | 3.301 | **0.001** |
| Year (2018) | 0.894 | 0.514 | 1.737 | 0.082 |
| Year (2019) | 2.155 | 0.581 | 3.711 | **<0.001** |
| Year (2020) | 1.570 | 0.544 | 2.887 | **0.004** |

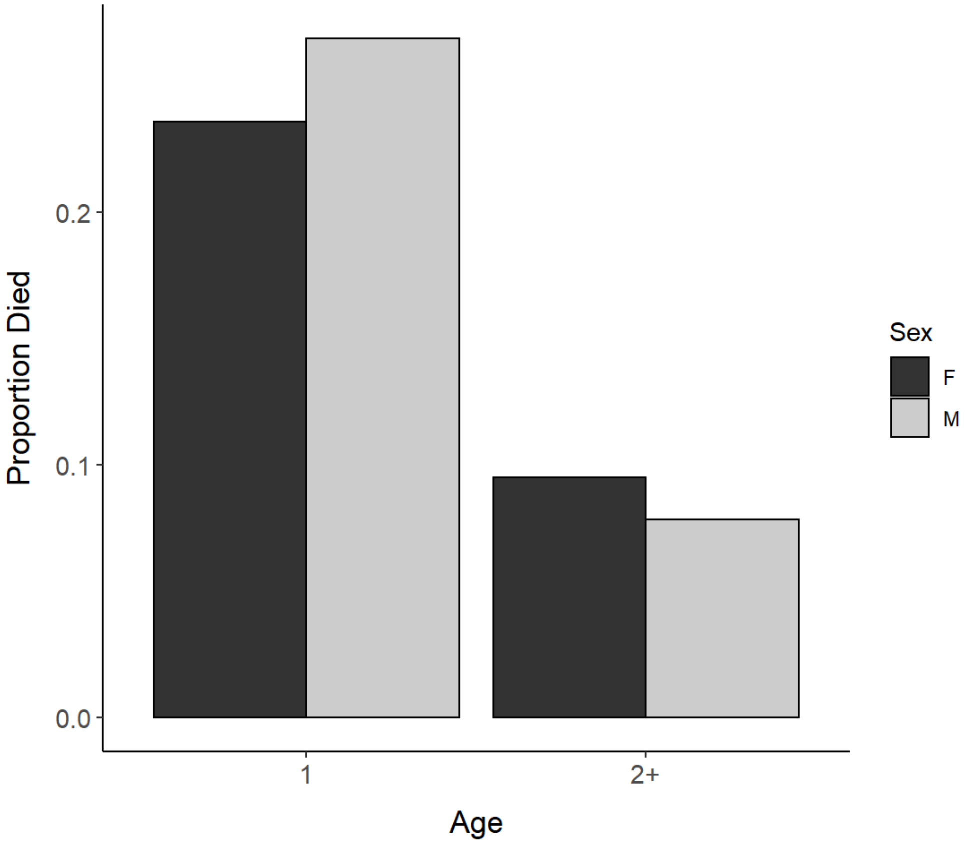

**Figure 8.** The proportion of blue tits of each age group and sex that were presumed dead. Birds that bred at the study site for one year only but were not seen in following years were presumed dead, while those seen at the site for two years or more were categorised as survivors.

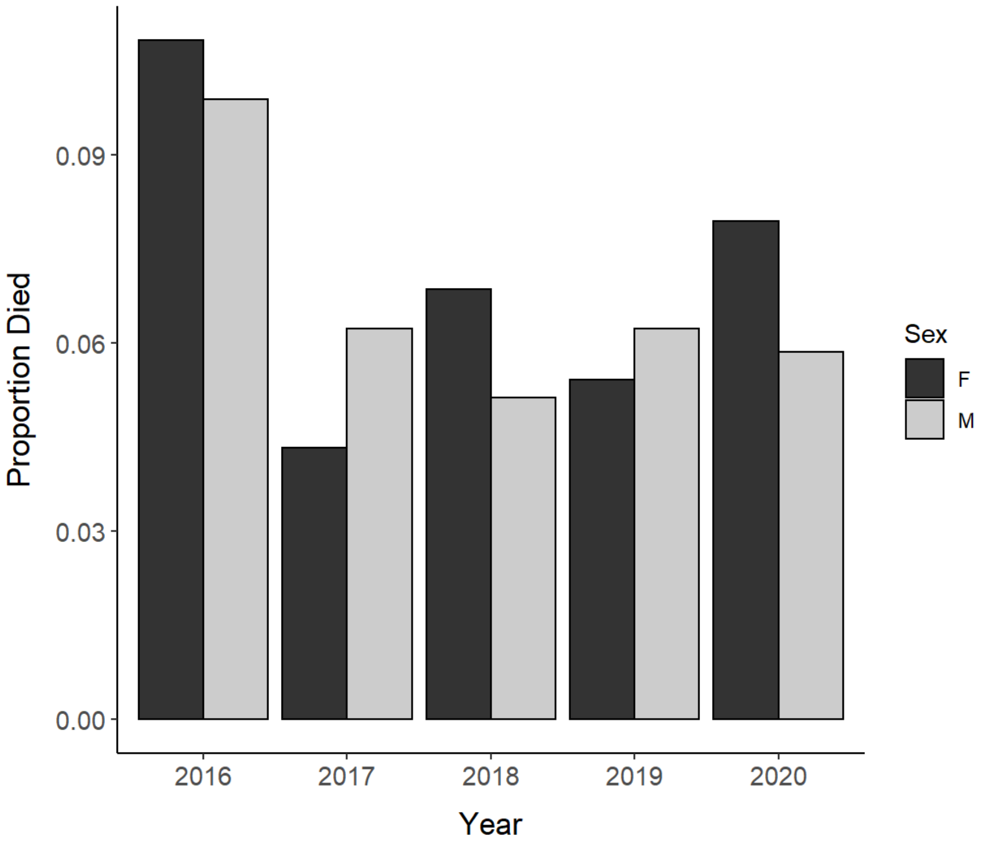

**Figure 9.** The proportion of blue tits from each year and sex that were presumed dead. Birds that bred at the study site for one year only but were not seen in following years were presumed dead, while those seen at the site for two years or more were categorised as survivors.

## Discussion

No significant effect of alternation or synchrony on pair divorce was found (Table 7, Table 8). However, increased mortality in those that alternated more often was found in females (Table 10). While not statistically significant ($P = 0.07$), the effect size and strength of this relationship suggests that it is worth investigation (Figure 7). This trend did not occur in males, suggesting sex differences in the costs of alternation (Table 9). This study is the first to find potential evidence for sex-specific costs of alternation.

This study presents evidence that alternation may impact on the costs of provisioning. Female blue tits that alternated less frequently were more likely to survive than those that alternated more often. Various studies manipulating demand for parental effort have found evidence of survival costs (Alonso-Alvarez and Velando, 2012), such as susceptibility to parasites resulting in reduced over-winter survival rates (Stjernman *et al.*, 2004), feather damage leading to post-breeding mortality (Merilä and Hemborg, 2000) and evidence of physiological stress in the form of elevated blood heat shock proteins (Merino *et al.*, 2006). Alternation during provisioning may lead to at least one of the pair increasing their provisioning rate in order to match with their partner, therefore increasing their parental effort. This may be more energetically demanding, resulting in costs leading to mortality such as those shown by manipulation studies. Given that alternation is expected to increase the efficiency of provisioning and decrease the costs of sexual conflict (Johnstone *et al.*, 2014), it is surprising that costs in the form of increased mortality were found in this study. It could be that alternation reduces the costs of sexual conflict for offspring by increasing the frequency and/or regularity of provisioning, but results in costs for the parents instead. With a trade-off between investment in the current reproductive attempt vs. future reproduction, this suggests that the benefits of alternation (i.e., increased brood size at day 14, Chapter 1) may outweigh the costs (i.e., reduced opportunity for future reproduction due to increased likelihood of mortality), suggesting that alternation may be an adaptive provisioning strategy. Further investigation into the mechanisms leading to mortality as a result of alternation would be beneficial to better understand this trend.

The difference between the sexes for the effect of alternation on mortality suggests key sex differences in the costs and benefits of alternation as a provisioning strategy. Previous research has suggested that males tend to suffer survival costs due to increased parental effort, while females do not (Santos and Nakagawa, 2012). Surprisingly, the opposite trend has been found in the present study, where females seemed to suffer a survival cost while males did not (Table 9, Table 10). Evidence of energetic costs of provisioning for females, but not for males, was also found in a previous study on blue tits by García-Navas and Sanz (2012). This study found that the more frequently females provisioned, the lower their body mass was, but this trend did not occur for males. Alternation is positively related to provisioning rate (Bebbington and Hatchwell, 2016), thus higher alternation can be expected to result in energetic costs. The sex-specific costs found in the present study and by García-Navas and Sanz (2012) suggest that more frequent provisioning is more costly for females than for males. If increased mortality is related to alternation, there may be sex differences in the function or mechanisms of alternation that cause this effect. Alternation might not be caused by both individuals - one of the pair could be actively alternating in response to their partner while the other provisions at their normal rate. If females actively alternate with their partner and males provision at their normal rate, the female may be investing more effort to maintain this pattern, potentially suffering more costs as a result. The causes of this sex difference should be investigated in further study.

Age of the individual and year were both significant predictors of mortality (Table 9, Table 10). Year is an expected predictor of mortality, given annual variation in factors such as weather and prey abundance that may influence survival. Mortality appears highest in 2016, where around 10% of breeding adults did not return to the breeding site in future years, presumed dead. As can be seen in Figure 8, individuals in their first breeding year (age 1) were more likely to be presumed dead than those aged 2 or older. One might expect mortality to be higher in older birds, however the trend seen in Figure 8 is likely due to the way this study categorised mortality, with individuals that bred at the study site for one season only and were not seen in following years being presumed dead. As a result, Figure 8 may reflect the methods used to isolate potential cases of mortality rather than actual mortality trends.

Contrary to expectation, neither alternation nor synchrony were significant predictors of divorce. Staying with a partner is generally beneficial due to the costs of changing mates and the benefits of staying with a familiar partner (Ens *et al.*, 1996; Culina *et al.*, 2015b). Perhaps alternation and synchrony do not influence divorce because the costs of finding a new partner may be higher than the costs of remaining in an uncoordinated partnership. Alternatively, pairs may divorce for reasons other than incompatibility or finding a better mate. Due to the higher mortality and short lifespan of blue tits, the likelihood of a partner returning to the breeding site is lower than in longer-lived species (Jeschke and Kokko, 2008). As a result, the benefits of spending time searching for a previous partner to pair with are reduced. Individuals may prioritise pairing up quickly with any partner over finding a previous one, so the performance of the previous partner might not play any role in divorce for blue tits. Evidence for this theory has been found by Gilsenan *et al*. (2017), who found that divorce in blue tits did not depend on breeding success in the previous year but was predicted by the difference in arrival date of the former pair members. Future studies on the effects on alternation and synchrony on divorce should be conducted on longer-lived species, where the certainty of divorce occurring due to a partner's reproductive performance is higher.

To my knowledge, this study is the first to find an effect of alternation on mortality. The findings of this study, that alternation may influence mortality in females, but not males, suggest potential sex differences in the mechanisms of alternation. As a result, further study is required to understand the potential causes of this effect. More evidence for the energetic costs of alternation would be beneficial. The small sample size for the divorce analyses in this study may have resulted in a small effect size - only 16 males and 10 females divorced their partners, with 38 pairs remaining together. Thus, any effect of alternation and synchrony on divorce may have been missed. Further studies on the effect of alternation and synchrony on divorce are required to better identify if these behaviours are related. Longer-lived species would be ideal for such studies, given that the benefits of mate retention are clearer in these species than short-lived ones (Pampus *et al.*, 2005).

This study found a trend in sex differences in the costs of alternation as a provisioning strategy, with female blue tits being more likely to die when alternation was high, but no effect of alternation on male mortality was found. As the reasons for this sex difference are unclear, further study is required to better understand the causes of such costs. Mortality costs due to alternation suggest a trade-off between optimising provisioning for the current brood via alternation vs. investment in future reproduction. Further investigation into the mechanisms of alternation is required to better understand this behaviour. No effect of alternation or synchrony on divorce was found. This is likely due to the short life span of blue tits reducing the likelihood that a partner will return to the breeding site, reducing the benefits of spending time finding a past partner instead of finding a new one (Jeschke and Kokko, 2008). As a result, future studies should further investigate the influence of alternation and/or synchrony on divorce in longer-lived species. This study highlights key areas that require further study in order to better understand the fitness costs and benefits of pair coordination. Whether coordination behaviours such as alternation and synchrony are adaptive behaviours has been disputed (Ihle *et al.*, 2019a; Santema *et al.*, 2019), however this study provides potential evidence for fitness consequences of alternation, suggesting that it may be an adaptive strategy.

# Overall Conclusions

Johnstone et al.'s (2014) model of alternation for conditional cooperation recently garnered attention due to its potential to explain how parents might reduce the costs of sexual conflict. Previous models of parental care suggested that the evolutionarily stable outcome of sexual conflict is for parents to only partially compensate for reductions in partner investment (McNamara *et al.*, 1999; Lessells and McNamara, 2012). This results in a reduction in parental investment to below optimal levels for offspring fitness, resulting in costs for offspring (Royle *et al.*, 2002; Royle *et al.*, 2010). Johnstone *et al.*'s (2014) model proposes that parents may reduce such costs of sexual conflict via conditional cooperation, by alternating provisioning visits. Various studies found evidence supporting that alternation of provisioning does indeed occur (Bebbington and Hatchwell, 2016; Iserbyt *et al.*, 2017; Savage *et al.*, 2017; Leniowski and Węgrzyn, 2018). In addition, synchrony of provisioning visits was found to be correlated with alternation (Bebbington and Hatchwell, 2016; Leniowski and Węgrzyn, 2018). High nest visit synchrony is thought to reduce the risk of predation by reducing the frequency of nest visits, thus reducing disturbance at the nest (Raihani *et al.*, 2010). Synchrony may also enable signalling of provisioning information (Doutrelant and Covas, 2007) and enhance provisioning and reproductive success (Mariette and Griffith, 2012). Given the correlation between alternation and synchrony, some have suggested that synchrony may enable partners to monitor one another's visit rate to allow effective alternation (Bebbington and Hatchwell, 2016).

While the theory of conditional cooperation seems promising as a conflict resolution strategy, some studies have pointed out that patterns of alternation may not be an active process, perhaps occurring passively due to temporal environmental variation (Baldan *et al.*, 2019; Ihle *et al.*, 2019a; Santema *et al.*, 2019). As a result, such studies argue that conditional cooperation has not yet been fully supported by existing research. To date, there is little evidence for any fitness benefits of coordination behaviours such as alternation and synchrony, with the only evidence so far being reduced predation risk with synchronous nest visits (Raihani *et al.*, 2010; Ihle *et al.*, 2019a). Exploration of the fitness consequences of coordination has therefore been suggested for future studies, as well as investigations into relationships between pair or brood characteristics and coordinated behaviours (Ihle *et al.*, 2019a). As a result, this thesis aimed to (i) explore the costs and benefits of alternation and synchrony, and (ii) identify relationships between pair/brood characteristics and alternation/synchrony. Chapter 1 investigated the prevalence of alternation and synchrony, the relationship between alternation and synchrony, and relationships between these behaviours and indicators of reproductive success. Following this, Chapter 2 investigated potential costs and benefits of alternation and synchrony, specifically looking at relationships with divorce and likelihood of mortality.

This study found evidence that breeding blue tits providing food for nestlings showed patterns of parental care that were consistent with coordinated provisioning behaviours (alternation and synchrony). Alternation and synchrony of provisioning visits by parents occurred more than expected by chance. Alternation and synchrony were also significantly correlated, as has been found in studies on other species (Bebbington and Hatchwell, 2016; Leniowski and Węgrzyn, 2018). This study also found that alternation appears to lead to increased reproductive success, supporting Johnstone *et al.*'s (2014) theory. Until this finding, the only known benefit of coordination was reduced predation rate with increased synchrony (Raihani *et al.*, 2010; Bebbington and Hatchwell, 2016). The finding of benefits of alternation is an important step in understanding whether this behaviour is adaptive. High alternation was associated with a higher chance of mortality in females, but not males, suggesting that alternation has sex-specific costs. These increased mortality costs suggest that alternating might transfer the costs of sexual conflict from the offspring to the parents. Further analysis of the costs and benefits of coordination are required to support the findings of this study and understand the adaptive significance of coordination. Studies investigating the effects of alternation and/or synchrony on parent mortality, and the mechanisms leading to mortality, would enhance understanding of the costs of these behaviours. In addition, the sex-specific costs suggested by this study require further investigation.

Surprisingly, synchrony was not related to many variables investigated in this study. It was expected that variables that were significantly related to pair alternation would also be related to synchrony, given the correlation between alternation and synchrony (Bebbington and Hatchwell, 2016; Chapter 1). This lack of relationships may be due to synchrony perhaps primarily functioning to reduce predation risk (Raihani *et al.*, 2010), such that it does not occur frequently if predation risk is low. Given that synchrony is thought to reduce predation risk, studies manipulating perceived predation risk may generate further insights into this behaviour. Predator presence could be simulated using model predators and audio playbacks of predator calls. Alternatively, if synchrony does function for partner monitoring to facilitate alternation (Doutrelant and Covas, 2007; Bebbington and Hatchwell, 2016), the effect of synchrony on reproductive success may be too indirect to show a relationship with variables indicating reproductive success. In addition, the methods used to quantify synchrony may be limited in that they required the arbitrary specification of a bandwidth to define synchronous nest visits. As a result, synchrony may not have been accurately defined in this study. Further development of methods to improve ways of defining synchrony would be advantageous.

Studies tend to consider alternation and synchrony together in order to develop a thorough picture of coordination during provisioning. However, the functions of these two behaviours seem to differ, with alternation theorised to increase the efficiency of provisioning (supported by Chapter 1 of this thesis) and reduce the costs of sexual conflict, while synchrony is thought to reduce nest predation (Raihani *et al.*, 2010). As a result, these two behaviours are likely influenced by different factors. Future studies should take these differences into account when developing and testing hypotheses about coordination, considering the separate factors that may impact alternation and synchrony when constructing models. For example, as mentioned above, synchrony is likely influenced by predation risk, so this should be considered in models exploring synchrony.

The relationships of alternation and synchrony with mate choice would be an interesting avenue for further study of coordination. If coordinated provisioning is adaptive, it would be expected that individuals will attempt to pair with mates that will show high coordination. If so, what characteristics might individuals use during mate choice to select a partner with whom they will be well coordinated? The present study investigated the effect of alternation and synchrony on divorce, aiming to explore whether pair coordination is important for mate retention. While this study found no significant effects of coordination on divorce, future studies are encouraged to investigate these relationships, particularly in longer-lived species where the certainty of divorce occurring due to a partner's reproductive performance is higher. Understanding whether individuals choose to stay paired to mates with whom they have experienced high coordination would provide insights into the importance of coordination in mate choice.

This study appears to have used one of the largest datasets of any coordination study. Using 6 years of blue tit breeding and provisioning data from a site with an average nest box occupancy of 75 boxes per year, this large dataset may be the reason that previously undetected effects were found in this study. For example, the relationship between brood size and alternation had been investigated in previous studies, but no relationship was found (Bebbington and Hatchwell, 2016; Griffioen *et al.*, 2019a; Lejeune *et al.*, 2019). This may mean that the effect of brood size on alternation is small. Larger datasets than are currently used in coordination studies may be required to detect relationships between coordination behaviours and brood characteristics, thus researchers in possession of such datasets are encouraged to contribute where possible.

## References

Alonso-Alvarez, C. and Velando, A. (2012) Benefits and costs of parental care. In: N. J. Royle, P. Smiseth and M. Kölliker (ed.). *The evolution of parental care*, pp**:** 40-61.

Alonzo, S.H. (2010) Social and coevolutionary feedbacks between mating and parental investment. *Trends in Ecology & Evolution,* 25, 99-108.

Alonzo, S.H. (2012) Sexual selection favours male parental care, when females can choose. *Proceedings of the Royal Society B: Biological Sciences,* 279, 1784-1790.

Alonzo, S.H. and Heckman, K.L. (2010) The unexpected but understandable dynamics of mating, paternity and paternal care in the ocellated wrasse. *Proceedings of the Royal Society B: Biological Sciences,* 277, 115-122.

Alonzo, S.H. and Klug, H. (2012) Paternity, maternity, and parental care. In: N. J. Royle, P. Smiseth and M. Kölliker (ed.). *The evolution of parental care*. Oxford: Oxford University Press, pp**:** 189-205.

Ayres, M.P. (1993) Plant defense, herbivory, and climate change. In: P. M. Karieva, J. G. Kingsolver and R. B. Huey (ed.). *Biotic interactions and global change*. Sunderland, MA, USA: Sinauer Associates Inc., pp**:** 75-94.

Baldan, D., Hinde, C.A. and Lessells, C.M. (2019) Turn-taking between provisioning parents: partitioning alternation. *Frontiers in Ecology and Evolution,* 7.

Balshine-Earn, S. and Earn, D.J.D. (1997) An evolutionary model of parental care in st. peter's fish. *Journal of Theoretical Biology,* 184, 423-431.

Barta, Z., Székely, T., Liker, A. and Harrison, F. (2014) Social role specialization promotes cooperation between parents. *The American Naturalist,* 183, 747-761.

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

Bebbington, K. and Hatchwell, B.J. (2016) Coordinated parental provisioning is related to feeding rate and reproductive success in a songbird. *Behavioral Ecology,* 27, 652-659.

Birkhead, T. and Møller, A. (1996) Monogamy and sperm competition in birds. In: J. Black (ed.). *Partnerships in birds*. Oxford: Oxford University Press, pp**:** 323-343.

Birkhead, T.R. and Møller, A.P. (1992) *Sperm competition in birds*. London: Academic Press.

Bonneaud, C., Mazuc, J., Gonzalez, G., Haussy, C., Chastel, O., Faivre, B. and Sorci, G. (2003) Assessing the cost of mounting an immune response. *The American Naturalist,* 161, 367-379.

Bowers, E.K., Nietz, D., Thompson, C.F. and Sakaluk, S.K. (2014) Parental provisioning in house wrens: effects of varying brood size and consequences for offspring. *Behavioral Ecology,* 25, 1485-1493.

Brennan, P.L.R. (2010) Clutch predation in great tinamous *Tinamus major* and implications for the evolution of egg color. *Journal of Avian Biology,* 41, 419-426.

Brennan, P.L.R. and Hyseni, C. (2008) Development of microsatellite markers for parentage analysis in the great tinamou (*Tinamus major*). *Molecular Ecology Resources,* 8, 933-935.

Burley, N.T. and Calkins, J.D. (1999) Sex ratios and sexual selection in socially monogamous zebra finches. *Behavioral Ecology,* 10, 626-635.

Chapman, T., Arnqvist, G., Bangham, J. and Rowe, L. (2003) Sexual conflict. *Trends in Ecology & Evolution,* 18, 41-47.

Clutton-Brock, T. (2017) Reproductive competition and sexual selection. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 372, 20160310.

Clutton-Brock, T.H. (1991) *The evolution of parental care*. Princeton: Princeton University Press.

Clutton-Brock, T.H. and Parker, G.A. (1992) Potential reproductive rates and the operation of sexual selection. *The Quarterly Review of Biology,* 67, 437-456.

Cockburn, A. (2006) Prevalence of different modes of parental care in birds. *Proceedings of the Royal Society B: Biological Sciences,* 273, 1375-1383.

Culina, A., Lachish, S. and Sheldon, B.C. (2015a) Evidence of a link between survival and pair fidelity across multiple tit populations. *Journal of Avian Biology,* 46, 507-515.

Culina, A., Radersma, R. and Sheldon, B.C. (2015b) Trading up: the fitness consequences of divorce in monogamous birds. *Biological Reviews,* 90, 1015-1034.

Dawkins, R. and Carlisle, T.R. (1976) Parental investment, mate desertion and a fallacy. *Nature,* 262, 131-133.

Dhondt, A.A. and Adriaensen, F. (1994) Causes and effects of divorce in the blue tit *Parus caeruleus*. *Journal of Animal Ecology,* 63, 979-987.

Dickinson, J.L. (2003) Male share of provisioning is not influenced by actual or apparent loss of paternity in western bluebirds. *Behavioral Ecology,* 14, 360-366.

DiSciullo, R.A., Thompson, C.F. and Sakaluk, S.K. (2019) Perceived threat to paternity reduces likelihood of paternal provisioning in house wrens. *Behavioral Ecology,* 30, 1336-1343.

Doutrelant, C. and Covas, R. (2007) Helping has signalling characteristics in a cooperatively breeding bird. *Animal Behaviour,* 74, 739-747.

Dubois, F. and Cézilly, F. (2002) Breeding success and mate retention in birds: a meta-analysis. *Behavioral Ecology and Sociobiology,* 52, 357-364.

Emlen, S.T. and Oring, L.W. (1977) Ecology, sexual selection, and the evolution of mating systems. *Science,* 197, 215-223.

Ens, B.J., Choudhury, S. and Black, J.M. (1996) Mate fidelity and divorce in monogamous birds. In: J. M. Black (ed.). *Partnerships in Birds: The Study of Monogamy*. Oxford: Oxford University Press, pp**:** 344-401.

Ens, B.J., Safriel, U.N. and Harris, M.P. (1993) Divorce in the long-lived and monogamous oystercatcher, *Haematopus ostralegus*: incompatibility or choosing the better option? *Animal Behaviour,* 45, 1199-1217.

Farmer, M.B. and Alonzo, S.H. (2008) Competition for territories does not explain allopaternal care in the tessellated darter. *Environmental Biology of Fishes,* 83, 391-395.

Fontaine, J.J. and Martin, T.E. (2006) Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecology Letters,* 9, 428-434.

Fowler, G.S. (1995) Stages of age-related reproductive success in birds: simultaneous effects of age, pair-bond duration and reproductive experience. *American Zoologist,* 35, 318-328.

Fromhage, L. and Jennions, M.D. (2016) Coevolution of parental investment and sexually selected traits drives sex-role divergence. *Nature Communications,* 7, 12517.

GarcÍa-Navas, V. and Sanz, J.J. (2012) Environmental and within-nest factors influencing nestling-feeding patterns of mediterranean blue tits (*Cyanistes caeruleus*). *The Condor,* 114, 612-621.

Gilsenan, C., Valcu, M. and Kempenaers, B. (2017) Difference in arrival date at the breeding site between former pair members predicts divorce in blue tits. *Animal Behaviour,* 133, 57-72.

Godfray, H.C.J. (1995) Evolutionary theory of parent–offspring conflict. *Nature,* 376, 133-138.

Gowaty, P.A. (1996) Battles of the sexes and origins of monogamy. In: J. Black (ed.). *Partnerships in birds: The study of monogamy*. Oxford: Oxford University Press, pp**:** 21-52.

Graves, J. (1991) Comments on the sample sizes used to test the effect of experimental brood enlargement on adult survival. *The Auk,* 108, 967-969.

Griffioen, M., Iserbyt, A. and Müller, W. (2019a) Handicapping males does not affect their rate of parental provisioning, but impinges on their partners' turn taking behavior. *Frontiers in Ecology and Evolution,* 7.

Griffioen, M., Müller, W. and Iserbyt, A. (2019b) A fixed agreement—consequences of brood size manipulation on alternation in blue tits. *PeerJ,* 7, e6826.

Haig, D. (2004) Genomic imprinting and kinship: how good is the evidence? *Annual Review of Genetics,* 38, 553-585.

Hamilton, W.D. (1964) The genetical evolution of social behaviour. *Journal of Theoretical Biology,* 7, 1-52.

Hansson, B., Bensch, S. and Hasselquist, D. (1997) Infanticide in great reed warblers: secondary females destroy eggs of primary females. *Animal Behaviour,* 54, 297-304.

Harris, M.P. (1973) The biology of the waved albatross *Diomedea irrorata* of Hood Island, Galapagos. *Ibis,* 115, 483-510.

Harrison, F., Barta, Z., Cuthill, I. and Székely, T. (2009) How is sexual conflict over parental care resolved? A meta-analysis. *Journal of Evolutionary Biology,* 22, 1800-1812.

Hinde, C.A. (2006) Negotiation over offspring care?—a positive response to partner-provisioning rate in great tits. *Behavioral Ecology,* 17, 6-12.

Hopwood, P.E., Moore, A.J., Tregenza, T. and Royle, N.J. (2015) Male burying beetles extend, not reduce, parental care duration when reproductive competition is high. *Journal of Evolutionary Biology,* 28, 1394-1402.

Houston, A. and Davies, N. (1985) The evolution of cooperation and life history in the dunnock. In: R. Sibly and R. Smith (ed.). *Behavioural Ecology*. Oxford: Blackwell Scientific, pp**:** 471-487.

Houston, A.I. and McNamara, J.M. (2002) A self–consistent approach to paternity and parental effort. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences,* 357, 351-362.

Houston, A.I., Székely, T. and McNamara, J.M. (2005) Conflict between parents over care. *Trends in Ecology & Evolution,* 20, 33-38.

Hunt, J. and Simmons, L.W. (2002) Confidence of paternity and paternal care: covariation revealed through the experimental manipulation of the mating system in the beetle *Onthophagus taurus*. *Journal of Evolutionary Biology,* 15, 784-795.

Ihle, M., Pick, J.L., Winney, I.S., Nakagawa, S. and Burke, T. (2019a) Measuring up to reality: null models and analysis simulations to study parental coordination over provisioning offspring. *Frontiers in Ecology and Evolution,* 7.

Ihle, M., Pick, J.L., Winney, I.S., Nakagawa, S., Schroeder, J. and Burke, T. (2019b) Rearing success does not improve with apparent pair coordination in offspring provisioning. *Frontiers in Ecology and Evolution,* 7.

Iserbyt, A., Fresneau, N., Kortenhoff, T., Eens, M. and Müller, W. (2017) Decreasing parental task specialization promotes conditional cooperation. *Scientific Reports,* 7, 6565.

Iserbyt, A., Griffioen, M., Eens, M. and Müller, W. (2019) Enduring rules of care within pairs - how blue tit parents resume provisioning behaviour after experimental disturbance. *Scientific Reports,* 9, 2776.

Jeschke, J.M. and Kokko, H. (2008) Mortality and other determinants of bird divorce rate. *Behavioral Ecology and Sociobiology,* 63, 1-9.

Johnstone, R.A. and Hinde, C.A. (2006) Negotiation over offspring care—how should parents respond to each other's efforts? *Behavioral Ecology,* 17, 818-827.

Johnstone, R.A., Manica, A., Fayet, A.L., Stoddard, M.C., Rodriguez-Gironés, M.A. and Hinde, C.A. (2014) Reciprocity and conditional cooperation between great tit parents. *Behavioral Ecology,* 25, 216-222.

Johnstone, R.A. and Savage, J.L. (2019) Conditional cooperation and turn-taking in parental care. *Frontiers in Ecology and Evolution,* 7.

Keenleyside, M.H.A. (1983) Mate desertion in relation to adult sex ratio in the biparental cichlid fish *Herotilapia multispinosa*. *Animal Behaviour,* 31, 683-688.

Klug, H., Alonzo, S.H. and Bonsall, M.B. (2012) Theoretical foundations of parental care. In: N. J. Royle, P. T. Smiseth and M. Kölliker (ed.). *The evolution of parental care*. Oxford: Oxford University Press, pp**:** 21-36.

Kokko, H. and Jennions, M.D. (2008) Parental investment, sexual selection and sex ratios. *Journal of Evolutionary Biology,* 21, 919-948.

Kokko, H. and Jennions, M.D. (2012) Sex differences in parental care. In: N. J. Royle, P. Smiseth and M. Kölliker (ed.). *The evolution of parental care*. Oxford: Oxford University Press.

Lack, D.L. (1968) *Ecological adaptations for breeding in birds*. London: Methuen.

Lehtonen, J., Parker, G.A. and Schärer, L. (2016) Why anisogamy drives ancestral sex roles. *Evolution,* 70, 1129-1135.

Lejeune, L., Savage, J.L., Bründl, A.C., Thiney, A., Russell, A.F. and Chaine, A.S. (2019) Environmental effects on parental care visitation patterns in blue tits *Cyanistes caeruleus*. *Frontiers in Ecology and Evolution,* 7.

Leniowski, K. and Węgrzyn, E. (2018) Synchronisation of parental behaviours reduces the risk of nest predation in a socially monogamous passerine bird. *Scientific Reports,* 8, 7385.

Lessells, C. (2012) Sexual conflict. In: N. Royle, P. Smiseth and M. Kölliker (ed.). *The evolution of parental care*: Oxford University Press 2012, pp**:** 150-170.

Lessells, C.M. (2006) The evolutionary outcome of sexual conflict. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 361, 301-317.

Lessells, C.M. and McNamara, J.M. (2012) Sexual conflict over parental investment in repeated bouts: negotiation reduces overall care. *Proceedings of the Royal Society B: Biological Sciences,* 279, 1506-1514.

Liker, A., Freckleton, R.P. and Székely, T. (2013) The evolution of sex roles in birds is related to adult sex ratio. *Nature Communications,* 4, 1587.

Liker, A., Freckleton, Robert P. and Székely, T. (2014) Divorce and infidelity are associated with skewed adult sex ratios in birds. *Current Biology,* 24, 880-884.

Lima, S.L. (2009) Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. *Biological Reviews,* 84, 485-513.

Low, M., Makan, T. and Castro, I. (2011) Food availability and offspring demand influence sex-specific patterns and repeatability of parental provisioning. *Behavioral Ecology,* 23, 25-34.

Magrath, M., J. L., Janson, J., Komdeur, J., Elgar, M.A. and Mulder, R.A. (2007) Provisioning adjustments by male and female fairy martins to short-term manipulations of brood size. *Behaviour,* 144, 1119-1132.

Mainwaring, M.C. and Griffith, S.C. (2013) Looking after your partner: sentinel behaviour in a socially monogamous bird. *PeerJ,* 1, e83.

Mariette, M.M. and Griffith, S.C. (2012) Nest visit synchrony is high and correlates with reproductive success in the wild Zebra finch *Taeniopygia guttata*. *Journal of Avian Biology,* 43, 131-140.

Martin, T.E., Scott, J. and Menge, C. (2000) Nest predation increases with parental activity: separating nest site and parental activity effects. *Proceedings of the Royal Society of London. Series B: Biological Sciences,* 267, 2287-2293.

Maynard Smith, J. (1977) Parental investment: A prospective analysis. *Animal Behaviour,* 25, 1-9.

McNamara, J.M., Gasson, C.E. and Houston, A.I. (1999) Incorporating rules for responding into evolutionary games. *Nature,* 401, 368-371.

McNamara, J.M., Székely, T., Webb, J.N. and Houston, A.I. (2000) A dynamic game-theoretic model of parental care. *Journal of Theoretical Biology,* 205, 605-623.

Meade, J., Nam, K.-B., Lee, J.-W. and Hatchwell, B.J. (2011) An experimental test of the information model for negotiation of biparental care. *PLoS one,* 6, e19684.

Merilä, J. and Hemborg, C. (2000) Fitness and feather wear in the collared flycatcher *Ficedula albicollis*. *Journal of Avian Biology,* 31, 504-510.

Merino, S., Moreno, J., Tomás, G., Martínez, J., Morales, J., Martínez-de la Puente, J. and Osorno, J.L. (2006) Effects of parental effort on blood stress protein HSP60 and immunoglobulins in female blue tits: a brood size manipulation experiment. *Journal of Animal Ecology,* 75, 1147-1153.

Mock, D.W., Schwagmeyer, P.L. and Parker, G.A. (2005) Male house sparrows deliver more food to experimentally subsidized offspring. *Animal Behaviour,* 70, 225-236.

Møller, A.P. (2000) Male parental care, female reproductive success, and extrapair paternity. *Behavioral Ecology,* 11, 161-168.

Møller, A.P. and Birkhead, T.R. (1993) Certainty of paternity covaries with paternal care in birds. *Behavioral Ecology and Sociobiology,* 33, 261-268.

Møller, A.P. and Cuervo, J.J. (2000) The evolution of paternity and paternal care in birds. *Behavioral Ecology,* 11, 472-485.

Müller, W., Lessells, C.M., Korsten, P. and von Engelhardt, N. (2007) Manipulative signals in family conflict? On the function of maternal yolk hormones in birds. *The American Naturalist,* 169, E84-E96.

Nakagawa, S., Gillespie, D.O.S., Hatchwell, B.J. and Burke, T. (2007) Predictable males and unpredictable females: sex difference in repeatability of parental care in a wild bird population. *Journal of Evolutionary Biology,* 20, 1674-1681.

Pampus, M., Schmidt, K.-H. and Wiltschko, W. (2005) Pair bond and breeding success in Blue Tits *Parus caeruleus* and Great Tits *Parus major*. *Ibis,* 147, 92-108.

Paredes, R., Jones, I.L. and Boness, D.J. (2005) Reduced parental care, compensatory behaviour and reproductive costs of thick-billed murres equipped with data loggers. *Animal Behaviour,* 69, 197-208.

Parker, G. (1979) Sexual selection and sexual conflict. In: M. Blum and N. Blum (ed.). *Sexual selection and reproductive competition in insects*. London: Academic Press, pp: 166.

Peterson, K.A., Thusius, K.J., Whittingham, L.A. and Dunn, P.O. (2001) Allocation of male parental care in relation to paternity within and among broods of the common yellowthroat (*Geothlypis trichas*). *Ethology,* 107, 573-586.

Queller, D.C. (1997) Why do females care more than males? *Proceedings of the Royal Society of London. Series B: Biological Sciences,* 264, 1555-1557.

Raihani, N.J., Nelson-Flower, M.J., Moyes, K., Browning, L.E. and Ridley, A.R. (2010) Synchronous provisioning increases brood survival in cooperatively breeding pied babblers. *Journal of Animal Ecology,* 79, 44-52.

Refsnider, J.M. and Janzen, F.J. (2010) Putting eggs in one basket: ecological and evolutionary hypotheses for variation in oviposition-site choice. *Annual Review of Ecology, Evolution, and Systematics,* 41, 39-57.

Reynolds, J.D., Goodwin, N.B. and Freckleton, R.P. (2002) Evolutionary transitions in parental care and live bearing in vertebrates. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences,* 357, 269-281.

Rice, W.R. and Holland, B. (1997) The enemies within: intergenomic conflict, interlocus contest evolution (ICE), and the intraspecific Red Queen. *Behavioral Ecology and Sociobiology,* 41, 1-10.

Roff, D.A. and Fairbairn, D.J. (2007) The evolution of trade-offs: where are we? *Journal of Evolutionary Biology,* 20, 433-447.

Royle, N.J., Hartley, I.R. and Parker, G.A. (2002) Sexual conflict reduces offspring fitness in zebra finches. *Nature,* 416, 733-736.

Royle, N.J., Schuett, W. and Dall, S.R.X. (2010) Behavioral consistency and the resolution of sexual conflict over parental investment. *Behavioral Ecology,* 21, 1125-1130.

Royle, N.J., Smiseth, P.T. and Kölliker, M. (2012) *The evolution of parental care*. Oxford: Oxford University Press.

Sakaluk, S.K. and Müller, J.K. (2008) Risk of sperm competition mediates copulation duration, but not paternity, of male burying beetles. *Journal of insect behavior,* 21, 153-163.

Sánchez-Macouzet, O., Rodríguez, C. and Drummond, H. (2014) Better stay together: pair bond duration increases individual fitness independent of age-related variation. *Proceedings of the Royal Society B: Biological Sciences,* 281, 20132843.

Santema, P., Schlicht, E. and Kempenaers, B. (2019) Testing the conditional cooperation model: what can we learn from parents taking turns when feeding offspring? *Frontiers in Ecology and Evolution,* 7.

Santos, E.S.A. and Nakagawa, S. (2012) The costs of parental care: a meta-analysis of the trade-off between parental effort and survival in birds. *Journal of Evolutionary Biology,* 25, 1911-1917.

Savage, J.L., Browning, L.E., Manica, A., Russell, A.F. and Johnstone, R.A. (2017) Turn-taking in cooperative offspring care: by-product of individual provisioning behavior or active response rule? *Behavioral Ecology and Sociobiology,* 71, 162.

Schlicht, E., Santema, P., Schlicht, R. and Kempenaers, B. (2016) Evidence for conditional cooperation in biparental care systems? A comment on Johnstone et al. *Behavioral Ecology,* 27, e2-e5.

Schöll, E.M., Ohm, J., Hoffmann, K.F. and Hille, S.M. (2016) Caterpillar biomass depends on temperature and precipitation, but does not affect bird reproduction. *Acta Oecologica,* 74, 28-36.

Schrader, M., Keller, M.K. and Lucey, G.F. (2020) Adaptation to monogamy influences parental care but not mating behavior in the burying beetle, *Nicrophorus vespilloides*. *Ecology and Evolution,* 10, 6525-6535.

Schuett, W., Dall, S.R.X. and Royle, N.J. (2011) Pairs of zebra finches with similar ‘personalities’ make better parents. *Animal Behaviour,* 81, 609-618.

Schwagmeyer, P.L., Mock, D.W. and Parker, G.A. (2002) Biparental care in house sparrows: negotiation or sealed bid? *Behavioral Ecology,* 13, 713-721.

Sheldon, B.C. (1994) Male phenotype, fertility, and the pursuit of extra-pair copulations by female birds. *Proceedings of the Royal Society of London. Series B: Biological Sciences,* 257, 25-30.

Sheldon, B.C. and Ellegren, H. (1998) Paternal effort related to experimentally manipulated paternity of male collared flycatchers. *Proceedings of the Royal Society of London. Series B: Biological Sciences,* 265, 1737-1742.

Simpson, K., Smith, J.N.M. and Kelsall, J.P. (1987) Correlates and consequences of coloniality in great blue herons. *Canadian Journal of Zoology,* 65, 572-577.

Slagsvold, T. and Lifjeld, J.T. (1988) Ultimate adjustment of clutch size to parental feeding capacity in a passerine bird. *Ecology,* 69, 1918-1922.

Spoon, T.R., Millam, J.R. and Owings, D.H. (2006) The importance of mate behavioural compatibility in parenting and reproductive success by cockatiels, *Nymphicus hollandicus*. *Animal Behaviour,* 71, 315-326.

Stearns, S.C. (1989) Trade-offs in life-history evolution. *Functional ecology,* 3, 259-268.

Stjernman, M., Råberg, L. and Nilsson, J. (2004) Survival costs of reproduction in the blue tit (*Parus caeruleus*): a role for blood parasites? *Proceedings of the Royal Society of London. Series B: Biological Sciences,* 271, 2387-2394.

Székely, T., Weissing, F.J. and Komdeur, J. (2014) Adult sex ratio variation: implications for breeding system evolution. *Journal of Evolutionary Biology,* 27, 1500-1512.

Tamburini, G., Marini, L., Hellrigl, K., Salvadori, C. and Battisti, A. (2013) Effects of climate and density-dependent factors on population dynamics of the pine processionary moth in the Southern Alps. *Climatic Change,* 121, 701-712.

Titulaer, M., Spoelstra, K., Lange, C.Y. and Visser, M.E. (2012) Activity patterns during food provisioning are affected by artificial light in free living great tits (*Parus major*). *PLoS One,* 7, e37377.

Trivers, R.L. (1972) Parental investment and sexual selection. In: B. Campbell (ed.). *Sexual Selection and the Descent of Man 1871-1971*. Chicago, IL: Aldine.

Van de Pol, M., Heg, D., Bruinzeel, L.W., Kuijper, B. and Verhulst, S. (2006) Experimental evidence for a causal effect of pair-bond duration on reproductive performance in oystercatchers (*Haematopus ostralegus*). *Behavioral Ecology,* 17, 982-991.

Van Rooij, E.P. and Griffith, S.C. (2013) Synchronised provisioning at the nest: parental coordination over care in a socially monogamous species. *PeerJ,* 1, e232.

Westneat, D.F. and Sargent, R.C. (1996) Sex and parenting: the effects of sexual conflict and parentage on parental strategies. *Trends in Ecology & Evolution,* 11, 87-91.

Wetton, J.H. and Parkin, D.T. (1991) An association between fertility and cuckoldry in the house sparrow, *Passer domesticus*. *Proceedings of the Royal Society of London. Series B: Biological Sciences,* 245, 227-233.

Wickham, H. (2009) *ggplot2: elegant graphics for data analysis (use R!)*. New York: Springer.

Williams, G.C. (1966) Natural selection, the costs of reproduction, and a refinement of Lack's principle. *The American Naturalist,* 100, 687-690.

Wilson, E.O. (1971) *The insect societies*. Cambridge: Harvard University Press.