Ph.D. Dissertation for the degree of Doctor of Philosophy

The pair coordination in provisioning behaviour of a group-living bird, the vinous-throated parrotbill (*Sinosuthora webbiana)*

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Graduate School of Biological Sciences

Seoul National University

Byoungsoon Jang

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Byoungsoon Jang

Confirming the Ph.D. Dissertation written by
Byoungsoon Jang
January 2023

Chair	Seunggwan Shin______	(seal/signature)
Vice Chair	Piotr G. Jablonski______	(seal/signature)
Examiner	Chang-Yong Choi_____	(seal/signature)
Examiner	Sang-im Lee_________	(seal/signature)
Examiner	Jin-Won Lee_________	(seal/signature)

Abstract

Behavioural coordination and synchronization in animals are common within breeding pairs as well as among group members. One of the less studied aspects in this field is the effect of interactions between breeding pairs and group members on the degree of coordination and synchronization within a breeding pair. Birds have been convenient subjects for the study of these phenomena. In this thesis, I investigate multiple aspects of synchronization and behavioural coordination of brood provisioning in a small passerine bird, the vinous-throated parrotbill *Sinosuthora webbiana*. This species can be used as a research model of a social, group-living animal in the natural habitat. Previous studies have suggested that vinous-throated parrotbills form social groups with complicated and long-lasting relationships among members. However, relatively few studies have been conducted on the links between social aspects of their biology and synchronization or coordination within a breeding pair in the breeding season. Therefore, in the three chapters (2, 3, 4) I focus on several aspects of behavioural synchrony and pair coordination during brood provisioning by the vinous-throated parrotbill.

Chapter 2 explored several mutually nonexclusive hypotheses that may explain synchronous nest vist. Parents may coordinate the timing of nest visits, thus decreasing the overall frequency of activity at the nest, in order to lower the risk of nest detection by predators. Parents may also simply move together for their own safety, or because foraging together increases foraging efficiency. In species that maintain social groups during the breeding season, the interactions with group members may affect the synchronization of parental visits to the nest. If other group members provide safety from predators, synchronous nest visit may not be needed for nest or parents' survival. If other group members help in finding food, then their presence increases foraging efficiency of a pair, and may therefore indirectly affect the degree of synchronous nest visits, especially if synchrony is caused by increase in foraging efficiency. Finally, presence of group members may cause many social interactions, which may disrupt normal nest provisioning pattern and decrease the synchrony of nest visits. Using observational evidence, I evaluated those hypotheses. I found that parents frequently synchronize provisioning visits (on average 66.7% of visits in each pair). Higher synchrony was not associated with higher nest survival, and higher local nest predation rate did not affect the level of synchrony of a pair. These results are inconsistent with the hypothesis that the function of synchrony is to avoid nest predation. Although at the population level, the average foraging efficiency of synchronous nest visits was not higher than that of asynchronous nest visits, the pairs increased the degree of synchrony in situations where the foraging efficiency associated with synchronous nest visits was higher than with asynchronous nest visits, but only at low local nest densities. This is consistent with the idea that at lower nest densities, when social interactions (e.g. mate-guarding) presumably do not strongly affect within-pair dynamics, parental synchrony helps in foraging. The level of synchrony was lower at nests with higher local nest density, and vice versa, and the pairs with multiple breeding attempts decreased their level of synchrony in response to increased nesting density over time. This is consistent with the idea that pairs may synchronize their visits to increase their foraging efficiency and/or their own safety, and that the presence of other group members either disrupts the synchrony through social interactions or because they provide alternative safety, so breeding pairs no longer need to synchronize their behaviour. However, longer inter-visit intervals in higher densities suggest that social disruption (e.g. mating guarding or competition over nest site) is a more likely explanation than the decreased perceived predation risk to adults. In conclusion, chapter 2 shows that parental coordination in group-living species is an outcome of within-pair mechanisms modified by social interactions with the group members.

The degree of coordination and synchronization of parents may decrease as nest density and thus interactions with neighbour increase. However, these effects may vary depending on the age and age-related experiences of a focal pair, and the breeding stages of other group members and neighbouring pairs (i.e. whether they are in the similar breeding stage with the focal pair or not). Hence, not only the local nest density, but also the breeding timing of the neighbouring pairs may affect the level of synchronous nest visit of a focal pair. Therefore, in chapter 3, I further investigated how provisioning rate, proportion of synchronous nest visit vary according to parental age, local nest density, and the proportion of neighbouring pairs that breed simultaneously or asynchronously with the focal pair. I found that older parents showed a higher level of synchronous nest visit than young parents among solitary breeders. However, there was no difference in the level of pair coordination according to parental age classes at high densities. Also, I found that the density of neighbours that breed simultaneously was not related to the level of pair coordination. However, when the number of neighbours that reproduce asynchronously with a focal pair (i.e. whether they do not breed or they are at different breeding stages) increased, the level of pair coordination decreased rapidly. These findings further confirm that a decrease in pair coordination level may be linked to the social interactions (disruptions of synchronous nest visit) with the social group members (local neighbours) that are not engaged in intense parental provisioning of their own broods.

The within-pair behavioural mechanisms by which synchrony is achieved and maintained are not fully understood. In chapter 4, I analysed several specific variables that may help to propose observation-based hypotheses regarding the behavioural mechanisms leading to synchrony in parrotbills. Specifically, I investigated the arrival patterns of breeding pairs, the volume of food per visit, the preceding inter-visit interval as a proxy of foraging trip duration, and overall foraging efficiency. I found that one of a breeding pair often spend a long time at the nest after visiting alone, and leave the nest together with its partner who arrive the nest later to feed nestlings. Our finding suggested that waiting for a partner at the nest is likely a mechanism for maintaining continued synchrony. Additionally, during synchronous nest visits, the parent who arrived at the nest first had a larger food load than the follower. Based on these observations, I hypothesize that the first-comer might be the leading individual initiating movement towards the nest and the partner will immediately follow him (or her), which leads to coordinated, synchronous nest visits.

Taken together, these results suggest that the breeding pairs of the vinous-throated parrotbills who live in groups developed behavioural mechanism that facilitate the rearing of offspring, with which they showed a very high level of coordination and synchronous nest visits during chick provisioning. However, the degree of parental coordination may vary depending on individual features (e.g. age, experience) and social environment (e.g. proportion of simultaneous breeding pairs).

Keyword: Behavioural synchrony, pair coordination, nesting density, parental age, vinous-throated parrotbill

Student Number: 2007-30774

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Chapter 1. General Introduction

1.1. Behavioural synchrony over parental care – the phenomenon and the search for the underlying mechanisms

Behavioural coordination and synchronization is widespread in animals ranging from humans (Gueguen, Jacob & Martin, 2009) to invertebrates (Ramírez Vila et al., 2011). In species that live in groups, behavioural synchronization is well developed, and it requires coordination among pair and group members. Also, this behaviour has adaptive value. For example, in birds and mammals, parents synchronize their actions to repel predators or do decrease predation risk. Simultaneous hatching in colonial birds can facilitate group defence by adults (Hernández-Matías, Jover & Ruiz, 2003). Such a synchronization can also bring benefits through group living. Parents can further contribute to protecting eggs from predators by simultaneously mobbing (while moving together) when a predator approaches. This synchronization behaviour can increase the efficiency of catching prey by reducing the time required for vigilance during foraging in groups (Ge, Beauchamp & Li, 2011).

Behavioural synchronization is common within pairs as well as groups. For example, when huddled with a mate the emperor penguins (*Aptenodytes forsteri*) save energy, and huddling leads to stronger an association between partners (Ancel et al., 2009). In the zebra finch (*Taeniopygia guttata*), the pairs who maintain a long-term relationship visit their nests in a more synchronous pattern (simultaneously), and their pair bond lasts longer (Prior & Soma, 2015). Synchronization of pair swimming in bottlenose dolphins (*Tursiops truncatus*) was highly correlated with their coordinated alliance (Jaakkola et al., 2018). The simultaneous or alternating provisioning visits seems to be achieved through active processes. In the great tit (*Parus major*), parents adjusted the provisioning rate by responding more actively to the partner's behaviour rather than the chicks' begging calls. This behaviour alleviates conflicts between partners (Savage et al., 2017) or between offspring (Shen et al., 2010) in the nest. Additionally, the simultaneous visits to the nest may reduce the chances of exposure to predators by reducing the number of visits, as has been demonstrated in several studies (Skutch., 1949; Martin, Scott & Menge, 2000; Ghalambor, Peluc & Martin, 2013). In a study of the long-tailed tit, alternating visits increased the provisioning rate and the chicks' survival rate (Bebbington & Hatchwell, 2016). In species where pair bonds are maintained throughout life, the breeding performance may be more dependent on parental cooperation through pair’s behavioural coordination rather than parental conflict involving attempts at exploitation between partners where one parent forces another to invest more in parental provisioning (Lessells & McNamara, 2012). The latter phenomenon, social effects on mates’ behavioural synchronization, has not been thoroughly studied, and my study species offers an opportunity to explore this issue. Therefore, I focus on behavioural synchronization between partners (e.g. synchronous nest visit) in the timing of their provisioning visits to the brood in Chapter 2, and I use observational evidence to evaluate several hypotheses concerning the factors that affect the behavioural synchronization of the brood provisioning visits.

Partners visiting the nest simultaneously or taking turns visiting the nest to feed their young are the two most often studied forms of coordination between partners. The synchrony visits or alternation visits require a coordination between the two parents, in which individual experience and age may play a role. Therefore, as the age increases, it is expected that the degree of collaboration or coordination between pair members (mates) may increase. Numerous studies have shown that older individuals have a higher reproductive success rate than younger individuals (Cichoñ, 2003; Pitera et al., 2021) However, very few studies have investigated whether parental coordination is associated with parental age or experience. Therefore, in chapter 3, I focus the relationship between coordination of provisioning effort and parental age class under different social conditions (e.g. nesting density, breeding synchrony, familiarity with neighbours). The vinous-throated parrotbills provide unique opportunities to explore these questions.

A synchronous nest visit to the nest may be a result of mates waiting for each other near the nest and entering the nest together, or it may be a result of the two mates travelling and foraging together between the consecutive visits. However, when male and female parents differ in their foraging success, they might show difference in the food load size and timing of arrival during a synchronous visit. I suggest hypotheses on the mechanisms involved in determining the moment when a foraging pair (a bird) decides to move synchronously to the nest with food loads collected by each mate during the foraging bout. Therefore, in Chapter 4 I focus on association between the food load size brought by each of the two parents and theirs order of arrival at the nest during synchronous visits. Arriving sequence might represent a temporary leader-follower relationship by pairs, which may be flexible from a trip to trip according to each individual's foraging success. Such a behaviour might be important in understanding the mechanisms responsible for parental coordination.

1.2. The ecology and ethology of the vinous-throated parrotbill

1.2.1 General information about the study species.

Colonial or semi-colonial breeding birds occur in various avian families (e.g. Brown & Brown, 2000)(Ecology, May & Minias, 2019). The evolution of these reproductive patterns has been mainly explained by the benefits and costs of group living. The benefits of group living during the breeding season include increased foraging efficiency or predator avoidance, while costs include competition for resources or predator attraction. Feeding efficiency in colonial birds is improved mainly through information exchange between colonial breeders (Brown & Brown, 2000). The joint or simultaneous defences against predator attacks can increase the survival of both young and adults of species that breed colonially. Relatively few studies have been conducted on species that maintain social bonds within stable social groups continuously throughout life, i.e. also beyond the breeding season (e.g. the zebra finch (*Taeniopygia guttata*; Prior & Soma, 2015; Mariette & Griffith, 2012). The vinous-throated parrotbill (*Sinosuthora webbiana* Lee et al. 2009a, 2010a) is one of such species and it can be used to explore general questions of behavioural synchronization and coordination within breeding pair in a social system comprising stable groups.

The vinous-throated parrotbill (Fig. 1.2) lives in groups of 30-120 individuals. Membership of group has been constant across the years (Lee et al., 2010). The birds spend most of their lives in the bushes, scrubs, and grasses and are organized in stable groups that occupy relatively small home ranges (Kim, 1998). Only juveniles disperse from the group, or may join other groups during the dispersal period of the juveniles (mainly 1.5months-2.5months after fledging). Although they do not show active group territorial behaviour, they do not mix with members of other groups (winter flocks) throughout year and avoid each other in the boundary area of the home range (Kim, 1998). Although detailed studies on the spatial distribution of nests during breeding season and the social organization of the wintering flocks have been conducted (Lee et al., 2009a; Lee, Lee & Hatchwell, 2010), more detailed studies are still needed on the composition of the spring flock and summer juvenile flocks.

Previous studies described the vinous-throated parrotbill as a semi-colonially breeding species. Nest distribution varies from solitary to colonial (Lee et al., 2009a). The observations suggested that this nesting density may be related to parental age, familiarity among members, and availability of vegetation structure needed for nest location. Competition for preferred nest sites in vegetation among individuals is strong during the nesting period. Aggressive behaviour (e.g. chasing off invaders in competition for nest sites among the group members) has been observed during the nesting period (BJ, personal observation). In general, older individuals tend to breed earlier and further away from the group, and younger individuals tend to breed in clusters around the same time in our study area (BJ, unpublished data). However, there is a large degree of variation with this respect, and it seems to be related to the availability of vegetation structure appropriate for nest location and to age-related traits among group members. Also, due to the high nest predation rate, many individuals frequently move, sometimes long distances after nest de-predation, and the membership (during the breeding season) between the locally breeding subgroups can be easily broken. Hence, while the membership in the main social group (possible to determine in winter flocks) remains stable, the membership in these locally breeding subgroups can be easily changed according to circumstances. Due to the movement of members and due to predation, it is difficult to describe the familiarity, affiliation, and membership bond among individuals. However, a recent study on the vinous-throated showed that the sibling birds tended to breed closer to each other (Lee et al., 2009a). In the zebra finch study, it has been assumed that the parents of individuals are free to determine their nesting site (Mariette & Griffith, 2012). However, in the parrotbill society, nest distribution might represent relationships among individual members (e.g., familiarity, relatives (especially siblings), parental age). Some members might limit their nesting site according to dominance relationships (adult-yearling relationship) although it was not proven yet.

1.2.2. Breeding ecology of the study species

The vinous-throated parrotbills (Fig. 1.2) live in groups throughout their lives. Members of a group almost always move collectively, except for some periods of the breeding season. Group life is also extended during the breeding season, and sometimes several pairs nest simultaneously next to each other in a small area. The vinous-throated parrotbill is a species with bi-parental care of brood (Fig. 1.1), like many other monogamous passerine species. Pair members of the vinous-throated parrotbill participate in almost all reproductive events (e.g. nesting building, incubation, brooding, provisioning) approximately equally between males and females (Kim, Satoshi & Won, 1995). There is currently no known unique task specialization of males and females during the breeding season of parrotbill parents. Parrotbills mate for life, and divorces are relatively rare. A small number of divorces have been reported in yearlings' parents (unpublished data). Pair change in vinous-throated parrotbill occurs with age after mainly the death of a partner. Because the parrotbills have winter-flock fidelity, old members who have long relationships are familiar each other, which will lead to closeness in their nest distribution and social relationships. Early studies of parrotbills have shown that individuals that are genetically close, such as male siblings, breed nearby (Lee et al., 2009a). Social members can form their relationships according to various factors, such as kinship, parental age, intimacy or exclusivity, and personality. The distribution and density of nests during the breeding season might represent results of these social relationships, sibling relationships, and parental age.

Outside of breeding season, parrotbills move in social groups. As the incubation period begins, the most basic movement unit changes from a group to a pair, and this continues into the nestling period. Pairs that fail to reproduce or individuals that do not acquire a suitable nest site (mostly yearlings) seem to continue group life even during the breeding season. In chapter 2, I extend the work of previous investigators who showed that parental synchrony visits decreased at high densities. I investigated a variety of plausible hypotheses and predictions about why this behaviour occurred. The density and distribution of nests might be consequences of social relationships among members in the complex social network of group-living birds. Because parrotbill members live together throughout their lives, they are expected to live in a highly complex, interconnected, structured society, and familiarity, intimacy, and affiliation among subgroup members may determine nesting distribution and density.

1.2.3. Specific information about the study population

Our population of parrotbills has been individually banded every year since winter 2004. A total of 8 winter flocks have been monitored, banded or recaptured, with more than 500 (capture rate of over 90%) individuals yearly for 6 years. I also have caught juveniles during the summer from the beginning of our study in 2007 until end of the study (100-250 per year). Contrary to the low rediscovery rate of nestlings, young birds (yearling) caught after fledging (probably completing natal dispersal) had a higher rediscovery rate in the following winter and breeding season. Since adult individuals are rediscovered in the same group for life after settlement, I determined their age class (categorized as old and yearling in our study) as adults. Juveniles become increasingly difficult to distinguish from older individuals after 2.5 months of age. The sex of a parrotbill is difficult to determine by appearance, although the shape of the cloaca (e.g. cloacal protuberance in male) may determine sex to some extent during the breeding season. Therefore, in this study, sex was determined by genetic analysis, for which I collected blood samples of individuals during the banding period of the winter flock.

Female and male parents of vinous-throated parrotbills have approximately equal provisioning rate at the population level. The timing of their arrivals and departures from the nest may vary while feeding the 6-9 day old nestlings. Sometimes, both parents leave the nest simultaneously after short provisioning, and sometimes a bird arrives alone and then quickly leaves after feeding (example in Fig. 1-1A). In other cases, however, a parent arrives at the nest alone and remains there until a partner arrives, then both leave the nest together (example in Fig. 1-1B). Sometimes after arriving together, the later arriving individual stays at the nest for a long time. In this case, the bird who arrives late may wait for the partner to return or leave alone after a long waiting (Figure 1-1C). Finally, although not common, there are cases where two individuals alternatively stay for a long time after provisioning, like a shift during incubation (Figure 1-1E). Pairs are likely to encounter each other or have contact with each other by calls when shifting. Nest visit patterns show that the parrotbill parents visit the nest in a coordinated way by interacting with each other and responding to each other’s behaviour.

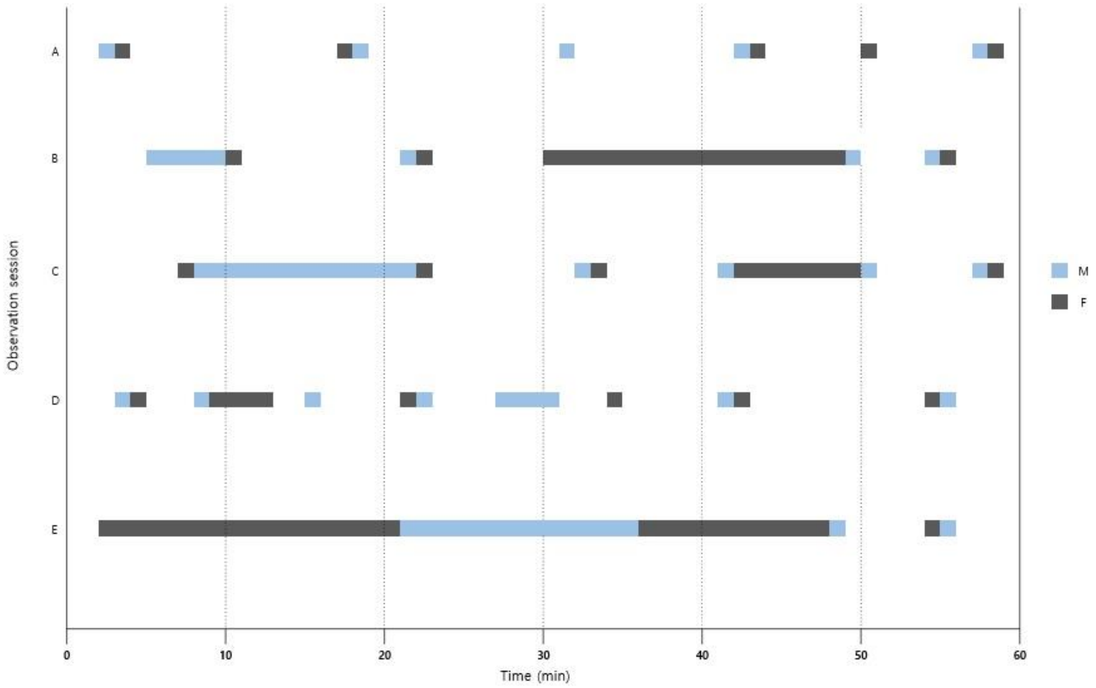

Figure 1.1. A graphical example illustrating variability (A-E) of the timeline (time on *x*-axis) of arrival, departure, duration (of time spent in the nest) of each parent's visit during an observation session (video recorded). Transition time (the latency between arrivals of the two parents) is not shown here if it is less than 1minute. M and F in the legend represent males and females.

Fig. 1-2. Parrotbill parents visit the nest simultaneously. One parent waits for nearby while the partner provision food to the chicks (A; shown red line for calculating prey size, a topic covered in chapter 2, 4). After one parent completes the provisioning, the next partner takes turns provisioning. The first feeding parent does not leave immediately but waits for another partner's provisioning by uttering constant contact call (B) during the most synchrony visit. In the end, the two leave the nest together.

Chapter 2

Foraging benefits and social disturbance shape the degree of synchrony of brood provisioning in a group-living bird.

Abstract

Avian parents often synchronize nest visits to feed chicks. Several non-mutually exclusive hypotheses have been proposed to explain this behaviour. Parents may coordinate the timing of nest visits to decrease the overall frequency of activity at the nest, and thus to lower the risk of nests being detected by predators who watch parents' movements. Parents may also simply move together for their own safety, or because foraging together increases foraging efficiency. Despite the adaptive values of synchronous provisioning, the presence of nearby neighbours often changes the degree of synchronization of parental visits in semi-colonially breeding species. Neighbours may indirectly increase pair's feeding efficiency by alerting predators or exchanging information about food sources, which results in reducing the need for synchronization of a pair. In contrast, the presence of neighbours can hinder a pair synchronizing due to antagonistic competition over nest sites or food sources. Here, we studied the parental synchrony in provisioning behaviour in a group-living passerine, the vinous-throated parrotbill, *Sinosuthora webbiana*. We found that parents frequently synchronize provisioning visits (on average, 66.7% of visits by a pair are synchronous). Higher synchrony was not associated with higher nest survival, and local predation intensity did not affect the level of synchrony. This is inconsistent with the hypothesis that synchrony is to avoid nest predation. Although at the populations level the foraging efficiency was not higher for synchronous than asynchronous visits, the pairs increased the proportion of synchronous visits when a synchronous visit was associated with higher foraging efficiency than an asynchronous visit, but only in pairs breeding in low local densities. The level of synchrony was lower in the nests breeding in higher local density (more neighbours nearby), and the same pairs with multiple breeding attempts decreased their level of synchrony in response to increased nesting density over time. Our results suggest that pairs may synchronize their visits to increase their foraging efficiency and/or their own safety, and that the presence of neighbours nearby either disrupts the synchrony through social interactions or makes a pair no longer need synchronization by securing safety and foraging. In conclusion, our study shows that parental coordination in group-living species is an outcome of within-pair mechanisms modified by social interactions with individuals breeding in the same area.

Keywords: nesting density, synchronous nest visit, vinous-throated parrotbill, *Sinosuthora webbiana*

2.1. **INTRODUCTION**

Animals that live in groups or pairs often perform their actions simultaneously. This behavioural synchronization occurs when the actions among group members switch at the same time (Duranton & Gaunet, 2016). Simultaneous movement between foraging patches requires a mechanism for consensus among members. For example, Rands et al. (2003) proposed a model that a temporary leader-follower could occur when the pair moved simultaneously between foraging patches, depending on their energetic reserve or predation risk.

Behavioural synchrony in social animals is widespread yet not fully understood phenomenon although there have been several theoretical studies addressing this issue (Conradt & Roper, 2005; Conradt & Roper, 2000; Dávid-Barrett & Dunbar, 2012; Duranton & Gaunet, 2016). Behavioural synchrony has adaptive values, such as decreasing the pressure of predation on offspring and increasing social cohesion within pairs or groups (Duranton & Gaunet, 2016), but it can also incur costs in the extra time and energy required to maintain synchrony (Conradt & Roper, 2010; Aivaz & Ruckstuhl, 2011). Models predict that behavioural synchrony should occur when the advantages of synchronized behaviour offset costs incurred through it (Aivaz & Ruckstuhl, 2011), but relatively few empirical studies examined behavioral synchrony in group living animals (King & Cowlishaw, 2009; Nishikawa, Suzuki & Sprague, 2021). Because birds may synchronize provisioning among care-givers (Raihani et al., 2010b; van Rooij & Griffith, 2013; Mariette & Griffi, 2012; Leniowski & Węgrzyn, 2018), avian parental provisioning is a good system to empirically study conditions that lead to behavioral synchrony between members of a reproductive unit (typically a pair in non-cooperative breeders or several individuals in cooperatively breeding birds). Particularly, the parental provisioning in altricial birds, where parents (or provisioners in cooperative breeders) bring food to their offspring in the nest, can be easily quantified. Additionally, parental provisioning in these birds is fundamental for nestling survival (Ricklefs, 2017), and so fitness consequences of various aspects of parental provisioning behaviour can be established.

There are several hypotheses that may explain synchronous provisioning by avian parents or generally by the care-givers (Table 1). Synchronous feeding decreases conspicuousness and movements at the nest, which may attract predators (*nest predation avoidance* hypothesis (Skutch., 1949; Martin, Scott & Menge, 2000; Ghalambor, Peluc & Martin, 2013; Bebbington & Hatchwell, 2016). Reduced visit frequency via synchronous provisioning had a positive effect on nestling survival in cooperatively breeding birds, such as the pied babbler *Turdoides bicolour*, as well as in monogamous birds like the zebra finch *Taeniopygia guttata* or the blackcap *Sylvia atricapilla* (Raihani et al., 2010b; Mariette & Griffith, 2012; Leniowski & Węgrzyn, 2018). Parents may also synchronize their visits in order to increase their own safety because they may warn each other about danger when they forage together which leads to synchronous visits (*parent predation avoidance* hypothesis (Fernández, Capurro & Reboreda, 2003; Ge, Beauchamp & Li, 2011; Ghalambor, Peluc & Martin, 2013; Duranton & Gaunet, 2016; Bebbington & Hatchwell, 2016). However, this may depend on the type of predator and its effect on parents vs offspring (Mahr, Riegler & Hoi, 2014). These two hypotheses are difficult to differentiate because they generate similar predictions: the degree of synchrony should be higher in the areas with higher predation. However, only the *nest predation avoidance* hypothesis predicts an association between the nest predation risk and the degree of synchrony of parental visits; i.e. only the *nest predation avoidance* hypothesis predicts that risk of nest predation is smaller when parents visit the nest synchronously. Finally, parents may also synchronize their visits when foraging together results in higher efficiency than foraging alone (*synchronous foraging benefits* hypothesis (Krebs, MacRoberts & Cullen, 1972; Swallows & Brown, 1988; Santema et al., 2009; Mariette & Griffith, 2013)). Foraging together automatically results in frequent synchronous visits to the nest. Additionally, there are two other hypotheses about the benefits of coordinated/synchronized provisioning, although I have not discussed them in detail (Table 1). First, synchrony and coordination can reduce sexual conflict between parents, allowing the more equitable sharing of workload (Baldan & Griggio 2019). Second, synchrony of nest visits may reduce offspring-offspring conflicts, allowing equal food distribution among the nestlings (Shen et al. 2010).

In social species that breed in groups/colonies of varying sizes and densities, several additional mechanisms should be considered. As other group members can help in detecting predators, parents no longer need to be synchronous in order to decrease predation risk for themselves or their broods (*group predator detection* hypothesis (Elgar, 1989; Ge, Beauchamp & Li, 2011)). This would result in lower synchrony in pairs breeding in locally high densities. If social foraging (foraging with other individuals; either mates or other members of social group) increases foraging efficiency, then not only foraging with the mate but also with any member of the group may be beneficial and this will modify the predictions from the *synchronous foraging benefits* hypothesis. In such a situation, parents who have more chances to forage socially with other group members are expected to be less synchronous within the pair because they may gain similar increase in foraging efficiency regardless (*group foraging benefits* hypothesis). Both, the *synchronous foraging* and the *group foraging* can be viewed as two types of a more general *social foraging* mechanism because in the two hypotheses the presence of a social partner or partners is assumed to help in foraging. This mechanism may lead to own increased foraging efficiency (especially for non-synchronous visits) and to a decreased rate of synchrony in higher local densities.

Despite the adaptive value of synchronous provisioning, however, parental synchrony may be broken by the antagonistic interaction with other individuals nearby. For example, the presence of other birds may create social disruptions of normal foraging and provisioning activities of pairs (*group disruption of foraging* hypothesis(Hake & Ekman, 1988; Tóth et al., 2017). From this hypothesis I expect, similarly to the *group foraging benefits* hypothesis, that the frequency of synchronous visits should be low in higher nesting density, and high in lower nesting density. However, in contrast to the *group foraging benefits* hypothesis, I expect that the interval between consecutive visits should be longer in higher nesting density due to social disruptions of foraging, and that foraging efficiency should not increase in the higher local breeding densities.

In this study, I tested those hypotheses by observing the parental provisioning behaviour of a semi-colonially breeding passerine, the vinous-throated parrotbill, *Sinosuthora webbiana*. The vinous-throated parrotbill is a small (ca.10g) and gregarious bird that is a common resident bird in South Korea. They live in large groups of 40-120 individuals in winter but split into smaller subgroups as the breeding season approaches (Lee, Lee & Hatchwell, 2010). Range and membership of large overwintering flocks remain constant across year (Lee et al., 2010). However, members of a subgroup show a form of fission-fusion during the breeding season, depending on their process of reproduction (i.e., the breeding schedule and location of an individual pair); therefore, the membership is not spatially and temporally stable. In that sense, the parrotbill is not a cooperative breeding bird (Kim, Yamagishi & Won, 1992; Lee, Kim & Hatchwell, 2010) but a pair is the primary reproductive unit in the parrotbill breeding system. Both parents contribute to the workload in approximately equal proportions at all

stages of reproduction (Lee, Kim & Hatchwell, 2010). Parents often defend around nests, especially during nest building, but no longer defend territories but share resources with neighbouring pairs during the rest of the breeding period. As a result, they show various form of nest distribution during the breeding season. Some parrotbill pairs breed in solitary while others breed semi-colonially at close range (Lee et al., 2009a), providing therefore a perfect system for examining the effect of social interaction on parental provisioning behaviour.
The aim of the research is to use observational evidence to evaluate predictions from these six hypotheses (summarized in Table 2-1) using observations of parental provisioning by in the Vinous-throated parrotbill *Sinosuthora webbiana* a socially monogamous group-living passerine with variable frequency of synchronized parental visits (Lee, Kim & Hatchwell, 2010).

Table 2-1. Simplified summary of the hypotheses and predictions explaining why synchronous or asynchronous nest visits occur in group-living birds.

	Hypothesis	Sub-hypothesis	Predictions
Adaptive explanation	avoidance of predation	*Nest predation avoidance*	**synchronous nest visits increase brood survival; when nest predation risk is high then parents are more synchronous**
		Parent predation avoidance	synchronous nest visits enhance parental survival; when adult predation risk is high then parents are more synchronous
	Social foraging	*Synchronous foraging benefit*	**foraging together (leading to synchronous visits) is more efficient than foraging alone**;
		Group foraging benefit	**foraging is more efficient at higher local densities because foraging with other members of social group increases foraging efficiency; the mechanism is the same as in the *synchronous foraging* hypothesis as both hypotheses are versions of a more *general social foraging* hypothesis, when foraging socially increases efficiency**
		Group predator detection	foraging is generally more efficient at higher local densities because other group members can help in detecting the predators
Non-adaptive process	social interactions influence	*Group disruption of foraging*	**foraging efficiency and degree of synchrony decrease (or at least do not increase) in higher local breeding densities because social interactions disrupt foraging and within-pair synchrony**

Bold text is the predictions tested in this study.

&

All the hypotheses predict that **parental synchrony decreases as the nesting density increases**, an effect already documented in the Vinous-throated parrotbill (Lee, Kim & Hatchwell, 2010). If I find no ***relationship between local predator activity and parental synchrony***, then the parent predation avoidance mechanism is an unlikely explanation for the synchronous foraging. If I find no ***relationship between nest predator's activity and parental synchrony***, and/or if parental synchrony does not result in enhancing nest survival, then the nest predation avoidance mechanism is an unlikely explanation for the synchronous foraging. If I find a ***positive association between the synchrony and foraging*** as well as the ***positive association between local density and foraging*** then the synchronous foraging benefit and group foraging benefit are likely to explain the synchrony, because both are just versions of the same general mechanism: foraging together (*social foraging*) increases foraging efficiency. However, if I find a ***positive association between nesting density, but not parental synchrony, and foraging,*** then <u>*group detection of predators*</u> mechanism would be a plausible hypothesis because it less likely that being joined by any group member increases foraging efficiency while being joined by the partner does not. In this situation, the <u>*group detection of predators*</u>, rather than <u>*group foraging benefit*</u>, mechanism would be more likely to be responsible for the positive association between local density and foraging because parent birds may focus on foraging when other group members are vigilant. Finally, if I observe that ***higher local density is associated with longer intervals between visits***, which may also lead to a ***decrease in foraging performance***, I would conclude that it is consistent with the <u>*group disruption of foraging*</u> hypothesis

2.2. METHODS

2.2.1. Study site and study species

The fieldwork was carried out during three breeding seasons, from 2007 to 2009, in Yangseo-myeon, Yangpyeong-gun, Gyeonggi-do, South Korea (37°32′N, 127°20′E). The study area (about 9km^2) includes farmland, woodland with scrubs and bushes at the edges. Further details about the study site could be found elsewhere (Kim C. H, Yamagishi S., 1995; Lee et al., 2009a). Open-cup nests are usually located in dense bushes, shrubs or small trees. A pair mates for life, and extra-pair copulations occurs at a low rate (Lee et al., 2009b). Parental roles such as nest building, incubation, chick-rearing are similar between sexes throughout the breeding cycle (Kim, 1998). Parrotbill young fledge at the age of 10-13 days (Kim, Satoshi & Won, 1995). The rate of nest predation in our population of the vinous-throated parrotbill is high (over 60%), and failed breeders attempt to renest. I observed 9 pairs with two breeding attempts within a year, and 2 pairs with three breeding attempts within a year.

Vinous-throated parrotbills spend the winter in groups of stable membership of approximately 40-120 individuals (Lee, Lee & Hatchwell, 2010). Large winter flocks split up into subgroups as the laying period approaches. Most pairs in the subgroups attempt to breed at close range from each other, but some pairs breed away from others. Therefore, the nests' distribution varies from solitary to loosely colonial (Kim, Satoshi & Won, 1995; Lee et al., 2009a).

2.2.2. Fieldwork

I caught parrotbills by placing mist nets near bushes or scrubs during the preceding non-breeding seasons (December-February), when they form large groups. I collected blood samples from all the birds (over 2500 individuals) that I color-banded from the late of the 2004 season through to the completion of the study (the early of the 2010 season). Blood samples (approximately 10-20 μl per bird) were taken from the brachial vein and were stored in absolute ethanol in the refrigerator. DNA was extracted from these samples in the lab before the breeding season. Sex was determined by the PCR-based technique (P2/P8 primers; (Griffiths et al., 1998). This allowed me to identify almost all breeding pairs (over 90%) during the subsequent breeding seasons. I searched for nests during the breeding seasons (April-July). Once I located a nest, I recorded nest position using

GPS, identified the parent’s colour rings, and then monitored the nests at the regular intervals of 1-3 days. I recorded parental visits to the nests using digital video cameras ((JVC GZ-MG7OKR and Sony Handycam SR62) positioned 2–8m from each nest to identify the provisioning adults from its unique colour-ring combination. I video- recorded parental feeding behavior for a mean duration of 4 h per nest (range 1.5–6.5h, n = 88 nests; once for each nest), during peak offspring demand (brood age 6–9 d, mean=7 days) in the morning (6:30-9:00am), except for bad weather. In general, young broods (nestling age 1-4 days) are visited by parents asynchronously because both parents take turns in brooding the chicks. Therefore, I focused on older broods. During the three breeding seasons of 2007-2009, I collected 304.7 hours of video at 88 nests, where I observed 1908 provisioning visits by parents. Brood size on the day of filming was on average 5 (range 3-7).

2.2.3. Variables used in the analyses

From the video, U recorded the time of each parent's arrival and departure (to the nearest 1s). The ***arrival time*** of a parent (I mark variable names with ***bold italic*** to indicate their specific meaning defined within this paper) was defined as the moment when a parent with food perched on/in a nest or in the nest tree (parents fed nestlings immediately after arrival without exception). The ***departure time*** of a parent was defined as the time when a parent flew away from the nest. Visits without food were rare (4 visits out of 1912 visits), and they were excluded from the analyses. I extracted two different groups of variables. One group was extracted for all 88 videotaped nests of 74 pairs. Additional variables were extracted for a smaller data set, for which the composition and size of prey brought to the nestlings were recorded. In the smaller data set of 27 broods, I aimed to compare synchronous and asynchronous visits within a pair where both types of visits were performed by the parents.

2.2.3.1. Variables for all nests (n=88)

Visit type- I followed the criterion of synchronous provisioning used by Lee et al. (2010). The *asynchronous nest visit* was defined as a visit of a single parent when its partner did not visit the nest within 1 min before or after the focal birds’ visit (following Mariette et al. 2012, I use the term ***transition time*** for this latency between visits of the two parents). If a visit involved arrivals of mates within the *transition time* of 1 minute from each other (the median transition was 4s; range 0 to 60s, n=775 transitions) and if none of the parents stayed in the nest for an excessively long time then the visit was considered a *synchronous visit*; otherwise, the visit was considered an *asynchronous visit*. A provisioning parent spent 2-2967seconds (median 22 s, n=1908) in the nest during an individual visit. However, among all the visits, 191 visits (67 visits in males, 124 visits in females) were associated with the subsequent excessive duration (defined as >2min) of staying in the nest by a visiting parent (median = 691s, 622s in male and female, respectively). If one parent stayed in the nest for the excessive duration (>2 min), I did not regard it as a synchronous provisioning even when parents arrived within 1 min of each other. During the monitoring period, parents visited their nests for feeding an average of 2.9 (male) and 2.8 (female) times. It indicates that the possibility of arriving by chance within a minute of each other is as low as 0.23% ((2.9 times x (1/60 min) x 2.8 x 1/60) x 100). Therefore, it is unlikely that random chance could explain the level of the synchronous provisioning observed between a pair.

Number of asynchronous visits or ***synchronous visits*** – the numbers directly observed in the video for each nest.

Proportion of synchronous visits – when used as an explanatory variable, it was calculated as (***number of synchronous visits***) / (***number of synchronous visits*** + ***number of asynchronous visits***). When analysing the proportion of synchronous visits as dependent (response) variable, the *cbind* function was used: *cbind* ((***number of synchronous visits***, ***number of asynchronous visits***).

Nesting density – The foraging distance of a pair is known to be 30-170 m from the nest (Kim, 1998). Therefore, as with Lee et al. (2010), I assumed that parents of the nests located within 200m or less from each other could frequently interact with each other. Therefore, for each of the 88 nests I calculated the local density as the maximal number of nests within 200 m radius that were active simultaneously with the focal nest. Nests were considered active from time the first egg was laid until nestlings either successfully fledged (sometimes until 2-3 days after fledging because parents stayed near their own nest with their young during that period) or until the nest failed. Nests were considered active simultaneously with the focal nest when there was any overlap between the active period of a nest and the focal nest. In total, 230 nests were considered in these calculations. Nesting density varied from 0 to 8 (mean±SD=3.02±2.03, n=88).

Predation intensity **-** Parents may experience how their nesting areas would be exposed to potential predators during the season because they could observe those predators even on their nests (unpublished data, JBS). I determined that predation intensity of the focal nest as the percentage of predation that occurred prior to the date of video-recording for all nests within 200 m of the focal nest. Predation that occurred after the video-recording may not associated with the provisioning behaviour of the focal nest parent at the time. In this study, the number of active nests located within 200m of the nest of the focal nest varied from 0 to 8 (average of 3 nests). The predation rate of the focal nest prior to video-recording ranged from 0 to100% with an average predation rate of 31.5%, which is naturally lower than the overall predation rate (66.5%, n=230). From video recordings, the primary predators of nestlings and eggs in our study area were the Eurasian jay (*Garrulus glandarius*) and Diones' ratsnake (*Elaphe dione*).

Brood survival – This is a binary variable describing if the brood survived until fledging or not and was calculated for all nests that survived until the hatching phase. This variable, albeit crude, was sufficient for our analyses aimed to test the predictions. Nestling starvation was rare throughout the breeding season (Kim, Yamagishi & Won, 1995; Lee et al., 2009b). Most nest failures were likely associated with nest predation (Kim, Yamagishi & Won, 1995).

Inter-visit interval **–** The inter-visit interval has been widely used to quantify carer behaviour, a variable that has been mathematically inversely related to provisioning rate (Savage & Hinde, 2019; Lejeune et al., 2019). I calculated inter-visit interval as the period from the moment the parent leaves the nest and the moment it arrives to the nest at the subsequent provisioning visit. As the filming was mostly done during the morning hours of high intensity of provisioning when birds mostly spent their time foraging between the subsequent visits, I use this as a rough proxy of time spent foraging by a male and a female separately. Naturally, occasionally the birds also can spend this time on other activities, and therefore inter-visit interval can only approximately be regarded as time spent foraging between visits. In the statistical analyses I used square-root transformation of this variable.

Maximum inter-visit interval – It is defined as the longest ***inter-visit interval*** observed for each bird (male and female within a pair separately). Outlier values of the inter-visit interval might indicate foraging trips that might have been interrupted by other activities (e.g. self-feeding, bathing, or possibly social interaction in colonial birds)(Savage & Hinde, 2019). If social disruption is involved, then I may expect that at least some of the ***inter-visit intervals*** may increase due to the social interactions, and therefore there is a possibility that the longest intervals may be an outcome of such a mechanism. However, simple self-maintenance activities (like bathing, preening, etc.) may also be responsible for the longest inter-visit intervals. In the statistical analyses I used square-root transformation of this variable.

PairID – Unique label for each pair. It was used as random variable in mixed models to control for repeat measures because I analysed/compared synchronous and asynchronous visits within a pair. Additionally, some pairs had a second (8) or third (n=2) brood, and those broods were also included in the dataset.

Other variables include ***Year (2007-2009)***, ***Laying date (***as the number of days from April 15th, ***Brood size*** (3-7), ***Brood age*** (6-9) and ***Sex***.

2.2.3.2. Additional variables for a subset of 27 nests

The restricted dataset comprised 27 nests from two breeding seasons (2008, 2009) for which diet data were available, and in which both types of visits were observed. For each bird, I estimated the prey load size at each visit. The length and width of prey items were measured by comparing it to the observable part of bill, tarsus, or color-band using a caliper on the screen. I extracted the following variables:

Number of prey items per visit – number of prey items brought by a bird in each visit (i.e. number of prey items in a prey load).

Prey load size - a sum of volume indices for all prey items brought during a visit (mm^3/visit). A ***prey volume index*** (mm^3) was calculated for each prey item using the estimated prey length (L; mm) and width (w; mm) according to the following formulas (Blondel et al., 1991; Bańbura et al., 1994).

- *prey volume index* = $(\pi /4) \times L \times \mathrm{w}^2$

(for Lepidoptera and for arthropods with cylindrical shape);

- *prey volume index* = $(\pi /6) \times L \times w^2$ for spiders,

Mean prey size index – calculated for each visit as an average ***prey volume index*** (mm^3/prey) from all prey items in a prey load (brought at one visit).

Foraging "efficiency" index - calculated for each visit of a parent by dividing the ***prey load size*** by the preceding ***inter-visit interval*** (mm^3/second). If I assume that inter-visit interval approximates the time spent foraging (see arguments above in the definition of ***Inter-visit interval***) between the subsequent visits, then the foraging efficiency index can be used as a proxy for foraging efficiency.

Maximal foraging efficiency - is defined as the largest of foraging "efficiency" index observed for each bird (male and female within a pair separately).

Relative foraging benefits from synchrony (shorter version ***Relative benefits from synchrony***) – it was calculated by subtracting the ***mean foraging "efficiency"*** for asynchronous visits from that of synchronous visits (***SmAEff***; mean ***S***ynchrony ***m***inus ***A***synchrony ***Eff***iciency at each nest) to the nest. This is an index of relative foraging superiority (or inferiority if values are negative) of synchronous over asynchronous foraging (and visits) for each bird (separately for a male and a female in a pair). If parents visit nest synchronously because of synchronous foraging benefits, then they may be sensitive to the local differences in foraging efficiency between synchronous and asynchronous visits. In this situation I may expect that birds increase the proportion of synchronous visits for locations in which foraging efficiency at the synchronous visits is higher than the efficiency at the asynchronous visits.

Brood size category – It was an ordinal variable based on the recorded ***brood size***: category 1= less than five chicks (mostly four chicks except one sample with 3 chicks), category 2 = 5 chicks, and category 3= more than five chicks (mostly 6 chicks except one sample with 7 chicks).

Brood age category – It was an ordinal variable based on ***brood age***: category 7= brood age of 6, 7 days (mostly 7 days: two sample size in 6 brood age); category 8=brood age of 8 days; category 9= brood age of 9 days.

2.2.4. Statistical analyses

2.2.4.1. General statistical methods

Statistical analyses were conducted in the R studio, version 3. 6. 3 (R Development Core Team, 2019) using the *lme4* package (Bates et al., 2015). Figures were produced using the "*ggplot2*" package (Wickham, 2016), "*ggpubr*" package (Kassambara, 2021), and "*ggeffects*" package (Lüdecke, 2018) for interaction effects. Model selection was performed using the *dredge* function in the package *MuMIn* (Barton & Barton, 2020). This function ranks the candidate models comprising all possible combinations of explanatory effects according to the Akaike Information Criterion (AICc). Models with lower AICc values are better supported by the data, and only models with ΔAICc < 4 were averaged according to the standard methodology (Burnham and Anderson, 2002; Grueber et al., 2011). The full (i.e. average estimates from which the variable was included in every model) and conditional model averaged estimates (i.e. average estimates from only those models in which the variable was included) were calculated. Effects were regarded as statistically significant when the 95% confidence intervals for a parameter estimate did not cross the zero (Burnham and Anderson, 2002).

The continuous variables were scaled and mean-centred (mean 0 and standard deviation 1) and unordered (e.g. sex, year, nest visit type) were standardized in all models using the *standardize* function (Eager, 2017) in *MuMIn* package. To check multi- collinearity among predictor variables, *VIF* (variance inflation factors) was calculated for each predictor in the global model using *performance* package (Lüdecke et al., 2021). *VIF* was <2.5 in all global models, indicating moderate level of collinearity among predictors (Freckleton, 2011). To avoid pseudo-replication due to repeated nesting attempts by the same pair, and due to synchronous and asynchronous visits by the same pair, I used ***pairID*** as a random factor in the statistical models.

2.2.4.2. General analyses of the synchronous provisioning visit (n=88)

Proportion of synchronous visits - I used the whole data set of 88 nests from three breeding seasons (2007-2009) to analyze factors influencing the proportion of synchronous nest visits. The response variable "***Proportion of synchronous visits***" in a GLMM with binomial distribution of errors and logit-link function was defined in the statistical analyses as *cbind* ***(number of synchronous visits/number of asynchronous visits).*** **Pair identities included random terms in the model.** The global model contained six independent variables: ***year*** (entered as category), ***laying date***, ***nesting density***, and ***predation intensity***, ***brood size***, ***brood age***; it also included six two-way interactions (***year*** x ***predation intensity***, ***year*** x ***nesting density***, ***year*** x ***brood age***, ***year*** x ***brood size***, ***nesting density*** x ***predation intensity, nesting density*** x ***laying date***). We include year as a fixed effect with its interactions in the model as some key parameters such as food availability and predation rate can vary greatly from year to year. I also used Spearman rank correlation to test if double-brooded pairs change their frequency of synchronous visits in response to the change in the nesting density between the consecutive breeding events within the same breeding season.

Nest predation risk - I used generalized linear mixed models (*glmer* function in R; R 3.6.3) with binomial error structure and logit-link function in order to investigate the effect of the ***proportion synchronous visits*** on ***brood survival*** from hatching to fledging (variable ***Brood Survival*** with two values: *1=survived, 0=depredated*).

2.2.4.3. Analyses of the foraging efficiency available prey load size (n=27 nests)

To analyze the comparison of foraging efficiency between synchronous and asynchronous visits, I used generalized linear mixed models (using the *lme4* packages) and the factors in the global (initial) model were the same as for the analysis of the proportion of synchronous visits (see above, analysis of the full data set), with additional factors added: ***nest visit type*** (synchronous or asynchronous), and bird ***sex*** (male or female). The pair ID was entered as random factor to account for repeated measures on the pair. I analysed the following response variables characterizing a visit: ***number of prey items***, ***prey load size***, ***mean prey size***.

Finally, using Generalized Linear Mixed Model analysis (GLMM) I determined if the ***relative foraging benefits from synchrony*** within a focal nesting site and other factors (***year, laying date***, ***nesting density***, ***predation intensity, brood size category*** and ***nestling age category***), affect the probability of a synchronous visit. I modelled ***nest visit type*** as a binary response (synchronous vs asynchronous visit) in a mixed model including ***pairID*** as a random effect and ***sex***, ***nesting density***, preceding ***inter-visit interval***, ***predation intensity***, ***brood***

age category, ***laying date***, ***year***, ***relative benefits from synchrony (SmAEff)*** as well as the following four interactions: ***nesting density*** x ***predation intensity***, ***nesting density*** x ***SmAEff***, ***nesting density*** x ***predation intensity***, ***predation intensity*** x ***SmAEff***. I excluded the first visit of each parent in all nests because the ***inter-visit interval*** for the first visit could not be calculated.

To explore the relationship between inter-visit intervals and synchrony (e.g. visit type) and environment factor (e.g. year, laying date), I analysed the ***inter-visit interval*** as Gaussian response variable in a mixed model including ***pair ID*** as a random effect and the following effects: ***visit type***, ***sex***, ***nesting density***, ***predation intensity***, ***brood age category***, ***brood size category***, ***laying date***, ***year***, including interactions of ***nesting density*** with other predictors (***visit type***, ***sex***, ***predation intensity***, ***brood age category***, ***brood size category***, ***year***).

2-3 RESULTS

As the main aim of all the analyses was to evaluate several hypotheses that may explain the degree of synchronous provisioning by the parrotbills, I added brief interpretation statements to each part of the results in order to keep the focus on the results' contribution to the evaluation of the hypotheses. In the discussion, I fully consider all the evidence together in the evaluation of the hypotheses.

General analyses of the synchronous provisioning visit (n=88 nests)

Parents visited the nest on average every 21.2±12 minutes (mean±SD throughout the paper; range: 0.7-73.3, n=1732 visits from 88 nests), leading to the provisioning rate of 5.7±1.89 visits/brood/hour. Both partners had similar provisioning rate (male: 2.8±1.0/hr vs. female: 2.9±1.2/hr, n=88). On average, partners conducted synchronous visits in 66.3±22.2% of the visits (0, 56.5%, 70.0%, 82.6%, 100% are the minimum, first quartile, median, third quartile and maximum respectively). The ***proportion of synchronous visits*** was higher in the pairs breeding in lower ***nesting density*** (Fig. 2-1A; Table 2-2), and it generally declined during a breeding season (Table 2) regardless of ***nesting density*** (interaction ***density*** x ***laying date*** not significant; Table 2-2). The ***proportion of synchronous nest visits*** was not affected (in statistical sense) by ***brood size, brood age***, ***predation intensity*** or ***year*** (Table 2-2).

In 10 double-brooded pairs within a season, the proportion of synchronous provisioning significantly decreased between consecutive breeding attempts as the nesting density increased between consecutive breeding attempts (Fig. 2-1B, Spearman's rank correlation, $r_s = -0.82$, $n = 10$, $p < 0.01$), indicating that the same pair decreased the degree of synchrony in response to increased nesting density (or increased their synchrony in response to decreased nesting density). These results indicate the possible role of the hypotheses involving direct effects of nesting density on synchrony.

There was no effect of local ***nest predation intensity*** on the degree of synchrony (Table 2-2), and the ***proportion of synchronous visits*** did not affect the nest success rate (Table 2-3, Fig. 2-S1). Hence, these results do not support the *nest predation avoidance hypothesis*.

Inter-visits intervals - The ***inter-visit interval*** was shorter for asynchronous visits (Fig. 2-2A; Table 4). Additionally, the inter-visit interval was shorter in older broods (Fig. 2-2B; Table 2-4). The ***maximum inter-visit interval*** did not depend on any factor (Table 2-5).

Table 2-2. Summary of model averaging to determine the predictor variables that affect the ***proportion of synchronous visits*** among all visits by a pair. The response variable was defined as *cbind* (number of synchronous visits, number of asynchronous visits). Sample sizes for the whole dataset are 88 broods. Italic in square brackets shows information concerning conditional averages (i.e. average estimates from only those models in which the variable was included). Bold indicates estimates that are significantly different from zero (at $p<0.05$). The 11 top models of ΔAICc < 4 were used in the model averaging. Global (Initial) model: *cbind* (No. of synchrony visit, No. of asynchronous visits) ~ Year+ Brood size (BS) + Brood age (BA) + Nesting density (DN) + Predation intensity (PI) + Laying date (LD) + Year: (PI +DN+ BA + BS) + DN: (PI + LD), random factor = pair identity, family = binomial. This table concerns Fig. 2-1A, and Table 2-S9 lists the top models.

	Estimate	Adjusted SE	z value	Pr(>|z|)	2.5%	97.5%
(Intercept)	0.83 [*0.83*]	0.12 [*0.12*]	7.06 [7.06]	0.00 [*0.00*]	0.60 [*0.60*]	1.06 [*1.06*]
Nesting density (ND)	-0.46 [-0.46]	0.12 [*0.12*]	3.86 [3.86]	0.00 [*0.00*]	**-0.70 [-0.70]**	**-0.23 [-0.23]**
Laying date (LD)	-0.21 [-*0.22*]	0.09 [*0.08*]	2.20 [*2.59*]	0.03 [*0.01*]	**-0.38 [-*0.38*]**	**-0.05 [-*0.05*]**
Brood age (BA)	-0.01 [-0.01]	0.09 [*0.11*]	0.10 [*0.12*]	0.92 [*0.90*]	-0.23 [-0.23]	0.20 [*0.20*]
Year 2007 ^{a}	0.02 [*0.04*]	0.12 [*0.16*]	0.19 [*0.26*]	0.85 [*0.79*]	-0.28 [-*0.28*]	0.36 [*0.36*]
Year 2008 ^{a}	0.05 [*0.10*]	0.13 [*0.17*]	0.41 [*0.60*]	0.68 [*0.55*]	-0.23 [-*0.23*]	0.43 [*0.43*]
BA:Year 2007 ^{a}	0.19 [*0.34*]	0.20 [*0.13*]	0.95 [*2.64*]	0.34 [*0.01*]	-0.09 [***0.09***]	0.60 [***0.60***]
BA:Year 2008 ^{a}	-0.31 [-*0.57*]	0.31 [*0.17*]	1.00 [*3.29*]	0.32 [*0.00*]	-0.91 [***-0.91***]	0.23 [***-0.23***]
Brood size	-0.01 [-*0.04*]	0.04 [*0.09*]	0.15 [*0.43*]	0.88 [*0.67*]	-0.23 [-*0.23*]	0.14 [*0.14*]
Predation intensity	0.01 [*0.05*]	0.04 [*0.09*]	0.21 [*0.53*]	0.84 [*0.60*]	-0.13 [-*0.13*]	0.23 [*0.23*]
ND:LD	0.01 [*0.06*]	0.04 [*0.11*]	0.17 [*0.51*]	0.86 [*0.61*]	-0.27 [-*0.27*]	0.16 [*0.16*]
ND:PI	-0.01 [-0.14]	0.04 [0.10]	0.18 [1.35]	0.85 [0.18]	-0.08 [-0.34]	0.68 [0.06]

^{a} (2009 reference category).

Table 2-3. Summary of GLMMs analysis of factors affecting the nest survival rate (response variable: ***Nest survival***). Sample sizes for the whole dataset are 88 broods. Italic in square brackets shows information concerning conditional averages (i.e. average estimates from only those models in which the variable was included). The 22 top models of ΔAICc < 4 were used in model averaging. Global (Initial) model: Survival (0,1) ~ Year + Nesting density + Predation intensity + Laying date + Proportion of synchronous visit, random factor = pair identity, family = binomial. Estimate from mean centred predictors. (Brood size, brood age, all interactions were not included in initial model because model failed to converse). This table concerns Fig. 2-3S, and Table 2-S10 lists the top models.

	Estimate	Adjusted SE	z value	Pr(>|z|)	2.5%	97.5%
(Intercept)	2.46 [*2.46*]	0.47 [*0.47*]	5.27 [*5.27*]	0.00 [*0.00*]	1.55 [*1.55*]	3.38 [*3.38*]
Year 2007[a]	-0.50 [-*0.90*]	0.61 [*0.56*]	0.82 [*1.60*]	0.41 [*0.11*]	-1.7 [-*1.99*]	0.70 [*0.20*]
Year 2008[a]	-0.23 [-*0.42*]	0.55 [*0.67*]	0.43 [*0.63*]	0.67 [*0.53*]	-1.3 [-*1.74*]	0.83 [*0.90*]
Laying date	-0.21 [-*0.54*]	0.39 [*0.46*]	0.54 [*1.17*]	0.59 [*0.24*]	-0.98 [-*1.45*]	0.56 [*0.37*]
Proportion of synchronous visits	-0.13 [-*0.41*]	0.33 [*0.47*]	0.41 [*0.89*]	0.68 [*0.37*]	-0.77 [-*1.33*]	0.51 [*0.50*]
Predation intensity	-0.06 [-*0.26*]	0.24 [*0.45*]	0.25 [*0.57*]	0.81 [*0.57*]	-0.53 [-*1.14*]	0.41 [*0.63*]
Nesting density	0.03 [*0.16*]	0.19 [*0.40*]	0.17 [*0.39*]	0.86 [*0.69*]	-0.35 [-*0.63*]	0.42 [*0.94*]

[a] 2009 (reference category)

Table 2-4. Summary of model averaging for predictors affecting the ***Inter-visit interval (seconds).*** Sample sizes for the whole dataset are 1732 observations from 88 broods. Italic in square brackets shows information concerning conditional averages (i.e. average estimates from only those models in which the variable was included). Bold indicates estimates that are significantly different from zero (at $p<0.05$). The 2 top models of ΔAICc < 4 were used in model. Bold indicates estimates that are significantly different from zero (at $p<0.05$). Global (Initial) model: Inter-visit interval ~ Visit type (VT) + Sex + Year + Brood size (BS) + Brood age (BA) + Nesting density (ND) + Predation intensity (PI) + Laying date + ND:(VT + Sex + PI + BA + BS +Year), random effect: pair identity. This table concerns Fig. 2-2, and Table S11 lists the top models.

	Estimate	Adjusted SE	z value	Pr(>|z|)	2.5%	97.5%
(Intercept)	0.06[*0.06*]	0.05[*0.05*]	1.14[*1.14*]	0.26[*0.26*]	-0.04[-*0.04*]	0.16[*0.16*]
Brood age	-0.26[-*0.26*]	0.04[*0.04*]	6.85[*6.85*]	0.00[*0.00*]	**-0.33[-*0.33*]**	**-0.18[-*0.18*]**
Visit type (Asynchrony)[a]	-0.10[-*0.10*]	0.03[*0.03*]	3.79[*3.79*]	0.00[*0.00*]	**-0.15[-*0.15*]**	**-0.05[-*0.05*]**
Nesting density	0.04[*0.10*]	0.05[*0.04*]	0.67[*2.35*]	0.50[*0.02*]	-0.07**[*0.02*]**	0.14**[*0.18*]**

[a] synchrony was set as the reference category (estimate of zero)

Table 2-5. Summary of GLMMs analysis of factors affecting the ***maximum inter-visit intervals***. Sample sizes for the whole dataset are 174 observations from 88 broods. For the maximum inter-visit interval, the longest inter-visit interval of male and female in each brood was the response variable. Italic in square brackets shows information concerning conditional averages (i.e. average estimates from only those models in which the variable was included). Bold indicates estimates based on full average that are significantly different from zero (at $p<0.05$). The 5 top models of ΔAICc < 4 were used in model averaging. Global (Initial) model: Maximum inter-visit interval ~ Year + Sex + Brood size (BS) + Brood age (BA) + Nesting density (ND) + Visit type +Predation intensity (PI) + Laying date (LD)+ Year: type + Sex:ND + Visit type:sex + DN:PI, random factor = pair identity, family = Gaussian. Estimate from mean centred predictors. Table 2-S12 lists the top models.

	Estimate	Adjusted SE	z value	Pr(>|z|)	2.5%	97.5%
(Intercept)	-0.01 [-*0.01*]	0.10[*0.10*]	0.07[*0.07*]	0.95[*0.95*]	-0.20[-*0.20*]	0.18[*0.18*]
Laying date	-0.08 [-*0.20*]	0.11[*0.09*]	0.71[*2.08*]	0.48[*0.04*]	-0.31[***-0.38***]	0.14[***-0.01***]
Visit type (asynchrony)	-0.02 [-*0.12*]	0.05[*0.08*]	0.36[*1.57*]	0.72[*0.12*]	-0.12[-*0.27*]	0.09[*0.03*]
predation intensity	0.02 [*0.13*]	0.06[*0.10*]	0.34[*1.40*]	0.74[*0.16*]	-0.10[-*0.05*]	0.14[*0.32*]

[a] reference category (synchronous visit)

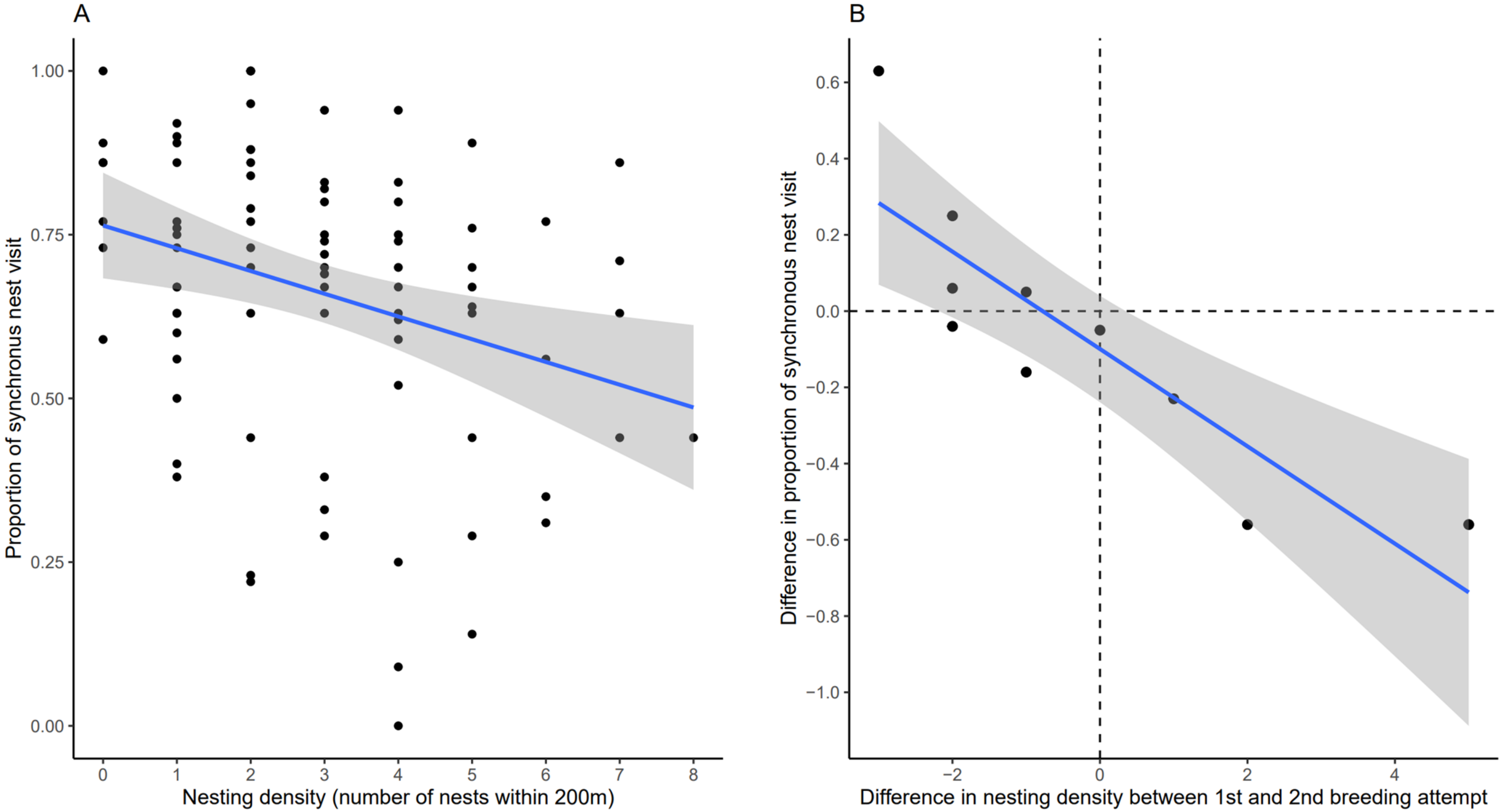

Fig. 2-1. Effect of nesting density (A) and the effect of change in local density between the first and second brood of the same pair within a season (B) on the proportion of synchronous provisioning visits among all visits by a pair.

Nesting density effects (A) are from the analysis with the whole dataset (88 nests). Graph was displayed by raw data in best model of Table 2-1A. The change of local density effect (B) are from 10 nests with double brooding within a season (Spearman correlation = -0.82, *n* = 10, *p* <0.01). Line display the predictions with its SE represented by shaded areas and black circles are observed data. Nesting density indicates the number of active neighbouring nests within a distance of 200m from the focal nest.

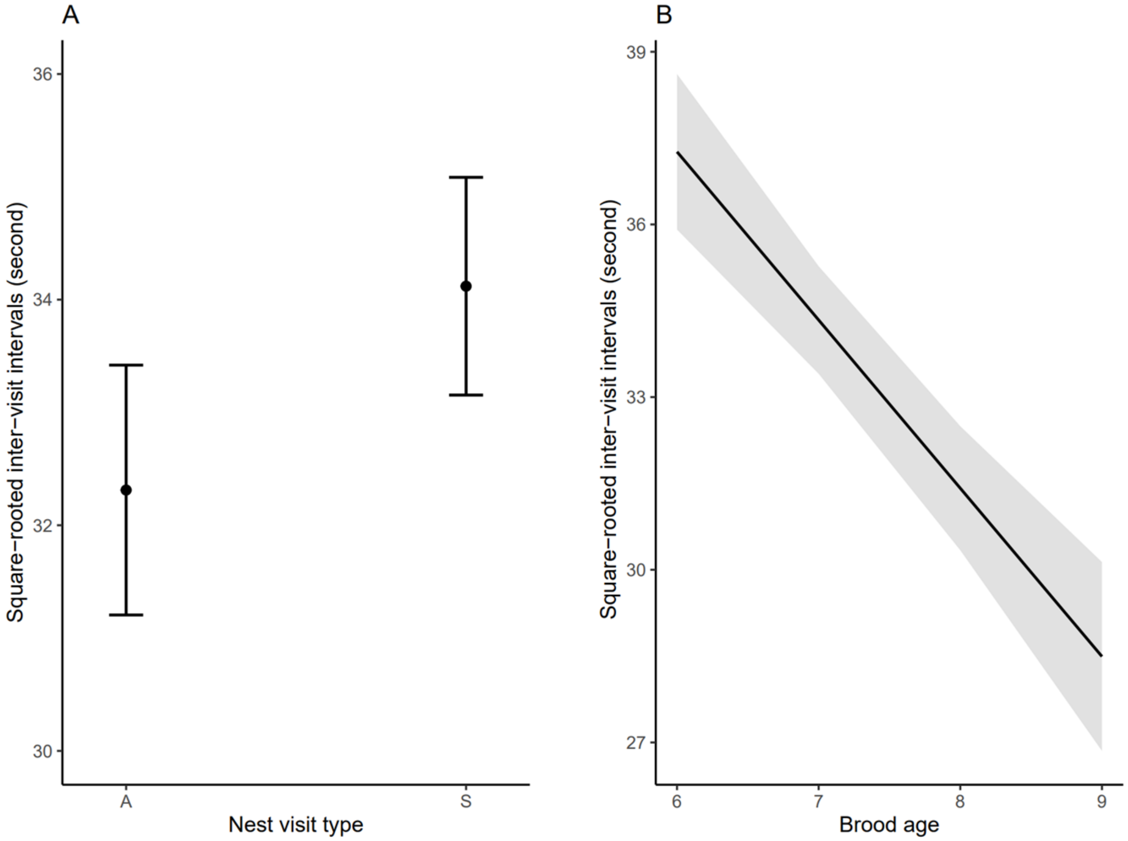

Fig. 2-2. Factor affecting inter-visit intervals in whole data set (1732 observation from 88 broods, 74 pairs). (A) – effect of visit type (synchronous vs asynchronous) on the inter-visit intervals; (B) – effect of brood age on the inter-visit intervals. Figures were produced with the ‘ggeffect’ function in R package ggeffects. Error bar in (A) and shaded area in (B) represent 95% confidence intervals around the estimated marginal means and the marginal effect regression line.

Analyses of the foraging efficincy via prey load size (n=27 nests)

Diet - Prey items brought to nests by the parrotbill parents include *Lepidoptera* (larvae, pupae), *Mantodea*, *Orthoptera*, *Diptera*, spiders and “unknown” arthropods (Jang et al, unpublished/in preparation). Parents usually bring 1-4 items (1.74±0.74(SD), n=467 from 27 nest) at one visit.

Foraging efficiency - The full analysis using generalized linear mixed models followed by model averaging (see Methods) showed that ***foraging efficiency*** (Table 6; Fig. 3) did not depend on any of the factors considered, including the ***type of visit*** (synchronous or asynchronous) and ***nesting density***. Additional analyses of ***prey load size***, mean ***prey size index, number of prey items per load***, and ***maximal foraging efficiency*** did not indicate any positive or negative effect of synchrony or higher density on those four response variables (Supplementary Materials: Table S1 –S8), albeit males brought significantly larger prey loads (Table S1, S2).

Inter-visits intervals – For full data set, the inter-visit interval was significantly shorter prior to an asynchronous than a synchronous visit (Fig. 2A). These results are consistent with the idea that the social interactions with other group members may cause an increase in the inter-visit intervals regarding visit type (Table 4). There was no consistent effect of local ***nest predation intensity*** on the ***inter-visit interval*** (Fig. 2A). For restricted dataset for diet analysis (n=27 nests), the duration of the ***maximum inter-visit interval*** increased with an increase of ***nesting density*** but only for the intervals ending with a visit of a single bird to the nest (the asynchronous visits; Fig. 4D; Table 8). The intervals preceding the synchronous visits to the nest were shorter in the birds breeding in the higher nesting density (Fig. 4D; Table 8). The results may be consistent to the *group disruption of foraging* hypothesis, assuming that singly foraging birds may be more susceptible to the social disruptions (see discussion for details of the hypothetical mechanism).

Do relative foraging benefits from synchrony affect the type of provisioning visit? - For the subset of 27 nests I could determine if birds are more synchronous when synchronous foraging is the better foraging option, and whether they are less synchronous when asynchronous foraging is the better option. The ***relative foraging benefits from synchrony*** was present in the best models, as was the ***nest density*** and interaction between these two variables (Table S16). These effects did not reach statistical significance (i.e. did not cross the zero) in analyses based on full averages (Table 9) that estimates from which the variable was included in every model. However, the interaction effect was statistically significant in analyses based on conditional averages (Table 9) that estimates from only those models in which the variable was included. Nevertheless, as these effects in full and conditional averaged estimate were consistnetly present in the best models, I think that I have any evidence to conclude that they affected birds’ behavior. Overall, the main effects (Table 9, Table S16) suggests that the ***frequency of synchronous visits*** was larger for locations where synchronous foraging was more efficient than the asynchronous foraging (Fig. 5A), and they were also more frequent at locations with low local ***nesting density*** (Fig. 5B; this is consistent with the analysis of the whole data set). However, the interaction term suggests that only in the lower local ***nesting density*** the birds increased synchronous foraging in response to an increase in the ***relative foraging benefits from synchrony***. In the higher local ***breeding density***, this relationship was reversed: decreased synchronous foraging was associated with an increase in the ***relative foraging benefits from synchrony*** (Fig. 5C). Like in the previous analysis of the whole data set, the local nest predation did not affect the type of visit (Table 9). These results are consistent with the idea that the birds breeding in lower nesting densities forage synchronously when synchronous foraging is more effficient, and those breeding in higher nesting densities are not sensitive to the benefits of synchronous foraging probably due to more frequent social interactions (disruptions) by group members.

Table 2-6. Summary of GLMMs analysis of factors affecting the ***foraging efficiency*** per nest visit (response variable: foraging efficiency=prey load size mm^3/ preceding inter-visit interval (second)). Sample sizes for the subset are 467 observations from 27 broods. Italic in square brackets shows information concerning conditional averages (i.e. average estimates from only those models in which the variable was included). Bold indicates estimates based on full average that are significantly different from zero (at $p<0.05$). The 3 top models of ΔAICc < 4 were used in model averaging.

Global (Initial) model: Foraging efficiency ~ Year + Sex + Brood size category (BS) + Brood age category (BA) + Nesting density (ND) + Predation intensity (PI) + Laying date + ND:(VT + Year + BS + BS+ PI), random factor = pair identity, family = Gaussian. Estimate from mean centred predictors. This table concerns Fig. 2-3, and Table 2-S13 lists the top models.

	Estimate	Adjusted SE	z value	Pr(>|z|)	2.5%	97.5%
(Intercept)	-0.01[-0.01]	0.07 [*0.07*]	0.14[*0.14*]	0.89[*0.89*]	-0.15[-*0.15*]	0.13[*0.13*]
Sex (Female)[a]	-0.01[-*0.08*]	0.03[*0.05*]	0.36[*1.79*]	0.72[*0.07*]	-0.08[-*0.17*]	0.05[*0.01*]
Year (2008)[b]	0.01[*0.10*]	0.04[*0.08*]	0.28[*1.30*]	0.78[*0.19*]	-0.07[-*0.05*]	0.09[*0.25*]

[a]male and [b]2009 was set as the reference category

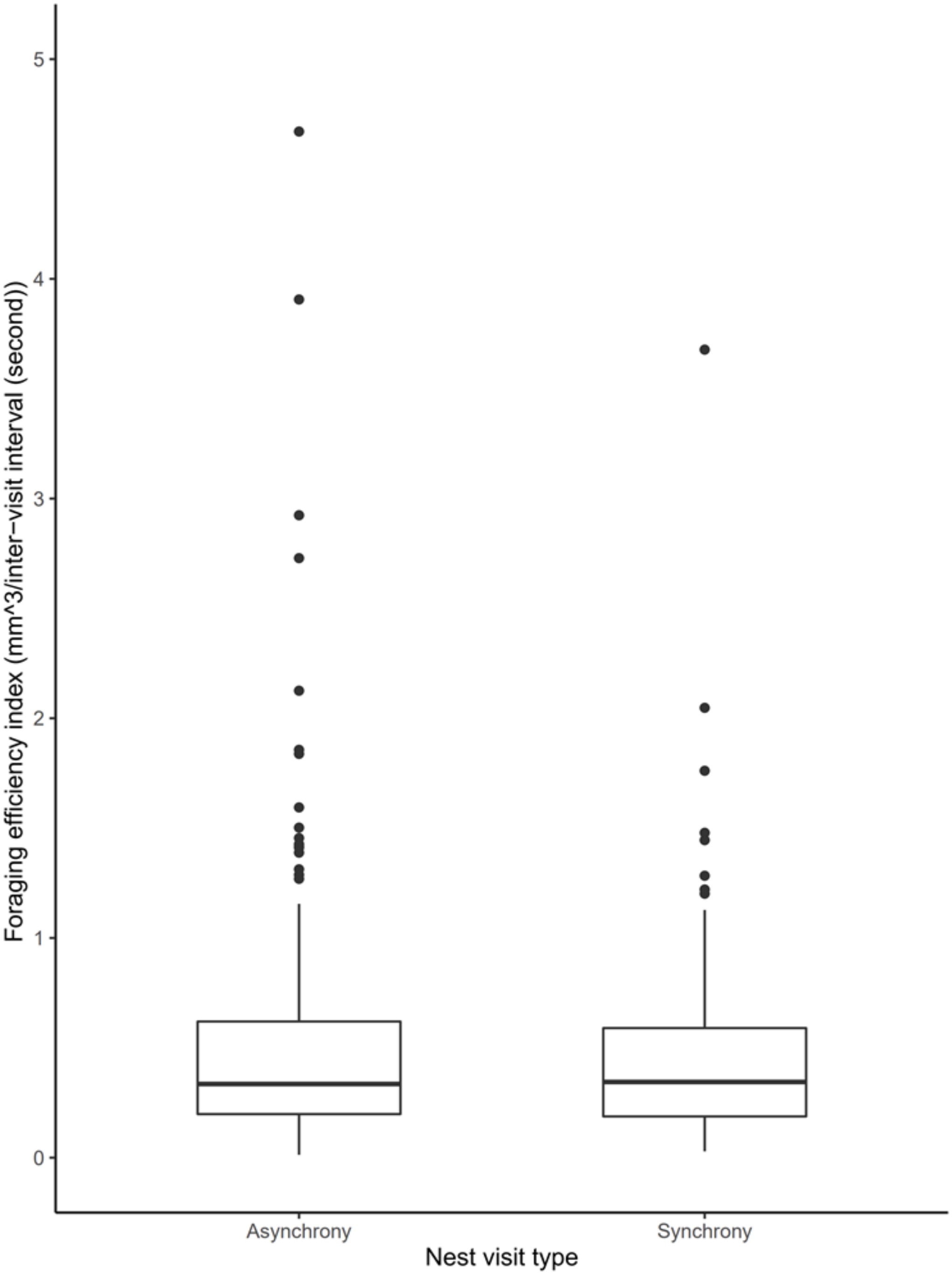

Fig. 2-3. Efficiency of foraging in synchronous and asynchronous trips. F*oraging efficiency index* was calculated for each visit of a parent by dividing the ***prey load size*** by the preceding ***inter-visit interval*** (mm^3/second). Boxes show the interquartile range, the thick line is the median, and the error bars (vertical lines) refer to the 1.5 interquartile. The extra data points are outliers

Table 2-7. Summary of model averaging for predictors affecting the ***Inter-visit interval (second).*** Sample sizes for the subset are 467 observations from 27 broods. Italic in square brackets shows information concerning conditional averages (i.e. average estimates from only those models in which the variable was included). Bold indicates estimates based on full average that are significantly different from zero (at $p<0.05$). The 41 top models of ΔAICc < 4 were used in model averaging. Global (Initial) model: Inter-visit interval ~ Visit type (VT) + Sex + Year + Brood size category (BS) + Brood age category (BA) + Nesting density (ND) + Predation intensity (PI) + Laying date + PI: Year + ND:VT + ND:PI + VT:PI, random effect: pair identity. This table concerns Fig. 2-4 (A, B, C), and Table 2-S14 lists the top models.

	Estimate	Adjusted SE	z value	Pr(>|z|)	2.50	97.50
(Intercept)	31.14[*31.14*]	0.61[*0.61*]	51.17[*51.17*]	0.00[0.00]	29.95[*29.95*]	32.33[*32.33*]
Nesting density (ND)	1.25[*1.25*]	0.52[*0.52*]	2.40[*2.40*]	0.02[*0.02*]	**0.23[*0.23*]**	**2.28[*2.28*]**
Predation intensity (PI)	-0.68[*-0.69*]	0.56[*0.56*]	1.21[*1.23*]	0.22[*0.22*]	-1.77[*-1.77*]	0.42[*0.40*]
Visit type (VT) (asynchrony)[a]	-0.78[*-0.87*]	0.48[*0.42*]	1.64[*2.07*]	0.10[*0.04*]	-1.71[*-1.69*]	0.15[*-0.05*]
Year (2008)[b]	1.59[*1.59*]	0.64[*0.64*]	2.49[*2.49*]	0.01[*0.01*]	**0.34[*0.34*]**	**2.84[*2.84*]**
ND: PI	-0.70[*-0.96*]	0.68[*0.62*]	1.03[*1.53*]	0.3[*0.13*]	-2.04[*-2.18*]	0.63[*0.27*]
PI: Year (2008)[b]	-1.83[*-1.86*]	0.77[*0.74*]	2.39[*2.50*]	0.02[*0.01*]	**-3.34[*-3.31*]**	**-0.33[*-0.4*]**
Brood size category	0.08[*0.33*]	0.31[*0.55*]	0.27[*0.60*]	0.79[*0.55*]	-0.53[*-0.75*]	0.69[*1.41*]
Laying date	-0.06[*-0.24*]	0.28[*0.53*]	0.21[*0.45*]	0.84[*0.66*]	-0.60[*-1.27*]	0.49[*0.80*]
Sex (female)[c]	-0.07[*-0.32*]	0.22[*0.40*]	0.30[*0.80*]	0.76[*0.42*]	-0.51[*-1.10*]	0.37[*0.46*]
Brood age category	0.01[*0.05*]	0.26[*0.55*]	0.05[*0.10*]	0.96[*0.92*]	-0.49[*-1.02*]	0.51[*1.12*]
PI: Visit type (VT) (asynchrony)[a]	-0.01[*-0.06*]	0.16[*0.42*]	0.06[*0.15*]	0.96[*0.88*]	-0.31[*-0.89*]	0.30[*0.76*]
ND: Visit type (VT) (asynchrony)[a]	0.01[*0.07*]	0.15[*0.41*]	0.06[*0.16*]	0.95[*0.87*]	-0.29[*-0.75*]	0.31[*0.88*]

[a]synchrony (reference category), [b]2009 (reference category), [c]male (reference category)

Table 2-8. Summary of model averaging for predictors affecting the ***maximum inter-visit intervals***. Sample sizes for the whole dataset are 97 observations from 27 broods. Italic in square brackets shows information concerning conditional averages (i.e. average estimates from only those models in which the variable was included). Bold indicates estimates based on full average that are significantly different from zero (at $p<0.05$). The 28 top models of ΔAICc < 4 were used in model averaging. Significant effects are in bold. Global (Initial) model: Maximum inter-visit interval ~ Year + Laying date + Brood age category + Brood size category + Predation intensity (PI) + Visit type (VT) + Nesting density (ND) + Sex + VT*ND + PI:VT + PI:ND + ND:PI, random factor = pair identity. This table concerns Fig. 4D, and Table 2-S15 lists the top models.

	Estimate	Adjusted SE	z value	Pr(>|z|)	2.50%	97.50%
(Intercept)	41.09[*41.09*]	1.08[*1.08*]	37.88[*37.88*]	0.00[*0.00*]	38.96[*38.96*]	43.21[*43.21*]
Nesting density	-0.03[*-0.03*]	1.03[*1.03*]	0.03[*0.03*]	0.97[*0.97*]	-2.05[*-2.05*]	1.98[*1.98*]
Sex (female)[a]	0.58[*0.95*]	0.68[*0.64*]	0.86[*1.5*]	0.39[*0.13*]	-0.75[*-0.29*]	1.92[*2.2*]
Nest visit type (asynchrony) [b]	-0.79[*-1.11*]	0.74[*0.65*]	1.06[*1.71*]	0.29[*0.09*]	-2.24[*-2.38*]	0.67[*0.16*]
Year (2008)[c]	1.06[*1.51*]	1.19[*1.16*]	0.89[*1.3*]	0.37[*0.19*]	-1.28[*-0.77*]	3.4[*3.79*]
Nesting density:nest visit type (asynchrony)[b]	2.15[*2.15*]	0.67[*0.67*]	3.22[*3.22*]	0.00[*0.00*]	0.84[*0.84*]	3.46[*3.46*]
Predation intensity	0.16[*0.37*]	0.72[*1.05*]	0.22[*0.35*]	0.82[*0.73*]	-1.24[*-1.69*]	1.56[*2.42*]
Laying date	0.04[*0.09*]	0.66[*1.02*]	0.06[*0.09*]	0.95[*0.93*]	-1.26[*-1.91*]	1.33[*2.09*]

[a] male (reference category), [b] synchrony (reference category), [c]2009 (reference category)

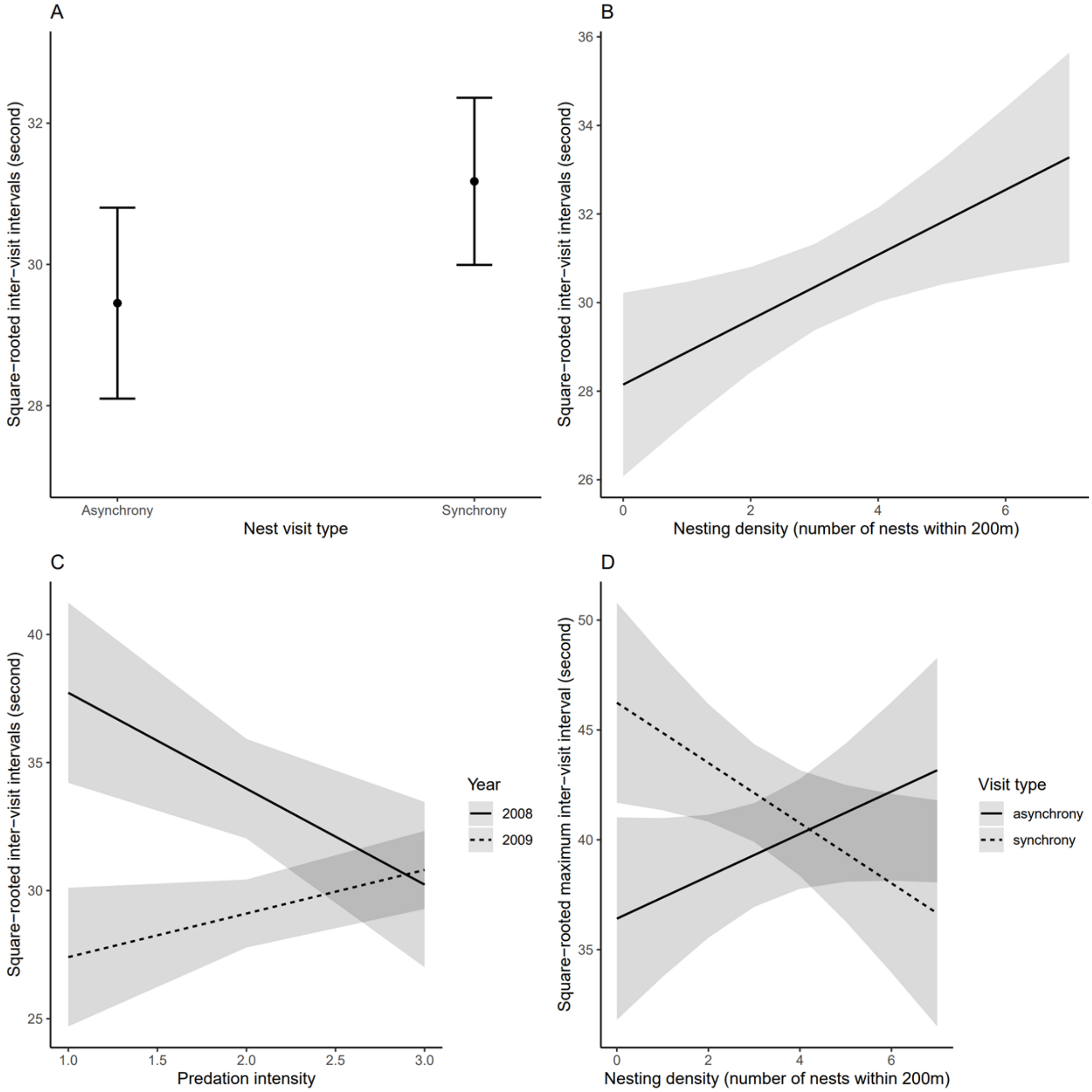

Fig. 2-4. Factor affecting inter-visit intervals in subset (467 observations from 27 broods). (A) – effect of visit type (synchronous vs asynchronous) on the inter-visit intervals; (B) – effect of nesting density on the inter-visit intervals; (C) – effect on local nest predation category on the inter-visit intervals; (D) – Effect of nesting density and type of visit (synchronous or asynchronous) on the maximum inter-visit intervals in two years (2008, 2009) of study. Figures were produced from the prediction of Table 6 (A, B, C) and Table 8 (D) using the 'ggeffect' function in R package ggeffects. Error bar (A) and shaded area in (B, C, D) represent 95% confidence intervals around the estimated marginal means and the marginal effect regression line. This figure concerns Table 2-7 (A, B, C) and Table 2-8D.

Table 2-9. Summary of GLMMs analysis of factors affecting the ***type of foraging visit*** (synchronous or asynchronous) for the two breeding seasons (2008, 2009) when foraging data were collected. Sample sizes for the subset are 467 observations from 27 broods. Italic in square brackets shows information concerning conditional averages (i.e. average estimates from only those models in which the variable was included). Bold indicates estimates based on full average that are significantly different from zero (at $p<0.05$). Global (Initial) model: Visit type (1, 0) ~ Predation intensity (PI) + Nesting density + Relative benefits from synchrony (SmAEff) + Sex + Brood age category + Brood size category + Year + Laying date + ND:PI + PI:SmAEff + DN:SmAEff + DN:PI, random factor = pair identity, family =binomial

This table concerns Fig. 2-5, and Table 2-S16 lists the top models.

	Estimate	Adjusted SE	z value	Pr(>|z|)	2.5%	97.5%
(Intercept)	0.31[*0.31*]	0.19[*0.19*]	1.66[*1.66*]	0.10[*0.10*]	-0.06[*-0.06*]	0.68[*0.68*]
Nesting density (ND)	-0.26[*-0.27*]	0.18[*0.17*]	1.40[*1.59*]	0.14[*0.11*]	-0.60[*-0.60*]	0.09[*0.06*]
Sex (female)[a]	-0.15[*-0.19*]	0.12[*0.10*]	1.22[*1.82*]	0.22[0.07	-0.39[*-0.40*]	0.09[*0.01*]
SmAEff [c]	0.20[*0.22*]	0.19[*0.18*]	1.05[*1.19*]	0.29[*0.23*]	-0.17[*-0.14*]	0.56[*0.58*]
ND:SmAEff	-0.38[*-0.43*]	0.23[*0.19*]	1.61[*2.25*]	0.11[*0.02*]	-0.83**[*-0.81*]**	0.08**[*-0.06*]**
brood size category	0.07[*0.25*]	0.17[*0.23*]	0.43[*1.09*]	0.67[*0.27*]	-0.26[*-0.20*]	0.40[*0.70*]
predation intensity (PI)	-0.04[*-0.09*]	0.13[*0.19*]	0.30[*0.50*]	0.77[*0.62*]	-0.29[*-0.46*]	0.21[*0.27*]
ND:PI	-0.08[*-0.29*]	0.16[*0.18*]	0.49[*1.56*]	0.63[*0.12*]	-0.39[*-0.65*]	0.24[*0.07*]
Laying date	-0.02[*-0.11*]	0.09[*0.19*]	0.21[*0.56*]	0.83[*0.57*]	-0.19[*-0.47*]	0.15[*0.26*]
Year (2008)[b]	-0.01[*-0.09*]	0.09[*0.22*]	0.14[*0.38*]	0.89[*0.70*]	-0.19[*-0.52*]	0.16[*0.35*]
brood age category	0.01[*0.04*]	0.07[*0.19*]	0.07[*0.19*]	0.94[*0.85*]	-0.14[*-0.34*]	0.15[*0.41*]
PI: SmAEff	0.01[*0.13*]	0.05[*0.19*]	0.14[*0.71*]	0.89[*0.48*]	-0.10[*-0.24*]	0.11[*0.50*]

[a] male (reference category), [b]2009 (reference category)

[c] SmAEff (SA) : Relative foraging benefits from synchrony

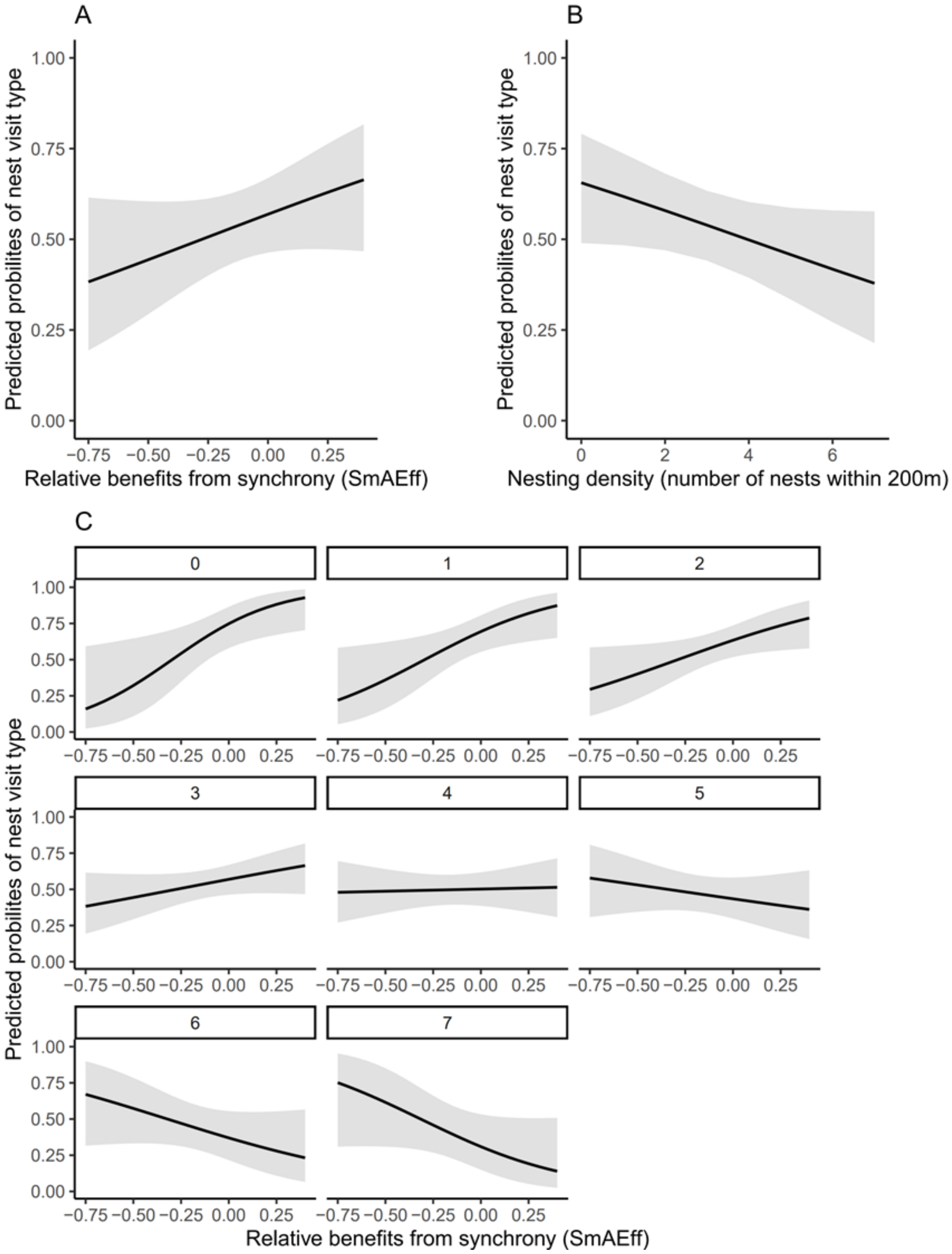

Fig. 2-5. Model effect of relative benefits from synchrony (SmAEff) (A), nesting density (B) and interaction between SmAEff and nesting density (C) on the probability of synchrony visit. SmAEff was calculated by subtracting the ***foraging "efficiency"*** for asynchronous visits from the foraging efficiency of synchronous visits (***SmAEff***; ***S***ynchrony ***m***inus ***A***synchrony ***Eff***iciency). Figures were produced with the 'ggeffect' function in R package ggeffects. Shaded area in (A, B, C) represent 95% confidence intervals around the estimated marginal means and the marginal effect regression line. The number in the facet label in (C) indicates the nesting density.

2-4 DISCUSSION

Synchrony – the outcome of behavioural flexibility

I showed that parents respond to the difference in nesting density between consecutive breeding attempts and decrease the level of synchrony when breeding in higher density. Hence, the association between high density of breeding pairs and low synchrony of parental visits already recorded by Lee et al (2010) appears to be the outcome of parental plasticity in response to social environment (presence of other breeders nearby). The results also suggest that this behavioral plasticity does not involve responses to increased nest predation risk, but that it may include responses to the foraging benefits from synchrony relative to asynchrony, and that these responses by a breeding pair are affected by the presence of other group members.

Below I discuss our observational data to evaluate the hypothetical mechanisms that may be responsible for this flexible synchronization of visits between the two parents. The hypotheses were presented in the introduction (Table 2-1), and they fall into three groups according to the main factor involved: predation risk, foraging efficiency, and social interactions. All the data are observational and the relationships are based on correlations which are not sufficient to extract any causative mechanisms. Therefore, my interpretation and evaluation of the hypotheses should be treated as the indication of the possible mechanisms shaping the flexibility of synchronous provisioning in the parrotbills.

Nest predation avoidance and *parent predation avoidance* hypotheses

If synchrony is an adaptation to decrease nest predation risk (*nest predation avoidance* hypothesis), I predicted that parents would visit the nest more synchronously in the locations with abundant predators in order to decrease the exposure of nests to predators (Eggers, Griesser & Ekman, 2005, 2008). Additionally, I expected to see an association between high level of synchrony and low risk of nest predation due to the lowered risk of revealing the nest to the predators by synchronous parents. However, I did not find any association between the level of synchrony and local nest predation risk. These results are inconsistent with the *nest predation avoidance* hypothesis.

Alternatively, parents may synchronize their behavior in order to increase anti-predator benefits for themselves. Vinous-throated parrotbills show a strong flocking habit with reluctance to be alone during the non-breeding season (Kim, Yamagishi & Won, 1992). They appear to retain this habit even during the breeding season when small foraging flocks (3-10 birds) are frequently observed (Kim, Yamagishi & Won, 1992). It may possibly benefit the adult birds by decreasing the risk of predation and it may underlie the trend to higher parental synchrony in lower local density observed in our study: with no alternative flocking members around at locally low nest densities, parents may be expected to show higher synchrony rate. The results do not contradict the *parent predation avoidance* hypothesis. However, I did not measure local predation risk for adults and therefore, I cannot fully evaluate this hypothesis.

Based on direct observations of some pairs (BSJ and JWL, pers. obs.), parent parrotbills, like zebra finch (Mariette & Griffith, 2015), seem to coordinate the whole foraging trip rather than merely coordinate by waiting for each near the nest to enter it together. Indeed, recent study using automated radiotracking technology shows that foraging pairs are highly coordinated in time and space during the chick-rearing period (Baldan & van Loon, 2022).

This indeed suggests that foraging together may have benefits such as decreased predation risk, which would be consistent with the *parent predation avoidance* hypothesis. However, as the *parent predation avoidance* hypothesis does not predict that ***inter-visit interval*** should increase with nest density, the observed increase of the ***inter-visit interval*** in pairs at higher ***nesting density*** indicate that the mechanisms responsible for the increased interval might have also caused a decrease in synchrony (see *social disruption* mechanisms discussed below.)

Synchronous foraging benefits and group foraging benefits **hypotheses**

Apart from reducing the predation risk for themselves (discussed above), foraging together may increase the foraging efficiency (Krebs, MacRobert & Cullen, 1972; Brown, 1988; Santema et al., 2009; Mariette & Griffith, 2013; Liebl et al., 2016). However, because there was no overall effect of ***nesting density*** on ***foraging efficiency*** (neighbors may also potentially help in foraging efficiently) or synchrony on foraging efficiency (no difference in ***foraging efficiency*** between ***synchronous*** and ***asynchronous*** visits), there is no straightforward support for a population-wide *synchronous foraging benefits* or *group foraging benefits*.

Although there is no straightforward support for a population-wide effect of social foraging on foraging efficiency, it does not mean that the birds were insensitive to the local differences in foraging efficiency between the single foraging trips (and the subsequent asynchronous visits) and the foraging together with their mates (and the subsequent synchronous visits). Our results showed that at very low density locations (or at solitary breeding area) the ***foraging efficiency*** was higher for ***synchronous*** visits while at other locations with high nesting density it was higher for the ***asynchronous*** visits. The evidence suggests that parrotbills breeding in lower ***nesting density*** behaved as if they were able to take this variation in foraging benefits from synchrony into account, and they increased the degree of synchrony when benefits from synchrony were larger (and *vice versa*). This is consistent with the idea that synchrony is a socially plastic behavioral trait, and that birds who are not involved in social interactions with local neighbors are sensitive to foraging efficiency and choose the behavior that brings higher foraging benefits. However, in higher ***nesting density*** this was no longer the case: the birds no longer switched to synchrony when synchrony was the better foraging option, and even the opposite trend was observed in the extremely large local densities. I hypothesize that the intensity of social disruption might have increased in response to the increase in the nesting density, which led to the lower synchrony in general, and it was associated with lack of adaptive shift to synchrony when it was the better foraging option (see discussion below).

Social disruption hypothesis

As the ***inter-visit intervals*** were longer for synchronous visits and for visits in higher densities it is possible that social interactions with a partner or with other group members are responsible for this lengthening of inter-visit intervals. The duration of the ***maximum inter-visit interval*** is especially likely to be associated with possible disruptions in the foraging routine due to non-foraging activities, including social interactions with (disruptions by) other group members. The increase of the ***inter-visit interval*** at high ***nesting density*** and the increase of the ***maximum inter-visit interval*** for ***asynchronous*** visits in response to increased ***nesting density*** may be viewed as consistent with the *group disruption of foraging* hypothesis. These results might have been an outcome of social interactions.

The presence of such an effect of density on maximum inter-visit interval for only the asynchronous visits may be hypothetically explained in by the stronger effect of social disruption on singly foraging birds leading to the delayed nest visit (longer interval between two consecutive single visits). Alternatively, social interaction might have delayed and caused a disruption of a joint foraging trip of a pair resulting in longer interval between leaving the nest together with a mate and arriving to the nest alone. The probability of such a hypothetical disruption of a synchronous foraging bout is expected to increase with time. Hence it is expected that longer foraging bouts of a pair are more often disrupted such that the consecutive nest visit is a visit by a single parent (asynchronous in our classification) leading to a bias in the duration of synchronous visits towards shorter values, especially at higher local densities. Possibly because of this, the intervals preceding synchronous visits to the nest (i.e. when two birds visit the nest together) were shorter in larger local-breeding densities. However, until information on bird behaviors during foraging trips is collected using radio-telemetry ((Keeling, Newberry & Estevez, 2017) all the above explanations are just the hypotheses consistent with the observational data collected at nests. Applying a recently developed technical methodology like recent radio-telemetry/GPS work (Rutz et al., 2012; Kavelaars et al., 2021; (Baldan & van Loon, 2022) and the use of proximity loggers (Rutz et al., 2012), more detailed future research on individual interaction and foraging movement in the parrotbill social system is needed.

Conclusions

In summary, my observations of bird behavior in the natural field conditions shows that parents frequently synchronize provisioning visits (on average 66.7% of visits by a pair are synchronous). Higher synchrony was not associated with higher nest survival, and local nest predation rate did not affect the level of synchrony. The level of synchrony was lower in the nests breeding in higher local density (more group members nearby), and the same pairs with multiple breeding attempts decreased their level of synchrony in response to increased nesting density over time. My results suggest parrotbills flexibly adjust the frequency of synchronous foraging trips and, if not socially disturbed by group members in high local breeding densities, the pairs appear to adaptively increase degree of foraging synchrony in response to increased relative foraging benefits from synchrony (relative to asynchrony).

Chapter 3

Pair coordination and provisioning effort in relation to parental age and social environment in the Vinous-throated parrotbill

Abstract

In group-living animals, parents that breed in densely populated areas may be affected by increased interactions with neighbours. This may have consequences for the reproductive effort and coordination of parental provisioning within a pair and those effects may depend on parental age. Additionally, not only the general local density, but also the breeding timing of the locally present pairs may affect parental effort and parental coordination of provisioning in a pair. To study these issues, I investigated how provisioning rate and the level of synchronous nest visit and the level of alternating visit in the Vinous-throated parrotbill vary according to parental age and the local density of neighbouring pairs that include both breeding at the same time and at different time with the focal pair. I found that older parents showed higher pair coordination than the younger parents in pairs breeding at low local densities (i.e. solitary breeders), but such age effect disappeared in pairs at the high local densities. Also, I found that the local density of breeding pairs that were at the similar stage of the breeding cycle (i.e. synchronous breeding) as the focal pair was not related to the level of synchronous nest visits. However, when the local density of pairs that breed asynchronously with the focal pair (i.e. were at a different stage of breeding cycle from the focal pair) increase, the level of provisioning coordination within the focal pair decreased rapidly. Our findings show that a decrease in pair coordination, which is mainly associated with an increase in the local density of asynchronous breeding pairs, may be linked to the social interactions (disruptions of synchronous provisioning) with the social group members (local neighbours) who are not engaged in intense parental provisioning of their own broods.

Key word; pair coordination, parental age, nesting density.

3-1 INTRODUCTION

Over the life history of various vertebrate taxa, from fish to humans, older parents tend to have higher reproductive success than younger parents. This has been often explained by age-related improvement of competence such as breeding experience, foraging ability, or access to resources (Forslund & Pärt, 1995). Parents coordinate common tasks in various reproductive activities, such as determining nesting sites, incubating eggs, or provisioning young. The importance of coordination between parents may increase if parental work is more evenly distributed rather than specialized between partners. Recent studies showed that pair coordination can improve with parental age and familiarity (Sánchez-Macouzet, Rodríguez & Drummond, 2014). Improvements in coordination may be related to the improved foraging ability with individual's age or familiarity with the habitat. In species where long-term pair bonds are maintained, there may be an improvement in pair compatibility as well. However, in species that breed colonially (in groups) or at high densities, some young individuals may be constrained by other members of social group in the level of coordination as well as in the access to resources.

Local nest densities vary among bird species from very low in solitary breeders to very high in colonial birds. Proximate mechanisms shaping nest density may include various ecological and social factors, such as nesting habitat's suitability, availability of food resources, and the presence of other individuals. If environmental or social pressures are density-dependent, individuals may prefer to reproduce at sites with appropriate nest densities according to their current environmental conditions (e.g. predation risks of individuals or nests). Differences in the characteristics of individuals or pairs can lead to asymmetries in the social environment in which reproductive performance is greatest (Roche & Brown, 2013; Brown, Roche & Bomberger, 2014). Studies have shown that individuals prefer to settle at different densities depending on their personality (shyness or aggressive individuals inherently) or dominance position (Serrano et al., 2019). In addition, age seems to be the most critical factor in individual characteristics that affect the decisions to settle (e.g. breed) in various densities (Brown et al., 2016). In the zebra finch *Taeniopygia guttata*, a species assumed to freely select nesting areas, older individuals bred more solitarily, and younger individuals reproduced colonially (Mariette & Griffith, 2013). Older individuals may outperform young individuals in the selection of nest sites, even in group-living birds. Therefore, older individuals may be freer to choose to settle in their preferred location depending on the current ecological situation. In contrast, younger individuals may be forced to breed colonially due to limited nesting places as a result of older individuals preoccupying suitable nesting places. In many social animals, the breeding density and spatial nest distribution in social birds may be determined by these ecological and social factors, such as aggregation composed of kin/siblings or cooperation between members composed of familiar or more compatible individuals (Lee et al., 2009a) (Hatchwell et al., 2001)(Brandl et al., 2021). Depending on the environmental pressure, the current nest density may affect the cooperation and coordination of the pair throughout the breeding season.

The previous studies on the parrotbill (Lee, Kim & Hatchwell, 2010) emphasized the importance of collaboration between individual members as provisioning rate increases when pairs breed at higher densities. However, in chapter 2, I found that parents breeding in locally high-densities had limited pair coordination, suggesting that this might be due to disruption by other social members. However, I did not explore the details of such a hypothetical disruption effect.

The spatial and temporal distribution of nests during the breeding season can represent social relationships among individuals. For example, several studies suggested that pair members with solid social ties attempted to reproduce in a colony simultaneously (Brandl et al., 2021), and that more familiar individuals (familiarity acquired in the preceding winter) established the territories near each other (Grabowska-Zhang, Wilkin & Sheldon, 2012). The pairs breeding near each other may benefit from joint vigilance against predators among familiar individuals. Individuals who succeeded in synchronous breeding in colonial species may benefit from rearing their offspring on a similar schedule (Brandl et al., 2021). Also, the benefits of group living are only possible if there is a smooth relationship among the members of the local social group who are spatially or temporally distributed, especially during the reproductive period. If unfamiliar and/or competitive individuals are present around a nest of a focal pair then, even in species breeding colonially, the cooperation or coordination between pair members is more likely to be difficult to achieve.

In this chapter, I first analyse the similarity of provisioning rates between partners according to age classes and breeding densities. Second, I investigate whether pairs composed of older individuals (i.e. experienced individuals paired with each other for a long time; parrotbills pair for life (Kim, Satoshi & Won, 1995)) exhibit greater coordination than those composed of younger individuals, and I also examine whether parental age affects the provisioning rate and the coordination between partners at different nesting densities ranging from solitary and colonial. Finally, I investigate the effect of the number of temporally synchronous and asynchronous breeding neighbours on the coordination level within a focal pair.

3.2. METHODS

3.2.1. Study species

Study site, study species and general field work procedure in detail can be shown in introduction and chapter 2.

Over the study period, more than 90% of the birds from 6-8 winter flocks of approximately 40-120 birds were captured every year using mist nets. Upon capture, birds were banded with a unique combination of three coloured leg ring on left tarsus to identify birds in field observation and an aluminium ring bearing a unique number on right tarsus, and blood was sampled (for sexing). Monitoring subgroups of birds in the spring, I found that the proportion of un-banded individuals was less than 10%, similar to the banding rates of winter flocks. Un-banded adults were later caught in the incubation period of the breeding season. The banding of newly recruited juveniles was conducted throughout the breeding season, when adults and young birds could be distinguished based on plumage.

The earlier studies on parrotbills found that the membership and home range of a large winter flock is maintained across years as well as within a season (Kim, Yamagish & Won, 1992; Lee et al., 2010). In the spring, subgroups (“pre-breeding transient flock” described by Lee et al.(Lee, Lee & Hatchwell, 2010); See Figure 1 representing annual cycle of parrotbill flock) disperse within and near their preceding winter home range, and usually attempt to nest synchronously near to each other, especially in the early spring (the first brood) although some pairs nest solitarily in both space and time.

The membership of subgroups and their spatial range may change during the breeding season according to their breeding status (e.g. success or failure), but generally birds retain highly structured social system with some degree of fission and fusion. I followed and observed subgroups in the early spring, 1–2 weeks before egg laying, to identify group members and examine their nest dispersion patterns.

3.2.2. Variables

The variables can be grouped into several types and they are listed and explained below.

3.2.2.1. Basic variables:

Hatching date – The date the egg was first hatched. In most nests, parrotbill chicks hatch on the same day; expressed in numerical format as number of days from April 15th in each year. In most nests, the hatching date was recorded by checking nests at daily intervals from the earliest expected hatching date.

Provisioning rate - From the video recordings, I calculated the total feedings as well as male and female feedings separately. *Provisioning rate* is defined as the number of times prey was brought to the nest per hour. Sample sizes for the whole dataset are 87 observations, 74 pairs (One Sample with extreme outlier of provisioning rate, which led to failure to normalize)

Mean inter-visit interval - I calculated the total inter-visit intervals as well as male and female inter-visit intervals separately. Inter-visit interval was defined as the period from the moment the parent leaves the nest and the moment it arrives to the nest at the subsequent provisioning visit. I calculated mean total inter-visit in each brood and mean of intervals of male and female separately in each brood.

Other variables include ***Year (2007-2009)***, ***Brood size*** (3-7), ***Brood age*** (6-9) and ***Sex***.

3.2.2.2. Provisioning effort within a pair

Provisioning equity is an index denoting the similarity (or difference) in provisioning rate in a pair. I followed calculation by Mariette and Griffith (2015) (Mariette & Griffith, 2015), which is: 1-|P_m(provisioning rate by a male/h) – P_f(provisioning rate by a female/h)|/total provisioning rate/h (P_t). A score of 1 indicates that the partners' provisioning rates were exactly the same. By using this variable, I can examine whether parental provisioning effort is similar between partners, and whether it is related to overall provisioning rate, pair characteristics (e.g. parental age class, pair bond duration) and the level of pair coordination (see variables below).

3.2.2.3. Pair coordination during provisioning.

A growing number of studies have shown that parental coordination leads to synchronization and alternation of nest visits by parents (Savage & Hinde, 2019; Mariette & Griffith, 2015; Baldan, Hinde & Lessells, 2019). Therefore, I used several variables that represent these two aspects of coordination

Visit type - First, I used ***visit type***, a binary variable already used in Chapter 2, to classify a visit by male or female as either synchronous or asynchronous. If both parents provided food to the nestlings in a 1 min time window, it was considered a "synchronous provisioning visit". Synchronous provisioning visit can occur when pair members travel together *en route* (Mariette & Griffith, 2012) to the nest or when the first-comer waits for a partner near the nest as shown in some cooperative breeders (Raihani et al., 2010a). Alternatively, it may also happen simply by chance. However, assuming that females visit the nest on average 2.9 times/hour and males visit the nest on average 2.8 times/hour, the chance of a nest being visited by the two parents by chance within 1min of each other is as low as 0.23% (2.9 times * (1min/60(1hr) * 2.8 times * (1/60) * 100)). Therefore, synchronous provisioning is unlikely to occur by chance and, as mentioned in Chapter 2. Synchronous *provisioning* can contribute to equal distribution of food among the nestlings (Shen et al., 2010) and it may lower the risk of nest predation by reducing the number of visits (Raihani et al., 2010a; Mariette & Griffi, 2012; Leniowski & Węgrzyn, 2018).

Proportion of synchronous visits – when used as an explanatory variable it was calculated as (***number of synchronous visits***) / (***number of synchronous visits*** + ***number of asynchronous visits***). When analysing proportion of synchronous visits as dependent (response) variable the *cbind* function was used: *cbind* (***number of synchronous visits***, ***number of number of asynchronous visits***).

Alternating succession - Second, I used a binary variable "***alternating succession***" to classify each visit as one of the two possible categories: *alternating rapid succession present* or *alternating rapid succession absent*. (in short*: present* or *absent*). The alternating visits in rapid succession (*alternating rapid succession present*) were defined as visits with the transition time of less than 30s (transition time is measured as the duration of time between leaving the nest by one parent and the arrival of the other parent). Synchronous provisioning can be achieved through alternating visit in rapid succession. However, alternating visit in rapid succession can also be achieved by actively waiting for a partner on the nest for a relatively long time even during peak demand period, which does not lead to synchronous provisioning and may result in a decreased provisioning rate. The proportion difference between synchronous provisioning visits and alternating visits in rapid succession within a pair varies from 0 % to 67 % (median 7.5%, n=88). Alternating visits in rapid succession after long duration in the nest by one parent may arise as the provisioning pairs re-schedule their timing of provisioning in order to maintain behavioural synchronization after separation due to disturbance or various reasons such as roosting, self-feeding.

Proportion of alternation succession – when used as an explanatory variable it was calculated as (***alternating rapid succession present***) / (***number of alternating rapid succession present + alternating rapid succession absent***). When analysing ***proportion of alternation rapid success*** as dependent (response) variable the *cbind* function was used: *cbind* (***number of alternating rapid succession absent, number of alternating rapid succession absent***).

3.2.2.4. Nesting density

Local density of the focal nest - I used the number of concurrently active nests on each day of the season (i.e. the day of video recording). I calculated the number of active nests around the focal nest on the day of video recording rather than the maximum number of active nests around the focal nest throughout the season as used in Chapter 2. I followed the criteria of 200 m used by Lee et al. (2010) (Lee, Kim & Hatchwell, 2010), as the distance at which group members would interact. Therefore, the l*ocal provisioned nest density* indicates the number of active neighbouring nests within 200m radius during the video of the focal nest.

Local density of provisioned nest category - I categorized density as solitary (no active neighbouring nest within 200m during the video), low density (1–2 active nests) or high density (3 –5 active nests) from *local provisioned nest density* because there is likely to be non-linear relationship between increasing nesting density as shown in some colonial species (Brown & Brown, 2000). The variable was treated as non-ordered (or ordered) class variable (solitary, low density, high density) or as a rank 1 (solitary), 2 (low density), 3 (high density)

Local density of broods at similar stage.

I considered as ***broods at similar stage*** when the absolute difference (in days) between the focal nest and neighbouring nests in first laying date is less than 6. The *local density of broods* at similar stage was defined as the number of synchronized broods alive around the focal nest within 200 m on the video-recording day (6-9 day old broods).

Local density of broods at different stage

I considered as ***broods at different stage*** when the absolute difference (in days) between the focal nest and neighbouring nests in first laying date is greater than 6. The *local density of broods at different stage* was the number of non-synchronized broods alive around the focal nest within 200 m on the day of video-recording (6-9 day old broods).

3.2.2.5. Parental age class

Most vinous-throated parrotbills have a short lifespan of approximately two years or less in our study area. However, 2.3% of 528 captured in the year (2005) of study initiation survived more than 4.5 years during the study period. I divided the age of parents into two categories: “old” and “young”. Individuals who had been colour-ringed for more than two years were classified as “old”. Also, because not only more than 90% individuals of winter flocks (6-8 flocks) have been captured and individually colour-ringed in each year but membership of winter flocks with stable home range also lasts for life (movement between winter flocks across year was less 5% in both our study and earlier studies (Lee et al., 2010)), thus, newly recruited individuals as well as ones banded as nestling and juveniles (in year; colour-ringed individually between July-August when we could determine their exact age) were considered as “young”. Support for treating newly recruited individuals as young comes from long-term studies of several species (Hatchwell et al., 2001; Brown, Roche & Brown, 201; Grabowska-Zhang, Wilkin & Sheldon, 2012) with a certain range of restricted study areas. In our study, I observed assortative mating with respect to parental age. Thus, older birds tended to have older mates, and younger birds tended to have younger mates. Mate retention was very high across the year as well as within a season, regardless of fail or success, thereby divorce where partners change while a mate still alive was rare (unpublished our data). Most mate changes occurred when a partner died and frequency of extra-pair nestlings was low (Lee et al., 2009b). I created ***age class*** (*AC*) variable for analysis. In some analyses, this was an ordered categorical variable characterizing a pair with the following classes ordered from older to younger: *old-old*, *old-*

young, *young-young* that corresponded to the variable values of 1, 2, and 3 respectively (e.g. Fig. 3.1). However, in some other analyses ***age class*** was treated as unordered categorical variable (e.g. Fig. 3.6) because its effect did not seem simply linear. The age class *old-young* was given to pairs regardless of which sex was the young (due to small sample size in *young male – old female* broods; n=5 out of a total of 88 broods).

3.2.2. Statistical analyses

All statistical analyses were conducted in the R studio, version 3. 6. 3 (R Development Core Team, 2019) using the lme4 package (Bates et al., 2015) and "emmean" package (Russell et al., 2022). Figures were produced using the "ggplot2" package (Wickham, 2009), "ggpubr" package (Kassambara, 2021) and "ggeffects" package (Lüdecke, 2018) for interaction effects. I described in captions of each graph details how the figure was obtained. The predictors that run all models represent in the caption of each table. A brood identity was included as a random effect. Sample sizes in each model represent in captions of each table.

Model selection was performed using the *dredge* function in the package *MuMIn* (Barton & Barton, 2020). This function constructs a series of candidate models of all possible combinations from the global model. I selected the top ranked models (< Δ4) according to the corrected Akaike Information Criterion (AICc) to use model averaging approach (Burnham KP, 2002). To be weighed the estimate and error of each predictor in top model, a parameter of zero is substituted into those model where the given parameter is not present. And then the parameter is obtained by averaging over all models in the top model set (< Δ4). Effects were regarded as statistically significant when the 95% confidence intervals for a parameter estimate did not cross the zero (Burnham and Anderson, 2002).

The continuous variables were scaled and mean-centred (mean 0 and standard deviation 1) and unordered (e.g. sex, year, nest visit type) and ordered factors (e.g. predation intensity as a category) were standardized in all models using the *standardize* function (Eager, 2017) in *MuMIn* package. To check multi- collinearity among predictor variables, *VIF* (variance inflation factors) was calculated for each predictor in the global model using *performance* package (Lüdecke et al., 2021). VIF was <2.5 in all global models, indicating moderate level of collinearity among predictors (Freckleton, 2011). I used AIC model selection to distinguish among a set of possible models describing the relationship between parental age class and parental effort, coordination. The best-fit model, < 4 ΔAICc, included every parameter with no interaction effects.

3.3. RESULTS

3.3.1. *Provisioning equity* index according to parental *age class*.

Overall, there was no difference in provisioning rates between partners (paired t test; t = 1.07, df = 86, p-value = 0.29, male; 2.7±0.7(SD)/hr vs female; 2.8±0.9(SD)/hr, n=87). Equity score of 1, a precisely equal value of provisioning rate between male and female parent, accounted for 18.4% (n=16 brood) of all nests (n=87), with the median of 91%. There was a significant relationship between the equity index and local density of provisioned nests ($\mathrm{t} = -2.23,\ p = 0.028;\ \mathrm{Figure}\ 3-1\mathrm{A}$), but did not reach statistical significance in relationship between equity and parental age class ($\mathrm{t} = -1.58,\ p = 0.117;\ \mathrm{Fiugre}\ 3-1\mathrm{B}$). As expected, the greater equity was associated with the higher levels of synchronous provisioning visits (Spearman's rank correlation, r_s = 0.47, n = 88, P<0.0001; Figure 3-2A) and alternating succession (r_s = 0.46, n = 88, *P*<0.0001; Figure 3-2B). Moreover, I found a significant positive relationship between provisioning rate and the proportion of synchronous visit (Pearson correlation: r_s = 0.275, n = 88, p = 0.013), but I did not find a significant relationship between provisioning rate and equity (r_s = 0.03, n = 88, p = 0.77).

For all three parental age classes, provisioning rate (Table 3-1; Figure 3-3A), and mean IVIs (Figure 3-3B) by one parent was highly correlated with its partner's, suggesting that a parent's provisioning visits and foraging activities are strongly linked with those of their partner's regardless of the pair's age class. In addition, there was an interaction between female provisioning rate and parental age class (Table 3-1) regarding male provisioning rate, but there was no interaction effect between male provisioning rate and age class regarding female provisioning rate (Table 3-1). This result suggested that males may respond differently to female provisioning rate depending on the pair's age class, but females are less sensitive with this respect.

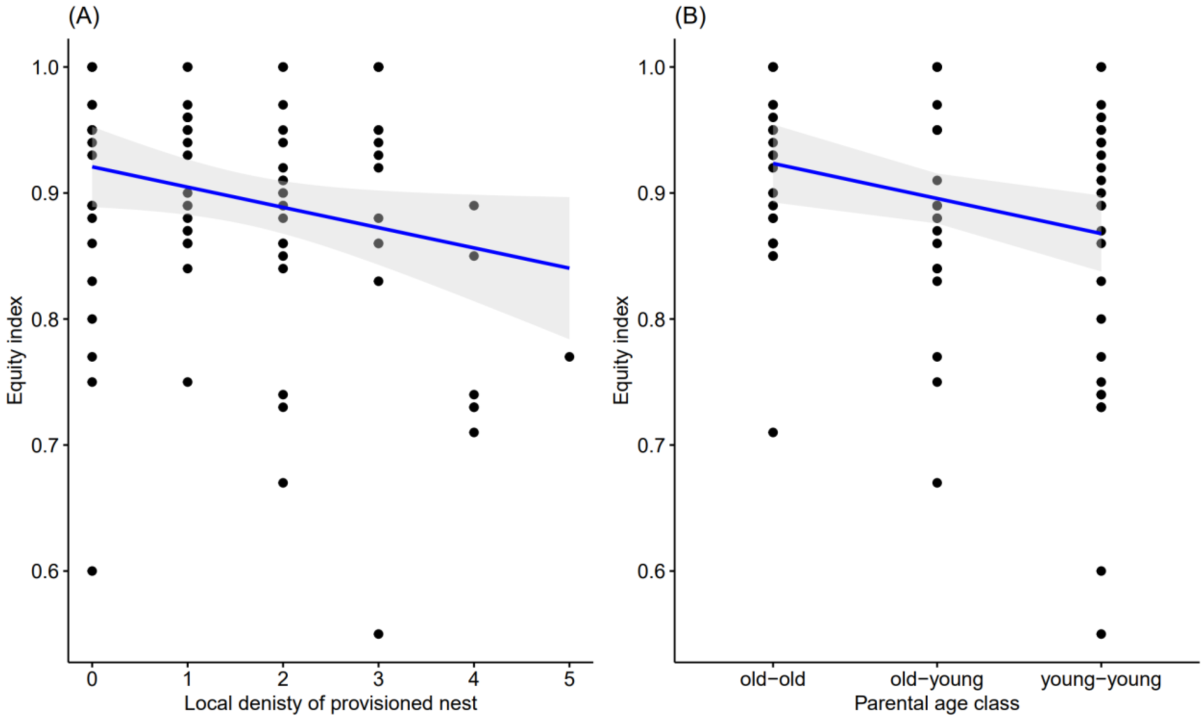

Figure 3-1 Equity index according to local density of provisioned nest (A) and parental age class (B). Equity index represents similarity in provisioning rate between male and female within a pair. I followed calculation of the equity index by Mariette et al (2015), which is 1-|P_m(provisioning rate in male/h) – P_f(provisioning rate in female/h)|/total provisioning rate/h (P_t). The *local density of provisioned nest* presents the number of active neighbouring nests within 200m during the video recording (6-9 days old nestlings). The regression lines of graphs (A,B), with SE represented by shading, are derived by a linear model using *Rfit* package, and show significant relationship between the equity index and local density of provisioned nests (estimate $\pm$se: -0.015 ± 0.0067, $\mathrm{t} = -2.23$, $p = 0.028$), and marginally non-significant effect for the relationship between equity and parental age class (estimate$\pm$se: -0.020 ± 0.013, $\mathrm{t} = -1.58$, $p = 0.117$) . Parental age class was treated as ordered factor (1:old-old, 2:old-young, 3:young-young) in the analyses.

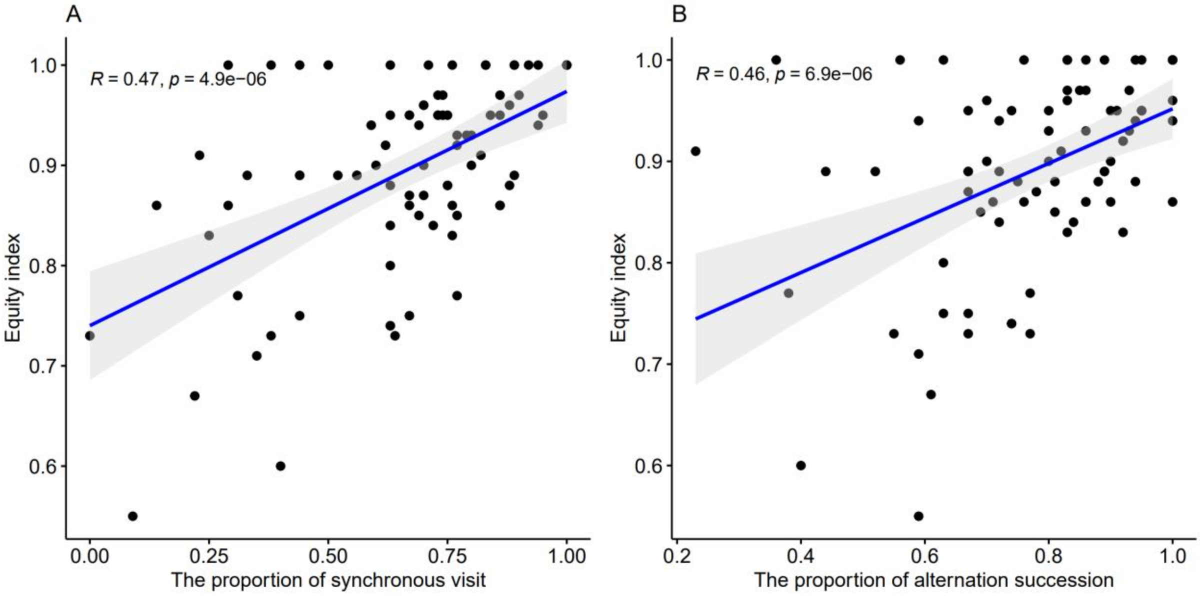

Figure 3-2. The correlation between equity and the proportion of synchronous visit (A) and the proportion of alternation succession (B). The regression line of graphs (A,B) with SE represented by shading is derived from value of predicted spearman's correlation and show a strong correlation between the equity index and the proportion of synchronous visit (spearman correlation = 0.47, n=88, p=4.9e-06) and between equity and the proportion of alternation succession (spearman correlation = 0.46, n=88, p=6.9e-06).

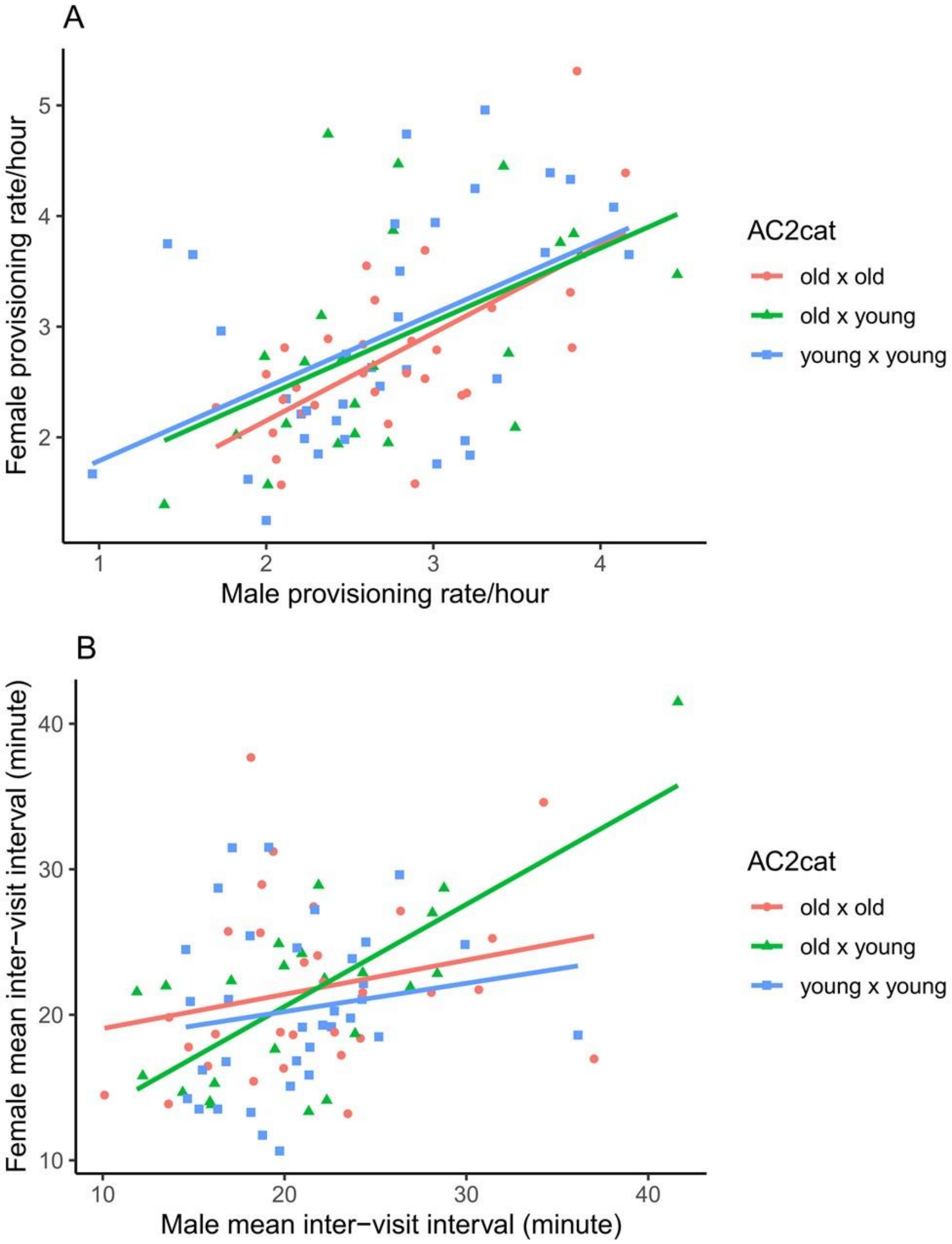

Figure 3-3. Correlation of provisioning rate (A) and mean inter-visit intervals (B) between female and male at the same nest among parental age class.

Table 3-1. Model of relationship between provisioning rate of one parent and its partner’s provisioning rate according to their parental age class. Initial model (above): female provisioning rate ~ male provisioning rate (MHR) + parental age class (AC) + MHR:AC. Initial model (below): male provisioning rate ~ female provisioning rate (FHR) + parental age class (AC) + FHR:AC

	Estimate	Std. Error	t value	Pr(>|t|)
Responsible variable : female parent provisioning rate				
(Intercept)	-0.378	0.578	-0.654	0.515
Male provisioning rate (FHR)	1.105	0.187	5.914	0.000***
Parental age class (AC)	0.547	0.307	1.785	0.0779.
MHR:AC	-0.163	0.104	-1.559	0.123
Responsible variable : male parent provisioning rate				
(Intercept)	-0.163	0.432	-0.377	0.707
Female provisioning rate (FHR)	1.091	0.135	8.103	0.000***
Parental age class (AC)	0.653	0.214	3.048	0.003**
FHR:AC	-0.261	0.068	-3.850	0.00023***

Parental age class was treated as ordered factor (1: old-old pair, 2: old-young pair, 3: young-young pair)

3.3.2. Variation of *provisioning rate* according to parental *age class* and *nest density category*.

The ***provisioning rate*** in 2009 was higher than in 2007 and 2008(Table 3-2, Figure 3-4(A)) although it does not reach a statistical significance in 2008 and provisioning rate increased with brood age (Table 3-2, Figure 3-4(B)). The provisioning rate in solitary was higher than in high density *categories* ((Table 3-2, Figure 3-5(A)) although it does not reach statistical significance. However, the provisioning rate does not differ among ***parental age class*** (Table 3-2, Figure 3-5(B)) and there was no interaction between nesting density category and parental age class (Table 3-2). From full averaging, the provisioning rate was not associated with the proportion of synchronous visit, but from conditional averaging, the provisioning rate was related to the proportion of synchronous visit (Table 3-2).

Table 3-2. Summary of model averaging from the two best fitting model ($\Delta AIC_c \leq 6$) for the predictors affecting ***provisioning rate*** during chick-rearing. Significant terms are shown in bold. Sample sizes for the whole dataset are 87 observations, 74 pairs (One Sample with extreme outlier of provisioning rate, which led to failure to normalize, was removed. Italic in square brackets shows information concerning conditional averages (i.e. average estimates from only those models in which the variable was included). *Provisioning rate* is defined as the number of times prey was brought to the nest per hour. The 10 top models of ΔAICc < 6 were in model averaging (see Table S3.1 of model selection). Confidence intervals that do not overlap zero are indicated in bold. Initial model : Provisioning rate ~ Year + hatching date + Brood age + Brood size + Nesting density category (NDC) + Parental age class category (PAC) + NDC*PAC, random factor = pair identity, family=Gaussian. This table concerns **Figure 3.4** and **3.5**

	Estimate	Adjusted SE	z value	Pr(>|z|)	2.5%	97.5%
(Intercept)	-0.09 [-*0.09*]	0.09 [*0.09*]	1.04 [*1.04*]	0.30 [*0.30*]	-0.27 [-*0.27*]	0.08 [*0.08*]
Brood age	0.59 [*0.59*]	0.19 [*0.19*]	3.19 [*3.19*]	0.00 [*0.00*]	**0.23 [*0.23*]**	**0.95 [*0.95*]**
Brood size	0.39 [*0.44*]	0.22 [*0.18*]	1.78 [2.43]	0.08 [*0.02*]	-0.04 [***0.09***]	0.82 [***0.80***]
Proportion of synchrony visit	0.38 [*0.43*]	0.22 [*0.18*]	1.77 [2.40]	0.08 [*0.02*]	-0.04 [***0.08***]	0.81 [***0.78***]
Year 2007	-0.58 [-*0.58*]	0.25 [*0.25*]	2.29 [2.29]	0.02 [*0.02*]	**-1.08 [-*1.08*]**	**-0.08 [-*0.08*]**
Year 2008	-0.53 [-*0.53*]	0.29 [*0.29*]	1.82 [*1.82*]	0.07 [*0.07*]	-1.10 [-*1.10*]	0.04 [*0.04*]
Hatching date	0.11 [*0.26*]	0.18 [*0.19*]	0.64 [*1.38*]	0.53 [*0.17*]	-0.24 [-*0.11*]	0.47 [*0.63*]
Nesting density category : parental age class (old x old)[a]	0.01 [*0.15*]	0.08 [*0.26*]	0.14 [*0.58*]	0.89 [*0.56*]	-0.14 -*0.35*]	0.16 [*0.65*]
Nesting density category : parental age class (old x young)[a]	0.00 [*0.05*]	0.07 [*0.26*]	0.05 [*0.20*]	0.96 [*0.84*]	-0.13 [-*0.46*]	0.14 [*0.56*]
Nest density (high)[b]	-0.01 [-*0.18*]	0.09 [*0.31*]	0.13 [*0.59*]	0.90 [*0.55*]	-0.18 [-*0.78*]	0.16 [*0.42*]
Nest density (low)[b]	0.00 [*0.03*]	0.06 [*0.23*]	0.04 [*0.15*]	0.97 [*0.88*]	-0.11 [-*0.42*]	0.12 [*0.49*]

[a] young x young is set as reference category, [b] solitary (reference category)

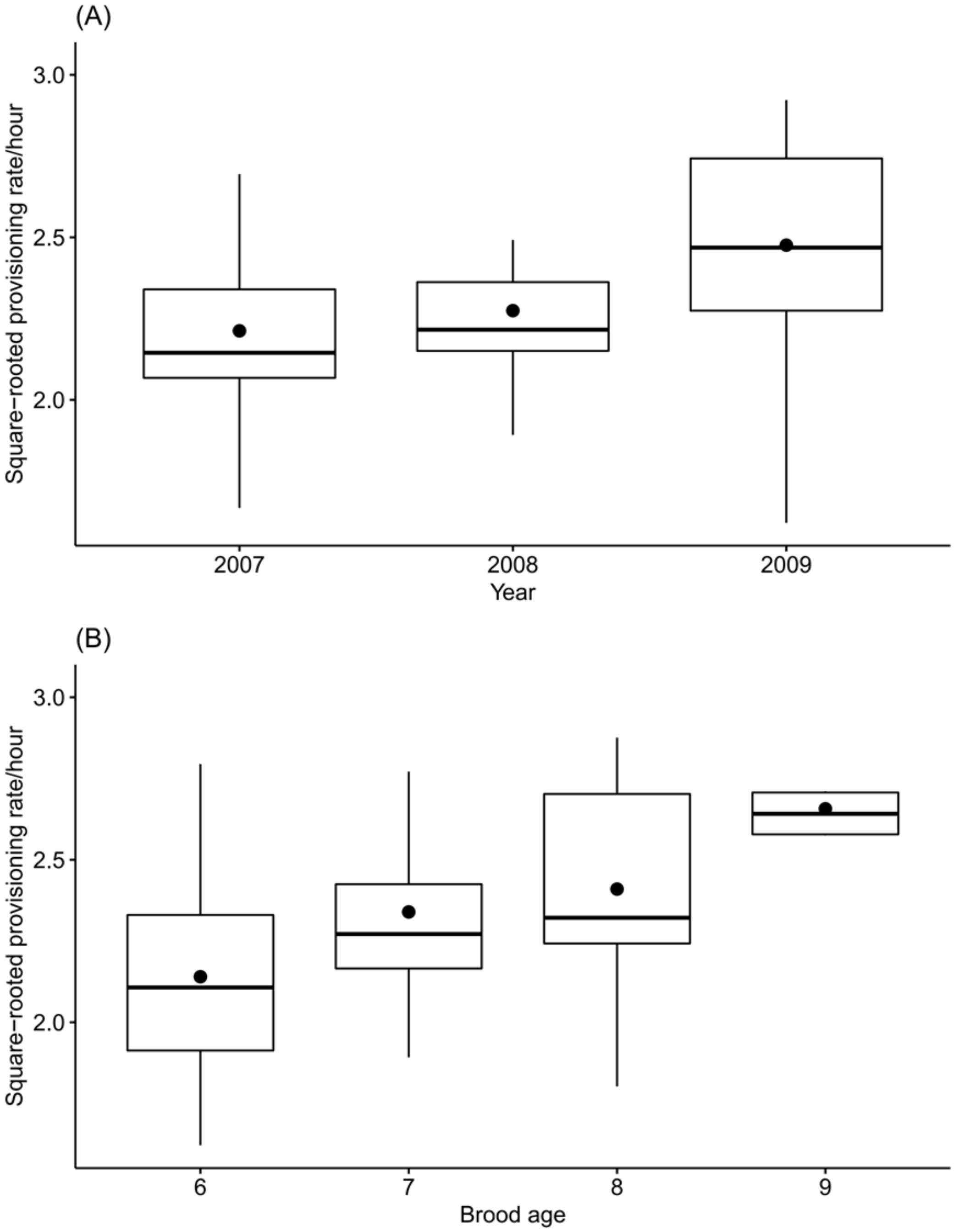

Figure 3-4 Provisioning rate in relation to year (A) and brood age (B). Sample size (A): 2007 (n=31), 2008 (n=19), 2009 (n=38), B: brood age 6 (n=17), 7 (n=41), 8 (n=23), 9 (n=7). This figure concerns Table 3.1
Boxes show the interquartile range, the thick line is the median, and the error bars (vertical lines) refer to the 1.5 interquartile. The extra data points in boxplot represent mean in each variable. This figure concern Table 3.2.

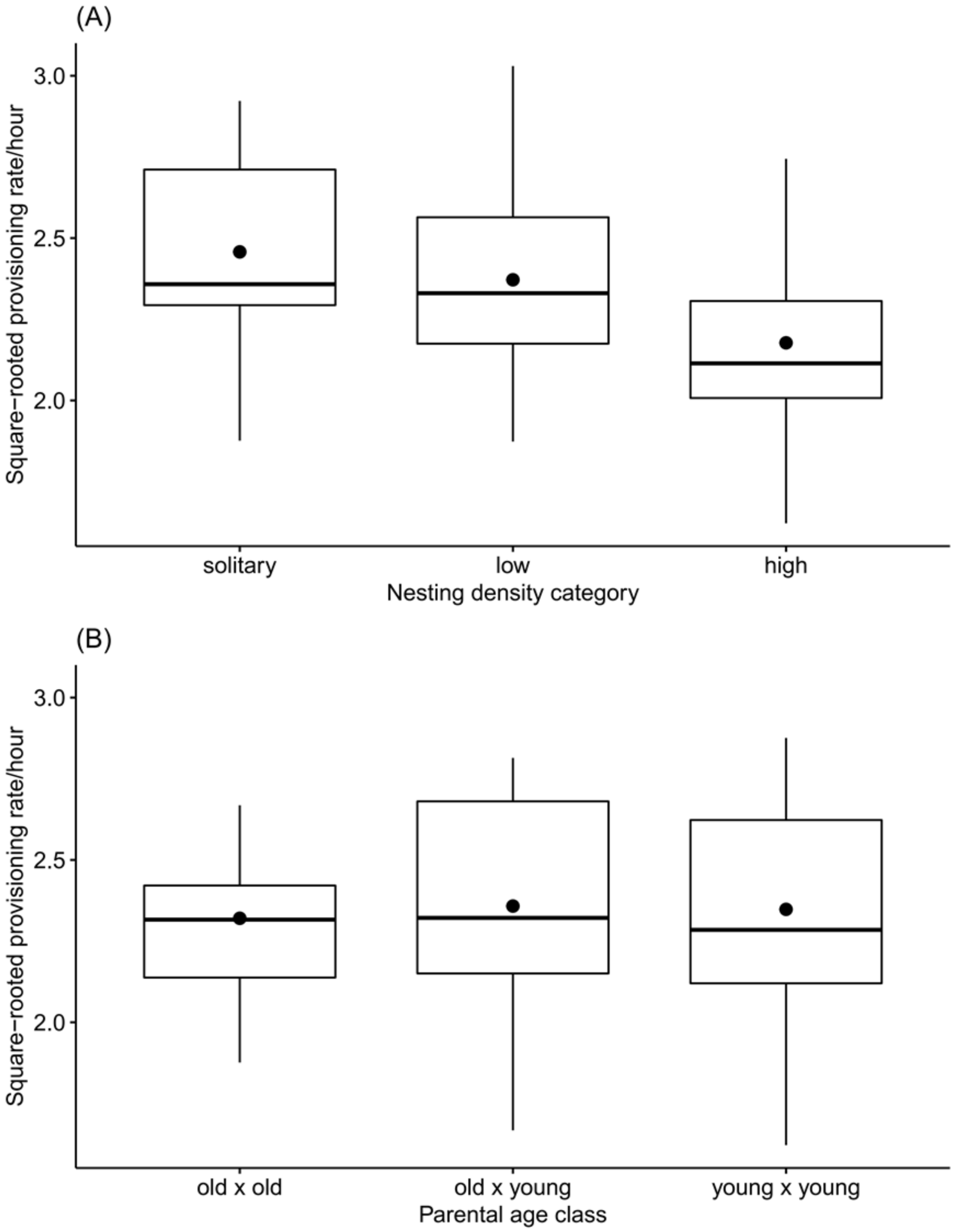

Figure 3-5 Provisioning rate in relation to nesting density category (A) and parental age class (B). Sample size (A): solitary (n=22,), low (n=46), high (n=23), (B): old x old (n=24), old x young (n=31), young x young (n=33) Boxes show the interquartile range, the thick line is the median, and the error bars (vertical lines) refer to the 1.5 interquartile. The extra data points in boxplot represent mean in each variable. This figure concern Table 3.2.

3.3.3. Within-pair coordination in relation to parental age class and local density: higher local density decreases synchronous provisioning, but old pairs are less susceptible to this effect

The vinous-throated parrotbill parents visited the nest in highly coordinated way. Of all nest visit (n=1911 from 88 nests), 67.7% (n=1294) had *synchronous provisioning visit* and 78.7 % (n=1504) had *alternating visit in rapid succession*.

The ***proportion of synchronous visits*** decreased in higher ***nest density*** as already shown in chapter 2, and it was not associated with year, brood size, or brood age. Although I did not detect significant main effect of parental age class on the ***proportion of synchronous visits,*** there was a significant interaction between ***nest density category*** and ***parental age class*** (Table 3-3) indicating that the effect of age was modified by density: in the solitary nests only the *young x young* pairs have decreased synchrony, in the low density the old x young pairs also have low synchrony, and in the high density all age classes have relatively low synchrony (Fig. 3-6 alternative) suggesting that *old x old* pairs are the most resistant to the disruptive effect of high density on synchrony of visits.

The level of ***alternating visit*** in rapid succession decreased in high density as the proportion of synchronous visit, and it was not related to year, brood size, brood age, parental age class (Table 3-4). However, there was an interaction between the age class and the nesting density with respect to the degree of alternating visit in rapid succession (Table 3-4, Figure 3-7). Post hoc test using emmean package showed that when parents had no neighbour' nest, old x old pairs and old x young pairs had significantly higher levels of CVR than young x young pairs (Figure 3-6, P=0.0003, Z-ratio= 3.871, SE=2.710, P=0.0314, Z-ratio= 2.522, SE=1.597).

Table 3-3. Summary of model averaging from the two best fitting model ($\Delta AIC_c \leq 4$) for the predictors affecting ***proportion of synchronous visit*** during chick-rearing. Significant terms are shown in bold. Sample sizes for the whole dataset are 88 observations, 74 pairs. Italic in square brackets shows information concerning conditional averages (i.e. average estimates from only those models in which the variable was included). The 5 top models of $\Delta AICc < 4$ were in model averaging (see Table S of model selection). Confidence intervals that do not overlap zero are indicated in bold. Initial model: cbind (synchrony, asynchrony) ~ Year + hatching date + Brood age + Brood size + Nesting density category (NDC) + Parental age class category (PAC) + NDC*PAC, random factor = pair identity, family=binomial
This table concerns Figure 3.6

	Estimate	Adjusted SE	z value	Pr(>|z|)	2.5%	97.5%
(Intercept)	0.86[*0.86*]	0.12[*0.12*]	7.15[*7.15*]	0.00[0.00]	0.62[*0.62*]	1.09[0.09]
Parental age class (PAC) (old x old) ^{a}	0.41[*0.41*]	0.33[*0.33*]	1.26[*1.26*]	0.21[*0.21*]	-0.23[*-0.23*]	1.06[1.06]
Parental age class (PAC) (old x young) ^{a}	0.51[*0.51*]	0.34[*0.34*]	1.50[*1.50*]	0.13[*0.13*]	-0.16[*-0.16*]	1.18[1.18]
Nesting density category (NDC) (high) ^{b}	-1.1 [*-1.15*]	0.29[*0.29*]	3.98[*3.98*]	0.00[*0.00*]	**-1.72[*-1.72*]**	**-0.59[-0.59]**
Nesting density category (NDC) (low) ^{b}	-0.02[*-0.02*]	0.27[*0.27*]	0.09[*0.09*]	0.93[*0.93*]	-0.55[*-0.55*]	0.50[0.50]
PAC (old x old) ^{a} **: NDC (high)** ^{b}	-1.59[*-1.59*]	0.75[*0.75*]	2.13[*2.13*]	0.03[*0.03*]	**-3.06[*-3.06*]**	**-0.12[-0.12]**
PAC (old x young) ^{a} **: NDC (high)** ^{b}	2.07[*2.07*]	0.82[*0.82*]	2.51[*2.51*]	0.01[*0.01*]	**0.45[*0.45*]**	**3.68[3.68]**
PAC (old x old) ^{a} : NDC (low) ^{b}	1.03[*1.03*]	0.74[*0.74*]	1.40[*1.40*]	0.16[*0.16*]	-0.41[*-0.41*]	2.47[2.47]
PAC (old x young) ^{a} **: NDC (low)** ^{b}	-2.45[*-2.45*]	0.75[*0.75*]	3.25[*3.25*]	0.00[*0.00*]	**-3.93[*-3.93*]**	**-0.97[-0.97]**
Brood age	0.09[*0.25*]	0.16[*0.19*]	0.52[*1.29*]	0.60[*0.20*]	-0.24[*-0.13*]	0.41[0.63]
Brood size	0.01[*0.03*]	0.08[*0.19*]	0.06[*0.15*]	0.95[*0.89*]	-0.16[*-0.34*]	0.17[0.40]
Year 2007^{c}	-0.04[*-0.36*]	0.16[*0.35*]	0.25[*1.02*]	0.81[*0.31*]	-0.36[*-1.05*]	0.28[0.33]
Year 2008^{c}	0.06[*0.52*]	0.20[*0.32*]	0.30[*1.63*]	0.77[*0.10*]	-0.33[*-0.11*]	0.44[1.15]

^{a} young x young is set as reference category, ^{b} solitary (reference category)

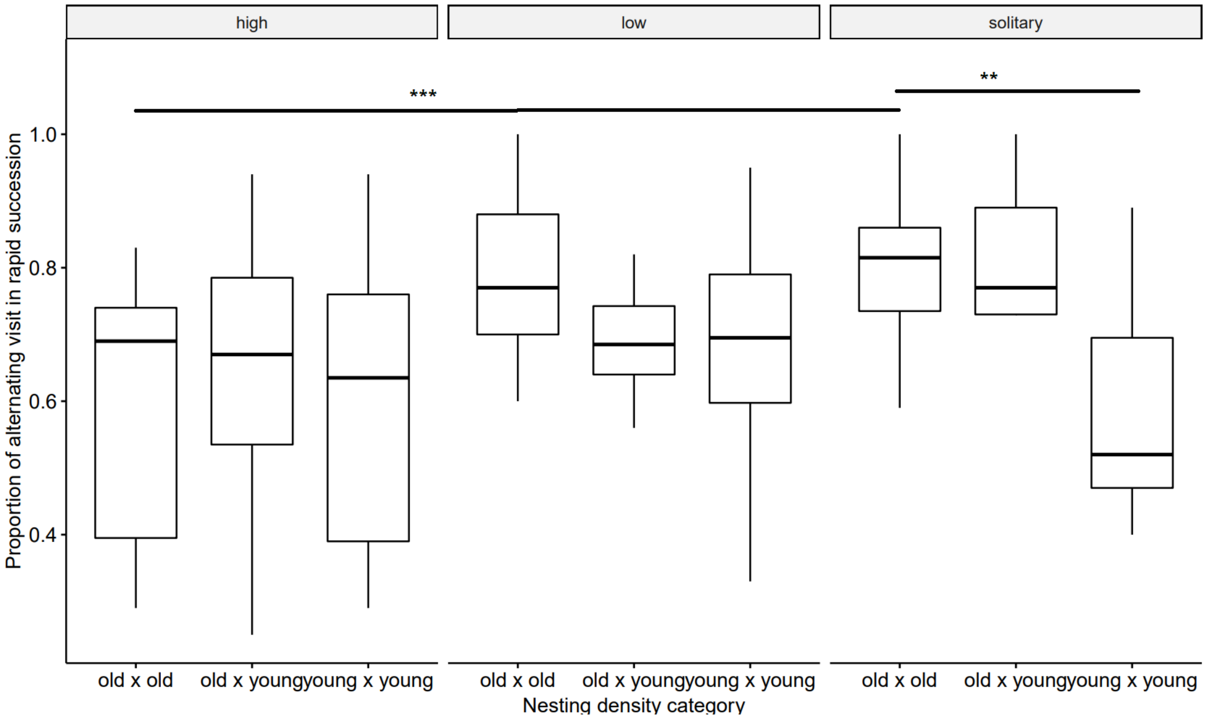

Figure 3-6 The level of ***synchronous provisioning*** in relation to the nesting density and parental age class. Boxes show the interquartile range, the thick line is the median, and the error bars (vertical lines) refer to the 1.5 interquartile. This figure concern **Table 3.3.** Sign of significance levels was represented from the summary table based on post-hoc analysis using emmean package (Supplementary Table 3-S3)

Table 3-4. Summary of model averaging from the two best fitting model ($\Delta AIC_c \leq 4$) for the predictors affecting **proportion of *alternating visit in rapid succession*** during chick-rearing. Significant terms are shown in bold. Sample sizes for the whole dataset are 88 observations, 74 pairs. Italic in square brackets shows information concerning conditional averages (i.e. average estimates from only those models in which the variable was included). The 8 top models of $\Delta AICc < 4$ were in model averaging (see Table S of model selection). Shown are model-averaged parameter estimates and 95% confidence intervals for each fixed effect. Confidence intervals that do not overlap zero are indicated in bold. Initial model: alternation success(1,0) ~ Year + hatching date + Brood age + Brood size + Nesting density category (NDC) + Parental age class category (PAC) + NDC*PAC, random factor = pair identity, family=binomial. This table concern **Figure 3.7**

	Estimate	Adjusted SE	z value	Pr(>|z|)	2.50%	97.50%
(Intercept)	1.54[*1.54*]	0.11[*0.11*]	13.89[*13.89*]	0.00[*0.00*]	1.32[*1.32*]	1.76[*1.76*]
Parental age class (PAC) (old x old) [a]	0.53[*0.53*]	0.33[*0.33*]	1.63[*1.63*]	0.10[*0.10*]	-0.11[*-0.11*]	1.17[*1.76*]
Parental age class (old x young) [a]	0.58[*0.58*]	0.31[*0.31*]	1.84[*1.84*]	0.07[*0.07*]	-0.04[*-0.04*]	1.19[*1.19*]
Nesting density category(NDC) (high) [b]	-0.77[*-0.77*]	0.29[*0.29*]	2.62[*2.62*]	0.01[*0.01*]	**-1.34[*-1.34*]**	**-0.19[*-0.19*]**
Nesting density category (low) [b]	-0.16[*-0.16*]	0.25[*0.25*]	0.63[*0.63*]	0.53[*0.53*]	-0.65[*-0.65*]	0.33[*0.33*]
PAC (old x old) [a] : NDC (high) [b]	-1.88[*-1.88*]	0.74[*0.74*]	2.53[*2.53*]	0.01[*0.01*]	**-3.34[*-3.34*]**	**-0.42[*-0.42*]**
PAC (old x young) [a] : NDC (high) [b]	1.34[*1.34*]	0.82[*0.82*]	1.64[*1.64*]	0.10[*0.10*]	-0.26[*-0.26*]	2.94[*2.94*]
PAC (old x old) [a] : NDC (low) [b]	-0.19[*-0.19*]	0.71[*0.71*]	0.26[*0.26*]	0.79[*0.79*]	-1.59[*-1.59*]	1.21[*1.21*]
PAC (old x young) [a] : NDC (low) [b]	-1.29[*-1.29*]	0.74[*0.74*]	1.76[*1.76*]	0.08[*0.08*]	-2.73[*-2.73*]	0.15[*0.15*]
Year 2007	0.22[*0.48*]	0.32[*0.33*]	0.67[*1.45*]	0.51[*0.15*]	-0.42[*-0.17*]	0.85[*1.12*]
Year 2008	0.06[*0.12*]	0.22[*0.31*]	0.26[*0.39*]	0.80[*0.69*]	-0.37[*-0.49*]	0.48[*0.73*]
Brood size	-0.09[*-0.24*]	0.17[*0.19*]	0.57[*1.29*]	0.57[*0.20*]	-0.42[*-0.61*]	0.23[*0.13*]
Brood age	-0.02[*-0.08*]	0.10[*0.19*]	0.18[*0.40*]	0.86[*0.69*]	-0.21[*-0.46*]	0.17[*0.30*]

[a] young x young is set as reference category, [b] solitary (reference category)

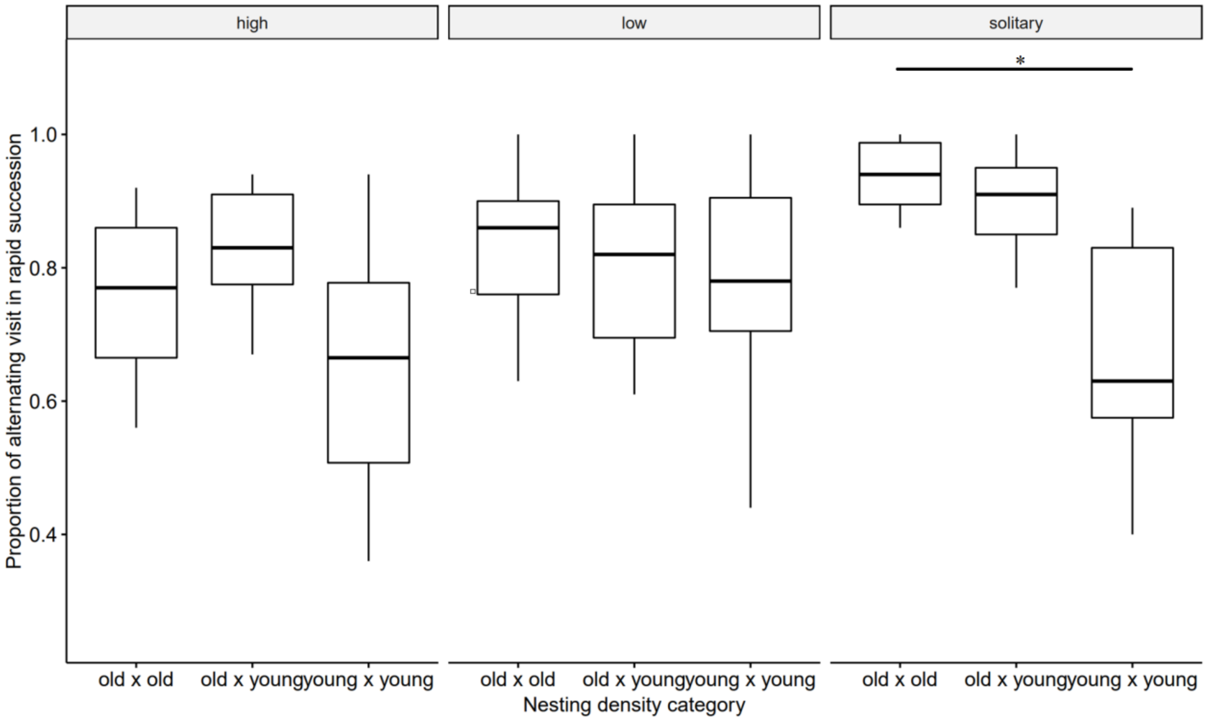

Figure 3-7 The level of alternating nest visits in rapid succession in relation to the nesting density and parental age class. Boxes show the interquartile range, the thick line is the median, and the error bars (vertical lines) refer to the 1.5 interquartile. The extra data points in boxplot represent mean in each variable. Sign of significance levels was represented from the summary table based on post-hoc analysis using emmean package (Supplementary Table 3-S3)

3.3.4. Provisioning visits synchrony in relation to the local breeding synchrony: locally non-synchronized breeders may cause decreased visiting synchrony within the focal pair.

Both types of provisioning visits, synchronous and asynchronous, were observed in pairs that bred synchronously as well as those that bred asynchronously with the local breeders (within 200 m radius). To explore if the proportion of synchronous visits in a focal nest depends on the local density of synchronously breeding pairs and/or the local density of non-synchronously breeding pairs I ran GLMM analysis that included several other variables as predictors (See caption to Table 3.5). The number of nesting pairs that breed synchronously around the focal nest was not associated with the proportion of synchronous provisioning in the focal nest (Table 3-5, Figure 3-8B), but the degree of synchronous provisioning visit decreased significantly as the number of nesting pairs that breed asynchronously increased (Table 3-5, Figure 3-8A).

Table 3-5. Summary of model averaging for predictors affecting the proportion of ***synchronous nest visit according to local density of synchronized brood and non-synchronized brood.*** Above: Initial model: Cbind (synchronous visit, asynchrony visit) ~ Year + Brood size + Brood age + local density of synchronized brood + Parental age class + (local density of synchronized brood)*Parental age class. Below: Initial model: Cbind (synchronous visit, asynchrony visit) ~ Year + Brood size + Brood age + local density of non-synchronized brood + Parental age class + (local density of non-synchronized brood)*Parental age class

	Estimate	Adjusted SE	z value	Pr(>|z|)	2.50%	97.50%
Model including local density of broods at similar stage						
(Intercept)	0.84	0.12	7.25	< 2e-16	0.61	1.06
Age class (old x old)[a]	0.52	0.37	1.41	0.16	-0.20	1.23
Age class (old x young) [a]	0.09	0.30	0.31	0.75	-0.50	0.69
Brood age	0.54	0.17	3.11	0.00	**0.20**	**0.88**
Local density of **broods at similar stage** (LDS)	-0.13	0.17	0.74	0.46	-0.46	0.21
AC (old x old)* LDS	-0.16	0.41	0.39	0.70	-0.96	0.64
AC (old x young)* LDS	0.16	0.40	0.40	0.69	-0.63	0.95
Year1	0.03	0.12	0.25	0.80	-0.20	0.27
BS	-0.01	0.08	0.11	0.92	-0.16	0.15
Model including local density of non-synchronized brood						
(Intercept)	0.83	0.11	7.32	<2e-16	0.61	1.06
Age class (old x old) [a]	0.45	0.36	1.25	0.21	-0.25	1.14
Age class (old x young) [a]	0.17	0.30	0.56	0.58	-0.42	0.75
Local density of broods at different stage (LDN)	-0.99	0.19	5.27	0.00	**-1.36**	**-0.62**
Brood age	0.06	0.14	0.45	0.65	-0.21	0.33
Brood size	0.05	0.12	0.39	0.70	-0.19	0.28
Year	-0.02	0.12	0.19	0.85	-0.26	0.22
AC (old x old)* LDN	-0.02	0.14	0.14	0.89	-0.29	0.26
AC (old x young)* LDN	0.00	0.11	0.04	0.96	-0.23	0.22

[a] Reference category is Age class (young x young)

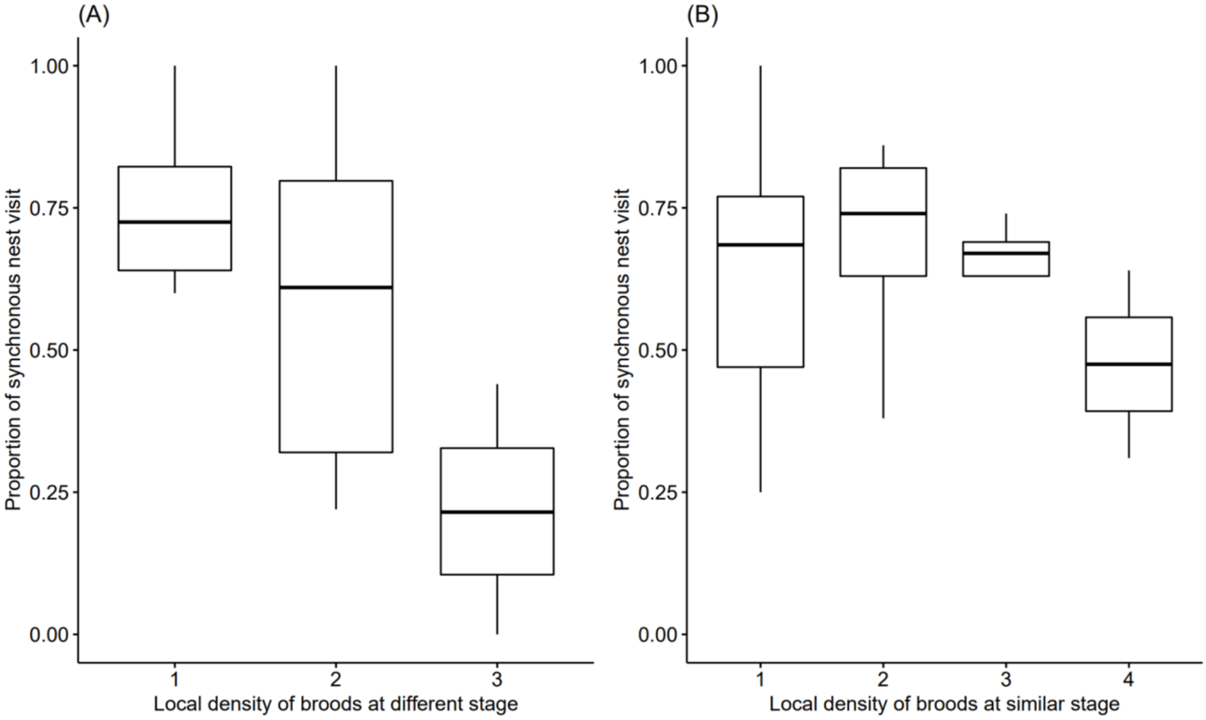

Figure 3.8. The level of synchronous provisioning in relation to the nesting density with asynchrony breeders (A) and synchrony breeders (B). Synchronous breeding was regarded as when the first egg of neighbouring's nest was laid in a nest six day before and after the first egg of the focal nest in local colony (within 200m radius of focal nest). Boxes show the interquartile range, the thick line is the median, and the error bars (vertical lines) refer to the 1.5 interquartile. The extra data points in boxplot represent mean in each variable. This figure concern Table 3.4. Sample size (A; 1 (n=26), 2 (n=16), 3 (n=4), B; 1(n=22), 2(n=13), 3(n=5), 4(n=2))

3.4. DISCUSSION

3.4.1. Overview

Previous work (chapter 2) on the vinous-throated parrotbill have suggested that pairs may increase synchrony of provisioning if it brings higher foraging benefits (and maybe also decreased predation risk to the parents) than solitary foraging and asynchronous provisioning. It was also suggested that this coordination within a pair is negatively affected by the hypothetical social disruption mechanism in the locally high nesting densities.

Here, in Chapter 3, I have expanded the notion of coordinated provisioning by including analysis of the degree of equity of parental provisioning between pair members and by analysis of the alternating provisioning visits coordinated among pair members. While the results are consistent with the previously proposed (Chapter 2) "social disruption" hypothesis, they provide more precision in determining how the mechanism may work, and how it may be affected by parental age and the associated individual experience. I have determined that the social hypothetically disruptive effects of local density on the coordination of provisioning, comprising visit synchrony and visit alternation, may be modified by the partners' age and experience as well as by the degree to which the timing of breeding of the local set of nests (within 200m form the focal nest) is synchronized with the timing of breeding of the focal pair. I show that older and therefore more experienced pairs are more coordinated with respect to both visit synchronization and visit alternation, but that this effect is clear only in solitary breeders, and the increasing local density attenuates the age effect. This effect of local density consists mostly of what appears to be a decrease in the proportion of synchronous nest visit and the level of alternation succession in old pairs as the density increases, suggesting that the social disturbance effect on older pairs (*old x old*, and *old x young*) hypothetically increases with local density. For young pairs, no such trend is evident, and it appears that intermediate densities may promote higher degree of coordination than either in solitary (non-significant difference) or in high (significant difference) density conditions. In other words, the hypothetical social disturbance effect on the focal pair's provisioning coordination affect all ages in high densities, but as the density decreases the older pairs can increase their coordination to the higher levels than young pairs, who remain relatively less coordinated in solitary conditions. The results also suggest that the proposed social disturbance effects on coordination are mostly caused by local breeders that are not synchronized in their timing of breeding with the focal pair. Below I present a more detailed discussion of these issues.

3.4.2. Similarity of provisioning rate between male and female according to parental age class

Large differences in provisioning rate between males and females may indicate the low level of coordination between parents, especially in monogamous species where no other task specialization (e.g. brooding) occurs during chick-rearing period (Bebbington & Hatchwell, 2016)(Mariette & Griffith, 2015). Additionally, this equal distribution of provisioning contributes to reducing the conflict between males and females (Hinde, 2006) and can also lead to an increase in the provisioning rate and in the level of pair coordination (Bebbington & Hatchwell, 2016).

I found that similarity between parents of the vinous throated parrotbills in provisioning rates was positively related to the level of pair coordination, but not to provisioning rate. Furthermore, the equity index value, which represents the similarity of the provisioning rate between parents was close to 1 (i.e., equal provisioning frequency between partners) in all age groups and combinations regardless of nesting density. Birds actively respond to their partner's activity, but may incur costs to maintain behavioural synchrony that requires coordination. For example, while synchronizing their foraging and nest visits, parents may spend additional time to achieve their synchrony, such as waiting time for partners when foraging rates are not matched between them or time looking for partners when separated. However, these costs can be reduced as parents become older and more experienced.

3.4.3. Provisioning rate among parental age class

Overall, provisioning rates decreased slightly at higher densities, although it did not reach statistical significance (Table 3-1). These results contradict a previous study (Lee, Kim & Hatchwell, 2010) on provisioning of the vinous-throated parrotbill, in which provisioning rates increased with increasing nesting density, probably through the benefit of group living, such as the increase in foraging efficiency with increased vigilance. Furthermore, my results show that there was no differences in overall provisioning rates according to parental age class and combination. However, I found that there was an interaction effect between provisioning rate and parental age class. Provisioning rates decreased significantly at high densities in young x young parents but this density dependence was not observed in older parents, implying that young parents may be more sensitive to increasing density while provisioning. Our anecdotal observations show that the collective movement among breeding pairs with nestlings or eggs is relatively uncommon, although there is an increased chance of encountering each other at higher densities, and small flocks (mostly consisted of failed breeders and nonbreeding pairs or juveniles) were often observed in the food-rich patch.

3.4.4. Pair coordination and provisioning rate

My results show that the proportion of synchronous visit is not related to the provisioning rate (Table 3-1), which is consistent with studies of the zebra finch *Taeniopygia guttata* (Mariette & Griffith, 2015), silver-throated tit (Wen et al., 2020), and blackcap (Leniowski & Węgrzyn, 2018), but in inconsistent with the long-tailed tit (Bebbington & Hatchwell, 2016), in which pair coordination is related to feeding rate. In species (e.g. zebra finch, vinous-throated parrotbill) where foraging synchrony leads to nest visit synchrony, it may incur costs to maintain synchrony (e.g. waiting time for a partner to finish foraging or provisioning, or finding a partner when they split up, all of which results in reduced provisioning rates). Therefore, the absence of relationship between pair coordination and provisioning rate may indicate that it may incur no cost to provisioning rate to achieve pair coordination (Mariette & Griffith, 2015).

3.4.5. Pair coordination with respect to parental age class and local density

Our results show that high nest densities limit coordination, but provisioning rates are not affected by increasing nest densities. I found an interaction between parental age class and nest density at the level of coordination. Why do young pairs do not increase their coordination as strongly as old pairs do when density decreases? Also, why this limiting effect on coordination is linked with the increasing density of local pairs that do not synchronize their timing of breeding with the focal pair, while no such effect is observed for pairs that breed synchronously with the focal pair (there is even a suggestion in the shape of the relationship in Fig. 3-7B that presence of a few synchronous breeders may aid in achieving provisioning coordination)? Pairs that bred synchronously at close range may be familiar and stronger social ties than pairs that bred asynchronously as shown in the recent study of the zebra finch (Brandl, Griffith & Schuett, 2019)(Brandl et al., 2021). Indeed, studies showed that breeders that nest synchronously in each colony are likely to maintain stable social relationships with tolerance and collaboration (e.g. communal mobbing toward predator or unfamiliar group members) (Grabowska-Zhang, Wilkin & Sheldon, 2012)(Brandl et al., 2021). Although the early spring subgroup membership has not been studied in detail, previous studies of parrotbills have revealed that male siblings nest closely together, based on genetic relatedness analysis (Lee et al., 2009a). Individuals that were born in the vicinity nest nearby in the following breeding season, even when their nesting location changed (unpublished data). A recent study shows that such a carryover effect of membership across years occurs in colonial species and even in territorial species (Brandl, Griffith & Schuett, 2018)(Firth & Sheldon, 2016).

Hence, I propose that in the parrotbill, the breeding pairs that occur locally near a focal nest are to a large extent members of a tight social group that synchronizes the timing of breeding and that interactions among those individuals do no lead to social disruption of pair coordination. However, some of locally present pairs are not members of this social group and I hypothesize that they are more likely to have non-synchronized timing of breeding with the other pairs. I suggest that with interactions between a focal pair and those individuals lead to the decrease in pair coordination in accordance with the “social disruption” hypothesis as already proposed in Chapter 2.

While the benefits of living in a group during the breeding season may be much more favourable among familiar individuals, unfamiliar members might be not to interact with each other, thereby no benefit of group-living. Individuals that reproduce asynchronously are likely to be individuals who did not group in a subgroup in the spring or those introduced into a new location after failure to produce. Our result shows that the density of neighbours that breed synchronously was not associated with the degree of synchronous provisioning visits, but the level of the degree of synchronous provisioning visits rapidly reduced as the number of non-simultaneously reproduced individuals increased (Table 3-5, Figure 3-8). I suggested that the interruption occurring during provisioning at high density in the previous analysis (chapter1) may be related to the exclusivity toward the recruited individuals. Conflicts between group members might occur more frequently than I thought in previous studies. The screaming call (vocalization produced during physical harassment) occurring in the parrotbill’s flocks is likely to result from conflict between individuals (Lee et al., 2015).

3.4.6. Conclusions

In conclusion, parrotbills have a much more complicated, structured, long-lasting social network system (like a human) and these diverse social relationships might be linked with provisioning effort and pair coordination. Cooperation between siblings, familiarity among members in each colony, and characteristics of an individual or the degree of sociality (e.g. solitary, colonial) may affect coordination or collaboration between paired mated or among group members. This coordination may contribute to survival. A more rigorous study of the social network system among group members in a more structured society needs further investigation.

Chapter 4

Arriving sequence and prey load size during synchronous provisioning visits in a group-living bird, the Vinous-throated parrotbill.

Abstract

In social birds, breeding parents often forage and visit nests in synchrony, which may benefit the breeding success and parental survival. However, the mechanisms by which synchrony is maintained are not fully understood. I investigated the arrival behaviour of partners after either synchrony visits or asynchrony visits, and the volume of food, the preceding travel length, and feeding efficiency between provisioning partners during synchrony nest visits. I found that parents often had long durations in the nest after visiting alone and leaving the nest together after the next partner arrived. Even after a synchrony visit, wait for the partner to arrive if a later fed parent had a long duration in the nest. Our finding suggested that waiting for a partner in the nest is likely a mechanism for maintaining continued synchrony. The nest seems to be the partner's predictable location and is relatively safer while separated. In addition, the parent arrived earlier at nest during synchrony visits had a higher feeding efficiency and quantity regardless of the partner's sex. The first-comer might be the leading individuals for initiating a movement to the nest during the synchronous visit. Our results show that the temporary leading and following relationships according to the status might occur trip to trip during synchrony visits, and the relationship can facilitate their ongoing coordination.

Key word; foraging synchrony, nest visit synchrony, Arriving order

4.1. INTROUDCTION

In monogamous species, such as long-tailed finch (van Rooij & Griffith, 2013), zebra finch *Taeniopygia guttata* (Mariette & Griffith, 2012) in which the pair forage together while raising their chicks, parents need to coordinate their behaviour when they move between foraging patches and their nest. Parents can have asynchronous provisioning visits, if one parent moves alone without waiting for the other partner. Such discrepancies in foraging trip between parents may arise due to differences in energy states between partners or disruption by others. For example, if both parents and nestlings have low hunger levels, it may be safer for the parent to wait for the partner even after foraging. When the parent also visits the nest solitarily, he (or she) can wait for a partner in the nest or rest in the nest after provisioning their chicks to keep foraging synchrony.

Previous theoretical studies considered that the individual's energy state determines foraging synchronization by a pair (Rands et al., 2003). Whether members of concurrently foraging pairs made each nest visit with optimal energy state and maximum food for nestlings has yet to be studied. However, since each individual at such visits may have different energy states or different feeding success rates, pair members can have a trade-off for the optimal timing of their visit to the nest. Comparing the amount of food, travel length, or feeding efficiency between parents who visit simultaneously within a pair may give insight into how each parent decided visiting timing depending on the amount of food within the pair. Theory predicts that the spontaneous leading or following conditions may emerge when moving between patches during foraging in groups or pairs, and movement timing may be determined flexibly from moment to moment according to factors, such as energetic state and predation risk (Rands et al., 2003).

In both monogamous species with parental care (van Rooij & Griffith, 2013) and some species with breeding in colonially or cooperatively, parents form behavioural synchrony during nest visit (Mariette & Griffith, 2015) (Raihani et al., 2010b). Synchronous nest visit is a form of pair coordination to provision food to chicks simultaneously, and little is known how to maintain constantly foraging synchrony or nest visit synchrony. Behavioural synchrony has many benefits, such as increased feeding efficiency and safety from predators, but it can also incur costs in the time and energy required to maintain synchrony. Waiting for partner in the nest or foraging patch might lower their provisioning rate for nestlings.

Previous studies and numerous anecdotal observations have shown that vinous-throated parrotbill parents mostly forage in a pair (foraging alone is relatively rare) or sometimes in a group during the chick-rearing (ref.). Therefore, a previous study suggested that synchronous foraging by pairs can lead to simultaneous nest visits (Lee, Kim & Hatchwell, 2010). Anecdotal observations (BSJ) show that pair members of vinous-throated parrotbills leave feeding patches simultaneously and arrive at the nest at the same time. After that, the parents leave together to the foraging patch after provisioning. During this process, pair members actively produce contact calls to keep them close, except when a partner approaches the nest to feed (presumably to avoid revealing nesting locations to predators). After feeding, the first comer (i.e. an partner that arrives first at the nest and feeds first) usually keep uttering soft calls around the nest to leave together with the late comer (Supplementary Material; video 1, 2).

To determine whether foraging synchrony and nest visit synchrony are maintained between parents by actively reacting with each other, I investigated how the arrival patterns of partners before and after asynchronous visits by single parents occur under multiple visit patterns (e.g. asynchronous visit after asynchronous visit, asynchronous visit after the synchrony visit, synchrony visit after solo visit in each individual level)

I investigated whether the order of arrival among pair members during simultaneous nest visits occurred randomly or in a specific way, and whether it was related to social environment or individual status, or pair characteristics. Specifically, I compared the amount of food, the number of food items, foraging efficiency between the first and late comer, regardless of sex during synchronous nest visits after foraging synchrony is likely to perform together in the foraging patch. Similarity of food quantity between males and females may facilitate continuous synchrony foraging.

4.2. METHODS

4.2.1. Study area and general field research methods

I conducted fieldwork in Buyong-ri, Yangpyeong-gun, Gyeonggi-do during the 2007-2009 breeding seasons. The research area includes open land near forests, streams, farmland, and villages. Parrotbills often forage in forests in early spring, but most of their foraging and nesting activities take place in areas composed of thickets and shrubs. In the study area, banding efforts continued since the winter of 2004 (Lee et al., 2010). I colour-banded most of the birds in the study area yearly until the winter of 2010. During the breeding season I searched for nests, and upon finding a nest, I monitored it regularly (every 1-3 days) to obtain general breeding parameters. The nestling diet and parental provisioning were recorded through a video camera installed near the nest (2-10 m away). Occasionally the birds seemed to be disturbed by the camera lens directed to the nest (e.g. behavioural indications of cautiousness), and I excluded those videos from the analyses. One recording at a nest lasted 4.5 hours and I have excluded the first 30 minutes from the analyses if during camera setting up the parents arrived at the nest area. However, the set up of the camera was usually quick and did not cause severe interruption in parental provisioning of a pair. The recordings were performed between 7 am and 9 am, unless times were changed due to weather conditions. It is generally not possible to identify gender based on appearance or behaviour in a video. Instead, I determined sex based on the individually unique colour band combinations put on the birds before the breeding season, combined with PCR-based sexing based on blood samples collected from banded birds (ref.).

4.2.2. Variables extracted from data

4.2.2.1 Environmental variables

Year – categorical (non-ordinal) variable with either three (2007, 2008, 2009) or two (2008, 2009) values.

Provisioned nest density- I used the number of concurrently active (active defined as nests with provisioned broods) nests within 200 meters radius from the focal nest on a day of the video recording. I calculated the density of nests around the focal nest during the video rather than the maximum number of active nests around the focal nest throughout the season used in the Chapter 2. I followed the criteria of 200 m by Lee et al. (Lee, Kim & Hatchwell, 2010), the distance at which group members would interact.

4.2.2.2 Basic breeding ecology variables

PairID – Unique label for each of the 74 pairs. Some pairs had a second (8 pairs) or third (2 pairs) brood.

Hatching date – The date when the first egg was hatched. In most nests, parrotbill chicks hatch on the same day; expressed in numerical format as the number of days from April 15th in each year. In most nests, the hatching date was recorded by checking nests at daily intervals from the earliest expected hatching date.

Brood age – Age of the nestlings in days from hatching at the time of the video recording.

Parental age class (*PAC*) – this variable was an ordered categorical variable characterizing a pair with the following classes ordered from older to younger: *old-old*, *old-young*, *young-young* that corresponded to the variable values of 1, 2, and 3 respectively.

4.2.2.3 Behavioral variables

Provisioning rate – From each video recording, I calculated the total number of provisioning visits to the brood by the male and the female separately. *Provisioning rate* was calculated by dividing the total number of visits by the total duration of the video recording and expressed as nr of visits/hour. Sample sizes for the whole dataset are: 86 observations (videos) collected at broods of 74 pairs comprising 64 pairs with one video (brood); 8 pairs with two videos (broods), and 2 pairs with three videos(broods).

Visit type- I followed the criterion of synchronous provisioning used by Lee et al. (2010). The *asynchronous visit* was defined as a visit of a single parent when its partner did not visit the nest within 1 min before or after the focal birds' visit (following Mariette et al. 2012, I use the term ***transition time*** for this latency between visits of the two parents) regardless of whether at the preceding visit the bird arrived at the nest alone or together with the partner. The remaining visits were classified as *synchronous visits* if none of the parents stayed in the nest for an excessively long time defined as more than 2 minutes from arrival at the nest. A provisioning parent spent 2-2967seconds (median 22 s., n=1908) in the nest during an individual visit.

Number of asynchronous visits and the ***number of synchronous visits*** – the numbers directly observed in the video for each nest.

Proportion of synchronous visits – when used as an explanatory variable it was calculated as (***number of synchronous visits***) / (***number of synchronous visits*** + ***number of asynchronous visits***). When analysing proportion of synchronous visits as dependent (response) variable the *cbind* function was used: *cbind* ((***number of synchronous visits***, ***number of number of asynchronous visits***).

Arriving sequence (variable generated for synchronous visits) - For every synchronous visit, I classified the parent arriving first to the nest as the "*first-comer*" and the subsequently arriving parent as the "*late-comer*". The first mate within the pair to arrive at the nest feeds nestlings first and leaves the nest first. Therefore, the order of parent's arrival at the nest is strictly the same as the order of provisioning and the order of leaving the nest after provisioning.

Long duration visits – this is a binary variable that classifies each provisioning visit into *long duration present* or *long duration absent* categories. Some of the video observations showed that the *first-comer* parent after provisioning the brood waited near the nest while his/her partner continued provisioning the brood. This could not have been checked it at all monitored nests because of the narrow field of view around the dense nesting area during the video, but whenever possible it was either directly observed in the video or acoustically determined by the presence of contact calls given by the *late-comer* parent near the nest. After the *late-comer* parent finished provisioning, then both parents often left the nest together. However, in about 10% of cases the *late-comer* parent did not leave the nest immediately after finishing provisioning (it is likely to occur in the absence of audible contact calls near the nest), and then stayed in the nest for an excessively ***long duration***: if a provisioning parent stayed on nest for more than 2 minutes during the peak food demand from the nestlings (6-9 days old), I regarded it as the ***long duration*** visit, regardless of the visit type (synchrony or asynchrony). I assumed that the function of the ***long duration*** of staying in the nest was not brooding because its frequency was not significantly higher for the younger than the older broods (age ranged from 6 and 9 days old) and because it occurred regardless of the season, even the warmer end of July (Table 4.1). However, long duration cannot completely rule out the extra effects of brooding heat as the parent sit on the chicks.

Waiting for the partner – For all long duration visits, I used this binary variable (waiting for the partner *observed* vs *not observed*) that codes for whether a bird waited for the partner in the nest or not during the long duration of staying in the nest. It is likely to occur when a later arriving parent loses its partner's contact call near the nest and subsequently stays in the nest for an excessively *long duration***.** If this *long duration* of staying in the in the nest continued until the subsequent visit to the nest by the partner, then I considered it "*waiting for a partner observed*". If the *long duration* of staying in the nest was terminated before the partner arrived, then it was classified as *waiting for the partner not observed*. s

4.2.2.4 Variables extracted from prey-load data

The restricted dataset with information on the diet comprised 41 nests from two breeding seasons (2008, 2009). At each parental visit, I classified prey items in a prey load brought to the nest in a bird's beak into three types, "caterpillar", "spiders", and "other arthropods". Parrotbills never fed plant food (e.g. seeds) to their chicks during the nestling period. Some visits were excluded from the analysis when the type of food and prey number could not be seen from the video. I extracted the detailed data from a digital recorder (JVC GZ-MG7OKR and Sony Handycam SR62) that can operate in slow-motion and frame-by-frame playback. The vinous-throated parrotbill is a multi-loader that is able to carry multiple prey items in a beak. I recorded the type and the number of food items delivered at each visit. I report the diet composition elsewhere (Jang et al in preparation). Here I extracted several variables crucial for the testing of the hypotheses.

Number of prey items per visit – number of prey items brought by a bird in each visit (i.e. number of prey items in a prey load).

Prey load size - a sum of volume indices for all prey items brought during the visit (mm^3/visit). The prey volume of each prey item was determined following Blondel et al. 1991 (See also details in Chapter2) (Blondel et al., 1991). Recent studies have shown that on-screen measurements can yield relatively accurate prey volumes of the actual prey (Sinkovics et al., 2018). The length and width of prey items were measured by comparing it to the observable part of bill, tarsus, or colour-band using a calliper on the screen. The ***prey volume index*** (mm^3) was calculated for each prey item using the estimated prey length (L; mm) and width (w; mm) according to the following formulas h (Blondel et al., 1991)(Bańbura et al., 1994).:

- *prey volume index* = $(\pi /4) \times L \times w^2$

(For Lepidoptera and for arthropods with cylindrical shape);

- *prey volume index* = $(\pi /6) \times L \times w^2$ for spiders,

The ***prey load size*** was a sum of prey volume indices of all prey items in a load.

Mean prey size index – calculated for each visit as an average ***prey volume index*** (mm^3/prey) from all prey items in a prey load (brought at one visit).

Foraging "efficiency" index - calculated for each visit of a parent by dividing the ***prey load size*** by the preceding ***inter-visit interval*** (mm^3/second). If I assume that inter-visit interval approximates the time spent foraging (see arguments above in the definition of ***Inter-visit interval***) between the subsequent visits then the foraging efficiency index can be used as a proxy for foraging efficiency.

4.2.3. Statistical analyses

I used the GLMM with distribution error specified in each analysis according to the type of the response variable. Pair ID was used as random factor. The global (initial) models varied from analysis to analysis and are specified in captions to the tables containing statistical results. Sample sizes in each model represent in captions of each table. Model selection was performed using the *dredge* function in the package *MuMIn* (Barton & Barton, 2020). This function constructs a series of candidate models form all possible combinations of predictors present in the global model. I selected the top ranked models (AICc $< \Delta 4$following the approach by (Burnham KP, 2002). The continuous variables were scaled and mean-centred (mean 0 and standard deviation 1) and unordered (e.g. sex, year, nest visit type) and ordered factors (e.g. predation intensity as a category) were standardized in all models using the *standardize* function (Eager, 2017) in *MuMIn* package. To check multi-collinearity among predictor variables, *VIF* (variance inflation factors) was calculated for each predictor in the global model using *performance* package (Lüdecke et al., 2021). VIF was <2.5 in all global models, indicating moderate level of collinearity among predictors (Freckleton, 2011). Effects were regarded as statistically significant when the 95% confidence intervals for a parameter estimate did not cross the zero (Burnham and Anderson, 2002).

4.3. RESULTS

4.3.1. Long duration visits and waiting for the partner

During the nest visits, the parents stayed at the nest for a median of 22 s (n=1911 from 88 nests; range: 2-2967, lower quartile: 16 s, upper quartile: 36 s). I observed 191 *long duration visits*, which included both the synchronous and asynchronous visits but less frequent in synchronous (5.4% of 1294 synchronous visits) than in asynchronous provisioning (25% of 617 asynchronous visits) (Figure 4-1A). 124 of the long duration visits were performed by females, and 67 by males (Figure 4-1(B)). Out of the 182 long duration visits of known duration (9 were excluded because the video recording ended during the long duration of one parent), 133 (73%) comprised a parent staying at the nest until the other partner come to feed (and then they left the nest together; Figure 4-2A). In 49 *long duration* visits, the parent left the nest alone prior to the arrival of the other partner. However, it cannot be ruled out the possibility that the parent might leave the nest upon hearing the call of the partner who waits for the mate.

The probability of the *long duration* visit was higher (in statistical sense) in the synchronous than the asynchronous visits, and in females than in males (Table 4-1). It was not affected by brood age, hatching date, or the preceding inter-visit interval (Table 4-1). The probability of "waiting for a partner" during the long duration visit was not affected by visit type, sex, nesting density, brood age, or brood size (Table 4-2).

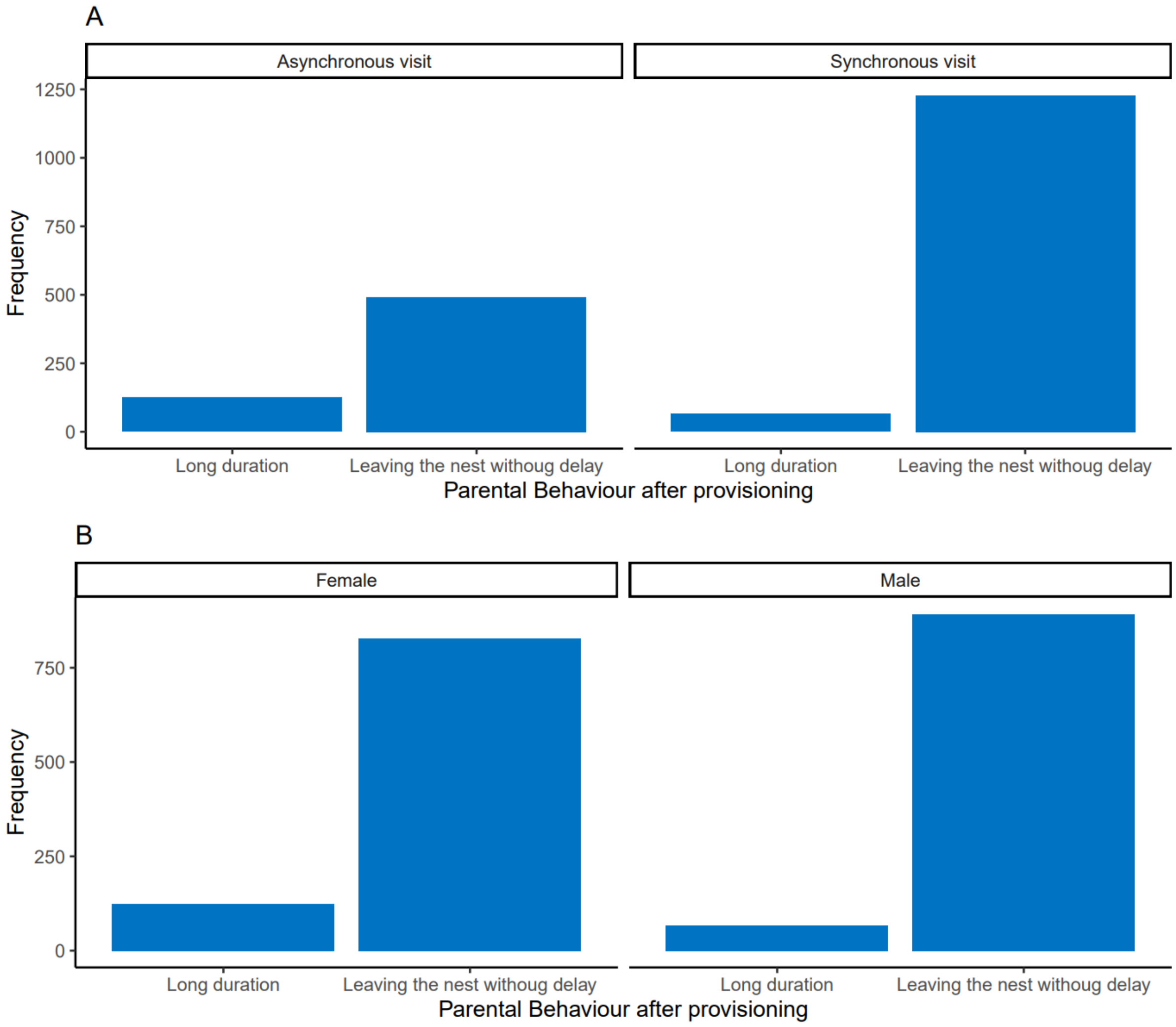

Figure 4-1. The effect of the type of visit (A) and sex (B) on the frequency of occurrence of *long duration* staying in the nest after a provisioning visit. The *Long duration* was defined as the case where the provisioning parent stayed in the nest for more than 2 minutes. Statistical results are in Table 4-1.

Table 4-1 Summary of GLMMs analysis of the factors affecting the **probability of the *long duration visit***. The *long duration* as a responsible variable was considered as excessively long staying (>2min) at nest after provisioning. Sample sizes were 1735 observations from 88 broods (First visits in each brood that cannot calculate inter-visit intervals were excluded). The top 17 models of ΔAICc < 4 were in model averaging (see Table 4-S1 for the list of models). Shown are model-averaged parameter estimates and 95% confidence intervals for each fixed effect. Confidence intervals that do not overlap zero are indicated in bold. Initial model: *cbind (long duration present (1), absent (0)) ~ Sex + Brood age + Brood size + Nest visit type + preceding inter-visit intervals+ Sex*Nest visit type + Sex*inter-visit intervals*, random factor = *pair identity*, family=binomial

	Estimate	Adjusted SE	z value	Pr(>|z|)	2.50%	97.50%
(Intercept)	-2.52	0.15	17.14	<2e-16	-2.81	-2.23
Brood age	-0.24	0.17	1.41	0.16	-0.58	0.09
Brood size	-0.11	0.14	0.83	0.41	-0.39	0.16
Sex (female)[a]	0.48	0.10	5.04	0.00	**0.30**	**0.67**
Hatching date	-0.05	0.11	0.48	0.63	-0.28	0.17
Visit type (asynchrony)[b]	0.76	0.10	7.88	<2e-16	**0.57**	**0.95**
Local density of provisioned nest	0.10	0.13	0.72	0.47	-0.16	0.35
Inter-visit interval*	-0.01	0.05	0.19	0.85	-0.11	0.09

[a] male is reference category, [b]synchronous visit is reference category.
*Preceding inter-visit interval in each visit.

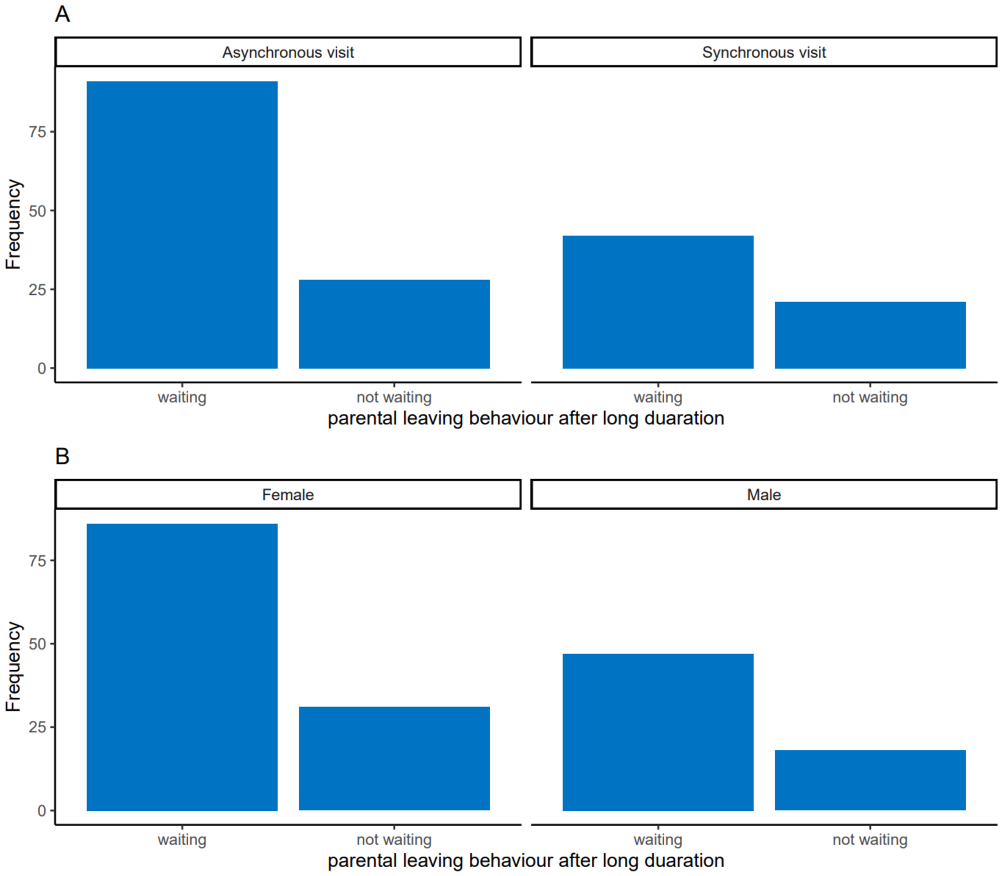

Figure 4-2. The effect of the type of visit (A) and sex (B) on the frequency of occurrence of *waiting for the partner* during *long duration* visits in the nest. Statistical results are in Table 4-2.

Table 4-2. Summary of GLMMs analysis of the factors affecting **the probability of the "*waiting for a partner*"** during a *long duration* visit (n=182 observations from 65 broods). The top 16 models of ΔAICc < 4 were used in model averaging (see Table 4-S2 for the list of top models). Shown are model-averaged parameter estimates and 95% confidence intervals for each fixed effect. Confidence intervals that do not overlap zero are indicated in bold. Initial model: *Sequence (waiting present (1) or absent (0) ~ Sex + Brood age + Brood size + Nest visit type + Local density of provisioned nest (LDP) + Sex*Nest visit type*, random factor = *pair identity*, family=binomial.

	Estimate	Std. Error	Adjusted SE	z value	Pr(>|z|)	2.5%	97.5%
(Intercept)	1.02	0.20	0.20	5.18	0.00	0.63	1.40
Visit type (asynchronous)[a]	0.11	0.16	0.16	0.70	0.48	-0.20	0.41
Local density of provisioned nest	-0.07	0.13	0.13	0.53	0.60	-0.32	0.18
Brood age	-0.01	0.08	0.08	0.13	0.90	-0.17	0.15
Sex (female)[b]	0.01	0.08	0.08	0.15	0.88	-0.14	0.17
Brood size	0.00	0.08	0.08	0.06	0.96	-0.15	0.15
Sex (female):visit type asynchronous)	0.01	0.03	0.03	0.17	0.87	-0.06	0.07

[a] Male is reference category, **[b]**synchronous visit is reference category.

4.3.2. Arriving sequence during synchronous visits

Overall, males arrived first more often than females during synchronous visits, and this was especially evident in pairs with a relatively low proportion of synchronous visits, indicating the presence of the significant interaction between sex and the proportion of synchronous visits (Table 4-3, Figure 4.3). The probability of arriving first within a pair was not associated with brood age, brood size and nesting density (Table 4-3).

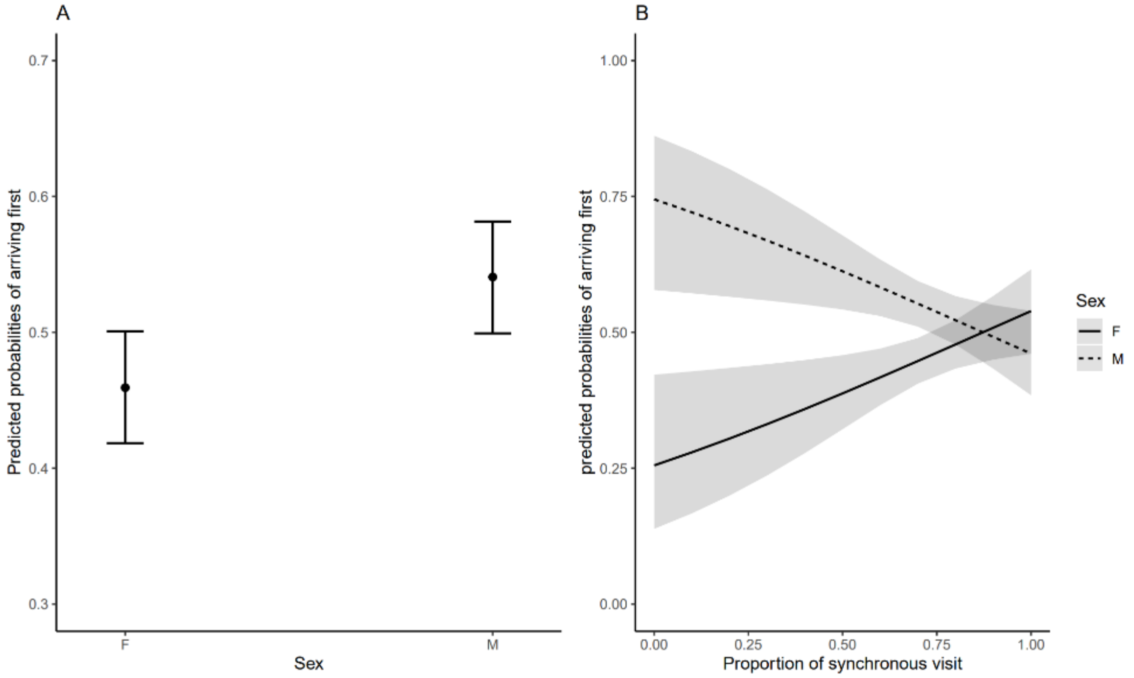

Figure 4-3. The effect of sex (A) and synchrony (proportion of synchronous visits; B) on the probability of arriving at the nest first (**probability of being the"*first-comer*").** Figures were produced from the prediction of Table 4-3 using the '*ggeffect*' function in R package *ggeffects*. Error bar (A) and shaded area in (B) represent 95% confidence intervals around the estimated marginal means and the marginal effect regression line. Statistical results are in Table 4-3.

Table 4-3. Summary of GLMMs analysis of the factors affecting the **probability of being the *first comer*** during a synchronous visit. The 5 top models of ΔAICc < 4 were in model averaging (Supplementary Table 4-S3 lists the top models produced by the *dredge* function). Shown are model-averaged parameter estimates and 95% confidence intervals for each fixed effect. Confidence intervals that do not overlap zero are indicated in bold.

Initial model: *Sequence(first(1), later(0) ~ Sex + Brood age + Brood size + Proportion of synchronous nest visit + Local density of provisioned nest (LDP) + Sex*(LDP*PS),* random factor = *pair identity*, family=binomial

Graphical representation of results is presented in Fig.4.3

	Estimate	Adjusted SE	z value	Pr(>|z|)	2.5%	97.5%
(Intercept)	0.00	0.06	0.00	1.00	-0.11	0.11
Sex (female)[a]	-0.21	0.06	3.74	0.00	**-0.32**	**-0.10**
Proportion of synchronous visit (PS)	0.00	0.06	0.00	1.00	-0.11	0.11
Sex (female):PS	0.17	0.06	2.95	0.00	**0.06**	**0.29**
Local density of provisioned nest (LDP)	0.00	0.04	0.00	1.00	-0.07	0.07
Sex (female):LDP	-0.02	0.05	0.43	0.66	-0.11	0.07
Brood age	0.00	0.02	0.00	1.00	-0.05	0.05
Brood size	0.00	0.02	0.00	1.00	-0.05	0.05

[a] male is reference category

4.3.3. Frequency of arriving at the nest first during synchronous visits by male and female parents.

For the data set of synchronous visits, I conducted separate analyses for each sex. In pairs where the male show higher provisioning rate than the female, the male was more likely to arrive at the nest before the female (Table 4.4, Figure 404A, B). On the other hand, the probability of the female arriving first at the nest increased in pairs with high female provisioning rate and low male provisioning rate (Fig. 4-4). Brood age, brood size, parental age class, nesting density and proportion of synchronous nest visits were not related to the probability of which sex came first. (Table 4-4).

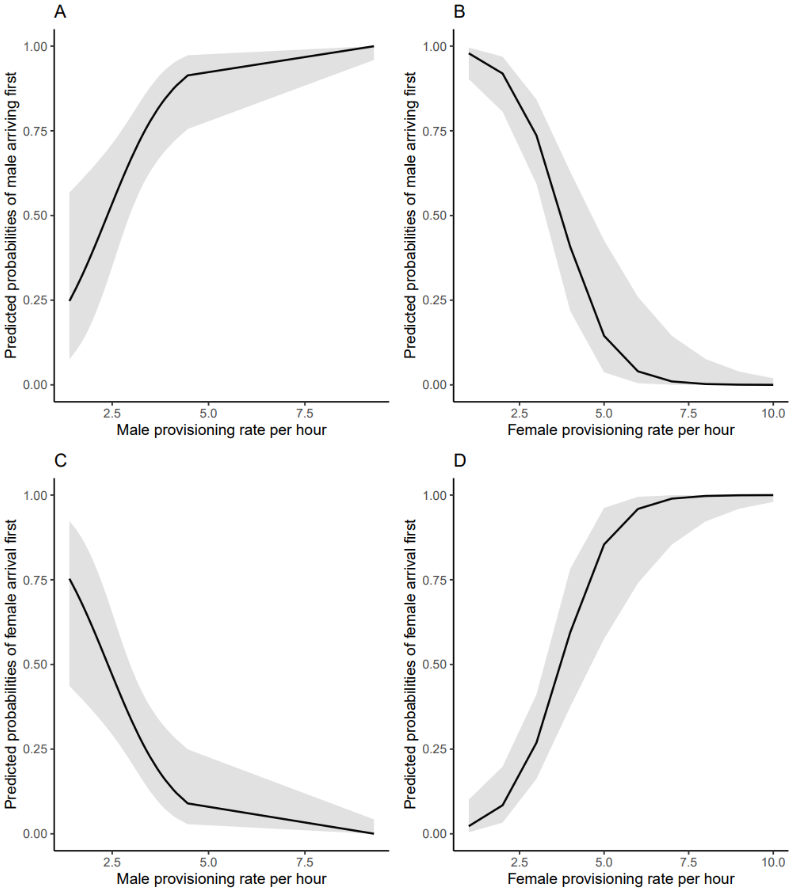

Figure 4-4. Effect plot showing possibility of male arriving first during the synchronous visit regarding to male provisioning rate per hour (A) and female provisioning rate per hour (B). Effect plot showing possibility of female arriving first during the synchronous visit regarding to male provisioning rate per hour (C) and female provisioning rate per hour (D). Figures were produced from the predictions of the statistical model presented in Table 4-4 using the '*ggeffect*' function in R package *ggeffects*. Shaded areas represent 95% confidence intervals around the estimated marginal effect regression line.

Table 4-4. Summary of GLMMs analysis of the factors affecting the probability that a male arrives at the nest first, i.e. before his partner (A), and factors affecting the probability that a female arrives et the nest first, i.e. before her partner (B) during the synchronous visit. Global model in (A): Sequence (male arriving first(1), later(0) ~ Brood age + Brood size + Proportion of synchronous nest visit + Female provisioning rate + Male provisioning rate + Local density of provisioned nest + Parental age class (PAC) + PAC*(PS+LDP), random factor = pair identity, family=binomial. Global model in (b): Sequence (female arriving first (1), later (0) ~ Brood age + Brood size + Proportion of synchronous nest visit + Female provisioning rate + Male provisioning rate + Local density of provisioned nest + Parental age class (PAC) + PAC*(PS+LDP), random factor = pair identity, family=binomial. *The 15 top models of ΔAICc < 4 (both A and B model) were in model averaging. Shown are model-averaged parameter estimates and 95% confidence intervals for each fixed effect. Confidence intervals that do not overlap zero are indicated in bold. Results are shown in Figure 4.4.

	Estimate	Adjusted SE	z value	Pr(>|z|)	2.5%	97.5%
Responsible variable : the probabilities of male arriving first (A)*						
(Intercept)	0.36	0.22	1.64	0.10	-0.07	0.80
Brood age	0.44	0.28	1.56	0.12	-0.11	1.00
Female provisioning rate (per hour)	-1.66	0.41	4.02	0.00	**-2.47**	**-0.85**
Male provisioning rate (per hour)	1.21	0.39	3.09	0.00	**0.44**	**1.98**
The proportion of synchronous visit (PS)	-0.31	0.24	1.27	0.20	-0.78	0.17
Parental age class (PAC)	0.12	0.20	0.58	0.56	-0.28	0.51
Local density of provisioned nest	0.03	0.12	0.21	0.83	-0.21	0.26
Brood size	-0.01	0.09	0.12	0.91	-0.19	0.17
PAC:PS	-0.01	0.06	0.16	0.88	-0.13	0.11
Responsible variable : the probabilities of female arriving first (B)*						
(Intercept)	-0.36	0.22	1.64	0.10	-0.80	0.07
Brood age	-0.44	0.28	1.56	0.12	-1.00	0.11
Female provisioning rate (per hour)[a]	1.66	0.41	4.02	0.00	**0.85**	**2.47**
Male provisioning rate (per hour)[a]	-1.21	0.39	3.09	0.00	**-1.98**	**-0.44**
The proportion of synchronous visit (PS)	0.31	0.24	1.27	0.20	-0.17	0.78
Parental age class (PAC)[b]	-0.12	0.20	0.58	0.56	-0.51	0.28
Local density of provisioned nest (LDP)	-0.03	0.12	0.21	0.83	-0.26	0.21
Brood size	0.01	0.09	0.12	0.91	-0.17	0.19
PAC:PS	0.01	0.06	0.16	0.88	-0.11	0.13

[a] Female (or Male) provisioning rate was calculated as the number of times prey was brought to the nest per hour by female (or Male). [b] Parental age class was treated as ordered factor (1: old-old, 2: old-young, 3: young-young)

4.3.4. Prey load size and foraging efficiency of the *first comer* and the *late comer* during a synchronous visit.

Prey load size during the synchronous visit was associated with sex and arrival sequence, but was not associated with year, nesting density, brood size and brood age, and hatching date (Table 4-4). Males feed on chicks larger prey than female during the synchronous nest visits. Furthermore, the *first comer* delivered larger prey to their brood than the *late comer* (Table 4.4, Figure 4.5A). Moreover, the foraging efficiency of the *first comer* was significantly higher than that of the *late comer* (Table 4-5, Figure 4.5B).

Table 4.5. Summary of model averaging for predictors affecting the ***prey load size during the synchronous provisioning***. Sample sizes were 498 observations from 41 brood. Global model in (A): ***prey load size*** ~ Year + Brood age + Brood size + Hatching date + arrival sequence(AS) + Local density of provisioned nest(LDP) + sex +AS*(Sex + LDP), random factor = pair identity, family=Gaussian. The 17 top models of ΔAICc < 4 (both A and B model) were in model averaging (see Table 4-S4 of model selection. Shown are model-averaged parameter estimates and 95% confidence intervals for each fixed effect. Confidence intervals that do not overlap zero are indicated in bold. Graphic presentation was shown in Figure 4.6A

	Estimate	Adjusted SE	z value	Pr(>|z|)	2.5%	97.5%
(Intercept)	18.20	0.44	41.21	< 2e-16	17.34	19.07
Sex	0.85	0.20	4.31	0.00	**0.47**	**1.24**
Arriving sequence	0.74	0.20	3.75	0.00	**0.35**	**1.13**
Year 2008	0.79	0.51	1.55	0.12	-0.21	1.79
Brood age	-0.10	0.28	0.35	0.72	-0.66	0.46
Local density of provisioned nest (LDP)	0.07	0.25	0.29	0.77	-0.42	0.56
Hatching date	-0.03	0.19	0.18	0.86	-0.41	0.34
Brood size	0.03	0.18	0.15	0.88	-0.33	0.38
Sex: Arriving sequence (first)	-0.01	0.08	0.14	0.89	-0.17	0.15
Arriving sequence (first): LDP	-0.01	0.06	0.15	0.88	-0.13	0.11

[a] late arrival is the reference category, [b] 2009 is the reference category

Table 4.6. Summary of model averaging analysis of the independent variable ***foraging efficiency index*** *for the synchronous provisioning*. Sample sizes were 498 observations from 41 brood. Graphic presentation was shown in Figure 4.6B. The ***foraging efficiency*** index was calculated by dividing the ***prey load size*** by the preceding ***inter-visit interval*** (mm^3/second). *The 11 top models of ΔAICc < 6 (both A and B model) were in model averaging (see Table 4-S5 of model selection). Shown are model-averaged parameter estimates and 95% confidence intervals for each fixed effect. Confidence intervals that do not overlap zero are indicated in bold. Global model: foraging efficiency ~ Year + Brood age + Brood size + Hatching date + arrival sequence(AS) + Local density of provisioned nest(LDP) + sex +AS*(Sex + brood size + brood age + Hatching date) + Year (LDP + sex + brood size + brood age + sequence + hatching date), random factor = pair identity, family=Gaussian

	Estimate	Adjusted SE	z value	Pr(>|z|)	2.5%	97.5%
(Intercept)	-0.04	0.06	0.61	0.54	-0.15	0.08
Arriving sequence (first)[a]	0.13	0.04	3.00	0.00	**0.05**	**0.22**
Sex	0.03	0.05	0.63	0.53	-0.06	0.12
Sex: Arriving sequence (first)	-0.02	0.05	0.44	0.66	-0.12	0.08
Local density of provisioned nest	0.00	0.02	0.21	0.83	-0.05	0.04
Parental age	0.00	0.01	0.12	0.91	-0.02	0.03
Year (2008)[b]	0.00	0.01	0.09	0.93	-0.03	0.02
Hatching date	0.00	0.01	0.09	0.93	-0.03	0.02
Brood age	0.00	0.01	0.05	0.96	-0.02	0.02
Brood size	0.00	0.01	0.03	0.98	-0.02	0.02

[a] late arrival is the reference category, [b] 2009 is the reference category

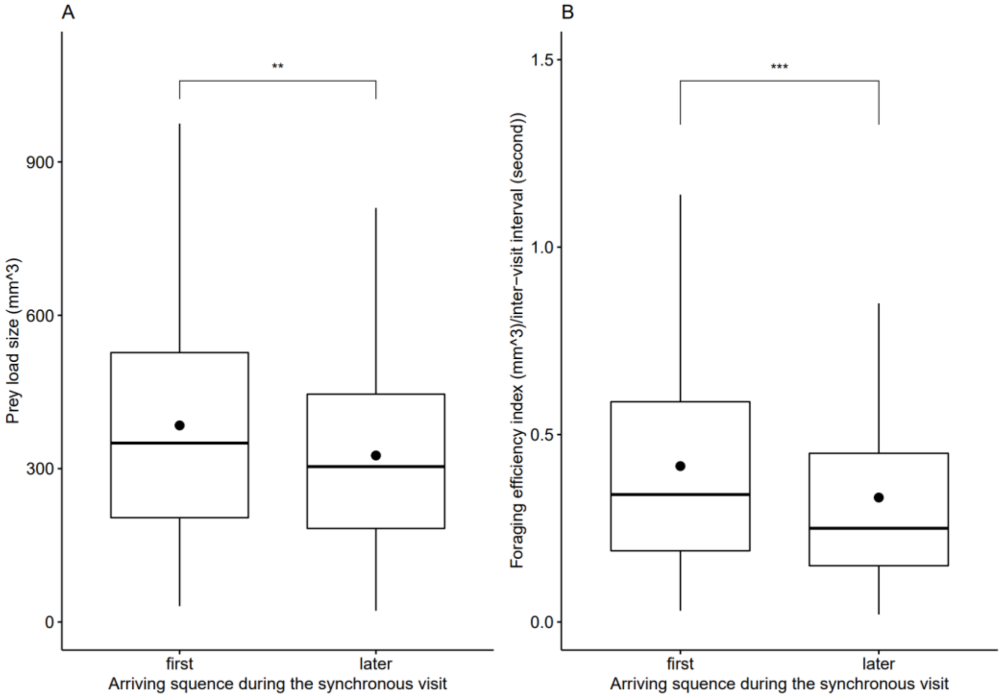

Figure 4.5. Comparison of prey load size (A) and foraging efficiency (B) between the first-comer and late-comer during the synchronous visits. Boxes show the interquartile range, the thick line is the median, and the error bars (vertical lines) refer to the 1.5 interquartile. The extra data points in boxplot represent mean in each variable. Statistical analyses are in Table 4.5(A) and Table 4.6(B)

4.4. DISCUSSION

4.4.1. Nest visits of long duration may play a function of waiting for the partner's arrival

In this chapter, I focused on detailed analyses of synchronous visits with the aim to provide insights into the behavioural mechanisms involved in maintaining synchrony between the pair members, and mechanisms of how social interactions with local breeders may affect the coordination between pair members. The results are consistent with the idea that the partners may actively promote synchrony by waiting for each other at the nest in order to initiate a foraging trip together, and that they follow each other during foraging and returning together. Below I discuss each of these aspects separately.

When parents visited their nest alone, they usually left the nest immediately after feeding. This was especially the case in the synchronous visits where 10% (134 of 1294) synchronous visits ended up in long stay in the nest. However, at the asynchronous visits, about 25% of times the birds stayed in the nest for an extended duration of time (*long duration* visits) after feeding the nestlings. Brooding of nestlings is not a likely explanation of the results because the frequency of this behaviour did not differ between brood age (6-9 days old) and hatching date (between early May to late July) (Table 4.1). It also appeared in nests with nestlings as young as 9 days old, which is near fledging time (normally, the young fledge when they are 10-12 days old). These results are consistent with the idea that the arrival at the nest together promotes departing the nest together after a short nest visit duration. The long duration in both synchrony and asynchrony visits lasted until the next partner arrived, and the waiting individual left the nest together with the partner. I hypothesize that the long duration presence in the nest may be related to waiting for a partner in order to initiate the synchronous foraging trip by leaving together with the partner after the partner completed brood provisioning.

If the primary purpose of waiting in the nest is to reunite with a partner, then it is one of crucial mechanisms responsible for sustaining foraging synchrony. To find the partner visually in the dense habitat where foraging occurs may be more challenging and riskier (predation risk due to higher chances to be visually detected on the move than sitting motionless in the nest) than just waiting at the nest. However, staying on the nest for extended periods can significantly reduce the feeding rate during the peak chick's demand. In such a case not waiting at the nest maybe a better option

The parrotbill, similarly to the group-living zebra finch (Loning, Griffith & Naguib, 2022), has a well-developed, unique long-distance call when separated from a group or pair. I propose that depending on the individual's energy status/hunger or perceived predation risk, the parrotbill parents may decide to find a partner in the foraging habitat by using vocal communication or in the nest by waiting for the partner.

4.4.2. Arriving sequence analysis suggests leader-follower roles within a pair

Different behaviours of parents during the synchronous visit may be related to their status or personality (Savage & Hinde, 2019), although this has never been proven empirically. Theoretical model (Rands et al., 2003) suggested that differences between individuals within a foraging pair (e.g. in the level of hunger or in motivation to forage) may lead to spontaneous emergence of a leader and a follower. I suspect that the arrival sequence during the synchronous visit and the difference in the food load size between the *first comer* and the *late comer* may be related to the leader-follower roles within a pair. As the *first comer* carried larger prey load than that of the *late comer* during the synchronous visits to the nest, I suggest that the *first comer's* decision to return from the foraging habitat to the nest to provision the nestlings may have been triggered by the large food load either because the beak was completely full (no option to grasp more items in the beak) or because it reached the size that maximizes the efficiency of central place foraging for the purpose of provisioning the brood most efficiently. However, at the time when one bird (pair-mate) already reached that moment of time of returning to the nest, the second bird (pair-mate) has not yet reached comparable food load size and in order to maintain synchrony the second pair-mate followed the leader by returning to the nest together. This hypothetical mechanism is consistent with small food loads, and with lower efficiency of provisioning by the *late comer*. The results are consistent with this explanation, assuming that the *first comer* status indeed indicated the bird who first decided to return to the nest. Such a temporary leader-follower relationship within a pair may be occurring near the end of foraging trip and/or during the return to the nest for provisioning.

Our direct qualitative evidence from field observations also indicated that an individual initiates departure from foraging habitat and moves /flies towards the nest to feed nestlings by making a unique contact call. This call may lead to emergence of transient leaders and followers en route to the nest through dense thickets and bushes. This hypothetical process leading to temporary leader-follower roles can be affected by interactions with locally present breeders and non-breeders. Our results indicated that young and old birds are differently affected by these hypothetical social interactions at higher nesting densities.

4.4.3. Conclusions

In conclusion, the results suggested that parrotbill parents achieve a high level of coordination through nest visit synchrony, and that parents are likely engaged in several mechanisms that can maintain coordination: waiting for the other partner in the nest (possibly in the foraging patch) and following the partner who decided to return to the nest for provisioning. Determining details of foraging, communication during foraging, and travel duration to the nest is a logical next step to fully understand the processes of within-pair coordination in the parrotbill, more detailed studies, including experimental approach, are needed.

Chapter 5. General discussion

The results provided a deeper understanding of pair coordination and behavioural synchronization during brood provisioning in a group-living bird (Fig. 5.1). I found that the vinous-throated parrotbill parents exhibited high levels of pair coordination during the chick-rearing period and the results suggested that this coordination is maintained because the pair-mates actively react to each other's behaviour. Synchronous nest visits are known mainly in granivorous species, which visit the nest infrequently (albeit more than once per hour) during the nestling period (Mariette & Griffith, 2015; van Rooij & Griffith, 2013). However, synchronous nest visits are little reported in insectivorous species with frequent nest visits. Instead, studies showed that parents achieve pair coordination by alternating nest visits in insectivores species with frequent provisioning visits (Bebbington & Hatchwell, 2016(Baldan & Griggio, 2019). It has been hypothesized that alternating nest visits and simultaneous visits reduce conflict between parents by distributing their work equally (Johnstone et al., 2014); (Johnstone & Savage, 2019). Parents may benefit from group living during synchronous nest visits, such as reducing predation risk or increased foraging efficiency. However, they may also incur high costs for synchrony and coordination, such as loss of time required for coordination, which is presumably why this behaviour has not been developed in many species. For example, males and females might differ in hunting time, prey types, and prey size during foraging trips for provisioning (Wiebe & Slagsvold, 2009). Asymmetry of status between the parents can lead to failure at the departure timing. Therefore, in order to keep coordinating their foraging trip or nest visiting, parents might continue the coordinated trip by waiting for the partner for the optimal time even though one parent is ready.

My study on the parrotbill contributed detailed insights into these processes of provisioning synchronization and coordination, starting from a general overall view in Chapter 2 and proceeding to detailed analyses in Chapter 3 and 4 that brought new level of understanding of the effect of social environment on provisioning, and allowed to formulate evidence-based hypotheses concerning within pair and within group social effect on provisioning rate, synchronization and coordination in birds in general.

I have focused on the hypothesis of coordination in parental efforts in the monogamous species, which is highly social, and maintains a pair-bond throughout life. This coordination may have an adaptive value, such as directly increasing the survival chance of parents (hypothetical explanation that cannot be excluded but the evidence did not allow to test it properly; Fig. 5.1) or increasing foraging efficiency (documented and summarized in Fig. 5.1). In chapter 2, I reviewed several hypotheses and predictions about why pair synchronous or asynchronous visits, a form of pair coordination, occur during nestling feeding. Contrary to expectations, no correlation was found between nestling survival and synchronous visits. Overall, nestlings that reached chick-rearing phase (despite high depredation during incubation) had a high probability of survival. One possible explanation for synchrony is related to the increase of survival of the parents themselves, although I cannot address it here (indicated by grey broken lines in Fig. 5.1). I presented evidence with indicating that pair coordination is likely to be flexible depending on social environment (e.g. nest density; Fig. 5.1) rather than ecological factor such as local predation intensity or nestling food demand (e.g. brood age, brood size). I showed that parents respond to change in nesting density between consecutive breeding attempts by decreasing synchrony in response to increasing density.

It is commonly believed that in highly social birds, high nesting density has the potential to increase the possibility of cooperation through information transmission of resources or increased predation vigilance, joint group mobbing (Ge, Beauchamp & Li, 2011). However, my study shows that social disturbance (e.g. increased social interactions) somewhat limits pair coordination. The parrotbill society may be considered more competitive for limited resources (especially nest site availability) during the breeding season than previously thought. My study in chapter 2 evaluated that another possibility of synchronous visits resulting from synchronous foraging was investigated whether foraging with parents as a pair rather than alone results in higher efficiency. At the population level, the foraging efficiency was, on average, not higher for synchronous than asynchronous visits. The pairs increased the degree of synchrony in situations when foraging efficiency associated with synchronous visits was higher than for asynchronous visits, but only in pairs at low local nest densities. The results of chapter 2 show that parental coordination in group-living species is an outcome of within-pair mechanisms modified by social interactions with the group members (summary in Fig. 5.1).

Theoretical and empirical evidence suggests that cooperation and coordination between pair members are crucial in their reproductive success in species where pair bonds are consistently maintained across the year (Burdick & Siefferman, 2020). The importance of cooperation between such pairs has been mainly studied in long-lived birds where pair bonds persist for an extended period (Sánchez-Macouzet, Rodríguez & Drummond, 2014). However, in short-lived species, pair-bonds are brittle, and divorce is common after their reproductive failure within a season and between years (Jeschke & Kokko, 2008). However, in short-lived species that form pair-bonds throughout life, such as parrotbills and zebra finch, cooperation and coordination can be as crucial to their reproductive success as in long-lived species. Cooperation and coordination between pairs may increase with age. Indeed, recent studies showed that pair coordination could improve with parental age and familiarity (Sánchez-Macouzet, Rodríguez & Drummond, 2014). Improvements in coordination may be related to the improved foraging ability with an individual's age or familiarity with the habitat. In species where long-term pair bonds are maintained, there may be an improvement in pair compatibility as well. As parrotbills breed in areas of various breeding densities, from solitary to colonial, the density effect is expected to frequently occur. In Chapter 2, I have already discussed that pair coordination is sensitive to the social environment. The effect of density may by modified by the parental age. Therefore, in a situation in which I consider the social environment, it is vital to consider pair coordination or parental effort along with age. I reviewed the predictions of the hypotheses concerning the changes in coordination with parental age in chapter 3. I found that older parents showed higher pair coordination than young parents among solitary breeders (summary in Fig. 5.1). However, there was no difference in the level of pair coordination according to parental age classes at high densities (this interaction effect is not indicated in the summary Fig. 5.1. for simplicity and clarity of the figure). I found that the density of neighbours that breed simultaneously was not related to the level of pair coordination, but when the number of neighbours that reproduced non-simultaneously (non-synchronous breeding) increased, the level of pair coordination decreased rapidly (summary in Fig. 5.1). My findings show that a decrease in pair coordination level, which is mainly associated with an increase in the density of asynchronously reproducing breeding pairs, may be linked to the social interactions (disruptions of synchronous provisioning)) with the social group members (local neighbours) that are not engaged in intense parental provisioning of their broods.

In chapter 4, I discussed the mechanisms by which synchrony is maintained. My study explains synchrony visits in which parents decide their visit type result from a combination of foraging efficiency (chapter 2) and social environment (e.g. nesting density), and partners' response (chapter 4). I have already revealed in Chapter 3 that parents distribute their provisioning rates equitably at the population level. This similarity in provisioning rate seems to have arisen from parental provisioning action seeking coordination. However, it was little about how this coordination is maintained. I found that parents often had long durations in the nest after visiting alone and leaving the nest together after the next partner arrived. Even after a synchrony visit, wait for the partner to arrive if a later fed parent had a long duration in the nest. My finding suggested that waiting for a partner in the nest is likely a mechanism for maintaining synchrony. The nest seems to be the partner's predictable location and is relatively safer while separated. In addition, the parent arrived earlier at the nest during synchrony visits had a higher feeding efficiency and quantity regardless of the partner's sex. The first-comer might be the leading individuals for initiating a movement to the nest during the synchronous visit. My results show that the temporary leading and following relationships according to the status might occur trip to trip during synchrony visits, and the relationship can facilitate their ongoing coordination.

This study system differs from some previously studies for social species because I detected negative rather positive effect of social interactions on provisioning. Studies on colonially breeding species reported that the provisioning rate increased in birds that breed colonially due to information exchange among breeders (Brown, 1988). In the zebra finch, the provisioning rate also increased for colony-breeding individuals than solitarily breeding individuals (Mariette & Griffith, 2013). However, our research found no positive effect of social interaction in the colonial breeding. If the cost outweighs the benefits of living in groups during breeding season, individuals are more likely to be spatially dispersed rather than colonially breeding. I proposed that the social bond via familiarity or kinship is an essential factor in the colonial breeding of the vinous-throated parrotbill.

The overall streamline from schematics (Figure 5-1) is as followed. (1)- Parents breed at locations with various local densities of breeding pairs, and density of pairs whose breeding is not synchronized with the focal pair is crucial ; (2)- in larger local densities the interactions with group members are more frequent, and especially with birds who are not involved in intensive provisioning, i.e. whose breeding is not synchronized with the focal breeding pair; (3) -more frequent interactions create more frequent disturbance in the provisioning activities and coordination within the focal pair; (4)- pairs that are disturbed less tend to forage together, and pay attention to the foraging efficiency benefit from synchronous foraging; (5)-

Foraging synchrony lead to synchronous provisioning visit; (6)-foraging synchrony also contribute to equity of provisioning between male and female; (7)-During foraging together, parents who collected full prey load decide to return to the nest and partners follow even if their prey load is smaller; (8)-parents with larger prey feed chicks first during a visit.

Conclusions

By using observational evidence collected in the natural habitat, I provided a uniquely detailed set of analyses aimed to understand why and how parental behavioural synchronization and pair coordination occur during the chick-rearing period in a group-living species, and the general summary of the results and their interpretation (hypothetical explanations) are presented in Fig. 5.1. Parrotbill pairs often make simultaneous nest visits during the chick-rearing. Synchronous nest visits require pair coordination and a mechanism to perform it continuously. Foraging in pairs may increase adults' survival and can increase foraging efficiency. I have shown that this parental effort and coordination is sensitive to social environments such as density and composition of local group (with respect to the stage of breeding by the local group members), and to foraging efficiency. The close relationship between these members of society can likely contribute more to coordination and provisioning efforts. The close relationship between these members of society can likely contribute more to coordination and provisioning efforts. I suggested that parents have a mechanism (e.g. waiting for a partner) to reunite in the event of separation by actively reacting to the behaviour of the partner in order to maintain coordination. In addition, I proposed that they smoothly maintain the synchrony through a temporary leader-follower relationship depending on their foraging success. The results expand our knowledge and advances our understanding of the complexity of factors that affect parental provisioning in social birds in general.

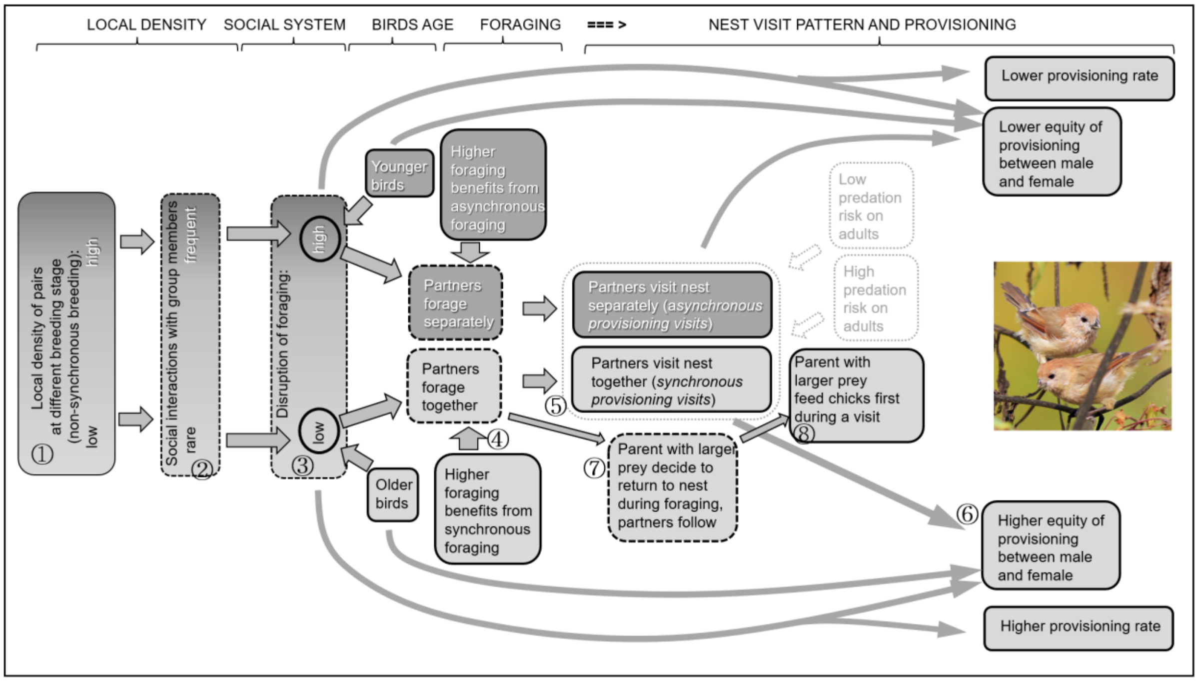

Figure 5.1: Simplified schematics of the main findings (solid lines) and the main proposed hypothetical explanations (broken lines) consistent with the findings. The gray broken lines and arrows indicate the hypothetical explanations that are not supported by the collected observational evidence, albeit they cannot be entirely excluded. See more explanations in the text. For simplicity and clarity of the schematics some of the complex effects that involve interactions are not depicted in the figure. (1)- Parents breed at locations with various local densities of breeding pairs, and density of pairs whose breeding is not synchronized with the focal pair is crucial ; (2)- in larger local densities the interactions with group members are more frequent, and especially with birds who are not involved in intensive provisioning, i.e. whose breeding is not synchronized with the focal breeding pair; (3) -more frequent interactions create more frequent disturbance in the provisioning activities and coordination within the focal pair; (4)- pairs that are disturbed less tend to forage together, and pay attention to the foraging efficiency benefit from synchronous foraging; (5)- Foraging synchrony lead to synchronous provisioning visit; (6)-foraging synchrony also contribute to equity of provisioning between male and female; (7)-During foraging together, parents who collected full prey load decide to return to the nest and partners follow even if their prey load is smaller; (8)-parents with larger prey feed chicks first during a visit. Photo by KW Im (under permission)

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Abstract in Korean

조류를 포함한 동물들에서 번식 쌍 사이에 협력적 관계는 흔히 발생한다. 특히 사회성이 강한 조류에서 번식 쌍과 그룹의 다른 구성원간의 상호작용이 부모의 협력적 관계에 영향을 미치는지에 관한 연구가 거의 시행되지 않았다. 본 논문은 참새목 조류인 붉은머리오목눈이의 번식기 동안 부모의 협력적 관계가 어떤 요인에 의해 발생하는지 조사했으며, 이에 대한 메커니즘에 관한 연구에 초점을 맞추었다. 본 종의 연구는 집단생활을 하는 동물의 연구 모델로 이용할 수 있을 것으로 기대된다. 이전 연구에서 붉은머리오목눈이는 구성원 사이에서 복잡한 사회적 관계를 지속적으로 유지하는 것으로 밝혀졌다. 부모의 새끼 양육 동안 지속적인 협력적 관계에 의해서 유지될 수 있는 번식 쌍의 동시 둥지 방문에 관한 주제를 각 장에서 토론하였다.

부모들은 새끼 양육에 필요한 먹이를 구하기 위해 암수가 함께 취식 활동을 하며 둥지에 동시에 함께 방문한다. 우리는 왜 암수의 둥지 동시방문 행동이 발생하는 지에 대해 제 2 장에서 여러 가능한 가설과 예견을 토대로 검토했다. 붉은머리오목눈이 부모 암수는 동시에 둥지를 방문하는 비율이 매우 높았으며, 이런 행동은 계절에 따라 변하는 둥지의 밀도에 따라 유동적인 것으로 나타났다. 동시 방문의 빈도는 번식(둥지) 밀도가 증가함에 따라 감소하였으며, 반대로 번식 밀도가 낮은 지역에서 동시방문 빈도는 증가하였다. 부모의 조화로운 협력 과정이 필요한 암수의 둥지 동시 방문은 둥지 인근에 위치한 다른 사회적 멤버들간의 사회적 상호작용의 증가로 인해 감소할 수 있다는 가설을 제시하였다. 또한 새끼에게 먹이 급여 효율성은 단독 혹은 낮은 밀도에서 증가 했으나 높은 밀도에서는 감소하였다.

우리는 이런 협력적 관계가 부모의 연령이나 둥지 주변의 사회구성원의 관계에 어떻게 달라지는지에 대해 제 3 장에서 토론했다. 부모들은 단독생활을 할 때 동시 방문의 빈도가 나이든 부모번식쌍에서 가장 높았으며, 1 년생 부모에서는 가장 낮게 나타났다. 그러나 밀도가 높아졌을 때 부모의 나이에 상관없이 전반적으로 낮게 나타났다. 또한 동시에 함께 번식한 이웃들이 함께 번식할 때 동시 둥지 방문 비율이 떨어지지 않았지만 비 동시에 번식한 이웃이 많았을 때는 크게 감소했다. 부모는 새롭게 유입된 번식 쌍이 많아질수록 조화로운 암수 간의 협력적 행동이 방해 받을 가능성을 높아진다는 결과를 제시하였다.

제 4 장에서는 두 부모가 지속적인 동시 둥지 방문을 위한 메커니즘에 대해 토론했다. 부모가 먹이 제공의 피크 기간 동안 둥지에서 오랜 시간 머무르는 것은 일시적으로 부모가 분리되었을 때 둥지에서 파트너를 기다리는 행동일 가능성이 있다는 가설을 제시하였다. 또한 동시 도착 동안 먼저 급여하는 개체와 나중에 급여하는 개체간의 먹이 양과 먹이효율성을 비교한 결과 먼저 먹인 개체는 암수에 상관없이 더 큰 먹이를 가져왔으며,

먹이 효율성도 높았다. 이것은 번식 쌍이나 개체의 특성에 보다 도착 순서에 의해 부모의 급이 먹이양에 차이가 나며, 더 성공적인 개체가 리더로서 일찍 도착하며 다른 파트너가 뒤따를 가능성이 높다는 것을 의미한다.

붉은머리오목눈이 부모는 육추기 동안 높은 수준의 협력적 관계를 유지했으며, 부모의 나이와 같은 개체의 특성과 번식 밀도와 같은 사회적 환경에 의해 영향을 받을 수 있다는 것을 본 연구를 통해 밝혀졌다. 또한 부모의 조화로운 협력관계는 번식 쌍의 성공적인 양육을 위한 매우 중요한 요인이라는 것을 논문에서 제시하였다.

SUPPLEMENTARY TABLES

Table 2-S1. Summary from GLMM-based model averaging for the top 25 models of ΔAICc < 4 generated in the analyses of the dependent variable ***prey load size*** (volume; ㎣) in the subset of data with diet information available (467 prey loads from 27 broods).
The global (initial) model: ***Prey load size*** ~ ***Year*** + ***Laying date*** + ***Brood age category*** + ***Brood size category*** + ***Predation intensity*** (*PI*) + ***Visit type*** (*VT*) + ***Nesting density*** (*ND*) + ***VT:ND*** + ***PI:VT*** + ***PI:ND*** + ***ND:PI***, random factor = ***Pair Identity***. The list of the top 20 models is in **Table 2-S2.**

	Estimate	Adjusted SE	Confidence interval	
			2.5%	97.5%
(Intercept)	18.565	0.565	17.458	19.671
Sex (female)[a]	**-0.759**	0.235	**-1.220**	**-0.298**
Year (2008)[b]	**1.304**	0.604	**0.120**	**2.488**
Predation intensity (PI)	0.208	0.403	-0.583	0.998
Brood age category	-0.035	0.281	-0.586	0.517
Laying date	-0.047	0.269	-0.574	0.479
Brood size category	-0.058	0.252	-0.551	0.436
Nesting density (ND)	-0.012	0.212	-0.428	0.403
Visit type (VT)	-0.012	0.085	-0.178	0.155
PI:VT	0.013	0.086	-0.157	0.182
ND:PI	-0.006	0.070	-0.143	0.132

[a]reference category (male), [b]reference category (2009)

Table 2-S2. Model selection table showing the top 20 models in the analyses of dependent variable ***prey load size*** (volume; ㎣) in the subset of data with diet information available (467 prey loads from 27 broods).

The global (initial) model: ***Prey load size*** ~ ***Year*** + ***Laying date*** + ***Brood age category*** + ***Brood size category*** + ***Predation intensity*** (*PI*) + ***Visit type*** (*VT*) + ***Nesting density*** (*ND*) + ***VT:ND*** + ***PI:VT*** + ***PI:ND*** + ***ND:PI***, random factor = ***Pair Identity***.

Model-averaged from the best fitting models ($\Delta AIC_c \leq 4$) highlighted in bold Each cell includes the value of the effect estimate or the mark "+" for categorical predictors that are included in the model. Blank cells indicated that the variable was not included in the cell.

Summary of averaging from the list of top 25 models of ΔAICc < 4 is shown in **Table 2-S1**.

Variables in the model									Statistical evaluation of the model's fit to data				
Brood age category	Brood size category	Nesting density	Laying date	Predation intensity (PI)	Sex	Visit Type(VT)	Year	PI: VT	df	logLik	AICc*	Delta	weight
					+		+		**5**	**-1431.29**	**2872.70**	**0.00**	**0.14**
				0.09	+		+		**6**	**-1430.60**	**2873.40**	**0.67**	**0.10**
-0.02					+		+		**6**	**-1431.00**	**2874.20**	**1.46**	**0.07**
			-0.03		+		+		**6**	**-1431.00**	**2874.20**	**1.46**	**0.07**
	-0.04				+		+		**6**	**-1431.00**	**2874.20**	**1.47**	**0.07**
		-0.01			+		+		**6**	**-1431.17**	**2874.50**	**1.81**	**0.06**
-0.03				**0.09**	+		+		**7**	**-1430.28**	**2874.80**	**2.08**	**0.05**
			-0.03	**0.09**	+		+		**7**	**-1430.30**	**2874.80**	**2.13**	**0.05**
	-0.04			**0.08**	+		+		**7**	**-1430.35**	**2875.00**	**2.24**	**0.05**
		-0.01		**0.09**	+		+		**7**	**-1430.49**	**2875.20**	**2.50**	**0.04**
					+	+	+		**6**	**-1431.56**	**2875.30**	**2.59**	**0.04**
-0.03	**-0.05**				+		+		**7**	**-1430.62**	**2875.50**	**2.76**	**0.04**
	-0.05		**-0.04**		+		+		**7**	**-1430.68**	**2875.60**	**2.88**	**0.03**
-0.02			**-0.03**		+		+		**7**	**-1430.68**	**2875.60**	**2.90**	**0.03**
				0.10	+	+	+	+	**8**	**-1429.71**	**2875.70**	**3.02**	**0.03**
	-0.05	**-0.02**			+		+		**7**	**-1430.85**	**2875.90**	**3.23**	**0.03**
-0.02		**-0.01**			+		+		**7**	**-1430.86**	**2876.00**	**3.25**	**0.03**
		-0.01	**-0.03**		+		+		**7**	**-1430.86**	**2876.00**	**3.26**	**0.03**
				0.09	+	+	+		**7**	**-1430.87**	**2876.00**	**3.28**	**0.03**
-0.04	**-0.05**			**0.09**	+		+		**8**	**-1429.93**	**2876.20**	**3.47**	**0.03**

* Akaike's Information Criterion corrected for small sample size (AICc).

Table 2-S3. Summary from GLMM-based model averaging for the top 4 models of ΔAICc < 4 generated in the analyses of the dependent variable ***mean prey size index*** in the subset of data with diet information available (467 prey loads from 27 broods).

Global (Initial) model: The global (initial) model: ***Mean prey size index*** ~ ***Year*** + ***Laying date*** + ***Brood age category*** + ***Brood size category*** + ***Predation intensity*** (*PI*) + ***Visit type*** (*VT*) + ***Nesting density*** (*ND*) + ***VT:ND*** + ***PI:VT*** + ***PI:ND*** + ***ND:PI***, random factor = pair identity. The list of the top 20 models is in **Table 2-S4**.

	Estimate	Adjusted SE	Confidence interval	
			2.5%	97.5%
(Intercept)	5.19	0.05	5.08	5.29
Sex	-0.07	0.03	-0.09	0.05
Year 2008[a]	0.03	0.05	-0.08	0.13

[a] reference category (2009)

Table 2-S4. The list of the top 20 models from the analyses of dependent variable: ***mean prey size index*** in the subset of data with diet information available (467 prey loads from 27 broods).

The global (initial) model: ***Mean prey size index*** ~ ***Year*** + ***Laying date*** + ***Brood age category*** + ***Brood size category*** + ***Predation intensity*** (*PI*) + ***Visit type*** (*VT*) + ***Nesting density*** (*ND*) + ***VT:ND*** + ***PI:VT*** + ***PI:ND*** + ***ND:PI***, random factor = pair identity. Model-averaged from the best fitting models ($\Delta AIC_c \leq 4$) highlighted in bold. Each cell includes the value of the effect estimate or the mark "+" for categorical predictors that are included in the model. Blank cells indicated that the variable was not included in the cell. Summary of averaging from the list of top 4 models of ΔAICc < 4 is shown in **Table 2-S3**.

Variables in the model							Statistical evaluation of the model's fit to data				
Brood age category	Brood size category	Nesting density	Laying date	Sex	Visit type	Year	df	logLik	AICc*	delta	weight
							3	**-473.305**	**952.70**	**0.00**	**0.42**
				+			**4**	**-473.129**	**954.30**	**1.68**	**0.18**
						+	**4**	**-473.278**	**954.60**	**1.98**	**0.16**
				+		**+**	**5**	**-473.2**	**956.50**	**3.87**	**0.06**
		-0.05					4	-475.174	958.40	5.77	0.02
			0.04				4	-475.215	958.50	5.85	0.02
-0.05							4	-475.216	958.50	5.86	0.02
	-0.03						4	-475.325	958.70	6.07	0.02
					+		4	-475.808	959.70	7.04	0.01
		-0.06		+			5	-474.893	959.90	7.25	0.01
			0.06			+	5	-475.038	960.20	7.55	0.01
			0.04	+			5	-475.041	960.20	7.55	0.01
-0.04				+			5	-475.09	960.30	7.65	0.01
	-0.03			+			5	-475.153	960.40	7.77	0.01
	-0.04					+	5	-475.266	960.70	8.00	0.01
0.01						+	5	-475.355	960.80	8.18	0.01
		0.004				+	5	-475.447	961.00	8.36	0.01
				+	+		5	-475.634	961.40	8.74	0.01
					+	+	5	-475.789	961.70	9.05	0.01
			0.06	+		+	6	-474.966	962.10	9.45	0.00

[*] Akaike's Information Criterion corrected for small sample size (AICc).

Table 2-S5. Summary from GLMM-based model averaging for the top 25 models of ΔAICc < 4 generated in the analyses of the dependent variable ***number of prey items per visit*** in the subset of data with diet information available (467 prey loads from 27 broods).
Global (Initial) model: Prey number ~ Year + Laying date + Brood age category + Brood size category + Predation intensity (PI) + Visit type (VT) + Nesting density (ND), random factor = pair identity. The list of the top 20 models is in **Table S6**.

			Confidence interval	
	Estimate	Adjusted SE	2.5%	97.5%
(Intercept)	0.663	0.246	0.200	1.165
Laying date	-0.003	0.002	-0.007	0.001
Year[a]	-0.090	0.093	-0.272	0.092
Sex	0.059	-0.085	0.145	0.149
Visit type	0.011	0.040	-0.067	0.088
Predation intensity	0.008	0.027	-0.045	0.061
Nesting density	0.002	0.010	-0.019	0.022
Brood age category	-0.005	0.027	-0.058	0.048
Brood size category	-0.001	0.017	-0.035	0.032

[a] Reference category (2009)

Table 2-S6. The list of the top 20 models from the analyses of dependent variable: ***number of prey items per visit*** in the subset of data with diet information available (467 prey loads from 27 broods).

Global (Initial) model: Prey number ~ Year + Laying date + Brood age category + Brood size category + Predation intensity (PI) + Visit type (VT) + Nesting density (ND), random factor = pair identity. Model-averaged from the best fitting models ($\Delta AIC_c \leq 4$) highlighted in bold. Each cell includes the value of the effect estimate or the mark "+" for categorical predictors that are included in the model. Blank cells indicated that the variable was not included in the cell. Summary of averaging from the list of top 25 models of ΔAICc < 4 is shown in **Table 2-S5**.

Variables and their interactions in the model								Statistical evaluation of the model's fit to data				
Brood age category	Brood size category	Nesting density	Laying density	Predation intensity	Sexy	Visit type	Year	df	logLik	AICc[*]	delta	weight
			-0.09				+	**4**	**-631.109**	**1270.3**	**0**	**0.114**
			-0.09		**0.06**		+	**5**	**-630.352**	**1270.8**	**0.53**	**0.087**
			-0.10					**3**	**-632.552**	**1271.2**	**0.85**	**0.074**
			-0.10		**0.06**			**4**	**-631.717**	**1271.5**	**1.22**	**0.062**
							+	**3**	**-632.844**	**1271.7**	**1.44**	**0.055**
			-0.09			**0.04**	+	**5**	**-630.841**	**1271.8**	**1.51**	**0.053**
			-0.09	**0.03**			+	**5**	**-630.859**	**1271.8**	**1.54**	**0.053**
		0.03	**-0.09**				+	**5**	**-630.939**	**1272**	**1.7**	**0.048**
-0.01			**-0.09**				+	**5**	**-631.079**	**1272.3**	**1.98**	**0.042**
	-0.01		**-0.09**				+	**5**	**-631.087**	**1272.3**	**2**	**0.042**
					0.06		+	**4**	**-632.113**	**1272.3**	**2.01**	**0.042**
			-0.11	**0.04**				**4**	**-632.149**	**1272.4**	**2.08**	**0.04**
			-0.10	**0.03**	**0.06**		+	**6**	**-630.105**	**1272.4**	**2.09**	**0.04**
-0.04			**-0.10**					**4**	**-632.175**	**1272.4**	**2.13**	**0.039**
			-0.09		**0.06**	**0.03**	+	**6**	**-630.154**	**1272.5**	**2.19**	**0.038**
			-0.10			**0.04**		**4**	**-632.211**	**1272.5**	**2.2**	**0.038**
		0.03	**-0.09**		**0.06**		+	**6**	**-630.222**	**1272.6**	**2.32**	**0.036**
			-0.11	**0.04**	**0.06**			**5**	**-631.323**	**1272.8**	**2.47**	**0.033**
	-0.01		**-0.09**		**0.06**		+	**6**	**-630.33**	**1272.8**	**2.54**	**0.032**
-0.01			**-0.09**		**0.06**		+	**6**	**-630.334**	**1272.9**	**2.55**	**0.032**

[*] Akaike's Information Criterion corrected for small sample size (AICc).

Table 2-S7. Summary from GLMM-based model averaging for the top 2 models of ΔAICc < 4 generated in the analyses of the dependent variable ***maximal foraging efficiency*** in the subset of data with diet information available (94 prey loads from 27 broods).

Global (Initial) model: Maximal foraging efficiency index ~ Year + Laying date + Brood age category + Brood size category + Predation intensity (PI) + Visit type (VT) + Nesting density (ND)+ VT:DN + VT:PI + VT:LD, random factor = pair identity. The list of the top 20 models is in **Table 2-S8**.

	Estimate	Adjusted SE	Confidence interval	
			2.5%	97.5%
(Intercept)	-0.355	0.078	-0.508	-0.203
Nesting density	-0.111	0.077	-0.117	0.082

Table 2-S8. The list of the top 20 models from the analyses of dependent variable: ***maximal foraging efficiency*** in the subset of data with diet information available (94 prey loads from 27 broods).

Global (Initial) model : Maximal foraging efficiency index ~ Year + Laying date + Brood age category + Brood size category + Predation intensity (PI) + Visit type (VT) + Nesting density (ND)+ VT:DN + VT:PI + VT:LD, random factor = pair identity. Model-averaged from the best fitting models ($\Delta AIC_c \leq 4$) highlighted in bold. Each cell includes the value of the effect estimate or the mark "+" for categorical predictors that are included in the model. Blank cells indicated that the variable was not included in the cell. Summary of averaging from the list of top 2 models of ΔAICc < 4 is shown in **Table 2-S7**.

Variables in the model								Statistical evaluation of the model's fit to data				
Brood age category	Brood size category	Nesting density	Laying density	Predation intensity	Sex	Visit type	Year	df	logLik	AICc*	delta	weight
								3	**-105.91**	**218.10**	**0.00**	**0.54**
		-0.151						**4**	**-106.50**	**221.50**	**3.36**	**0.10**
						+		4	-107.08	222.60	4.52	0.06
							+	4	-107.17	222.80	4.69	0.05
	0.028							4	-107.53	223.50	5.41	0.04
				0.016				4	-107.55	223.60	5.46	0.04
					+			4	-107.56	223.60	5.47	0.04
0.005								4	-107.56	223.60	5.48	0.04
			0.002					4	-107.56	223.60	5.48	0.04
		-0.205					+	5	-107.02	224.70	6.62	0.02
		-0.153				+		5	-107.64	226.00	7.88	0.01
		-0.152		0.022				5	-108.13	226.90	8.85	0.01
0.019		-0.153						5	-108.14	227.00	8.86	0.01
	0.003	-0.151						5	-108.14	227.00	8.87	0.01
		-0.152			+			5	-108.15	227.00	8.88	0.01
		-0.152	0.009					5	-108.15	227.00	8.89	0.01
						+	+	5	-108.32	227.30	9.22	0.01
-0.038							+	5	-108.66	228.00	9.91	0.00
	0.034					+		5	-108.68	228.00	9.95	0.00
				0.021		+		5	-108.71	228.10	10.01	0.00

* Akaike's Information Criterion corrected for small sample size (AICc).

Table 2-S9. The list of the top 10 models from the analyses of dependent variable ***proportion of synchronous visits*** in the full set of data (88 broods). The global (initial) model: *cbind* (No. of synchrony visit, No. of asynchrony visit) ~ Year+ Brood size (BS) + Brood age (BA) + Nesting density (DN) + Predation intensity (PI) + Laying date (LD) + Year: (PI +DN+ BA + BS) + DN: (PI + LD), random factor = pair identity, family = binomial. Each cell includes the value of the effect estimate or the mark "+" for categorical predictors that are included in the model. Blank cells indicate that the variable was not included in the model. Summary of averaging from the list of the 10 models of ΔAICc < 4 is shown in **Table 2-2,** and the results are graphically presented in **Fig. 2-1A**.

Variables and their interactions in the model									Statistical evaluation of the model's fit to data				
Brood age (BA)	Brood size	Nesting density (ND)	Laying date (LD)	Predation intensity (PI)	Year	BA:Year	ND:LD	ND:PI	df	logLik	AICc[*]	delta	weight
		-0.07	**-0.03**						**4**	**-246.34**	**501.2**	**0**	**0.21**
0.01		**-0.07**	**-0.03**						**5**	**-245.97**	**502.7**	**1.51**	**0.10**
0.00		**-0.05**	**-0.03**		**+**	**+**			**9**	**-241.18**	**502.7**	**1.51**	**0.10**
	-0.01	**-0.08**	**-0.04**						**5**	**-246.19**	**503.1**	**1.95**	**0.08**
		-0.08	**-0.03**	**0.00**					**5**	**-246.30**	**503.3**	**2.18**	**0.07**
		-0.07	**-0.03**				**0.00**		**5**	**-246.31**	**503.4**	**2.2**	**0.07**
0.01	**-0.01**	**-0.07**	**-0.03**						**6**	**-245.74**	**504.5**	**3.36**	**0.04**
0.01		**-0.07**	**-0.03**				**0.01**		**6**	**-245.85**	**504.7**	**3.57**	**0.04**
0.01		**-0.07**	**-0.03**	**0.00**					**6**	**-245.93**	**504.9**	**3.74**	**0.03**
0.00	**-0.01**	**-0.05**	**-0.03**		**+**	**+**			**10**	**-241.02**	**504.9**	**3.74**	**0.03**
0.00		-0.05	-0.03		+	+	0.00		10	-241.15	505.2	4.01	0.03
0.00		-0.05	-0.03	0.00	+	+			10	-241.18	505.2	4.06	0.03
	-0.01	-0.07	-0.03				0.00		6	-246.13	505.3	4.15	0.03
	-0.01	-0.08	-0.04	0.00					6	-246.16	505.3	4.19	0.03
0.01		-0.05			+	+			8	-243.78	505.4	4.22	0.03
		-0.08	-0.03		+				6	-246.21	505.4	4.29	0.03
		-0.08	-0.03	-0.01				0.00	6	-246.27	505.6	4.41	0.02
		-0.07	-0.03	0.00			0.00		6	-246.28	505.6	4.45	0.02
0.02	-0.01	-0.07	-0.03				0.01		7	-245.52	506.4	5.27	0.02
0.01	-0.01	-0.07	-0.03	0.00					7	-245.70	506.8	5.65	0.01

[*] Akaike's Information Criterion corrected for small sample size (AICc).

Table 2-S10. The list of the top 22 models from the analyses of dependent variable ***nest survival*** in the full set of data (88 broods).

Initial model: Survival (1,0) ~ Year + Nesting density + Predation intensity + Laying date + Proportion of synchronous visit, random factor = pair identity, family = binomial.

Model-averaged from the best fitting models ($\Delta AIC_c \leq 4$) highlighted in bold. Each cell includes the value of the effect estimate or the mark "+" for categorical predictors that are included in the model. Blank cells indicated that the variable was not included in the cell.

Summary of averaging from the list of the 10 models of $\Delta AICc < 4$ is shown in **Table 2-3,** and the results are graphically presented in **Fig. 2-S3**.

Variables in the model					Statistical evaluation of the model's fit to data					
Nesting density (ND)	Laying date (LD)	Predation intensity (PI)	The proportion of synchronous visit	Year	df	logLik	AICc[*]	delta	weight
					2	**-26.81**	**57.8**	**0**	**0.12**
				+	**4**	**-24.71**	**57.9**	**0.15**	**0.11**
	-2.17			**+**	**5**	**-23.72**	**58.2**	**0.42**	**0.10**
			-1.47		**3**	**-26.29**	**58.9**	**1.1**	**0.07**
	-1.06				**3**	**-26.44**	**59.2**	**1.4**	**0.06**
	-2.41		**-1.59**	**+**	**6**	**-23.18**	**59.4**	**1.64**	**0.05**
			-1.25	**+**	**5**	**-24.35**	**59.4**	**1.68**	**0.05**
		-1.17		**+**	**5**	**-24.40**	**59.5**	**1.77**	**0.05**
	-2.33	**-1.39**		**+**	**6**	**-23.31**	**59.7**	**1.91**	**0.05**
0.59					**3**	**-26.71**	**59.7**	**1.95**	**0.05**
0.78				**+**	**5**	**-24.52**	**59.8**	**2.01**	**0.04**
		-0.31			**3**	**-26.78**	**59.8**	**2.09**	**0.04**
	-1.25		**-1.69**		**4**	**-25.79**	**60.1**	**2.31**	**0.04**
0.71	**-2.08**			**+**	**6**	**-23.58**	**60.2**	**2.44**	**0.04**
		-0.30	**-1.46**		**4**	**-26.26**	**61**	**3.25**	**0.02**
0.19			**-1.41**		**4**	**-26.28**	**61**	**3.28**	**0.02**
	-2.51	**-1.24**	**-1.47**	**+**	**7**	**-22.87**	**61.1**	**3.38**	**0.02**
		-1.09	**-1.17**	**+**	**6**	**-24.09**	**61.2**	**3.46**	**0.02**
0.42	**-0.98**				**4**	**-26.39**	**61.3**	**3.5**	**0.02**
	-1.03	**-0.20**			**4**	**-26.42**	**61.3**	**3.57**	**0.02**
0.47				**+**	**6**	**-24.29**	**61.6**	**3.86**	**0.02**
0.55		**-0.98**		**+**	**6**	**-24.30**	**61.6**	**3.89**	**0.02**

[*] Akaike's Information Criterion corrected for small sample size (AICc).

Table 2-S11. The list of the top 2 models from the analyses of dependent variable ***inter-visit interval*** in the full set of data (88 broods).
Initial model: Inter-visit interval ~ Visit type (VT) + Sex + Year + Brood size (BS) + Brood age (BA) + Nesting density (ND) + Predation intensity (PI) + Laying date + ND*(VT + Sex + PI + BA + BS +Year), random effect: pair identity. Model-averaged from the best fitting models ($\Delta AIC_c \leq 4$) highlighted in bold. Each cell includes the value of the effect estimate or the mark "+" for categorical predictors that are included in the model. Blank cells indicated that the variable was not included in the cell. Summary of averaging from the list of the 2 models of ΔAICc < 4 is shown in **Table 2-4,** and the results are graphically presented in **Fig. 2-2**.

Variables and their interactions in the model									Statistical evaluation of the model’s fit to data				
Brood age	Brood size	Nesting density (ND)	Sex	Predation intensity (PI)	Visit type (VT)	Year	BA:ND	DN2:VT	df	logLik	AICc[*]	delta	weight
-0.26					**+**				**5**	**-2379.91**	**4769.8**	**0**	**0.433**
-0.24		**0.10**			**+**				**6**	**-2379.44**	**4770.9**	**1.09**	**0.252**
-0.26				-0.07	+				6	-2380.98	4774	4.16	0.054
-0.26					+	+			7	-2380	4774.1	4.23	0.052
-0.25	-0.06				+				6	-2381.16	4774.4	4.53	0.045
-0.24	-0.09				+	+			8	-2379.62	4775.3	5.48	0.028
-0.23	-0.06	0.09			+				7	-2380.74	4775.6	5.71	0.025
-0.25		0.08			+		0.06		7	-2380.89	4775.9	6.01	0.021
-0.25									4	-2384.1	4776.2	6.39	0.018
-0.25		0.08		-0.04	+				7	-2381.31	4776.7	6.85	0.014
-0.26			+		+				6	-2382.5	4777.1	7.21	0.012
-0.25		0.07			+	+			8	-2380.62	4777.3	7.47	0.01
-0.25		0.09			+			+	7	-2382.01	4778.1	8.25	0.007
-0.24		0.10	+		+				7	-2382.06	4778.2	8.35	0.007
-0.25	-0.05			-0.06	+				7	-2382.46	4779	9.13	0.005
-0.23	-0.09	0.07			+	+			9	-2380.53	4779.2	9.32	0.004
-0.24		0.08							5	-2384.59	4779.2	9.36	0.004
-0.26				-0.05	+	+			8	-2381.67	4779.4	9.58	0.004
-0.24	-0.06	0.08			+		0.06		8	-2382.1	4780.3	10.45	0.002
-0.25						+			6	-2384.13	4780.3	10.46	0.002

[*] Akaike’s Information Criterion corrected for small sample size (AICc).

Table 2-S12. The list of the top 5 models from the analyses of dependent variable ***maximum inter-visit intervals*** in the full set of data (88 broods)
Global (Initial) model: **maximum inter-visit intervals** ~ Year + Sex + Brood size (BS) + Brood age (BA) + Nesting density (ND) + Visit type +Predation intensity (PI) + Laying date (LD)+ Year: type + Sex:ND + Visit type:sex + DN:PI, random factor = pair identity, family = Gaussian. Model-averaged from the best fitting models ($\Delta AIC_c \leq 4$) highlighted in bold. Each cell includes the value of the effect estimate or the mark "+" for categorical predictors that are included in the model. Blank cells indicated that the variable was not included in the cell. Summary of averaging from the list of the 5 models of ΔAICc < 4 is shown in **Table 2-5**.

Variables in the model								Statistical evaluation of the model's fit to data				
Brood age	Brood size	Nesting density	Sex	Laying date	Predation intensity	Visit type	Year	df	logLik	AICc*	delta	weight
								3	**-229.361**	**464.9**	**0**	**0.292**
				-0.16				**4**	**-228.749**	**465.7**	**0.87**	**0.188**
						+		**4**	**-229.066**	**466.4**	**1.51**	**0.137**
				-0.14		**+**		**5**	**-228.814**	**468**	**3.12**	**0.061**
		0.10						**4**	**-230.208**	**468.7**	**3.79**	**0.044**
-0.12				-0.18				5	-229.362	469.1	4.22	0.035
-0.07								4	-230.608	469.5	4.59	0.029
					0.06			4	-230.718	469.7	4.81	0.026
		0.09		-0.15				5	-229.696	469.7	4.89	0.025
	0.01							4	-230.924	470.1	5.22	0.021
-0.09						+		5	-229.995	470.3	5.49	0.019
-0.14				-0.17		+		6	-229.023	470.5	5.69	0.017
		0.09				+		5	-230.106	470.6	5.71	0.017
				-0.15	0.05			5	-230.153	470.7	5.8	0.016
			+					4	-231.214	470.7	5.8	0.016
	-0.03			-0.16				5	-230.231	470.8	5.96	0.015
					0.05	+		5	-230.489	471.3	6.47	0.011
			+	-0.16				5	-230.591	471.5	6.68	0.01
	-0.01					+		5	-230.636	471.6	6.77	0.01
							+	5	-230.742	471.8	6.98	0.009

[*] Akaike's Information Criterion corrected for small sample size (AICc).

Table 2-S13. The list of the top 3 models from the analyses of dependent variable ***foraging efficiency*** in the subset of data with diet information available (27 broods). Global (Initial) model: Foraging efficiency ~ Year + Sex + Brood size category (BS) + Brood age category (BA) + Nesting density (ND) + Predation intensity (PI) + Laying date + ND:(VT + Year + BS + BS+ PI), random factor = pair identity, family = Gaussian. Model-averaged from the best fitting models ($\Delta AIC_c \leq 4$) highlighted in bold. Each cell includes the value of the effect estimate or the mark "+" for categorical predictors that are included in the model. Blank cells indicated that the variable was not included in the cell. Summary of averaging from the list of the 3 models of ΔAICc < 4 is shown in **Table 2-6,** and the results are graphically presented in **Fig. 2-3**.

Variables in the model								Statistical evaluation of the model's fit to data				
Brood age category	Brood size category	Nesting density	Laying date	Predation intensity	Sex	Visit type	Year	df	logLik	AICc[*]	delta	weight
								3	**-657.439**	**1320.9**	**0**	**0.512**
					+			**4**	**-658.02**	**1324.1**	**3.2**	**0.103**
							+	**4**	**-658.25**	**1324.6**	**3.66**	**0.082**
		-0.05098						4	-658.938	1326	5.03	0.041
				0.04442				4	-659.002	1326.1	5.16	0.039
			-0.03833					4	-659.024	1326.1	5.2	0.038
-0.02073								4	-659.15	1326.4	5.46	0.033
						+		4	-659.154	1326.4	5.46	0.033
	-0.02517							4	-659.181	1326.4	5.52	0.032
					+		+	5	-658.88	1327.9	6.96	0.016
		-0.0522			+			5	-659.506	1329.1	8.21	0.008
				0.06657			+	5	-659.54	1329.2	8.28	0.008
				0.04489	+			5	-659.58	1329.3	8.36	0.008
					+	+		5	-659.585	1329.3	8.37	0.008
			-0.03836		+			5	-659.606	1329.3	8.41	0.008
-0.01685					+			5	-659.748	1329.6	8.7	0.007
	-0.024				+			5	-659.771	1329.7	8.74	0.006
		-0.04171					+	5	-659.849	1329.8	8.9	0.006
			-0.02877				+	5	-659.905	1329.9	9.01	0.006
						+	+	5	-659.943	1330	9.09	0.005

[*] Akaike's Information Criterion corrected for small sample size (AICc).

Table 2-S14. The list of the top 41 models from the analyses of dependent variable ***inter-visit interval*** in the subset of data with diet information available (27 broods). Global (Initial): Inter-visit interval ~ Visit type (VT) + Sex + Year + Brood size category (BS) + Brood age category (BA) + Nesting density (ND) + Predation intensity (PI) + Laying date+ PI: Year + ND:VT + ND:PI + VT:PI, random effect: pair identity.

Each cell includes the value of the effect estimate or the mark "+" for categorical predictors that are included in the model. Blank cells indicated that the variable was not included in the cell. Summary of averaging from the list of the 41 models of ΔAICc < 4 is shown in **Table 2-7,** and the results are graphically presented in **Fig. 2-4A, 2-4B, 2-4C**.

Variables and their interactions in the model												Statistical evaluation of the model's fit to data				
Brood age category	Brood size category	Nesting density (ND)	Laying date	Predation intensity (PI)	Sex	Visit type (VT)	Year	ND:PI	ND:VT	PI:VT	PI:Year	df	logLik	AICc*	delta	weight
		0.15		**-0.09**		+	+	**-0.11**			+	**9**	**-1658.44**	**3335.3**	**0**	**0.086**
	0.04	**0.15**		**-0.08**		+	+	**-0.13**			+	**10**	**-1657.92**	**3336.3**	**1.06**	**0.051**
		0.13		**-0.06**		+	+				+	**8**	**-1660.03**	**3336.4**	**1.11**	**0.049**
		0.15	**-0.02**	**-0.08**		+	+	**-0.10**			+	**10**	**-1658.13**	**3336.7**	**1.47**	**0.041**
		0.14		**-0.09**	+	+	+	**-0.11**			+	**10**	**-1658.13**	**3336.7**	**1.48**	**0.041**
0.00		**0.15**		**-0.09**		+	+	**-0.11**			+	**10**	**-1658.17**	**3336.8**	**1.56**	**0.039**
		0.15		**-0.09**		+	+	**-0.11**		+	+	**10**	**-1658.38**	**3337.2**	**1.97**	**0.032**
		0.15		**-0.09**		+	+	**-0.11**	+		+	**10**	**-1658.39**	**3337.3**	**2**	**0.032**
		0.13	**-0.04**	**-0.06**		+	+				+	**9**	**-1659.51**	**3337.4**	**2.15**	**0.029**
		0.13		**-0.09**			+	**-0.12**			+	**8**	**-1660.63**	**3337.6**	**2.3**	**0.027**
0.02	**0.05**	**0.16**		**-0.08**		+	+	**-0.13**			+	**11**	**-1657.54**	**3337.7**	**2.39**	**0.026**
		0.13		**-0.06**	+	+	+				+	**9**	**-1659.7**	**3337.8**	**2.53**	**0.024**
	0.04	**0.16**	**-0.01**	**-0.08**		+	+	**-0.12**			+	**11**	**-1657.61**	**3337.8**	**2.54**	**0.024**
	0.04	**0.15**		**-0.08**	+	+	+	**-0.13**			+	**11**	**-1657.63**	**3337.8**	**2.57**	**0.024**
0.00		**0.13**		**-0.06**		+	+				+	**9**	**-1659.75**	**3337.9**	**2.62**	**0.023**
	0.01	**0.13**		**-0.06**		+	+				+	**9**	**-1659.78**	**3338**	**2.69**	**0.022**
		0.14	**-0.02**	**-0.08**	+	+	+	**-0.10**			+	**11**	**-1657.82**	**3338.2**	**2.95**	**0.02**
0.00		**0.15**	**-0.02**	**-0.08**		+	+	**-0.11**			+	**11**	**-1657.84**	**3338.3**	**2.99**	**0.019**
	0.04	**0.16**		**-0.08**		+	+	**-0.13**		+	+	**11**	**-1657.85**	**3338.3**	**3.01**	**0.019**
		0.13		**-0.06**		+	+			+	+	**9**	**-1659.95**	**3338.3**	**3.02**	**0.019**
	0.04	**0.15**		**-0.08**		+	+	**-0.13**	+		+	**11**	**-1657.86**	**3338.3**	**3.04**	**0.019**
0.00		**0.14**		**-0.09**	+	+	+	**-0.11**			+	**11**	**-1657.87**	**3338.3**	**3.04**	**0.019**

		0.13		**-0.06**		+	+		+		+	**9**	**-1659.98**	**3338.4**	**3.09**	**0.018**
	0.04	**0.14**		**-0.08**			+	**-0.14**			+	**9**	**-1660.11**	**3338.6**	**3.35**	**0.016**
		0.15	**-0.02**	**-0.09**		+	+	**-0.10**		+	+	**11**	**-1658.06**	**3338.7**	**3.44**	**0.015**
		0.14		**-0.09**	+	+	+	**-0.11**		+	+	**11**	**-1658.07**	**3338.7**	**3.46**	**0.015**
		0.13		**-0.09**	+		+	**-0.12**			+	**9**	**-1660.17**	**3338.7**	**3.46**	**0.015**
		0.15	**-0.02**	**-0.08**		+	+	**-0.10**	+		+	**11**	**-1658.08**	**3338.7**	**3.47**	**0.015**
		0.14		**-0.09**	+	+	+	**-0.11**	+		+	**11**	**-1658.09**	**3338.8**	**3.49**	**0.015**
0.00		**0.15**		**-0.09**		+	+	**-0.11**		+	+	**11**	**-1658.11**	**3338.8**	**3.54**	**0.015**
0.00		**0.15**		**-0.09**		+	+	**-0.11**	+		+	**11**	**-1658.12**	**3338.8**	**3.55**	**0.015**
		0.13	**-0.04**	**-0.06**	+	+	+				+	**10**	**-1659.18**	**3338.8**	**3.58**	**0.014**
0.00		**0.13**	**-0.04**	**-0.06**		+	+				+	**10**	**-1659.22**	**3338.9**	**3.65**	**0.014**
		0.14	**-0.02**	**-0.08**			+	**-0.11**			+	**9**	**-1660.29**	**3339**	**3.71**	**0.013**
	0.01	**0.14**	**-0.04**	**-0.05**		+	+				+	**10**	**-1659.26**	**3339**	**3.73**	**0.013**
0.00		**0.14**		**-0.09**			+	**-0.12**			+	**9**	**-1660.34**	**3339.1**	**3.81**	**0.013**
0.02	**0.05**	**0.16**	**-0.01**	**-0.08**		+	+	**-0.13**			+	**12**	**-1657.21**	**3339.1**	**3.85**	**0.013**
		0.12		**-0.05**			+				+	**7**	**-1662.44**	**3339.1**	**3.86**	**0.012**
		0.13				+	+					**6**	**-1663.49**	**3339.2**	**3.89**	**0.012**
0.02	**0.05**	**0.15**		**-0.08**	+	+	+	**-0.13**			+	**12**	**-1657.24**	**3339.2**	**3.9**	**0.012**
		0.15		**-0.09**		+	+	**-0.11**	+	+	+	**11**	**-1658.33**	**3339.2**	**3.97**	**0.012**
0.01	0.01	0.14		-0.05		+	+				+	10	-1659.41	3339.3	4.04	0.011
0.01		0.13		-0.06	+	+	+				+	10	-1659.42	3339.3	4.06	0.011
		0.14	-0.04	-0.06		+	+			+	+	10	-1659.42	3339.3	4.06	0.011
	0.04	0.15	-0.01	-0.08	+	+	+	-0.12			+	12	-1657.32	3339.3	4.06	0.011

[*] Akaike’s Information Criterion corrected for small sample size (AICc).

Table 2-S15. The list of the top 16 models from the analyses of dependent variable ***maximum inter-visit interval*** in the subset of data with diet information available (27 broods).

Global (Initial) model: **maximum inter-visit intervals** ~ Year + Sex + Brood size (BS) + Brood age (BA) + Nesting density (ND) + Visit type +Predation intensity (PI) + Laying date (LD)+ LD:Visit type + LD:ND + Visit type:DN + DN:PI, random factor = pair identity, family = Gaussian. Model-averaged from the best fitting models ($\Delta AIC_c \leq 4$) highlighted in bold. Each cell includes the value of the effect estimate or the mark "+" for categorical predictors that are included in the model. Blank cells indicated that the variable was not included in the cell. Summary of averaging from the list of the 16 models of ΔAICc < 4 is shown in **Table 2-8,** and the results are graphically presented in **Fig. 2-4D**.

Variables and their interactions in the model							Statistical evaluation of the model's fit to data				
Nesting density (ND)	Laying date	Predation intensity	Sex	Visit type (VT)	Year	ND:VT	df	logLik	AICc*	delta	weight
0.01			**+**	**+**	**+**	**+**	**8.00**	**-309.49**	**636.70**	**0.00**	**0.13**
0.02		**0.06**	**+**	**+**	**+**	**+**	**9.00**	**-308.47**	**637.10**	**0.40**	**0.11**
0.02	**0.02**		**+**	**+**	**+**	**+**	**9.00**	**-308.58**	**637.30**	**0.62**	**0.09**
0.01				**+**	**+**	**+**	**7.00**	**-311.13**	**637.50**	**0.89**	**0.08**
0.02	**0.02**	**0.06**	**+**	**+**	**+**	**+**	**10.00**	**-307.54**	**637.70**	**1.05**	**0.08**
0.01		**0.06**		**+**	**+**	**+**	**8.00**	**-310.11**	**637.90**	**1.24**	**0.07**
-0.05			**+**	**+**		**+**	**7.00**	**-311.37**	**638.00**	**1.38**	**0.07**
0.01	**0.02**			**+**	**+**	**+**	**8.00**	**-310.22**	**638.10**	**1.47**	**0.06**
0.02	**0.02**	**0.06**		**+**	**+**	**+**	**9.00**	**-309.18**	**638.50**	**1.83**	**0.05**
-0.05		**0.01**	**+**	**+**		**+**	**8.00**	**-310.48**	**638.60**	**1.98**	**0.05**
-0.05	**0.00**		**+**	**+**		**+**	**8.00**	**-310.48**	**638.60**	**1.98**	**0.05**
-0.06				**+**		**+**	**6.00**	**-313.01**	**639.00**	**2.32**	**0.04**
-0.05	**0.00**	**0.01**	**+**	**+**		**+**	**9.00**	**-309.56**	**639.20**	**2.59**	**0.04**
-0.05		**0.01**		**+**		**+**	**7.00**	**-312.11**	**639.50**	**2.86**	**0.03**
-0.05	**0.00**			**+**		**+**	**7.00**	**-312.11**	**639.50**	**2.86**	**0.03**
-0.05	**0.00**	**0.01**		**+**		**+**	**8.00**	**-311.19**	**640.10**	**3.40**	**0.02**
			+	+	+		6.00	-315.88	644.70	8.06	0.00
		0.07	+	+	+		7.00	-314.86	645.00	8.35	0.00
				+	+		5.00	-317.20	645.10	8.43	0.00
0.00			+	+	+		7.00	-315.01	645.30	8.65	0.00

* Akaike's Information Criterion corrected for small sample size (AICc).

Table 2-S16. The list of the top 43 models from the analyses of dependent variable ***nest visit type*** in the subset of data with diet information available (27 broods).
Global (Initial) model: Visit type (0, 1) ~ Predation intensity (PI) + Nesting density + Relative benefits from synchrony (SmAEff) + Sex + Brood age category + Brood size category + Year + Laying date + ND:PI + PI:SmAEff + DN:SmAEff + DN:PI, random factor = pair identity, family =binomial.
Model-averaged from the best fitting models ($\Delta AIC_c \le 4$) highlighted in bold. Each cell includes the value of the effect estimate or the mark "+" for categorical predictors that are included in the model. Blank cells indicated that the variable was not included in the cell.
Summary of averaging from the list of the 43 models of ΔAICc < 4 is shown in **Table 2-9,** and the results are graphically presented in **Fig. 2-5A, 2-5B, 2-5C**.

Variables and their interactions in the model											Statistical evaluation of the model's fit to data				
Brood age category	Brood size category	Nesting density (ND)	Laying date	Predation intensity (PI)	sex	SmAEff	Year	ND:PI	SmAEff :ND	PI:SmA Eff	df	logLik	AICc*	delta	weight
		-0.58			**+**	**0.45**			**-0.75**		**6**	**-291.98**	**596.10**	**0.00**	**0.09**
	0.35	**-0.53**			**+**	**0.51**			**-0.87**		**7**	**-291.58**	**597.40**	**1.25**	**0.05**
		-0.54				**0.47**			**-0.75**		**5**	**-293.65**	**597.40**	**1.29**	**0.05**
	0.66	**-0.49**		**-0.19**	**+**	**0.38**		**-0.7384**	**-1.78**		**9**	**-289.58**	**597.60**	**1.41**	**0.04**
		-0.56	**-0.26**		**+**	**0.47**			**-0.75**		**7**	**-291.73**	**597.70**	**1.55**	**0.04**
		-0.57		**-0.18**	**+**	**0.33**		**-0.4958**	**-1.30**		**8**	**-290.76**	**597.80**	**1.69**	**0.04**
		-0.57		**-0.17**	**+**	**0.46**			**-0.80**		**7**	**-291.87**	**598.00**	**1.83**	**0.04**
		-0.62			**+**	**0.42**	**+**		**-0.76**		**7**	**-291.92**	**598.10**	**1.93**	**0.03**
0.03		**-0.58**			**+**	**0.44**			**-0.75**		**7**	**-291.98**	**598.20**	**2.06**	**0.03**
		-0.55			**+**						**4**	**-295.12**	**598.30**	**2.17**	**0.03**
	0.36	**-0.49**				**0.53**			**-0.88**		**6**	**-293.22**	**598.60**	**2.48**	**0.03**
	0.67	**-0.45**		**-0.19**		**0.41**		**-0.7348**	**-1.78**		**8**	**-291.24**	**598.80**	**2.64**	**0.02**
		-0.53	**-0.26**			**0.49**			**-0.75**		**6**	**-293.40**	**599.00**	**2.82**	**0.02**
					+						**3**	**-296.46**	**599.00**	**2.83**	**0.02**
	0.33	**-0.52**	**-0.24**		**+**	**0.52**			**-0.87**		**8**	**-291.37**	**599.10**	**2.90**	**0.02**
		-0.53		**-0.19**		**0.36**		**-0.492**	**-1.30**		**7**	**-292.45**	**599.10**	**2.99**	**0.02**
0.27	**0.75**	**-0.50**		**-0.24**	**+**	**0.35**		**-0.7654**	**-1.85**		**10**	**-289.37**	**599.20**	**3.07**	**0.02**
	0.63	**-0.40**		**-0.24**	**+**	**0.56**		**-0.7363**	**-1.78**	**0.30**	**10**	**-289.38**	**599.20**	**3.09**	**0.02**
		-0.54		**-0.18**		**0.48**			**-0.79**		**6**	**-293.53**	**599.20**	**3.10**	**0.02**
	0.35	**-0.53**		**-0.17**	**+**	**0.52**			**-0.92**		**8**	**-291.47**	**599.30**	**3.10**	**0.02**
	0.36	**-0.59**			**+**	**0.48**	**+**		**-0.89**		**8**	**-291.50**	**599.30**	**3.15**	**0.02**
		-0.47		**-0.24**	**+**	**0.54**		**-0.5055**	**-1.32**	**0.35**	**9**	**-290.46**	**599.30**	**3.16**	**0.02**
0.14	**0.39**	**-0.54**			**+**	**0.49**			**-0.89**		**8**	**-291.52**	**599.30**	**3.20**	**0.02**
		-0.57				**0.45**	**+**		**-0.76**		**6**	**-293.62**	**599.40**	**3.27**	**0.02**
0.00		**-0.54**				**0.47**			**-0.75**		**6**	**-293.65**	**599.50**	**3.34**	**0.02**

	0.66	**-0.54**		**-0.24**	+	**0.36**	+	**-0.7231**	**-1.80**		**10**	**-289.51**	**599.50**	**3.36**	**0.02**
		-0.48		**-0.22**	+	**0.65**			**-0.80**	**0.31**	**8**	**-291.62**	**599.60**	**3.41**	**0.02**
		-0.56	**-0.25**	**-0.16**	+	**0.47**			**-0.79**		**8**	**-291.63**	**599.60**	**3.42**	**0.02**
		-0.62	**-0.27**		+	**0.44**	+		**-0.77**		**8**	**-291.64**	**599.60**	**3.44**	**0.02**
	0.67	**-0.49**	**0.03**	**-0.19**	+	**0.38**		**-0.7502**	**-1.80**		**10**	**-289.58**	**599.60**	**3.49**	**0.02**
		-0.52			+	**0.28**					**5**	**-294.77**	**599.70**	**3.52**	**0.02**
		-0.52									**3**	**-296.84**	**599.70**	**3.58**	**0.02**
		-0.64		**-0.24**	+	**0.42**	+		**-0.84**		**8**	**-291.72**	**599.80**	**3.61**	**0.01**
0.03		**-0.57**	**-0.26**		+	**0.46**			**-0.75**		**8**	**-291.72**	**599.80**	**3.61**	**0.01**
		-0.62		**-0.23**	+	**0.31**	+	**-0.4809**	**-1.32**		**9**	**-290.70**	**599.80**	**3.64**	**0.01**
		-0.57	**-0.10**	**-0.18**	+	**0.35**		**-0.4677**	**-1.27**		**9**	**-290.73**	**599.90**	**3.71**	**0.01**
		-0.54		**0.06**	+			**-0.5156**	**-0.52**		**6**	**-293.84**	**599.90**	**3.71**	**0.01**
0.06		**-0.58**		**-0.19**	+	**0.32**		**-0.4948**	**-1.31**		**9**	**-290.75**	**599.90**	**3.75**	**0.01**
		-0.54	**-0.22**		+						**5**	**-294.93**	**600.00**	**3.84**	**0.01**
0.06		**-0.58**		**-0.19**	+	**0.45**			**-0.80**		**8**	**-291.85**	**600.00**	**3.87**	**0.01**
					+	**0.35**					**4**	**-295.97**	**600.00**	**3.88**	**0.01**
											2	**-298.02**	**600.10**	**3.91**	**0.01**
-0.02		**-0.62**			+	**0.42**	+		**-0.76**		**8**	**-291.92**	**600.10**	**4.00**	**0.01**
	0.34	-0.49	-0.24			0.55			-0.87		7	-293.01	600.30	4.12	0.01
			-0.58								5	-295.09	600.30	4.16	0.01

SmAEff (SA) : Relative foraging benefits from synchrony

[*] Akaike's Information Criterion corrected for small sample size (AICc).

SUPPLEMENTARY FIGURES:

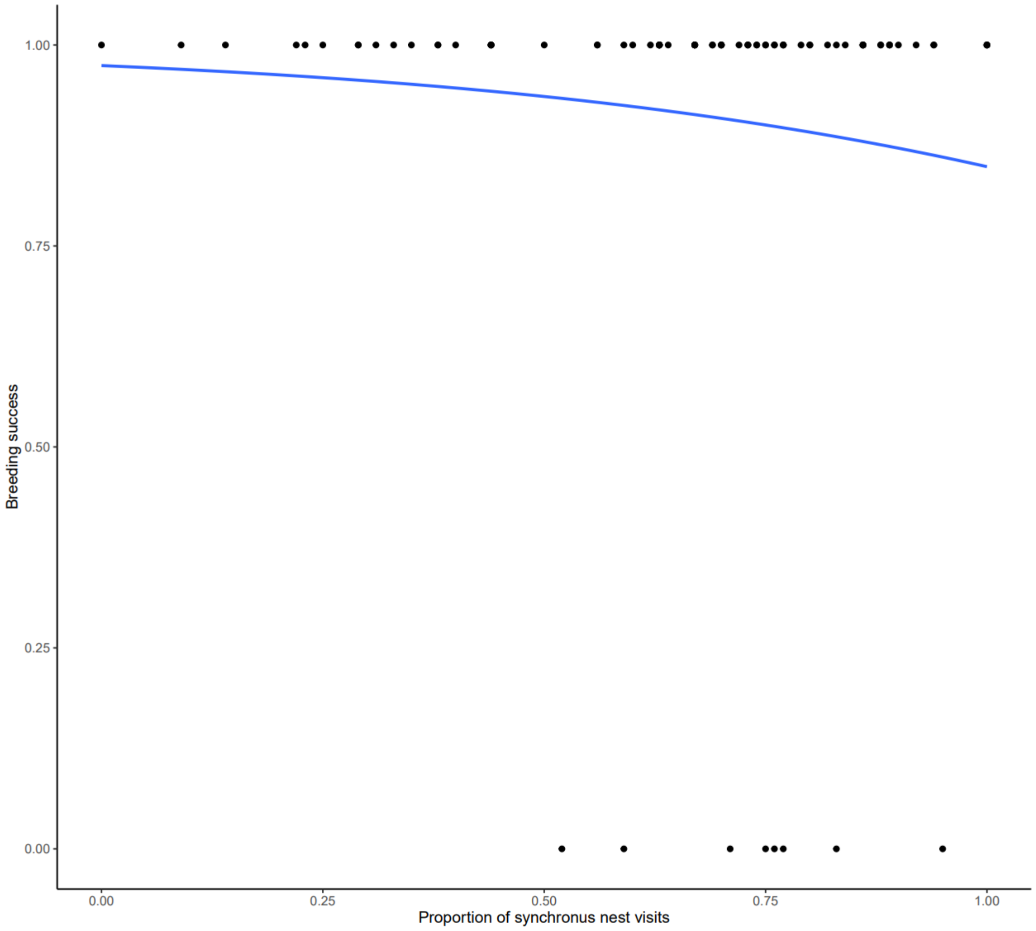

Fig. 2-S1. The effect of synchronous provisioning behaviour of parents on the probability of nestling survival. The solid line represented the mean survival probability and was generated from the predictions of Table 3 using mean values for the synchronous nest visit. The points are the mean observed levels of synchronous nest visits for each brood (n=88; some data points with the same value of the level of synchronous nest visit were overlaid). This figure concerns Table 2-3 and Table 2-S10.

Table 3-S1. Predictor variables that affect provisioning rate, model selection tables showing the 20 top models for each GLMM. Delta represent the difference in AICc. Model-averaged from the best fitting models ($\Delta AIC_c \leq 4$) highlighted in bold. Each cell includes the value of the effect estimate (+ value in standardized categorical predictors indicate that the variable included in the model). Blank cells indicated that the variable was not included in the cell. Initial model: Provisioning rate ~ Year + hatching date + Brood age + Brood size + Nesting density category (NDC) + Parental age class category (PAC) + NDC*PAC, random factor = pair identity, family=Gaussian This table concerns **Table 3.2** and **Figure 3.4, 3.5**.

Age class category	Brood age	Brood size	Nest density category	Hatching date	Proportion of synchrony visit	Year	df	logLik	AICc	delta	weight
	0.28	**0.21**			**0.22**	**+**	**8**	**-101.96**	**221.80**	**0.00**	**0.32**
	0.31	**0.24**		**0.13**	**0.21**	**+**	**9**	**-100.88**	**222.10**	**0.31**	**0.27**
	0.30				**0.23**	**+**	**7**	**-104.67**	**224.80**	**2.99**	**0.07**
	0.31	**0.22**				**+**	**7**	**-105.00**	**225.40**	**3.64**	**0.05**
	0.34	**0.25**		**0.14**		**+**	**8**	**-103.84**	**225.50**	**3.75**	**0.05**
+	0.28	0.21			0.20	+	10	-101.53	226.00	4.18	0.04
	0.26	0.20	+		0.20	+	10	-101.69	226.30	4.50	0.03
	0.32			0.08	0.23	+	8	-104.32	226.50	4.72	0.03
+	0.31	0.24		0.13	0.20	+	11	-100.62	226.80	4.98	0.03
	0.30	0.23	+	0.13	0.20	+	11	-100.77	227.10	5.29	0.02
+	0.31	0.22				+	9	-103.87	228.10	6.31	0.01
	0.28	0.20	+			+	9	-103.88	228.10	6.32	0.01
	0.28		+		0.20	+	9	-104.14	228.60	6.83	0.01
		0.24			0.26	+	7	-106.64	228.70	6.93	0.01
	0.34					+	6	-107.87	228.80	7.01	0.01
+	0.34	0.25		0.12		+	10	-103.02	228.90	7.15	0.01
+	0.31				0.21	+	9	-104.31	228.90	7.17	0.01
	0.31	0.23	+	0.12		+	10	-103.10	229.10	7.32	0.01
	0.30		+			+	8	-106.24	230.30	8.55	0.00
	0.36			0.08		+	7	-107.49	230.40	8.63	0.00

Shown are the Akaike’s Information Criteria corrected for small sample size (AICc).

Table 3-S2. Predictor variables that affect ***the proportion of synchronous visit***, model selection tables showing the 20 top models for each GLMM. Delta represent the difference in AICc. Model-averaged from the best fitting models ($\Delta AIC_c \leq 4$) highlighted in bold. Each cell includes the value of the effect estimate (+ value in standardized categorical predictors indicate that the variable included in the model). Blank cells indicated that the variable was not included in the cell. Global(Initial) model : Visit type (0, 1) ~ Predation intensity (PI) + Nesting density + Relative benefits from synchrony (SmAEff) + Sex + Brood age category + Brood size category + Year + Laying date + ND:PI + PI:SmAEff + DN:SmAEff + DN:PI, random factor = pair identity, family =binomial
This table concerns **Table 3.3 and Figure 3.6**.

Brood age	Brood size	Nesting density (ND)	Year	Parental age class:ND	df	logLik	AICc	delta	weight
		+		**+**	**10**	**-241.07**	**505**	**0**	**0.352**
0.02		**+**		**+**	**11**	**-240.21**	**505.9**	**0.89**	**0.225**
	0.00	**+**		**+**	**11**	**-241.04**	**507.6**	**2.56**	**0.098**
		+	**+**	**+**	**12**	**-239.75**	**507.7**	**2.67**	**0.093**
0.02	**0.00**	**+**		**+**	**12**	**-240.21**	**508.6**	**3.58**	**0.059**
0.01		+	+	+	13	-239.23	509.4	4.39	0.039
		+			6	-248.64	510.3	5.31	0.025
	0.00	+	+	+	13	-239.74	510.4	5.41	0.024
0.02		+			7	-247.76	510.9	5.92	0.018
		+			4	-251.46	511.4	6.41	0.014
0.01	0.00	+	+	+	14	-239.19	512.1	7.14	0.01
0.02		+			5	-250.74	512.2	7.22	0.01
	0.00	+			7	-248.59	512.6	7.58	0.008
0.02	-0.01	+			8	-247.63	513.1	8.09	0.006
	0.00	+			5	-251.41	513.6	8.56	0.005
		+	+		8	-248.09	514	9	0.004
0.02	-0.01	+			6	-250.62	514.3	9.28	0.003
		+	+		6	-250.64	514.3	9.33	0.003
0.01		+	+		9	-247.41	515.1	10.14	0.002
0.01		+	+		7	-250.09	515.6	10.58	0.002

Shown are the Akaike's Information Criteria corrected for small sample size (AICc).

Table 3-S3. Predictor variables that affect ***alternating visit in rapid succession***, model selection tables showing the 20 top models for each GLMM. This table concerns Shown are the Akaike's Information Criteria corrected for small sample size (AICc). Delta represent the difference in AICc. Model-averaged from the best fitting models ($\Delta AIC_c \leq 4$) highlighted in bold. Each cell includes the value of the effect estimate (+ value in standardized categorical predictors indicate that the variable included in the model). Blank cells indicated that the variable was not included in the cell. Initial model : cbind(alternation succession present, not present ~ Year + Hatching date + Brood age + Brood size + Nesting density category (NDC) + Parental age class category (PAC) + NDC*PAC, random factor = pair identity, family=binomial

Table 3.4 and **Figure 3.7**.

Parental age class (PAC)	Brood age	Brood size	Nesting density (ND)	Year	PAC:ND	df	logLik	AICc	delta	weight
+			**+**		**+**	**10**	**-209.68**	**442.2**	**0**	0.251
+			**+**	**+**	**+**	**12**	**-207.41**	**443**	**0.77**	0.171
+		**-0.02**	**+**	**+**	**+**	**13**	**-206.16**	**443.2**	**1.04**	0.149
+		**-0.01**	**+**		**+**	**11**	**-209.05**	**443.6**	**1.37**	0.127
+	**-0.01**		**+**		**+**	**11**	**-209.56**	**444.6**	**2.39**	0.076
+	**-0.01**		**+**	**+**	**+**	**13**	**-207.30**	**445.5**	**3.31**	0.048
+	**0.00**	**-0.02**	**+**	**+**	**+**	**14**	**-206.12**	**446**	**3.79**	0.038
+	**0.00**	**-0.01**	**+**		**+**	**12**	**-209.01**	**446.2**	**3.96**	0.035
+			+	+		8	-214.77	447.4	5.16	0.019
+			+			6	-217.18	447.4	5.18	0.019
+		-0.02	+	+		9	-213.55	447.4	5.2	0.019
+		-0.01	+			7	-216.48	448.4	6.15	0.012
+	-0.01		+			7	-216.97	449.3	7.13	0.007
+	-0.01		+	+		9	-214.56	449.4	7.22	0.007
+	-0.01	-0.02	+	+		10	-213.41	449.7	7.47	0.006
		-0.02	+	+		7	-217.29	450	7.77	0.005
			+	+		6	-218.65	450.3	8.13	0.004
+	-0.01	-0.01	+			8	-216.35	450.5	8.32	0.004
+						4	-221.48	451.4	9.24	0.002
	-0.01	-0.02	+	+		8	-217.06	451.9	9.73	0.002

Table 4-S1 Model selection table showing the top 20 models for each GLMM, predictors the probability of long duration at nest after provisioning visit. Initial model: cbind (long duration present (1), absent (0)) ~ Sex + Brood age + Brood size + Nest visit type + preceding inter-visit intervals+ Sex*Nest visit type + Sex*inter-visit intervals, random factor = pair identity, family=binomial. Delta represent the difference in AICc. Model-averaged from the best fitting models ($\Delta AIC_c \leq 4$) highlighted in bold. Each cell includes the value of the effect estimate “+” value in standardized categorical predictors indicate that the variable included in the model). Blank cells indicated that the variable was not included in the cell. Summary of averaging from the list of the 24 models of ΔAICc < 4 is shown in **Table 4-1,** and the results are graphically presented in **Fig. 5A, 5B, 5C**.

Brood age	Brood size	Sex	Hatching date	Inter-visit interval	Visit type	Nesting density	df	logLik	AICc	delta	weight
-1.14	**-0.78**	**+**	**-0.67**		**+**		**7**	**-468.52**	**951.1**	**0.00**	**0.09**
-0.99	**-0.65**	**+**			**+**		**6**	**-469.54**	**951.1**	**0.02**	**0.09**
-0.89		**+**			**+**	**0.63**	**6**	**-469.65**	**951.4**	**0.24**	**0.08**
-0.82	**-0.59**	**+**			**+**	**0.58**	**7**	**-468.66**	**951.4**	**0.28**	**0.08**
-1.08		**+**			**+**		**5**	**-470.68**	**951.4**	**0.28**	**0.08**
-0.98	**-0.72**	**+**	**-0.54**		**+**	**0.44**	**8**	**-468.04**	**952.2**	**1.06**	**0.06**
-1.20		**+**	**-0.47**		**+**		**6**	**-470.17**	**952.4**	**1.28**	**0.05**
	-0.67	**+**			**+**	**0.78**	**6**	**-470.25**	**952.5**	**1.43**	**0.05**
-1.00		**+**	**-0.33**		**+**	**0.55**	**7**	**-469.42**	**952.9**	**1.78**	**0.04**
-1.17	**-0.80**	**+**	**-0.68**	**-0.14**	**+**		**8**	**-468.43**	**952.9**	**1.83**	**0.04**
-1.01	**-0.66**	**+**		**-0.13**	**+**		**7**	**-469.47**	**953.0**	**1.88**	**0.04**
		+			**+**	**0.86**	**5**	**-471.51**	**953.1**	**1.94**	**0.04**
-0.84	**-0.61**	**+**		**-0.15**	**+**	**0.59**	**8**	**-468.55**	**953.2**	**2.08**	**0.03**
-0.91		**+**		**-0.13**	**+**	**0.64**	**7**	**-469.57**	**953.2**	**2.08**	**0.03**
-1.10		**+**		**-0.10**	**+**		**6**	**-470.63**	**953.3**	**2.19**	**0.03**
	-0.77	**+**			**+**		**5**	**-471.91**	**953.9**	**2.74**	**0.02**
-1.01	**-0.73**	**+**	**-0.55**	**-0.15**	**+**	**0.45**	**9**	**-467.92**	**954.0**	**2.84**	**0.02**
-1.22		**+**	**-0.47**	**-0.11**	**+**		**7**	**-470.12**	**954.3**	**3.18**	**0.02**
	-0.73	**+**	**-0.22**		**+**	**0.74**	**7**	**-470.13**	**954.3**	**3.22**	**0.02**
	-0.68	**+**		**-0.11**	**+**	**0.79**	**7**	**-470.19**	**954.4**	**3.33**	**0.02**
-1.02		**+**	**-0.33**	**-0.13**	**+**	**0.57**	**8**	**-469.33**	**954.7**	**3.63**	**0.02**
		+		**-0.09**	**+**	**0.87**	**6**	**-471.47**	**955.0**	**3.88**	**0.01**
		+			**+**		**4**	**-473.50**	**955.0**	**3.92**	**0.01**
		+	**0.00**		**+**	**0.86**	**6**	**-471.51**	**955.1**	**3.95**	**0.01**
	-0.86	+	-0.37		+		6	-471.59	955.2	4.12	0.01

Shown are the Akaike’s Information Criteria corrected for small sample size (AICc).

Table 4-S2 Model selection table showing the top 20 models for each GLMM, predictors the probability of "waiting for a partner" during long durations at nest. Initial model: Sequence (waiting for present (1), absent (0) ~ Sex + Brood age + Brood size + Nest visit type + Local density of provisioned nest (LDP) + Sex*Nest visit type, random factor = pair identity, family=binomial. Shown are the Akaike's Information Criteria corrected for small sample size (AICc). Delta represent the difference in AICc. Model-averaged from the best fitting models ($\Delta AIC_c \leq 4$) highlighted in bold. Each cell includes the value of the effect estimate "+" value in standardized categorical predictors indicate that the variable included in the model). Blank cells indicated that the variable was not included in the cell. Summary of averaging from the list of the 24 models of $\Delta AICc < 4$ is shown in **Table 4-2**

Brood age	Brood size	Sex	Visit type (VT)	Nesting density	Sex : VT	df	logLik	AICc	delta	weight
						2	**-105.23**	**214.5**	**0.00**	**0.16**
			+			**3**	**-104.49**	**215.1**	**0.58**	**0.12**
				-0.41		**3**	**-104.81**	**215.8**	**1.22**	**0.09**
			+	**-0.46**		**4**	**-103.95**	**216.1**	**1.59**	**0.07**
-0.13						**3**	**-105.19**	**216.5**	**1.99**	**0.06**
		+				**3**	**-105.20**	**216.5**	**2.00**	**0.06**
	0.06					**3**	**-105.22**	**216.6**	**2.05**	**0.06**
		+	**+**			**4**	**-104.36**	**217.0**	**2.43**	**0.05**
	0.10		**+**			**4**	**-104.46**	**217.1**	**2.61**	**0.04**
-0.07			**+**			**4**	**-104.47**	**217.2**	**2.64**	**0.04**
-0.21				**-0.46**		**4**	**-104.70**	**217.6**	**3.10**	**0.03**
		+		**-0.41**		**4**	**-104.79**	**217.8**	**3.28**	**0.03**
	0.01			**-0.41**		**4**	**-104.81**	**217.8**	**3.31**	**0.03**
		+	**+**	**-0.44**		**5**	**-103.86**	**218.1**	**3.54**	**0.03**
-0.15			**+**	**-0.48**		**5**	**-103.89**	**218.1**	**3.59**	**0.03**
		+	**+**			**5**	**-103.92**	**218.2**	**3.65**	**0.03**
	0.05		**+**	**-0.45**		**5**	**-103.94**	**218.2**	**3.70**	**0.03**
-0.14		+				4	-105.15	218.5	4.00	0.02
-0.14	0.08					4	-105.17	218.6	4.05	0.02
	0.06	+				4	-105.19	218.6	4.08	0.02

Shown are the Akaike's Information Criteria corrected for small sample size (AICc).

Table 4-S3 Model selection table showing the top 20 models for each GLMM, predictors influencing the probability of arriving first in synchronous nest visit. Initial model : Sequence(first(1), later(0) ~ Sex + Brood age + Brood size + Proportion of synchronous nest visit + Local density of provisioned nest (LDP) + Sex*(LDP*PS), random factor = pair identity, family=binomial. Shown are the Akaike's Information Criteria corrected for small sample size (AICc). Delta represent the difference in AICc. Model-averaged from the best fitting models ($\Delta AIC_c \leq 4$) highlighted in bold. Each cell includes the value of the effect estimate "+" value in standardized categorical predictors indicate that the variable included in the model). Blank cells indicated that the variable was not included in the cell.

Summary of averaging from the list of the 5 models of ΔAICc < 4 is shown in **Table 4-3,** and the results are graphically presented in **Fig 4.3**

Brood age	Brood size	Sex	Proportion of synchrony visit (PS)	Nesting density (ND)	Sex:PS	Sex:ND	df	logLik	AICc	delta	weight
		+	**0.00**		**+**		**5**	**-882.32**	**1774.7**	**0.00**	**0.29**
		+	**0.00**	**0.00**	**+**	**+**	**7**	**-881.29**	**1776.7**	**1.97**	**0.11**
0.00		**+**	**0.00**		**+**		**6**	**-882.32**	**1776.7**	**2.02**	**0.10**
	0.00	**+**	**0.00**		**+**		**6**	**-882.32**	**1776.7**	**2.02**	**0.10**
		+	**0.00**	**0.00**	**+**		**6**	**-882.32**	**1776.7**	**2.02**	**0.10**
0.00		+	0.00	0.00	+	+	8	-881.29	1778.7	4.00	0.04
	0.00	+	0.00	0.00	+	+	8	-881.29	1778.7	4.00	0.04
0.00	0.00	+	0.00		+		7	-882.32	1778.7	4.04	0.04
0.00		+	0.00	0.00	+		7	-882.32	1778.7	4.04	0.04
	0.00	+	0.00	0.00	+		7	-882.32	1778.7	4.04	0.04
		+		0.00		+	5	-884.90	1779.9	5.17	0.02
		+					3	-887.19	1780.4	5.71	0.02
0.00	0.00	+	0.00	0.00	+	+	9	-881.29	1780.7	6.03	0.01
0.00	0.00	+	0.00	0.00	+		8	-882.32	1780.8	6.07	0.01
0.00		+		0.00		+	6	-884.90	1781.9	7.19	0.01
	0.00	+		0.00		+	6	-884.90	1781.9	7.19	0.01
		+	0.00	0.00		+	6	-884.90	1781.9	7.19	0.01
0.00		+					4	-887.19	1782.4	7.72	0.01
	0.00	+					4	-887.19	1782.4	7.72	0.01
		+	0.00				4	-887.19	1782.4	7.72	0.01

Table 4-S4 Model selection table showing the top 20 models for each GLMM, predictors influencing mean prey load size index. Global model in (A): ***prey load size*** ~ Year + Brood age + Brood size + Hatching date + arrival sequence(AS) + Local density of provisioned nest(LDP) + sex +AS*(Sex + LDP), random factor = pair identity, family=Gaussian. Shown are the Akaike's Information Criteria corrected for small sample size (AICc). Delta represent the difference in AICc. Model-averaged from the best fitting models ($\Delta AIC_c \leq 4$) highlighted in bold. Each cell includes the value of the effect estimate "+" value in standardized categorical predictors indicate that the variable included in the model). Blank cells indicated that the variable was not included in the cell.

Summary of averaging from the list of the 24 models of ΔAICc < 4 is shown in **Table 4-4,** and the results are graphically presented in **Fig. 4.5A**

Brood age	Brood size	Sex	Hatching date	Arriving sequence (AS)	Nesting density (ND)	Year	Sex : AS	AS:ND	df	logLik	AICc	delta	weight
		+		**+**		**+**			**6**	**-1814.64**	**3641.4**	**0.00**	**0.19**
-0.06		**+**		**+**		**+**			**7**	**-1814.29**	**3642.8**	**1.35**	**0.09**
		+		**+**	**0.04**	**+**			**7**	**-1814.45**	**3643.1**	**1.66**	**0.08**
		+	**-0.03**	**+**		**+**			**7**	**-1814.53**	**3643.3**	**1.83**	**0.07**
	0.03	**+**		**+**		**+**			**7**	**-1814.57**	**3643.3**	**1.91**	**0.07**
		+		**+**		**+**	**+**		**7**	**-1814.95**	**3644.1**	**2.66**	**0.05**
		+		**+**					**5**	**-1817.14**	**3644.4**	**2.95**	**0.04**
-0.07		**+**	**-0.04**	**+**		**+**			**8**	**-1814.11**	**3644.5**	**3.03**	**0.04**
-0.05		**+**		**+**	**0.04**	**+**			**8**	**-1814.14**	**3644.5**	**3.09**	**0.04**
-0.06	**0.02**	**+**		**+**		**+**			**8**	**-1814.23**	**3644.7**	**3.29**	**0.04**
-0.10		**+**		**+**					**6**	**-1816.31**	**3644.8**	**3.33**	**0.04**
		+		**+**	**0.04**	**+**		**+**	**8**	**-1814.28**	**3644.8**	**3.37**	**0.03**
		+		**+**	**0.09**				**6**	**-1816.34**	**3644.8**	**3.39**	**0.03**
	0.03	**+**		**+**	**0.05**	**+**			**8**	**-1814.34**	**3644.9**	**3.49**	**0.03**
		+	**-0.02**	**+**	**0.04**	**+**			**8**	**-1814.34**	**3644.9**	**3.50**	**0.03**
	0.02	**+**	**-0.03**	**+**		**+**			**8**	**-1814.46**	**3645.2**	**3.75**	**0.03**
-0.06		**+**		**+**		**+**	**+**		**8**	**-1814.57**	**3645.4**	**3.97**	**0.03**
-0.08		+		+	0.08				7	-1815.77	3645.7	4.30	0.02
		+		+	0.04	+	+		8	-1814.77	3645.8	4.35	0.02
	0.06	+		+					6	-1816.83	3645.8	4.38	0.02

Table 4-S5 Predictor variables that affect the foraging efficiency, model selection tables showing the 20 top models for each GLMM. Delta represent the difference in AICc. Model-averaged from the best fitting models ($\Delta \mathrm{AIC}_c \leq 6$) highlighted in bold. Each cell includes the value of the effect estimate "+" value in categorical predictors indicate that the variable included in the model). Blank cells indicated that the variable was not included in the cell. Global model: foraging efficiency ~ Year + Brood age + Brood size + Hatching date + arrival sequence(AS) + Local density of provisioned nest(LDP) + sex +AS*(Sex + brood size + brood age + Hatching date) + Year (LDP + sex + brood size + brood age + sequence + hatching date), random factor = pair identity, family=Gaussian

Summary of averaging from the list of the 3 models of ΔAICc < 4 is shown in **Table 4-5,** and the results are graphically presented in **Fig. 4.5B**.

Parental age	Brood age	Brood size	Gender	Hatching date	Arrival sequence (AS)	Nesting density	Year	Sex:AS	df	logLik	AICc	delta	weight
					+				**4.00**	**-837.58**	**1683.20**	**0.00**	**0.40**
			+		**+**			**+**	**6.00**	**-836.54**	**1685.20**	**1.99**	**0.15**
			+		**+**				**5.00**	**-837.59**	**1685.30**	**2.05**	**0.15**
					+	-0.07			5.00	-838.83	1687.80	4.54	0.04
+					+				5.00	-839.24	1688.60	5.35	0.03
					+		+		5.00	-839.26	1688.60	5.40	0.03
				-0.04	+				5.00	-839.27	1688.60	5.42	0.03
	-0.02				+				5.00	-839.41	1688.90	5.68	0.02
									3.00	-841.47	1689.00	5.75	0.02
		0.01			+				5.00	-839.50	1689.10	5.87	0.02
			+		+	-0.08		+	7.00	-837.46	1689.10	5.88	0.02
			+		+	-0.07			6.00	-838.81	1689.80	6.53	0.02
			+						4.00	-840.96	1690.00	6.77	0.01
			+		+		+		6.00	-839.26	1690.70	7.44	0.01
			+	-0.04	+				6.00	-839.29	1690.70	7.48	0.01
			+	-0.03	+			+	7.00	-838.31	1690.80	7.58	0.01
			+		+		+	+	7.00	-838.32	1690.80	7.61	0.01
	-0.03		+		+			+	7.00	-838.32	1690.80	7.61	0.01
	-0.02		+		+				6.00	-839.42	1691.00	7.74	0.01
+			+		+			+	7.00	-838.46	1691.10	7.89	0.01

Shown are the Akaike's Information Criteria corrected for small sample size (AICc)