Paying attention but not coordinating: Parental care in European starlings (*Sturnus vulgaris*)

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Joanna Enns

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Declaration of Committee

Name: **Joanna Enns**

Degree: **Master of Science**

Title: **Paying attention but not coordinating: Parental care in European starlings (*Sturnus vulgaris*)**

Committee: **Chair:** **Bernard Crespi**
Professor, Biological Sciences

Tony Williams
Supervisor
Professor, Biological Sciences

David Green
Committee Member
Professor, Biological Sciences

Leithen M’Gonigle
Committee Member
Associate Professor, Biological Sciences

John Reynolds
Examiner
Professor, Biological Sciences

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Abstract

Sexual conflict occurs in biparental species because working together provides shared benefits while incurring individual costs. In birds, coordination of provisioning visits via turn-taking has been proposed as a strategy to mitigate this conflict. However, alternation of visits requires that birds have access to reliable information on their partner's behaviour. I investigated coordination in the European starling, *Sturnus vulgaris*, where direct access to information is variable and limited. Using observational data and a short-term mate removal experiment, there was evidence that individuals adjusted their behaviour in response to their partner. Both sexes decreased their provisioning in the hour the partner was removed but returned to pre-experimental levels within 24 hours, which is consistent with "matching" of parental effort, rather than a "compensation" response widely reported in other studies. Despite this, there was no evidence of coordination, both alternation and synchrony of visits did not differ from that expected by chance.

Keywords: Biparental care, provisioning, mate removal, coordination, alternation, synchrony

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Vector drawing of a female European starling by Joanna Enns

Chapter 1.

General Introduction

1.1. Background

Parental care occurs whenever parents increase the growth and survival of their offspring, which can range from choosing a nesting site to providing protection (through building nests, attending and brooding eggs/offspring, caring for offspring after they are nutritionally independent) and offering food to offspring (Smiseth et al. 2012; Kölliker et al. 2014). While parental care enhances offspring fitness, it also comes at a cost to parental fitness due to the energy expenditure that it takes to care for offspring (Trivers 1972). An individual's ability to produce and raise future offspring may be reduced by providing for current offspring, meaning that parental care will only be worthwhile when the benefits to offspring outweigh the costs to the parents (Alonso-Alvarez and Velando 2012). Different strategies exist among species for providing care to offspring, including: uniparental care (maternal or paternal), where only one parent cares for the offspring; biparental care, where both parents care for the offspring at some stage of the parenting process; and cooperative care, where both parents are assisted by other group members (often categorized as a form of biparental care). In biparental species, sexual conflict exists between parents due to the inherent costs present in providing care and as a result of this conflict, both sexes benefit from the other parent investing more (Wedell et al. 2006; Lessells 2012). Rates of biparental care vary greatly across taxonomic groups; biparental care is absent in squamate reptiles; present at low levels in amphibians, teleost fishes, and non-primate mammals; present at high levels in cichlid fishes, crocodilians, and primates; and present in almost all avian species (81%, 90% including cooperative species; Reynolds et al. 2002; Cockburn 2006). With co-parenting so prevalent among birds, there has been major interest into how parents have evolved to deal with this sexual conflict.

Previous studies have proposed and built on theories over the past few decades for how levels of investment should be decided between partners. While often not explicit, theories have focused on allocation of food to offspring and mostly use bird species with central-place foraging as models. Houston and Davies' (1985) paper was seminal in introducing the first theory of co-investment, known as the “sealed bid” model. The sealed bid model relies on the assumption that levels of parental effort are genetically determined and change over an evolutionary timescale, resulting in each sex offering a single, fixed level of optimal effort. Results from this model state that the evolutionary stable strategy for parents is to partially compensate if they encounter a change in their partner’s investment, i.e., parents will increase their effort in response to a decrease in their partner’s effort (and vice versa) but the total effort will remain lower than the initial effort with two parents working. Building on this theory, McNamara et al. (1999; 2003) proposed a negotiation model where partial compensation is the predicted outcome, but investment is instead negotiated between partners on a behavioural timescale. In response to a discrepancy in the results of real-world experiments testing these models, Johnstone and Hinde (2006) proposed a different type of negotiation model which they deem the “information” model of investment. Like the previous negotiation model, the information model relies on the assumption that parents negotiate their investment over a behavioural timescale but the response of one parent to a change in their partner’s behaviour is based on the level of information that parents have of brood need. This model predicts partial compensation only when brood need doesn’t vary and parental assessment of brood need is very accurate, but predicts a matching response when brood need does vary and parental assessment of brood need is incomplete. More recently, Johnstone et al. (2014) took the negotiation model a step further by suggesting parents cooperate conditionally in their effort. They propose that individuals may take turns in providing effort, and by doing this can keep track of their partner’s effort, responding in a sort of “tit-for-tat”. When applied to central-place provisioning birds, parents can coordinate their provisioning effort by synchronizing or alternating their visits to the nest.

Much interest has focused on whether birds coordinate parental care during chick rearing and numerous studies provide evidence of parents alternating and/or synchronizing their provisioning visits above the level of chance (Mariette and Griffith 2012; van Rooij and Griffith 2013; Johnstone et al. 2014; Mariette and Griffith 2015; Bebbington and Hatchwell 2016; Koenig and Walters 2016; Savage et al. 2017; Ihle, Pick, Winney, Nakagawa, and Burke 2019; Lejeune et al. 2019). However, there has been little consideration of what information parents have, or need, of their partner’s behaviour to facilitate alternation. In this study, I investigate coordination in the European starling (*Sturnus vulgaris*), a species with imperfect information on partner behaviour.

1.2. Study Species

The European starling is a well-studied species with biparental care. They make an ideal species for studying in the field because they are commonly found in urban and agricultural environments, readily adapt to nesting in man-made nest boxes, and willingly nest as close as 0.5m to each other (Kessel 1957; Feare 1984). At the start of the breeding season, males select, defend and prepare a nesting site (in addition to displaying via song, posture, and behaviour; Eens et al. 1991) to solicit females to mate with them. Once mated, females will lay one egg each day up until clutch completion, laying an average of 5 eggs in peak broods (T.D. Willams, unpub. data). Despite the difference in laying date, eggs hatch within a couple of days of each other due to delayed onset of incubation, which the female begins upon clutch completion and lasts for ~11 days. Starlings are highly synchronous in their egg-laying and hatching of chicks, with a peak in hatching activity occurring over 4 days (in British Columbia, Williams 2012). There are two main peaks of laying that occur over the breeding season, with intermediate nests often occurring between these two peaks. Both sexes may help to brood the young (Kessel 1957) and switch from spending most of their time brooding to provisioning around day 6 post-hatching for an average 21 days. European starlings are flexible in their biparental care, with most nests receiving care from both female and male parents while some nests only receive maternal care. This is because they are facultatively polygynous, meaning males may mate with multiple females and subsequently provision multiple nests, providing the most care to their primary nest (36% of male feeding visits) and less to a secondary nest (10%; Smith et al. 1994). Singularly-mated males will only provision to one nest and are considered monogamous (Pinxten and Eens 1994; Smith et al. 1994). Due to this polygyny, nests differ in how much provisioning they receive from males.

1.3. Thesis Objectives

In the first chapter I review relevant background on biparental care, coordination, and the study species in this thesis, the European starling. In the second chapter I investigate parental care, partner responsiveness, and coordination in European starlings. My objectives were to: 1) explore the effect of mate status on female quality and breeding productivity by comparing laying dates, clutch sizes, nest success, and brood size at fledging between partnered and un-partnered females; 2) describe provisioning rate and determine the factors that affect provisioning rate in females and males such as year, brood type, brood size, chick age, and partner's provisioning rate; 3) explore the timing of female provisioning visits in relation to male provisioning by comparing inter-visit interval lengths between partnered and un-partnered females and between visits (from nests with male help) with more recently visiting males; 4) experimentally manipulate partner information through the use of a short-term (1-hour) mate removal study on both females and males; 5) investigate coordination by looking at whether synchrony and alternation of nest visits occur above the levels of chance. In the third chapter I provide a summary of my main findings and suggest future studies.

Chapter 2.

Paying attention but not coordinating: Parental care in European starlings (*Sturnus vulgaris*)

2.1. Introduction

Parental care increases offspring survival, and therefore the inclusive fitness of parents (Alonso-Alvarez and Velando 2012). Consequently, in many species, parents care for their young in some capacity by providing warmth, protection, or sustenance, and this is essential to offspring development (Smiseth et al. 2012; Kölliker et al. 2014). In birds, biparental care is the most common system of parental investment, and both sexes provide care in approximately 81% of all species (Cockburn 2006). However, co-parenting is also thought to be a source of sexual conflict because, while partners share in the reproductive fitness benefits of joint care, each parent incurs individual costs, either from the physical effort required for care or from lost mating opportunities (Trivers 1972; Houston et al. 2005; Lessells 2012). Given sexual conflict, there should be selection for individuals to contribute as little as possible to parental care in order to maximize their benefits by ‘free-riding’ off their partner’s efforts. However, if the other parent is unwilling to compensate for their partner’s reduced provisioning, this will generate a cost to both parents in terms of decreased offspring health and, ultimately, decreased parental fitness (McNamara et al. 1999; Royle et al. 2002; Houston et al. 2005; Lessells and McNamara 2012). A possible solution to this sexual conflict is parental cooperation, such as conditional cooperation: where each sex provides food only after their partner has done so, leading to a pattern of alternation or turn-taking (Johnstone et al. 2014). By sharing the workload, provisioning can be a coordinated effort where individuals hold their partner accountable.

In recent years, numerous studies have investigated whether birds coordinate parental care during chick rearing (van Rooij and Griffith 2013; Johnstone et al. 2014; Mariette and Griffith 2015; Bebbington and Hatchwell 2016; Koenig and Walters 2016; Iserbyt et al. 2017; Khwaja et al. 2017; Savage et al. 2017; Takahashi et al. 2017; Tyson et al. 2017; Leniowski and Węgrzyn 2018). Parental cooperation can present as visible alternation of feeding visits between parents or synchrony of feeding visits. Several species have been shown to alternate visits more often than expected by chance (Johnstone et al. 2014; Bebbington and Hatchwell 2016; Savage et al. 2017), and/or synchronize their visits to the nest (Mariette and Griffith 2012; Bebbington and Hatchwell 2016; Leniowski and Węgrzyn 2018), providing evidence of coordination. However, models of parental cooperation rely on the assumption that, a) birds have ongoing information of their partner's recent provisioning behaviour, and b) that individuals can then adjust their behaviour in response to that of their partner. Ongoing information could be gathered directly through observation of their partner's behaviour, or indirectly through access to nestling begging intensity (Hinde 2006; Meade et al. 2011). To date, few studies have focused on this "informational" component of cooperation between parents. Further, most previous studies have involved species where partners either spend considerable time together at the nest, i.e. visit synchrony is high (long-tailed tits, *Aegithalos caudatus*, Bebbington and Hatchwell 2016; chestnut-crowned babblers, *Pomatostomus ruficeps*, Savage et al. 2017), or species where both partners forage close to the nest (<45 m in great tits, *Parus major,* and blue tits, *Cyanistes cauruleus,* Naef-Daenzer and Keller 1999; Johnstone et al. 2014; Baldan, Curk, et al. 2019; Lejeune et al. 2019). In these scenarios, birds could directly observe their partner's foraging behaviour and/or nest visits, providing them a source of direct information on their partner's behaviour (Naef-Daenzer and Keller 1999; Savage et al. 2017). In contrast, many avian species forage at much greater distances from their nest site, with no evidence of parents foraging together so that partners are less likely to encounter each other while foraging or directly observe each other bringing food to the nest.

It remains unknown whether species with this 'direct knowledge gap' of their partner's behaviour are capable of alternation. If such species still show evidence of conditional cooperation in the absence of 'direct' information on their partner's behavior this would suggest that alternation can be based on 'indirect' information, e.g. cues associated with chick demand, hunger, and begging. One way to distinguish these different sources of information in parental coordination studies is to temporarily remove one partner (and therefore any 'direct' information on this birds behaviour) and determine if the remaining partner adjusts its provisioning behaviour. Only one such study employing temporary mate removal to investigate alternation has been reported so far (Iserbyt et al. 2019) and this was conducted on blue tits (*Cyanistes caeruleus*), a species that forages close to the nest site and synchronizes provisioning visits (Lejeune et al. 2019).

European starlings (*Sturnus vulgaris*) forage at considerable distances from the nest (200-1600 m, average 400 m), there is no evidence that pairs forage together, and synchrony at the nest appears to be low, if present at all (Cabe 1993; Williams and Fowler 2015; T.D. Willams, unpub. data). Thus, this is an example of a species that might be limited in its access to direct information on the provisioning effort of the partner. European starlings also show marked variation in the amount of paternal care they provide: some females receive no help from males while others receive comparable levels of help from their male partners. This provides a unique opportunity to compare the provisioning behaviour of females between those that receive male help (and have information on their partners behaviour) and those that do not.

Here I investigated whether European starlings adjust their provisioning effort and timing based on knowledge of their partner's provisioning behaviour (either from direct information of partner presence or from indirect cues via chicks) using rates and arrival times of provisioning nest visits. First, I determined if mate status of females (with/without a male partner) was related to female quality (laying date, clutch size) or breeding productivity to determine how important males are in this system. Secondly, I asked how provisioning rate varied with ecological context (year, first vs. second broods, brood size). Third, I looked at the timing of female provisioning visits in relation to male presence (using inter-visit intervals) to explore the responsiveness of females where they have information or totally lack information on a partner. I then tested the short-term responsiveness of both sexes to information on their partner's behaviour directly by removing one (randomly-caught) partner from the nest. Finally, I asked whether European starlings show evidence of coordination by comparing their levels of alternation and synchrony to those expected by chance.

2.2. Methods

2.2.1. Study System

Fieldwork was conducted between April through early July 2017-2020 on a nest box-breeding population of European starlings (*Sturnus vulgaris*) located at Davistead

Farm, Langley, British Columbia, Canada (49°10'N, 122°50'W; established in 2001). In all years, nest boxes were checked daily starting April 1 to record laying date (1st egg date), clutch size (number of eggs at clutch completion), hatching date (when half or more eggs had hatched in each clutch), and brood size (number of surviving chicks). Brood size was recorded at hatching, at day 6 post-hatching, and at fledging on day 21. Chicks from all nests were measured for mass (± 0.1 g) and tarsus length (± 0.01 mm) at 17 days post-hatching. Adult females were caught in nest boxes between days 6-10 of incubation, weighed, and fitted with two unique colour bands and a metal identification band (Environment Canada banding permit for TDW #10646). Males were not captured or banded, and thus, identity of males is unknown.

All nest measures were recorded for first, second, and intermediate nests. First clutches or broods were defined as those initiated during the "peak" of laying in the 12 days after the earliest first nest initiation date in each year (Williams et al. 2015). Pairs that successfully fledged a first brood often initiated a second breeding attempt (see Cornell and Williams 2016) and nests were categorized as "second broods" if they were initiated within a period determined by the earliest laying date of known, banded birds that successfully fledged a peak brood. Nests initiated between the peak and second broods were categorized as intermediate nests. All research was conducted under Simon Fraser University animal care permit 1172B-96, following guidelines of the Canadian Council of Animal Care.

2.2.2. Observations of Provisioning Rate

Behavioural watches of chick-rearing parents were conducted at individual nest boxes between 0900-1500 hours with chicks aged 6-8 days (chick age counted in days post-hatch, with hatch date as day 0) to obtain observational data on provisioning rate (nest visit rate). Observations were taken in-person using binoculars or using video cameras for a minimum of 30 minutes and maximum of 147 minutes. For all observations, the arrival time of each provisioning visit (visit where the individual is carrying food) and the sex of the visiting individual were recorded, identified by the presence of leg bands (bands = female, no bands = male). Video observations were watched at 5x the speed to collect data on timing of visits. In instances where it was unclear whether the visiting bird had food, the visit was counted as provisioning provided it was 30+ seconds from the last provisioning visit made by that individual.

2.2.3. Mate Removal Experiment

Experimental manipulations of provisioning rate via mate removal were conducted between 1000-1500 hours. All experimental nests were observed for a minimum of 30 minutes on the day prior to removal, and for 60 minutes on the day of mate removal but preceding removal (”pre-experiment”). Many experimental nests also had observational data recorded during days 6-8 post-hatch prior to the experiment. Following the “pre-experiment” observation period, either individual of the pair (female or male) was caught using nest box traps (Van Ert Enterprises, Leon, IA). The bird was then weighed and held in a covered metal cage for 60 minutes. During this hour, provisioning rate and timing of nest visits were recorded for the remaining partner at the nest (“experiment” data). At the completion of the 60 minutes, the captured bird was released at its nest box. All experimental nests were then observed for 60 minutes the following day (“post-experiment”).

All mate removals occurred when chicks were between 7-14 days old and were conducted no more than once for each brood. Because some individuals laid multiple broods, they experienced two mate removals total throughout the season. Mates or partners were temporarily removed from a total of n = 60 nests in 2019, removing females in n = 44 instances and males in n = 16 nests. In 2020, n = 45 nests were manipulated in total, n = 24 of which had females removed and n = 21 that had males removed. Only one nest from 2019 (second brood, brood size of 2) and one nest from 2020 (first brood, brood size of 5) failed to fledge chicks from all manipulated nests; all other experimental nests successfully fledged chicks (98.1%).

2.2.4. Statistical Analysis

The complete non-experimental dataset was filtered to remove all observations without provisioning visits and all observations with ‘unknown’ visits where the sex of the visitor (and therefore order and timing of visits by sex) could not be determined. Observational analyses on mate status, provisioning rate, inter-visit intervals, alternation, and synchrony were conducted using pre-experimental observations from 2017, 2018, 2019, and 2020. All observational analyses were restricted to first and second nests (i.e. intermediate nests were excluded, these only comprised 6.7% of all nests that were observed).

Experimental analyses of provisioning rate used observations from manipulated nests in 2019 and 2020 and included nests from first broods (70.6% of nests), second broods (19.1% of nests), and intermediate broods (10.3% of nests). Brood type was included as an interaction term in applicable analyses due to known biological differences between first and second broods (Cornell and Williams 2016). Additionally, analyses were separated by brood type when this interaction was significant. All statistical analyses were completed in R version 3.6.1 (R Core Team 2019).

Mate Status

Individual quality of females was assessed in relation to female's mate status, i.e., whether females had a male partner helping out at the nest or not. Females were categorized as being partnered with a mate if there were one or more provisioning visits from a male in any observations of a nest. Female quality was assessed using laying date and clutch size (Williams 2012). Linear mixed-effect models were run separately for each brood type (1st and 2nd), with date of laying or clutch size as the dependent variable, mate status as the main effect, and year and female band number as random factors. Samples sizes were n = 158 nests for 1st broods: n = 24 nests of un-partnered females ("F") and n = 134 nests of partnered females ("F+M"), and n = 65 nests for 2nd broods: n = 23 nests of un-partnered females and n = 42 nests of partnered females.

Female mate status was also used to examine the effect of paternal care on the probability of nest success. Nest success was defined as nests where at least one chick fledged (recorded at chick age 21) whereas nest failure describes nests where no chicks survived to the time of fledging. This analysis was restricted to nests that were observed, starting at chick age 6, as this was the only way to determine presence of males. It is therefore unrepresentative of overall nest success in the population because the majority of nest failure occurs before day 6 (Korpimäki 1978; Stouffer and Power 1991). The number of fledged nests versus failed nests was compared in relation to mate status using Fisher's exact tests. There were n = 155 nests in brood 1 and n = 64 nests in brood 2 (Table 2.1). In addition, among females that fledged broods, brood size at fledge was compared between partnered and un-partnered females to investigate the effect of paternal care on breeding productivity. Brood size at fledge was modelled for each brood separately using a linear mixed-effects model, with mate status as the main effect, and year and female band number as random factors (year was included as a random factor due to the small sample size of nests belonging to un-partnered females in some years). This analysis included n = 145 first brood nests (F = 19, F+M = 126) and n = 56 second brood nests (F = 16, F+M = 40).

Provisioning Rate

Provisioning rate was calculated as the number of nest visits, for each sex, divided by the length of the observation period (decimal minutes) and was then standardized as provisioning rate/30 minutes (following Fowler and Williams 2015). Data were square-root transformed to normalize the distribution. Males were not observed feeding chicks at 47/223 nests (21.1%), which were designated as female-only nests. Provisioning rate was therefore analyzed for, a) females, using all nests (n = 585 observations at 223 nests); b) males, using all nests, i.e. including nests where male partners were not observed and therefore given a value of 0 for male provisioning rate (n = 585 observations at 223 nests), and c) males, using only nests where a male partner was observed feeding chicks (n = 503 observations at 176 nests).

Differences in provisioning rate between males and females within pairs were analyzed using paired-tests. Variation in provisioning rate for each of the three categories above were analyzed using linear mixed effects models, with provisioning rate as the dependent variable, year, brood type (1st or 2nd broods), and their interaction as main effects, brood size and chick age as covariates, and female band number as a random factor. Subsequently, using a dataset that excluded female-only nests, I examined the relationship between female and male provisioning rate with brood type as an interaction term and female band number as a random factor.

Inter-visit Intervals

Inter-visit interval (IVI), or the interval of time between consecutive visits from the same parent, was used as a measure of timing for provisioning visits (Johnstone et al. 2014; Savage et al. 2017; Baldan, Curk, et al. 2019; Ihle, Pick, Winney, Nakagawa, and Burke 2019). For all applicable analyses, inter-visit intervals were $\log_{10}$ transformed and provisioning rates were square-root transformed to normalize their respective distributions.

The relationship between timing of provisioning and provisioning rate was explored for each sex separately using a linear mixed-effects model with IVI as the dependent variable, provisioning rate, brood type, and their interaction as main effects, and female band number as a random factor. These analyses used n = 3,592 female IVIs from 530 observations of 216 nests and n = 2,036 male IVIs from 378 observations of 160 nests.

Female inter-visit intervals from visits that directly followed another female visit were compared in relation to mate status and sex of the previous visiting bird using linear mixed-effects models. When comparing IVIs in relation to the sex of the previous visiting bird (order of visits: female, female, female verses male, female, female), only visits from nests where both partners had been observed were used. In these models, the dependent variable was female IVI, the main effect was mate status or sex of the previous visiting bird, covariates included chick age and brood size, and random effects were year and female band number. In the analysis comparing female IVIs in relation to sex of the previous visiting bird for first broods, year was included as a covariate instead of a random effect due to the model not converging. For mate status, there was n = 1,806 IVIs from 337 observations of 148 first-brood nests and n = 571 IVIs from 128 observations of 58 second-brood nests. To analyze the effect of the previous visiting bird, n = 1,101 IVIs from 242 observations of 118 first-brood nests and n = 265 IVIs from 73 observations of 34 second-brood nests were used.

Mate Removal

Provisioning rates were compared between observations taken before the day of mate removal, and observations taken in the hour preceding mate removal ("pre-experimental" observations) using linear mixed-effects models. Provisioning rate was the dependent variable, observation type (before or on the day of removal) was the main effect, and female band number was included as a random factor. This included n = 86 observations of 27 nests for females and n = 104 observations of 35 nests for males.

Linear mixed-effects models were used to compare provisioning rates between observation types: pre-experimental, experimental, and post-experimental. Here, provisioning rate was the response variable, observation type was the main effect, and female band number was included as a random factor. The experimental dataset was filtered to remove nests without pre-experimental observations. These analyses used n = 75 observations of 27 nests for females and n = 114 observations of 41 nests for males.

Coordination

Visit synchrony is the simultaneous arrival of both partners and/or potential overlap in time spent at the nest and, therefore, the most direct way for birds to obtain information on their partner's behaviour. Here, an individual's visit was considered synchronous if it occurred shortly after a visit from its partner, i.e., the interval between alternating visits was within a certain threshold. Alternation occurs when a parent provisions their chicks after their partner (and before their partner makes another visit), meaning it can be calculated simply from the order of provisioning visits.

To determine an appropriate threshold for synchrony, I measured the time birds spent in the nest box during a feeding visit (i.e., the time during which a partner could also arrive) for n = 30 visits chosen randomly from nests in 2019. Time spent inside the nest box during a provisioning or chick-feeding visit averaged 10.0 ± 1.0 seconds (range: 2.0 – 27.0 seconds). 97.4% of alternating visits had intervals greater than this 10 second mean. Previous studies have used intervals of 1 or 2 minutes as a threshold for measuring synchrony (Bebbington and Hatchwell 2016; Ihle, Pick, Winney, Nakagawa, Schroeder, et al. 2019), however this seemed somewhat arbitrary and too large given the short time European starlings spend provisioning at the nest. With this in mind, I modelled synchrony using two thresholds: 1) an interval of 30 seconds, slightly larger than the maximum time we found starlings spent at the nest, and 2) an interval of 1 minute, a more conservative estimate closer to what has been used in previous studies.

The number of alternated and synched visits (occurring within 30 or 60 seconds) were calculated for each observation and compared to random following a "within individual within nest watch" randomization procedure (Johnstone et al. 2014; Ihle, Pick, Winney, Nakagawa, and Burke 2019). To generate the number of alternated and synched visits that would be expected by chance, inter-visit intervals were first randomly sampled without replacement within each sex and observation. New visit times were then calculated using the random order of IVIs for each sex respectively, and visits from both sexes were then combined to generate a new order of visits. Counts of alternated and synched visits were calculated from this new order of visits. This randomization process was repeated 10,000 times to create a null distribution for each observation where the median value was recorded. Observed alternation and synchrony counts were compared to random (median values from null distributions) using generalized linear mixed models with Poisson distributions (Model iv from Ihle, Pick, Winney, Nakagawa, and Burke 2019). Alternation or synchrony was the dependent variable and main effects were: type (observed vs. random)*brood type, type*chick age, type*brood size, type*total number of visits per 30 minutes, and type*absolute difference between number of male and female visits per 30 minutes. Female band number and year were included in all models as random factors. There were 424 observations of 176 distinct nests used in each model.

2.3. Results

2.3.1. Mate Status, Female Quality, and Breeding Productivity

Female laying dates varied in relation to mate status, i.e., whether females had a male partner or not, for first broods ($F_{1,123.0} = 7.07$, $P = 0.009$), but not for second broods ($F_{1,59.9} = 2.67$, $P = 0.108$) when controlling for year (Figure 2.1). In first broods, females with male partners laid 0.9 days earlier than females without male partners (first egg date 102.0 ± 1.0 versus 103.0 ± 1.0, respectively; pooling years). Clutch size was independent of mate status for first broods ($F_{1,116.5} = 3.77$, $P = 0.055$) and second broods ($F_{1,49.7} = 1.49$, $P > 0.20$; Figure 2.1).

For broods that survived to day 6 post-hatching, there was a significant effect of mate status on successful fledging versus total brood failure in both first broods (odds ratio = 6.50, $P = 0.009$) and second broods (odds ratio = 7.24, $P = 0.016$; Table 2.1). Females with male partners were more likely to successfully fledge chicks in first broods (96% of nests) and second broods (95% of nests) compared to females without partners (79% in first broods and 73% in second broods).

In nests that successfully fledged chicks, mate status had a significant effect on the brood size at fledging for first broods ($F_{1,97.5} = 9.79$, $P = 0.002$) and second broods ($F_{1,53.9} = 4.55$, $P = 0.037$; Figure 2.1). Females with male partners had 0.8 more chicks at the time of fledging in first broods (brood size 4.7 ± 0.1 versus 3.9 ± 0.3, respectively) and 0.7 more chicks in second broods (brood size 3.0 ± 0.2 versus 2.2 ± 0.3, respectively) compared to that of females with no identified male partner.

2.3.2. Variation in Provisioning Rate due to Ecological Factors

Female provisioning rate was independent of the year*brood type interaction ($F_{3,571.7} = 1.80$, $P = 0.15$; Table 2.2) and there was no difference in female provisioning rate among brood types (first and second broods, $F_{1,511.8} = 1.07$, $P > 0.30$). However, there was an effect of year on mean female provisioning rate ($F_{3,500.9} = 5.90$, $P < 0.001$). Females visited 1.3 more times per 30 minutes in 2017 (5.2 ± 0.4 visits/30 min) than in 2018 (3.9 ± 0.3; $P = 0.003$) and 1.2 more times than in 2019 (4.0 ± 0.3; $P = 0.008$). Females also provisioned more in 2020 (4.8 ± 0.3) when compared with 2018 (3.9 ± 0.3; $P = 0.003$) and 2019 (4.0 ± 0.3; $P = 0.006$).

Considering all nests (i.e., including nests where a male partner was not observed), male provisioning rate was independent of the year*brood type interaction ($F_{3,572.2} = 0.27$, $P > 0.80$) and brood type ($F_{1,538.8} = 2.33$, $P = 0.127$; Table 2.2). Male provisioning rate also varied with year ($F_{3,543.0} = 8.54$, $P < 0.001$). Male provisioning rates were highest in 2020 (3.6 ± 0.2 visits/30 min) when compared with 2017 (2.1 ± 0.4; $P < 0.001$), 2018 (2.3 ± 0.2; $P < 0.001$), and 2019 (2.5 ± 0.2; $P < 0.001$). Overall, male provisioning rates for all nests (2.6 ± 2.5 visits/30 min) were lower than females (4.5 ± 2.8; $T_{584} = 13.86$, $P < 0.001$).

Similar results were obtained for male provisioning rate when excluding nests where only females were observed. Male provisioning rate was independent of the year*brood type interaction ($F_{3,468.7} = 0.23$, $P > 0.80$) and brood type ($F_{1,402.1} = 2.91$, $P = 0.089$), while year had an effect ($F_{3,397.2} = 3.34$, $P = 0.019$; Table 2.2). Males still provisioned most in 2020 (3.8 ± 0.2), but only compared to 2018 by 1.0 visit (2.8 ± 0.3; $P = 0.008$) and 2019 by 0.9 visits (2.8 ± 0.3; $P = 0.010$). For nests where both males and females were observed, mean male provisioning rate (3.1 ± 2.5 visits/30 min) was still lower than mean female provisioning rate (4.5 ± 2.8; $T_{502} = 9.40$, $P < 0.001$).

Provisioning rates varied with brood size for females ($F_{1,375.6} = 6.12$, $P = 0.014$, $R^2 = 0.02$), males ($F_{1,444.3} = 70.63$, $P < 0.001$, $R^2 = 0.13$), and males when female-only nests were excluded ($F_{1,309.7} = 40.13$, $P < 0.001$, $R^2 = 0.08$; Figure 2.2). While all parents increased the frequency of their provisioning in response to larger brood sizes, there was a stronger effect on males ($\beta = 0.8 \pm 0.1$ visits/30 min) and males excluding female-only nests ($\beta = 0.8 \pm 0.1$) than females ($\beta = 0.2 \pm 0.1$). However, there was marked residual variation for any brood size, e.g., for females with 5 chicks, provisioning rate varied from 0.5 to 14.5 visits/30 min, and for males with 5 chicks, provisioning rate varied from 0.5 to 11.8 visits/30 min (Figure 2.2). Provisioning rates also varied in relation to chick age for females ($F_{1,524.8} = 41.51$, $P < 0.001$, $R^2 = 0.06$), but not for males ($F_{1,504.0} = 2.01$, $P > 0.15$), or males when female-only nests were excluded ($F_{1,449.6} = 0.62$, $P > 0.40$; Figure 2.2). While females increased their provisioning rate with older chicks, there was marked residual variation for any chick age, e.g., for nests where the majority of chicks were 7 days old, female provisioning rate varied from 0.5 to 16.2 visits/30 min (Figure 2.2).

Female provisioning rate was independent of the male provisioning rate*brood type interaction, i.e., the relationship between female and male provisioning rates did not differ between first and second broods ($F_{1,404.0} = 0.24$, $P > 0.60$). There was a significant, albeit weak, positive relationship between female and male provisioning rates ($F_{1,409.3} = 9.50$, $P = 0.002$, $R^2 = 0.02$), where female rate increases from 4 to 6 visits/30 min over the range of 0 to 12 male visits/30 min (Figure 2.3). Brood type had no effect on female provisioning rates ($F_{1,410.9} = 3.12$, $P = 0.078$).

2.3.3. Variation in Timing of Inter-visit Intervals

Inter-visit intervals decreased as provisioning rate increased for females ($F_{1,567.0} = 895.47$, $P < 0.001$, $R^2 = 0.30$) and males ($F_{1,726.1} = 504.37$, $P < 0.001$, $R^2 = 0.28$) but with considerable variance around the line (Figure 2.4). Inter-visits intervals were independent of the provisioning rate*brood type interaction for females ($F_{1,1125.1} = 2.83$, $P = 0.093$) and males ($F_{1,745.1} = 0.83$, $P > 0.30$), and there was no effect of brood type for either sex (female: $F_{1,1455.1} = 1.82$, $P > 0.15$; male: $F_{1,926.2} = 1.38$, $P > 0.20$).

Female inter-visit intervals from visits that directly followed another female visit did not vary in relation to mate status, i.e., whether a female was partnered with a male or not, for first ($F_{1,1235.9} = 1.60$, $P > 0.20$) or second broods ($F_{1,292.9} = 1.94$, $P > 0.15$; Figure 2.5). However, female IVIs did vary in relation to which sex visited previously for first broods ($F_{1,1090.3} = 7.69$, $P = 0.006$; Figure 2.5). In first broods, females took 33.6 seconds longer to return to the nest to provision if the preceding visit was from a male (IVI 3.66 ± 0.19 versus 3.10 ± 0.18, respectively). No difference was found between female IVIs based on the previous visiting bird in second broods ($F_{1,258.6} = 0.93$, $P > 0.30$).

2.3.4. Provisioning Rate Response to Mate Removal

Provisioning rates differed between observations taken 1-8 days before mate removal (chick ages 6-13) and observations taken in the hour preceding mate removal for females ($F_{1,62.4} = 5.91$, $P = 0.018$), but not for males ($F_{1,71.0} = 1.27$, $P > 0.20$). The average female provisioning rate in observations conducted before the day of removal was lower by 0.9 visits per 30 minutes when compared with observations conducted in the hour preceding removal (4.8 ± 0.4 versus 5.7 ± 0.4, $P = 0.018$). Due to this, only pre-experimental observations were used in the subsequent analysis.

Provisioning rates differed among pre-experimental, experimental, and post-experimental observation types for females ($F_{2,50.1} = 5.15$, $P = 0.009$) and males ($F_{2,75.6} = 9.28$, $P < 0.001$) in similar ways (Figure 2.6). There was a marginally significant decrease in female provisioning rate between pre-experimental and experimental observations, where females made 1.1 fewer visits while their partner was removed from the nest (5.6 ± 0.5 versus 4.5 ± 0.5, respectively, $P = 0.049$). Males also decreased their provisioning rates in the hour when their partner was removed from the nest compared to pre-experimental observations (2.9 ± 0.3 versus 4.4 ± 0.4, respectively, $P < 0.001$). Both females and males increased their provisioning rates post-experiment, by 2.1 and 1.4 visits, respectively (female: 6.6 ± 0.6, $P = 0.003$; male: 4.3 ± 0.4, $P < 0.001$), compared to experimental levels of provisioning. Finally, there was no difference between provisioning rates of pre- and post- experimental observations for females ($P > 0.20$) or males ($P > 0.70$).

2.3.5. Coordination via Alternation and Synchrony

The level of alternation observed in nest watches did not differ from those expected when nest visit intervals of males and females were randomized ($z = -0.40$, $P > 0.60$; Figure 2.7; all interactions between data type and brood type, chick age, brood size, total provisioning rate, provisioning rate difference: $P > 0.40$). Alternation counts did vary in relation to brood type ($z = 2.07$, $P = 0.038$), chick age ($z = 5.38$, $P < 0.001$), total provisioning rate (z = 24.35, P < 0.001), and provisioning rate difference (z = -12.70, P < 0.001), but not with brood size (z = 1.42, P > 0.15).

Counts of synched visits, defined as any visit occurring within 30 seconds or 1 minute of the nest partner, did not differ between observed and randomized data using either the 30-second threshold (z = -1.46, P = 0.146) or 1-minute threshold (z = 0.58, P > 0.50; Figure 2.7; all interactions between data type and brood type, chick age, brood size, total provisioning rate, provisioning rate difference: P > 0.10). With both thresholds, synchrony varied with total provisioning rate (30 sec: z = 11.28, P < 0.001; 1 min: z = 20.27, P < 0.001), and provisioning rate difference (30 sec: z = -2.77, P = 0.006, 1 min: z = -6.53, P < 0.001). When the 30-second threshold was used, synchrony varied with brood size (z = 2.06 P = 0.040), but not chick age (z = -0.68, P > 0.40). The opposite was found when the 1-minute threshold was used, where synchrony varied with chick age (z = 3.61, P > 0.001), but not brood size (z = 0.69, P > 0.40).

2.4. Discussion

In this study I determined if there was evidence for coordination (*sensu* Johnstone et al. 2014) during chick provisioning in European starlings by investigating: a) the importance of mate status for females, having a male partner or not (i.e., having partner information, or not), b) ecological drivers of provisioning rate, and c) responsiveness of birds to information on their partners behaviour using i) observational and ii) experimental data, and d) potential true (non-random) coordination of behaviour via alternation and synchrony of visits. There was some evidence that females with male partners are higher quality than un-partnered females given their earlier laying dates in first broods. Females with male partners were also found to successfully fledge more chicks on average. Among nests with both male and female parents contributing to care, females had overall higher provisioning rates than males and there was a weak positive relationship in provisioning rates between partners. Both female and male provisioning rates varied across years and increased with brood size; female provisioning rates also increased with chick age – though these relationships were weak with large residual variation. In first broods, inter-visit intervals from visits that occurred directly after another female visit which had been preceded by a male visit (order of visits: male, female, female) were longer than those that had been preceded by another female visit (order of visits: female, female, female). Additionally, I found that both females and males responded to the hour-long removal of their partner by decreasing their provisioning rates immediately during removal before increasing them back to pre-experimental levels the day after removal (once reunited). These results suggest that birds do adjust their behaviour in relation to information about their partner’s behaviour or presence. However, despite the experimental evidence that European starlings respond to information on their partner’s behaviour, there was no evidence of coordination via alternation or synchrony (i.e., this was not different from random).

2.4.1. Impact of Female Mate Status

Exploring female quality in our system is important for accurately interpreting subsequent analyses that compare partnered and un-partnered females, as well as the impact of males on breeding productivity. An obvious difference to consider at the outset is that females with no mates lack all relevant information and therefore behave ‘independently’ by definition. In contrast, females with male partners have the potential to respond to their partner’s behaviour and so can vary in the extent to which they do so. Many studies across a wide range of avian species (including passerines, waterfowl, seabirds, and raptors) have shown that females that lay earlier also tend to lay larger clutches and raise more chicks (Perrins 1970; Williams 2012). Further, male and female mate choice (in birds generally and especially in European starlings where not all nests receive male care) can result in males contributing care to the nests of the highest quality females in the population, increasing the male’s likelihood of nest success (Sandell et al. 1996; Schuett et al. 2010; Schroeder et al. 2013). Female European starlings from first broods were found to lay eggs 0.9 days earlier if they had a male partner, providing evidence that partnered females might be higher quality than females who haven’t succeeded in securing a male partner that contributes to parental care. While this difference is not large, European starlings are highly synchronous in their laying and appear to adjust clutch size over just 4-5 days (Williams 2012), so this difference in laying date could be biologically significant. However, there was no difference between clutch sizes in relation to female mate status, which is considered one of the most important determinants of reproductive effort and is therefore a key indicator of female quality (Williams 2012). In summary, there is some evidence that females with male partners in this system are of higher quality, support for this idea is weak overall, given that clutch sizes across partnered and un-partnered females did not differ.

In our population of European starlings, males contributed to provisioning at 79% of nests and both nest success and fledging productivity were significantly higher in nests that received care from both parents. While this outcome could exclusively be due to partnered females being of higher quality compared to un-partnered females (as discussed above), it is more likely that the male contribution to chick provisioning plays a role. This is because mate status had a substantial effect on likelihood of nest success and brood size at fledging among first broods (1.2x more successful nests and 0.8 more chicks) and second broods (1.3x more successful nests and 0.7 more chicks), while female quality was only found to affect laying dates of first broods. These results suggest that the provisioning contribution of males significantly increased nest productivity in our study system. Previous studies on European starlings have reported equivocal results in terms of male impact on nest success despite differences in defining male effort. In European starlings, males with multiple mates will provision most to their primary nest and less to their secondary nest, (see General Introduction), whereas monogamous males will only provision to one nest (Pinxten and Eens 1994; Smith et al. 1994). When categorized by nest type, Pinxten and Eens (1994) found that nestling mortality was higher and chick weight at day 15 post-hatching was lower in secondary nests compared to primary nests. Similarly, Smith et al. (1994) found that secondary females experienced lower fledging success and produced chicks with lower masses and smaller tarsus lengths on average compared to females from monogamous and primary nests. In contrast to these findings and the result of the current study however, a previous analysis using the same population of birds found no difference in either the mean brood size or chick mass at fledging between nests with and without male help (Fowler and Williams 2015). As in this study, Fowler and Williams (2015) did not differentiate between the different types of nests (monogamous, primary, and secondary) because males in the population are not banded and consequently remain unidentified. The distinction between nests with and without male help may have been too crude to detect an impact of males in their study.

2.4.2. Ecological Drivers of Provisioning Rate

Analyses on provisioning rates of females and males were included to provide sufficient background context on the parental care behaviour of European starlings in our population. Overall, female European starlings had higher provisioning rates than males, even at nests where females had male partners. While males contributed to the provisioning at 79% of total nests in this study, the ratio of provisioning effort was skewed towards females, with females visiting an average of 4.5 times per 30 minutes and males visiting an average of 3.1 times (excluding female-only nests) and 2.6 times overall (including female-only nests). Further, there was large variation in the amount of male help that each nest received, likely in part due to the polygynous nature of males, and male effort ranged from 2.2% to 81.8% of total provisioning visits observed for a nest. The finding of female bias towards provisioning is consistent with previous research on European starlings (Pinxten and Eens 1994; Sandell et al. 1996; Fowler and Williams 2015). Using the same population of birds, Fowler and Williams (2015) reported an average female rate of 4.4 visits/30 min and average male rate of 2.5 visits/30 min (including female-only nests), which is directly comparable with our results. Despite differences from the current study in categorizing male help (with or without male help versus monogamous, primary, and secondary), Pinxton and Eens (1994) similarly found that male provisioning rates in primary broods were significantly lower than female rates when chicks were 12-13 days old and male provisioning rates in monogamous broods were lower on average, though non-significant, than female rates across all chick age categories.

Ecological factors that affect provisioning effort in the current study were identified in order to account for them in subsequent analyses. Provisioning rate in European starlings varied across years, brood sizes, and chick ages. Perhaps surprisingly, yearly differences in provisioning rate could not be explained by 'good' versus 'poor' years, as annual variation in provisioning rate did not match up with annual variation in mean breeding productivity. For example, provisioning rate was much lower in 2018 (females 3.9 visits/30 min; males 2.3 visits/30 min) compared with 2020 (females 5.6, males 3.8), i.e. 66% higher in 2020. However, mean annual productivity in both years was very similar: 4.1 and 4.0 chicks fledging, and both years were relatively 'good' years compared to the overall mean brood size at fledging of 3.3 chicks (2002-2020, TDW unpublished data). This is consistent with the relatively weak positive relationship between provisioning rate and brood size in both sexes because we would expect to see higher provisioning rates in good years if this relationship was stronger. Despite its low predictive power, the positive relationship between brood size and provisioning rate in both sexes is present and has been reported in previous research on European starlings (Wright and Cuthill 1990; Pinxten and Eens 1994; Fowler and Williams 2015). In the current study, sex differences between provisioning rate in relation to brood size and chick age were as follows: males increased their provisioning more with brood size than females did and females increased their provisioning in relation to chick age, unlike males. This could be due to differences in reproductive investment. For example, males may respond more to brood size because a larger brood may be indicative of increased fitness benefits (more offspring). Whereas females may respond more to actual nest demand, demonstrated by their provisioning rate increasing with chick age, i.e., offspring growth.

The positive relationship between female and male provisioning rate in the current study provides some evidence that higher quality females are socially partnered with higher quality males in regards to provisioning effort. This could be due to increased compatibility between social pairs achieved through mate choice (Spoon et al. 2006; Fraser and Bugnyar 2010), or could potentially indicate responsiveness between partners due to matching of provisioning effort. If the latter explanation is true, it provides evidence that parents may be matching their partner's effort, increasing or decreasing their provisioning frequency in response to an increase or decrease in their partner's frequency, respectively. Nonetheless, this relationship was weak with large variation; for example, female provisioning rate varied from 1 to 9 visits given a male provisioning rate of 3 visits. So, regardless of the explanation for a positive relationship between partner's provisioning, the overall benefit of that provisioning was low.

2.4.3. Behavioural Responsiveness of Females to Male Provisioning

In European starling nests where both partners contribute to provisioning, females are exposed to information on their partner's visits either directly through observation of their partner's behaviour or indirectly through cues from chicks (Meade et al. 2011). This can be contrasted with nests where males do not contribute, in which females have no external information from male partners that could affect their behaviour, i.e., they can behave 'independently'. I predicted that in females with male partners, information from the male's provisioning effort might affect female return time and result in different female inter-visit interval lengths (from back-to-back female visits) in nests with both partners compared to nests without males. In other words, females would adjust their behaviour based on information from their males. However, this was not the case: solitary females had the same return times on average as partnered females, which potentially have to factor in their partner's behaviour. Taken alone, this result suggests females are not responding to information on their partner's provisioning. In contrast, there was a significant difference between female return times to the nest in relation to sex of the bird making the most recent nest visit (though only in first broods). Female European starlings took longer to return to the nest with food when a male had visited more recently (order of visits: male, female, female), than when a male hadn't visited as recently (order of visits: female, female, female). This would support the idea that females may alter their time of return based on (direct or indirect) information from males, returning more slowly when they have obtained information that their partner visited. One explanation for why this difference was only found among first broods could be that second brood pairs are generally higher quality, i.e., only the most successful birds are able to rear a second brood (Cornell and Williams 2016). Females in second broods may therefore have to respond less to information cues from males because they are better matched to their partner. However, the dataset also had reduced power to detect differences, due to the much smaller sample size of second brood intervals (n = 265 IVIs) compared to first broods (n = 1,101 IVIs).

2.4.4. Provisioning Decrease in Response to Mate Removal

Although there was only weak or equivocal evidence for European starlings changing their provisioning behaviour in response to their partners behaviour based on correlative data (above), there was clear evidence of partner responsiveness in the mate removal experiment of this study. Both females and males responded to the short-term loss of their social partner by decreasing their provisioning visits during the hour of removal before returning to pre-experimental levels of provisioning the day after. These results provide evidence that European starlings have sufficient information on the behaviour of their partner in order to respond within a short (1 hour) time period. The removal response shown here is also consistent with the idea that parents are matching their partner's provisioning, as predicted within the framework of both the information model and conditional cooperation model (Hinde 2006; Johnstone and Hinde 2006; Johnstone et al. 2014). Johnstone and Hinde's (2006) information model predicts a matching response between partners when parents have incomplete information on brood need, resulting in parents using information of their partner’s provisioning to decide their own level of provisioning, i.e., increasing visits when their partner has increased their visits and decreasing visits when their partner has decreased their visits. Conditional cooperation predicts the same matching outcome, but uses reciprocity between partners to explain why: parents will decrease their provisioning in response to a decrease in their partner’s provisioning, utilizing a “tit for tat” response rule to minimize sexual conflict (Johnstone et al. 2014). Another possibility to consider is that the decrease in provisioning rate shown by both sexes was not due to partner matching of workload but was instead a disturbance response to trapping. That is to say, the focal parent may have decreased their provisioning rate out of fear after witnessing their partner being trapped or hearing their partner’s distress calls. A counterpoint to this is that the trapped individual was removed as soon as possible, usually within minutes of triggering the trap, and placed in a cloth bag immediately to minimize potential calls. Nonetheless, this effect may account for some of the variation in responses among individuals and is important to consider.

A *decrease* in provisioning rate, as seen in European starlings in the current study differs markedly from the majority of studies that employ mate removal or a form of handicapping to reduce parental care of one partner. The most common response of focal birds to the absence of their partners is to partially compensate for the loss of provisioning effort from the removed partner (meta-review using 54 studies by Harrison et al. 2009). One factor that might explain these seemingly contradictory responses is the length of the removal period between studies. The information model suggests that partial information of brood need may cause a parent to match their partner’s effort in the short term, due to the assumption that their partner has brood knowledge that they don’t have, until they can gather more information on brood need (Johnstone and Hinde 2006). Once birds have more accurate information on brood need, through changes in chick begging that occur over a longer time period, they are predicted to respond with partial compensation. In this way, both matching and partial compensation are expected responses to changes in partner provisioning but occur in different contexts. The decrease in provisioning demonstrated in the current study is similar to results of a recent study on blue tits, where individuals responded to the short-term (20 minute) removal of their partner by decreasing their provisioning rates (Mainwaring and Hartley 2020). Great tits and long-tailed tits (in separate studies) were also found to respond to a short-term experimental change in partner work rate by matching, though this was demonstrated by a change in the opposite direction: focal birds increased their provisioning in response to an increase in their partner's provisioning (Hinde 2006; Meade et al. 2011). Given this framework, European starlings in the current study demonstrated their ability to respond to short-term changes in the provisioning effort of their partner by matching effort, which is a necessary first step toward potential coordination, but in itself does it not prove that birds are coordinating effort.

2.4.5. Lack of Coordination

True parental coordination requires evidence of alternation or turn-taking at a rate greater than predicted by random chance, and the most parsimonious way this can be achieved, in terms of knowledge of partner behaviour, would be high, non-random, levels of synchrony when pairs visit the nest (Bebbington and Hatchwell 2016). European starlings spent on average only 10 seconds inside the nest box during a provisioning visit (even though partners could, in theory, be observed arriving or leaving the nest for slightly longer period than this). Perhaps not surprisingly therefore, levels of synchrony (i.e., parents arriving together at the nest), in the current study were very low and not higher than expected by chance, even using a conservative 30 second and 1 minute threshold. This lack of synchrony agrees with anecdotal observations while collecting provisioning data: when encountering each other at the nest box, individuals would often startle and the second visiting parent would alter their behaviour, i.e., fly away and wait till the first visitor had left before entering the nest box (J.L. Enns, pers. obs). Synchrony is the simplest (i.e., most direct) method for pairs to track each other's provisioning behaviour; Bebbington and Hatchwell (2016) even suggest that synchrony may be necessary for alternation to occur. However, our results suggest that this can be discounted as a mechanism related to partner information underpinning coordination in our species. Clearly, synchrony at the nest is an important component of parental care in some other species and has been suggested as a method of predator avoidance and shown to improve nestling growth and survival (Raihani et al. 2010; Mariette and Griffith 2012), potentially by facilitating food partitioning among chicks (Shen et al. 2010).

However, empirical data on duration of synchronous visits and behaviour during these visits appears to be very limited in other taxa such as passerines, which generally have high nest visit rates (Williams 2012). Some passerines have long visit durations and high levels of synchrony (>70% of visits) but these tend to be species with low nest visit rates (<1/hr, Mariette and Griffith 2012; ~1/hr, van Rooij and Griffith 2013). Further, there is no clear methodology for choosing a species-appropriate threshold for synchrony; thresholds chosen have been longer than the time spent at the nest (5 min threshold versus 3.4 or 1.75 min average times, van Rooij and Griffith 2013; 2 min threshold versus 0.3 min median time, Ihle, Pick, Winney, Nakagawa, Schroeder, et al. 2019; Ihle, Pick, Winney, Nakagawa, and Burke 2019), shorter than the time spent at the nest (2 min threshold versus 4.8 min average time, Mariette and Griffith 2012), or do not report of the average time spent at the nest at all (1 min threshold, Bebbington and Hatchwell 2016). Using an incorrectly large threshold, for instance, might greatly over-estimate the time pairs have to encounter and obtain information on their partner's behaviour, and thus over-estimate this key component of coordination. Future studies would benefit from using a standardized approach, one that has not yet been created, to select a threshold for synchrony. Ideally, such a standard would be species-specific, taking into account the baseline provisioning behaviour.

Alternation, i.e., non-random turn-taking, of nest visits between European starling pairs was also not significantly different from the randomized order of nest visits in this study. So, while European starlings demonstrated they were able to respond to a short-term decrease in their partner's provisioning, and did so by decreasing their own provisioning, I found no evidence to indicate they are alternating their visits more than predicted by chance. So far, alternation of provisioning visits above the level of chance has been suggested to occur in great tits (Johnstone et al. 2014; Baldan, Curk, et al. 2019), long-tailed tits (Bebbington and Hatchwell 2016), acorn woodpeckers, *Melanerpes formicivorus* (Koenig and Walters 2016), canaries, *Serinus canaria* (Iserbyt et al. 2017), chestnut-crowned babblers (Savage et al. 2017), rock sparrows, *Petronia petronia* (Baldan and Griggio 2019), house sparrows, *Passer domesticus* (Ihle, Pick, Winney, Nakagawa, and Burke 2019), and blue tits (Lejeune et al. 2019). Of these species, most also synchronize their nest visits (long-tailed tits, acorn woodpeckers, rock sparrows, house sparrows, blue tits) or visit the general nesting area together (chestnut-crowned babblers), and/or have short foraging distances (<45 m in great and blue tits, Naef-Daenzer and Keller 1999; <70 m in house sparrows, Peach et al. 2008; <100 m in long-tailed tits, Bebbington and Hatchwell 2016). Additionally, many seabirds have prolonged, complex “turn-taking ceremonies”, however these occur when duties of brooding and provisioning are exchanged between partners, components of which may provide information that allows the partner to mediate their own behaviour or indicate readiness to take on parental duties (Takahashi et al. 2017; Gillies et al. 2021). Overall, given the commonalities among species used to test the conditional cooperation model, studies providing evidence of alternation may be less representative than implied. Without synchrony (as described above) and given their long foraging distances (average 400 m from the nest), European starlings presumably have little access to direct information on their partner’s behaviour and may have to rely on incomplete information gathered through chick demand. Begging is well known as a signal of chick demand; however, assessment of chick need over a short-term via begging is unlikely to be perfectly accurate (Schwagmeyer et al. 2002). Therefore, while European starlings have access to enough information on their partner’s provisioning to respond (demonstrated via mate removal), they may not have the information required to coordinate visits through alternation, i.e., on a visit-by-visit time frame.

Despite the large amount of recent interest in coordination, studies have used various approaches to measure this emergent behaviour, some of which are more robust than others. True turn-taking is notoriously difficult to measure for a couple of reasons. First, levels of passive coordination (the amount of alternated/synched visits that arise naturally and will be present in any system with 2+ provisioning parents) must be considered in order to detect true, active coordination (Bebbington and Hatchwell 2016; Baldan, Hinde, et al. 2019). It has even been suggested that true coordination may be impossible to detect given that environmental factors affect timing of visits simultaneously (Ihle, Pick, Winney, Nakagawa, and Burke 2019). Second, coordination is intrinsically related to total provisioning rate mathematically, i.e., rates of alternated and synched visits will increase with the number of provisioning visits. This is a problem because coordination may then be spuriously correlated with any measure that is correlated with provisioning rate, such as reproductive success. An improved measure of coordination, such as that proposed by Ihle, Pick, Winney, Nakagawa, Schroeder, et al. (2019) and subsequently used in this study, should take this relationship into account. Given the difficulties in measuring coordination discussed above, it is inconclusive how widespread true alternation is. I recommend future studies be conducted on a wider range of species with a) different absolute total provisioning rates, and b) different foraging ranges and behaviour in order to test the applicability of this theory.

2.5. Tables

Table 2.1 **Percentages (with sample sizes in parentheses) of nests that failed or successfully fledged, grouped by parental mate status and separated by brood. Only nests with observations (starting at day 6) were included in order to determine mate status of the female. Nests were considered to have both parents present if there were any observations that included at least one female visit and at least one male visit.**

Brood	Mate status	Failed nests	Fledged nests	Total nests
1	Female only	21%	79%	15%
		(5)	(19)	(24)
	Female + male	4%	96%	85%
		(5)	(126)	(131)
2	Female only	27%	73%	34%
		(6)	(16)	(22)
	Female + male	5%	95%	66%
		(2)	(40)	(42)

Table 2.2 **Means ± SD for provisioning visits per 30 minutes of European starlings observed during chick rearing (chicks aged 5 to 14 days old). Sample sizes are in parentheses where the first number is the number of observations and the second in the number of distinct nests used to calculate each mean. Visit means were calculated using all observations other than in column 5 where nests of un-partnered females were excluded.**

Year	Brood	Female visits	Male visits	*Male visits excl. female-only nests	Total visits
2017	1	4.25 ± 2.17	2.04 ± 2.49	3.00 ± 2.49	6.29 ± 2.75
		(28, 20)	(28, 20)	(19, 14)	(28, 20)
	2	4.93 ± 2.58	1.20 ± 2.18	3.00 ± 2.61	6.13 ± 3.14
		(15, 13)	(15, 13)	(6, 5)	(15, 13)
2018	1	3.89 ± 2.70	2.25 ± 2.29	2.58 ± 2.27	6.15 ± 3.97
		(95, 50)	(95, 50)	(83, 42)	(95, 50)
	2	3.12 ± 2.00	1.45 ± 2.01	2.35 ± 2.12	4.57 ± 2.86
		(42, 20)	(42, 20)	(26, 11)	(42, 20)
2019	1	4.85 ± 3.27	2.50 ± 2.41	2.86 ± 2.37	7.35 ± 3.66
		(158, 47)	(158, 47)	(138, 38)	(158, 47)
	2	3.65 ± 2.35	1.68 ± 2.05	2.16 ± 2.09	5.33 ± 3.03
		(54, 15)	(54, 15)	(42, 10)	(54, 15)
2020	1	5.61 ± 2.73	3.75 ± 2.62	3.80 ± 2.60	9.36 ± 3.46
		(140, 41)	(140, 41)	(138, 40)	(140, 41)
	2	3.84 ± 1.93	3.24 ± 2.45	3.36 ± 2.41	7.07 ± 3.65
		(53, 17)	(53, 17)	(51, 16)	(53, 17)
All years	1 + 2	4.53 ± 2.82	2.62 ± 2.50	3.05 ± 2.45	7.14 ± 3.79
		(585, 223)	(585, 223)	(503, 176)	(585, 223)

2.6. Figures

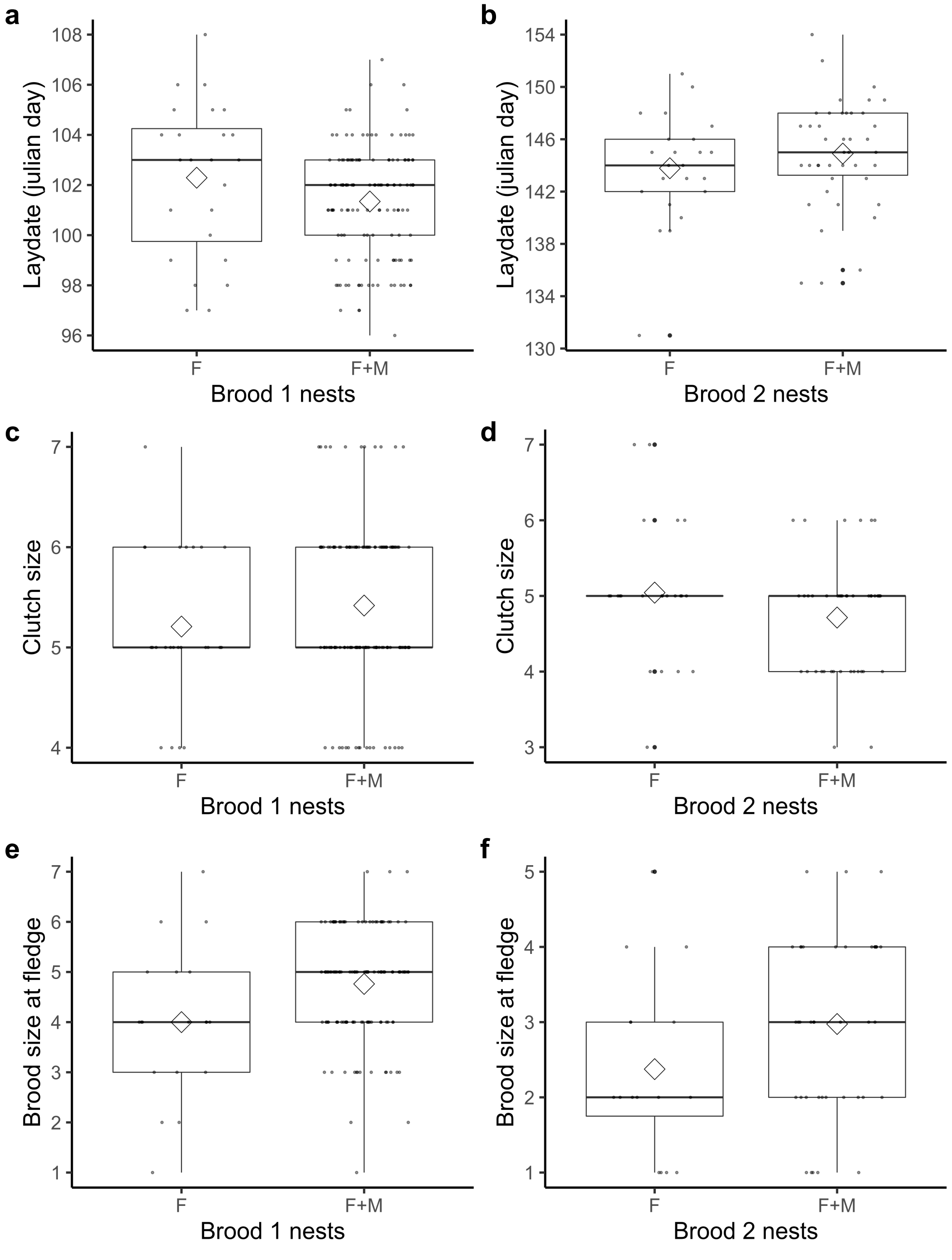

Figure 2.1 **Comparison of (a, b) laying dates (first broods n = 158; second broods n = 65), (c, d) clutch sizes (first broods n = 158; second broods n = 65), and (e, f) brood sizes at time of fledging (first broods n = 145; second broods n = 56) between nests belonging to unpartnered females (F) and partnered females (F+M). Laying dates, clutch sizes, and brood sizes were pooled across all years of the study (2017, 2018, 2019, 2020).**

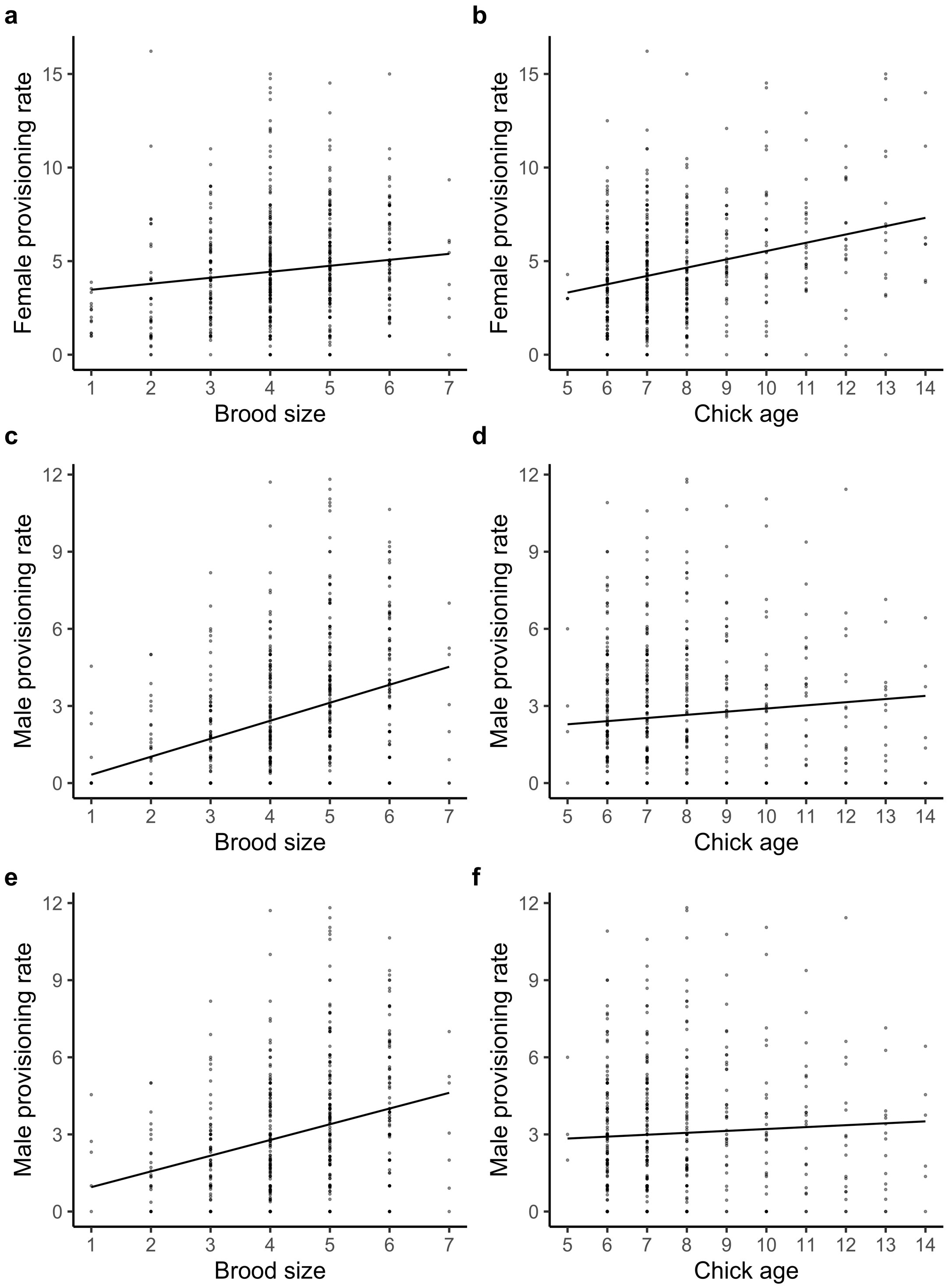

Figure 2.2 Provisioning rates of (a, b) females (n = 585), (c, d) males including all nests (n = 585), and (e, f) males excluding female-only nests (n = 503) for chicks as a function of (a, c, e) brood size, i.e., number of chicks on day of observation and (b, d, f) chick age. Provisioning rate was standardized as the number of feeding visits by each parent in a 30 minute observation period.

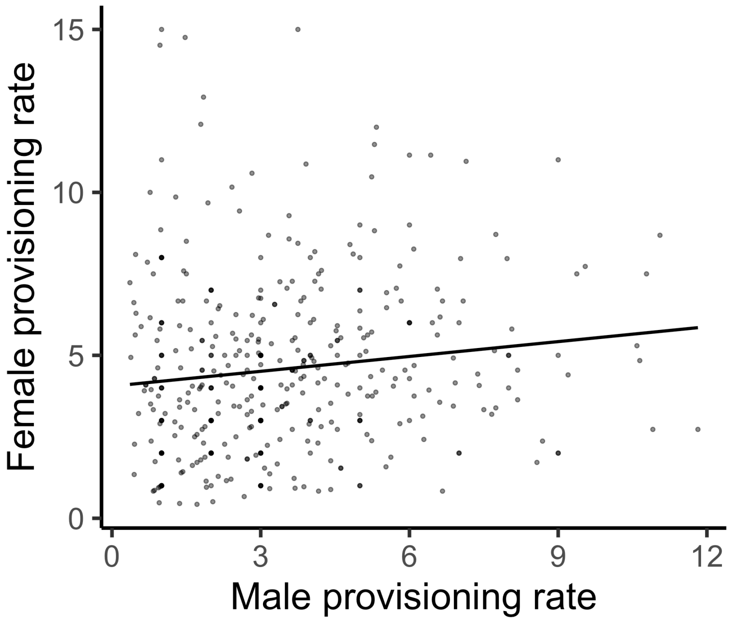

Figure 2.3 **Female provisioning rate as a function of male provisioning rate for social partners (n = 424). Provisioning rate was standardized as the number of feeding visits by each parent in a 30 minute observation period.**

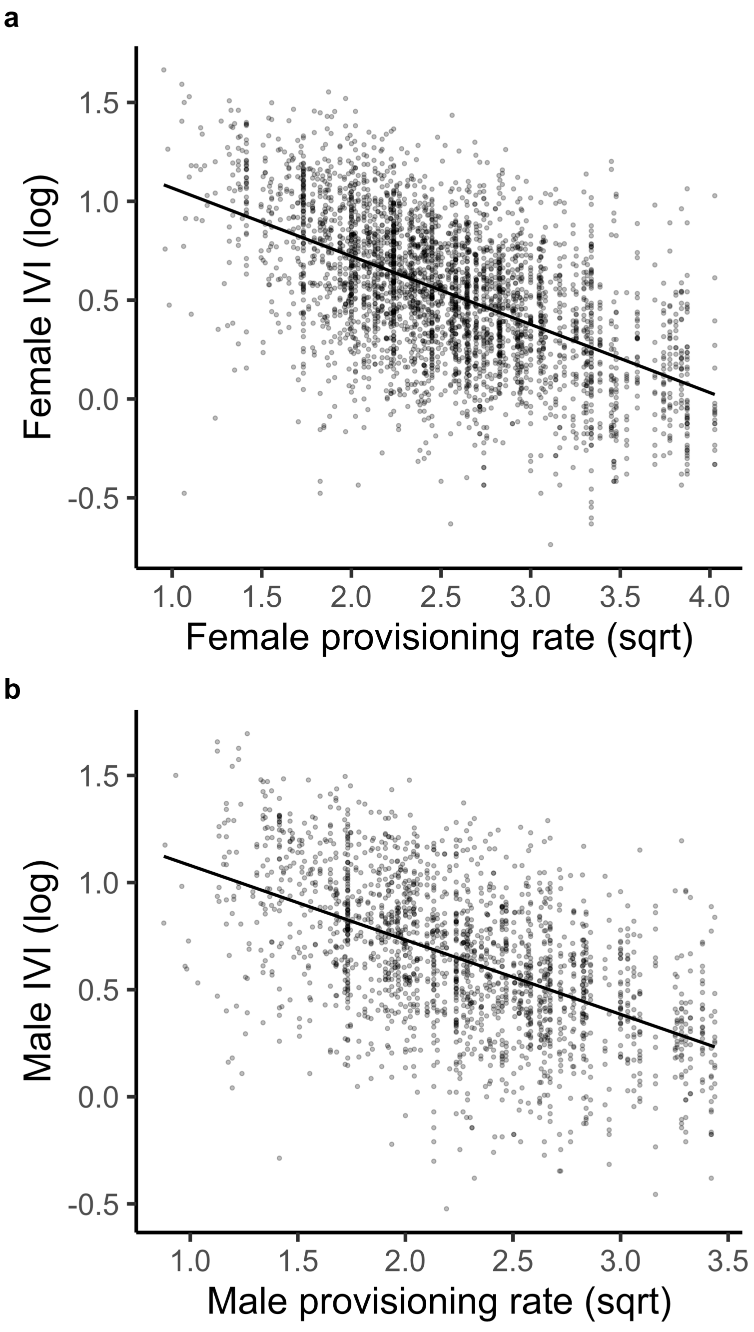

Figure 2.4 **Inter-visit intervals as a function of provisioning rate for (a) females (n = 3,592 IVIs) and (b) males (n = 2,036 IVIs). Intervals have been $\log_{10}$ transformed to normalize their distribution. Provisioning rate was standardized as the number of feeding visits by each parent in a 30 minute observation period and have been square-root transformed to normalize their distribution.**

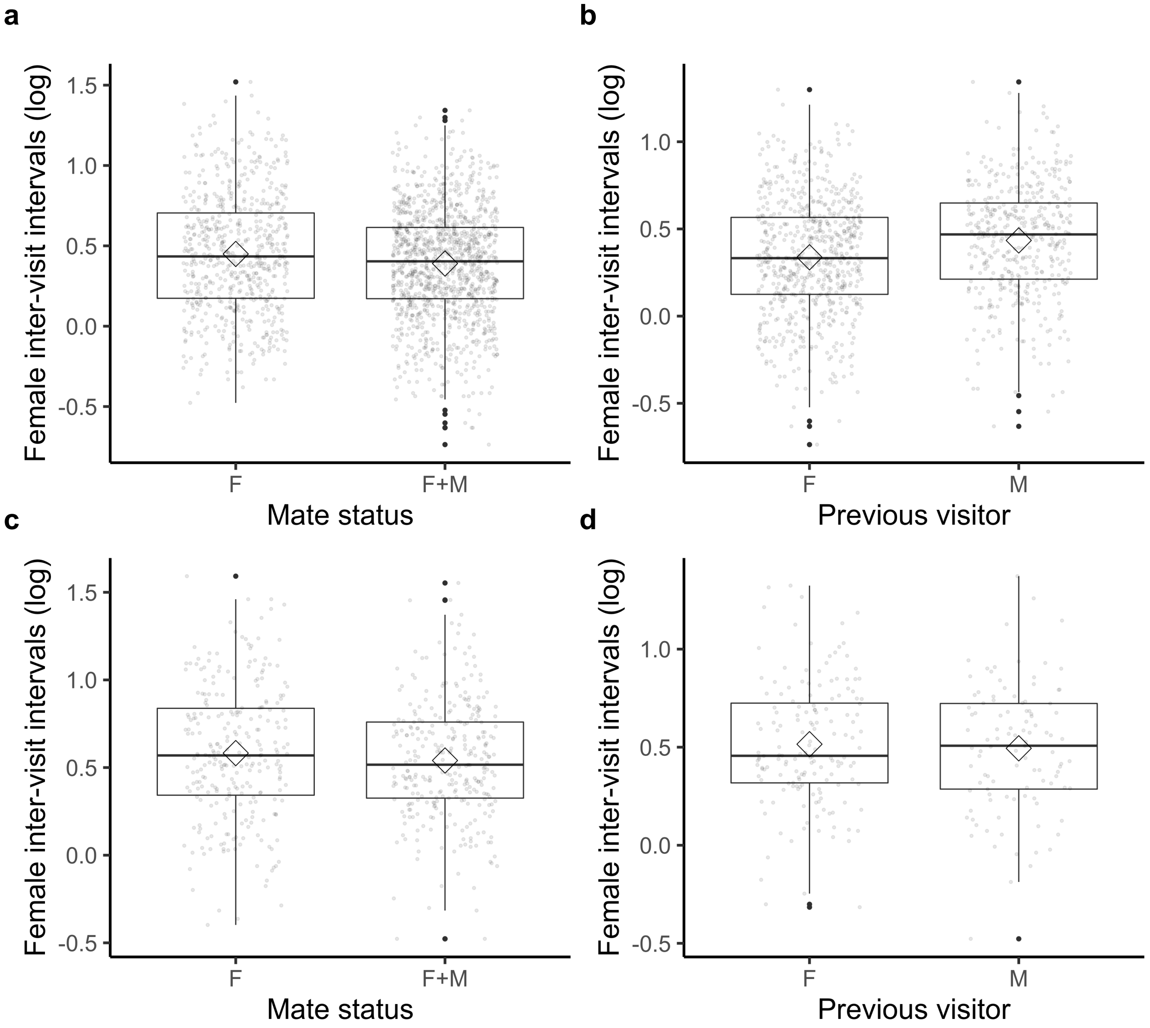

Figure 2.5 **Comparison of female inter-visit intervals between (a, c) nests belonging to unpartnered females (F) and partnered females (F+M) and (b, d) visits where the previous visitor was female (F) or male (M) for (a, b) first broods (n = 1806; n = 1101) and (c, d) second broods (n = 571; n = 265). Intervals have been $\log_{10}$ transformed to normalize their distribution.**

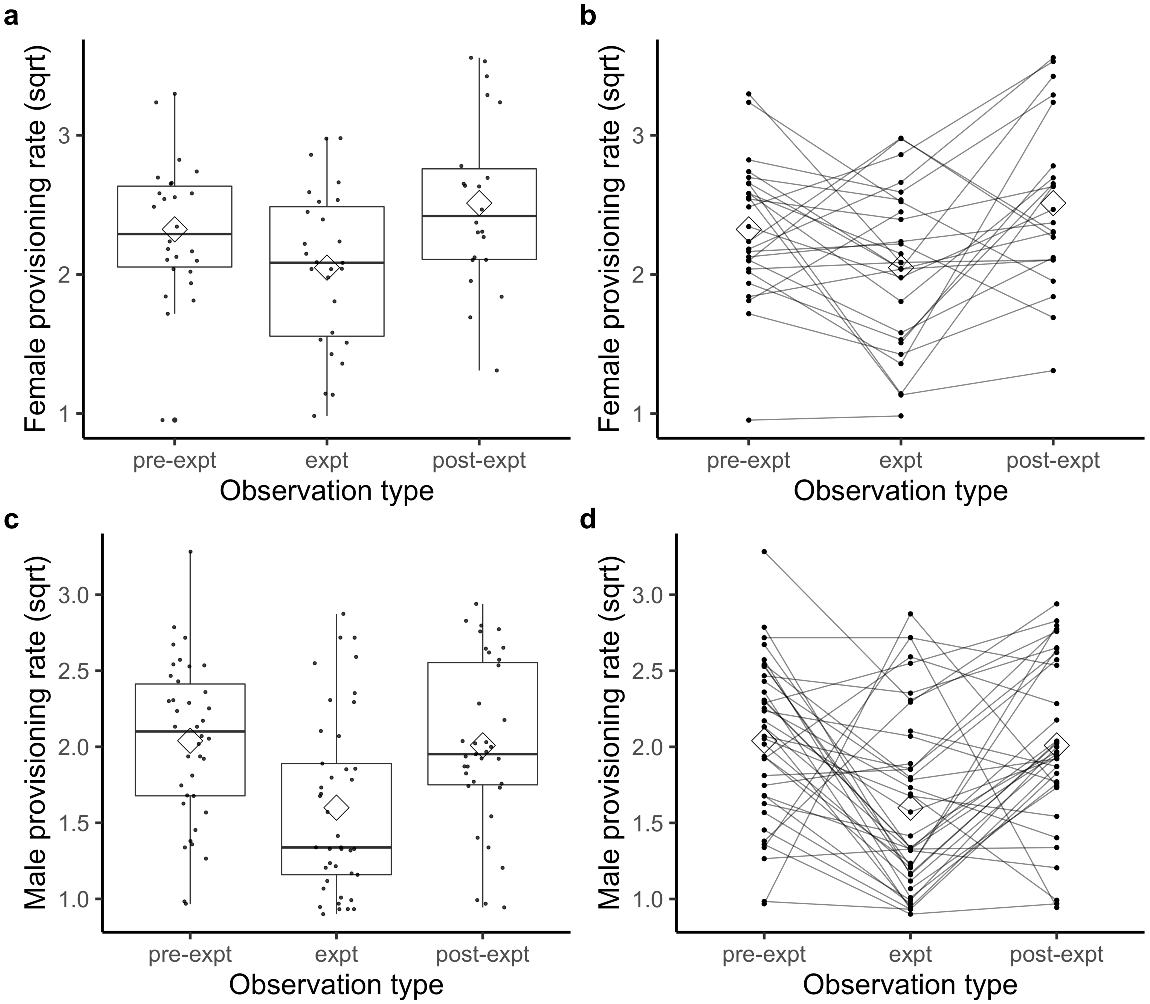

Figure 2.6 **Comparison of provisioning rates between observation types: pre-experimental, experimental, and post-experimental for (a, b) females (n = 75) and (c, d) males (n = 114) in 2019 and 2020. The focal bird's partner was removed from the nest for 1 hour during the experimental observation. Provisioning rate was standardized as the number of feeding visits by each parent in a 30 minute observation period.**

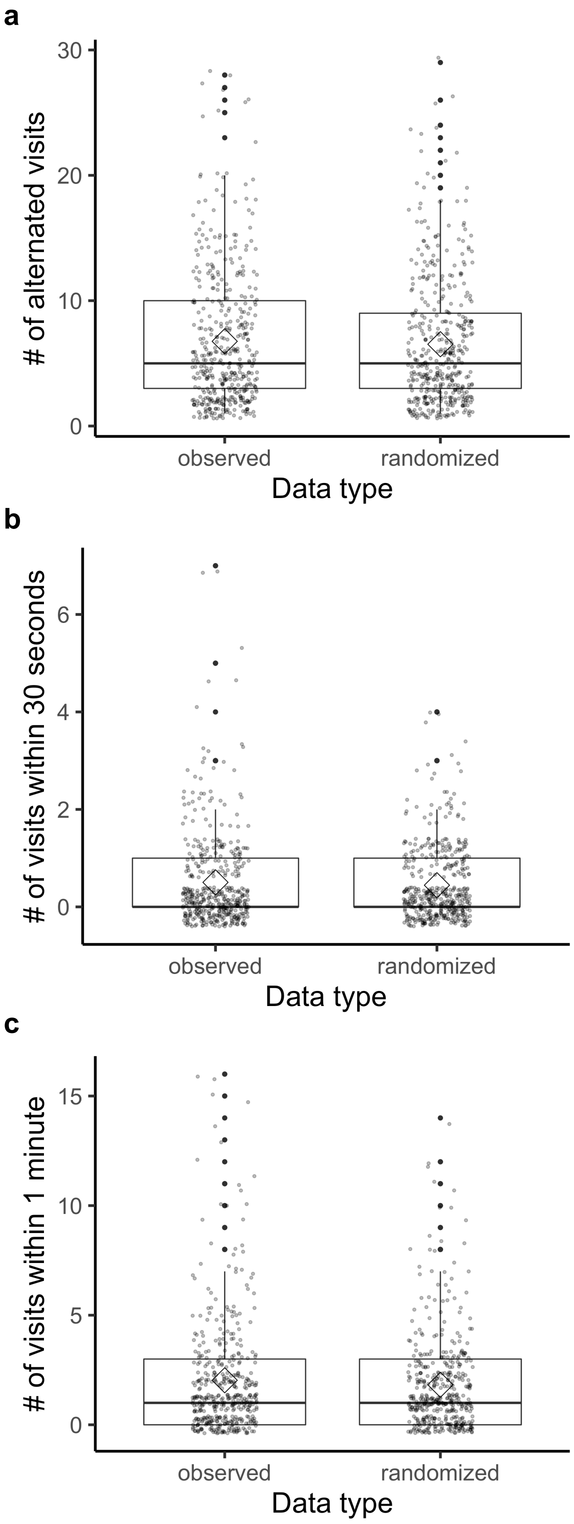

Figure 2.7 **Comparison of (a) alternated visits and (b, c) synched visits, using a threshold of (b) 30 seconds and (c) 1 minute, between observed and randomized data types (n = 424 observations).**

Chapter 3.

General Conclusion

In this thesis, I found that European starlings do not coordinate their parenting via synchrony or alternation of nest visits. Yet, they still demonstrated a clear ability to respond to short-term changes in the provisioning behaviour of their partners. Further, the matching response (decrease in provisioning by the focal parent in response to a perceived decrease in provisioning by the partner) demonstrated by both sexes in the mate removal experiment most closely resembles the outcomes predicted by the information model of investment proposed by Johnstone and Hinde (2006). However, it remains unresolved how European starling parents access up-to-date information about their partners and further studies are needed to explore this fundamental aspect of biparental care.

Investigating the flexibility of parental care is essential for placing alternation and synchrony in context, especially in regards to what information parents have access to on their partners. Recent studies on coordination have begun to include experimental manipulations of provisioning behaviour using brood size manipulations (Baldan, Curk, et al. 2019; Griffioen, Müller, et al. 2019), feather clipping handicaps (Griffioen, Iserbyt, et al. 2019), and short-term mate removal (via catch and release, Iserbyt et al. 2019) – as is presented in this study. More of this research is needed to tease apart a) whether active coordination is occurring and b) what mechanisms are used to maintain coordination. Studies have also begun to examine how coordination varies with factors such as: workload (great tits, Baldan, Curk, et al. 2019; blue tits, Griffioen, Müller, et al. 2019; Griffioen, Iserbyt, et al. 2019), breeding phenology and meteorological conditions (chestnut-crowned babblers, Nomano et al. 2019), reproductive success (long-tailed tits, Bebbington and Hatchwell 2016; house sparrows, Ihle, Pick, Winney, Nakagawa, Schroeder, et al. 2019), ecological conditions (blue tits, Lejeune et al. 2019; house wrens, *Troglodytes aedon*, Baldan and Ouyang 2020), brood desertion (rock sparrows, Baldan and Griggio 2019), and nest site competitors (eastern bluebirds, *Sialia sialis*, Burdick and Siefferman 2020). However, due to differences in how alternation and synchrony are measured and the confounding effect of provisioning rate in most coordination measures (see Discussion), studies may be overstating the apparent effects of coordination. Additionally, the emphasis on birds as models for coordination has not gone unnoticed (Savage et al. 2020). Very few studies investigating coordination have been conducted on non-avian species; these include: Taborsky and Riebli's (2020) work illustrating that cooperatively-breeding daffodil cichlids (*Neolamprologus pulcher*) show evidence of temporal coordination and conditional cooperation and Smiseth's (2019) review of burying beetle research, where he suggests that parents show negotiation of workload despite the lack of explicit study into coordination in beetles. This demonstrates how little is known about coordination in contexts other than provisioning in central-place foraging birds and reveals another area of future interest.

In combination with the difficulties in accurately measuring coordination, the evidence that alternation may be limited to species that synchronize their effort (see Discussion), and the specific focus on turn-taking in birds, conditional cooperation (as it has been researched so far) may not be widely representative as a theory of resolving conflict. In regards to parental care in European starlings, I think much could be gained from investigating what access parents have to information on their partner's behaviour. Ongoing work on the same population of European starlings studied in this thesis includes using radio telemetry to track the movements of fledglings. Similar methods could easily be co-opted to track the movements of parents in order to determine whether they truly are foraging separately and not congregating somewhere outside the nest territory. It would also be fruitful to conduct augmented begging experiments as in Hinde (2006), Meade et al. (2011), and Lendvai et al. (2018) to test whether European starlings respond by matching when partner workload is manipulated in the opposite direction, i.e., whether parents increase their provisioning rate in response to an increased provisioning rate of their partner. The information hypothesis proposed by Johnstone and Hinde (2006) highlights another possible area of research, as there are still unresolved discrepancies between responses to changes in partner provisioning. If partner response depends on assessment of brood need as suggested in this model, individuals should respond to short-term changes in care with matching and longer-term changes in care with partial compensation (see Discussion). This could be tested within the same species by using different treatments to adjust the length of time that parents are exposed to a change in their partner's effort (e.g. augmented begging played in the nest box for a varying lengths of time between pairs). If observed, the change in behavioural response from matching to compensation of effort should also indicate how long it takes for parents to gather accurate information of brood need through chick demand. In conclusion, there is still much to be learned about parental negotiation of care, in birds and among other, less-studied taxa.

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