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SYNCHRONOUS PROVISIONING OF THE COOPERATIVELY BREEDING CHESTNUT-CROWNED BABBLER, *POMATOSTOMUS RUFICEPS*

By

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A dissertation submitted to the Graduate School of Environmental Science,
Hokkaido University, Sapporo, in partial fulfilment
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General introduction

Cooperative breeding is defined as a breeding system where individuals other than parents help to rear offspring, typically by delaying dispersal from the natal territory. Such systems are widespread, occurring in many species of insect, bird and mammal (Wilson 1971; Stacey & Koenig 1990; Choe & Crespi 1997; Solomon & French 1997). Why such altruistic helping behaviour evolves has been explained by kin selection (Hamilton 1964; Emlen & Wrege 1988; Russell & Hatchwell 2001). Helpers are mostly offspring of breeders and likely to gain kin-selected indirect benefit from caring brothers and sisters. Why helpers delay dispersal sacrificing their own breeding opportunities is a separate question from why individuals provide help (Brown 1987; Emlen 1991). Constraints imposed on independent breeding by low availability of habitats or mates outside the natal territories have been found in a number of species (Pruett-Jones & Lewis 1990; Koenig et al. 1992; Komdeur et al. 1995; Pasinelli & Walters 2002). Therefore, helping is considered as a secondary option in case where young individuals are unlikely to find their own breeding opportunity and they benefit from staying at home to avoid increased mortality risk that they would take if they become floaters (e.g. Ridley et al. 2008). Helpers may also benefit from increased probability of inheriting the natal territory once breeders die if they stay at home (Woolfenden & Fitzpatrick 1978).

In addition to kin-selected benefits, a series of hypotheses on direct fitness benefit of helping behaviour have been proposed and tested empirically (Cockburn 1998). The group augmentation (or pseudo-reciprocity) hypothesis suggests that helpers gain direct benefit by increased group size as a result of raising offspring who also stay in the natal territory (Woolfenden 1975; Kokko et al. 2001). Helpers may also gain benefit if acquisition of parenting skills through helping improves their own reproductive success once they start their own breeding, compared to individuals who

did not help while they are young (Skutch 1961; Komdeur 1996). It is also known in a few species that unrelated male helpers have chances of mating with breeding females in the future breeding attempt by helping her current breeding (Reyer 1984; Sherley 1989, 1990; Fessl et al. 1996; Slone 1996).

Another important question is how societies of cooperative breeding are organised. The pattern of mating is a basic social organisation in cooperative breeders as well as in other animals. Mating system in cooperative breeding is associated with helping. For example, Wrege and Emlen (1994) found that females of the White-fronted Bee-eaters (*Merops bullockoides*) preferred to mate with males who are more likely supported by helpers. Females would benefit from enhanced productivity when more helpers are present. Further, the relation between breeding males and females becomes more complex if more than one breeding male or female are present in a group, an issue that has received much attention in the last decade (Magrath et al. 2004). Under such situation, there could be various levels of reproductive sharing among breeders. Reproductive skew is the degree of sharing of reproduction among the same sex. The skew is complete when a dominant breeder monopolises the reproduction and the skew is low when group members of the same sex equally share the reproduction. A number of models have been proposed to explain why and how the degree of reproductive skew varies both across groups or populations of the same species and across species, based on an assumption that interactions between dominants and subordinates of the same sex determine the share of reproduction (Magrath et al. 2004). In these models, both indirect and direct benefits from helping are important parameters, as expected.

Apart from the mating and reproductive competition within groups, organisations of social relationship in cooperatively breeding birds are poorly understood, even though coordination among carers would be an important factor

affecting the fledging success of chicks. Most studies assume that individual contributions to provisioning are determined independent of behaviours of other carers, but carers are likely to adjust their behaviours with each other during cooperative provisioning. There are at least four types of interaction during their cooperative provisioning, (1) despotic or coercive interactions, (2) signalling their contribution toward group members, (3) negotiation of the amount of contribution, and (4) dependence between carers caused by social preference, which are mentioned below.

A common assumption in the studies of cooperative breeding is that helpers are subordinate to breeders. If this is true, the contribution by helpers to offspring care is more or less influenced by dominant breeders. For example, the recruitment of helpers with coercion by breeders has been observed in the White-fronted Bee-eaters (Emlen & Wrege 1992). In the Superb Fairy-wrens (*Malurus cyaneus*), male helpers who did not provide help during the nestling period received punishment from dominant males (Mulder & Langmore 1993). The dominant males become aggressive to helpers during only this period, since they need their helping (Mulder et al. 1994). Even in species where the clear evidence of coercion is absent, dominants may be able to suppress reproduction of subordinates (Young et al. 2006, but see Komdeur 2005), thereby, forcing them to engage in helping to seek only indirect benefits which is an inferior option for helpers in many cases. Further investigation is necessary to elucidate the prevalence of the despotic organisations in cooperative breeding.

Zahavi (1974, 1995) claimed that helping can be a signal toward potential mates or coalition partners in the future rather than the investment to gain indirect benefit assisting kin or gain direct benefit from increased group size through group augmentation. Under the ‘social prestige’ hypothesis, helpers are predicted to show-off their contribution toward other group members. Another type of signalling is related to

the dominant-subordinate interaction mentioned above. If helpers benefit from staying at the home territory, it is expected that helpers increase their contribution to allo-parental care and signal their willingness to provide care toward breeders to avoid punishment or eviction from the group (Gaston 1978). However, empirical evidence of these 'helping-as-a-signal' hypotheses is still scarce.

The cooperative provisioning might be organised in democratic, or at least less coercive, manners. For example, negotiation of parental cares observed in biparental care systems (Johnstone & Hinde 2006; Hinde & Kilner 2007) may also be present in cooperative breeders (Hatchwell 1999; Johnstone 2011). Carers may change their provisioning rate to compensate the change in the amount of care by other carers. Alternatively, carers may respond to others to match the amount of their contribution with other carers. Which response carers take would be dependent on the cost of offspring care, survival probability of offspring, and information that carers have on the need of offspring (Hatchwell 1999; Johnstone & Hinde 2006).

A much less studied factor that may influence the coordination of cooperative provisioning is social preference among group members. Social network analyses in a variety of social animals have revealed that social preference varies even in species that are not regarded as highly social (e.g. Croft et al. 2004). Further, simulation studies showed that social preference can influence the stability of group during collective movements (Ballerini et al. 2008; Bode et al. 2011). Social preference between carers may also influence the coordination of cooperative offspring care if individuals prefer to forage with specific individuals and tend to provision nests together. Such dependency between carers due to social preference has not been examined explicitly in avian cooperative breeders. Most cooperatively breeding avian species forms groups comprising of individuals with different levels of familiarity to each other (e.g.

immigrant and natal individuals), and those individuals differ in relatedness to each other as well as to offspring they care. It is highly likely that such heterogeneity in the group composition provides an opportunity for cooperative breeders to develop non-random social preference between specific combinations of individuals within groups.

The quantification of social preference or behavioural organisation among carers is best achieved by simultaneous monitoring of behaviours of all carers in a group. In studies on how helping improves the growth and survival of the offspring in avian cooperative breeders, observation of provisioning behaviours of all group members has been a standard procedure, but the adjustment of provisioning involving all carers received attention only recently (Raihani et al. 2010; Shen et al. 2010). Especially when the group size is large, simultaneous observation of multiple individuals is difficult, and analyses of such data become complicated. Nests of cooperative breeders have been traditionally monitored with direct observation video cameras for limited time periods (typically only a few hours per day over 3-5 days), although long-lasting observation is needed for the reliable quantification of interactions between every combination of group members. Recent advance in the monitoring technique is expected to eliminate such difficulty and facilitate the studies of the coordination of group provisioning (e.g. Shen et al. 2010).

In this thesis, I investigate how carers interact to each other while provisioning offspring in a cooperatively breeding Chestnut-crowned Babbler (*Pomatostomus ruficeps*) by monitoring nest visits of all group members using a PIT (passive integrated transponder) -tag data logger. Chapter 1 establishes a method of social network analysis to study social preference on the basis of the pattern of synchronous provisioning. Chapter 2 provides an empirical test of one of the helping-as-a-signal hypotheses, 'social prestige', and Chapter 3 tests another signal-based hypothesis, 'pay-to-stay'.

Chapter 1

A social network analysis of nest visit synchrony monitored with PIT-tag system

Introduction

Individuals within populations commonly show affiliative behaviour with conspecifics. The social preferences underpinning repeated affiliative interactions between individuals in a population can be characterised using a social network (Croft et al. 2008; Sih et al. 2009). Over the past decade, significant evidence has accumulated in support of the occurrence of heterogeneous networks of social affiliation within animal populations, and in a variety of contexts (Croft et al. 2005; McDonald 2007; Blumstein et al. 2009; Croft et al. 2008; Voelkl & Kasper 2009; Nagy et al. 2010). This body of work provides important new insights into the ecological causes and consequences of social behaviour. For example, description of social structure is important for the studies of infectious disease or mating systems (e.g. Poulin 2010). Alternatively, given that individual fitness will often be enhanced through behavioural coordination with others in their group, and that this might be facilitated through a social network, it follows that individual behaviour within a group might be less independent than is typically considered (Voelkl & Kasper 2009; Naug 2009; Bode et al. 2011). Despite these facets, our awareness of the contexts in which social networks are quantified in the animal kingdom is still relatively limited.

This paucity is partly caused by a lack of efficient methods for collecting large amounts of data on social interactions from wild animals over the diversity of behavioural contexts. Data collection for social network analysis is challenging since it requires substantial social interaction data for every combination of individuals within a social group or population. Recent developments of automated monitoring systems for wild animals provide one potential solution to this problem (Krause et al. 2011). Automated behavioural recording are particularly useful in species in which individuals

are difficult to observe due to their cryptic nature or fast movement during social interactions, or do not habituate well to the presence of observers. Although behavioural monitoring of relatively large animals with GPS (e.g. Leu et al. 2010; Nagy et al. 2010) and proximity (e.g. Ji et al. 2005; Rutz et al. 2012) loggers is growing, the financial costs of attaching such loggers simultaneously to all individuals in multiple groups can be prohibitive, and small animals can seldom carry such loggers for sufficient durations.

Passive integrated transponder (PIT) tags provide a low cost method for automated monitoring of individual behaviour (Gibbons & Andrews 2004; Bridge & Bonter 2011). Tags are 1x6 mm or 2x12 mm and carry a unique identity code that can be detected by an antenna linked to a reader. The antennae may be set where social interactions are expected and with the readers recording individual identity along with date and time of detection. The co-occurrence of individuals in antennae proximity can be used as an indicator of either social association (Kerth et al. 2006; Patriquin et al. 2010) or behavioural synchrony (Korslund 2006) depending on the contexts in which the data is collected. The PIT-tag reader allows monitoring of relatively small animals for days at a time, far longer than conventional methods of human observers and video camera. This is because PIT-tag readers consume little battery power and its simple data structure (tag ID, date and time) does not require large memory. Its application has facilitated the analysis of social network structure in species for which direct observations are difficult (e.g. bats, Kerth et al. 2006; Patriquin et al. 2010, small passerine birds, Aplin et al. 2012), but is still limited partly owing to analytical difficulties.

One field in which social networks of affiliative interactions have been under-explored is in cooperative breeders (Madden et al. 2009; Drewe 2010; Schürch et al. 2010), although there is compelling evidence for the importance of social networks in

eusocial insects (Fewell 2003). Cooperative breeders represent a specific case of group-living species where individuals, in addition to parents, contribute to rearing offspring. Such systems offer a particularly exciting system for investigating social network structure, since cooperating group members are a major determinant of group breeding success (Dickinson & Hatchwell 2004; Russell 2004), but the efficiency with which cooperation can be coordinated is likely to decline with increasing group size due to reduction of information concerning offspring need (Dall et al. 2012). Coordination and information transfer can be influenced by the structure of group social networks. For example, individuals with a strong association for all other group members can unify a group together when performing collective activity, even if only a small number of individuals have such a high connectedness (or 'centrality') in the network (Bode et al. 2011). By contrast, networks can be segregated into sub-networks (or 'communities') when subsets of group members have stronger preference amongst themselves than for the rest of the group (Lusseau et al. 2006; Wolf et al. 2007; Oh & Badyaev 2010). Community structuring of individuals within groups can be driven by preferences by individuals with similar phenotypes, 'motivations', or familiarity (Griffiths & Magurran 1999; Croft et al. 2005). While division of group into sub-groups specialising in different tasks has been shown to be important in social insects, in which a clear division of labour occurs among the helping caste (Fewell 2003), whether or not this is true of cooperative vertebrates, wherein task partitioning is uncommon (Clutton-Brock et al. 2003), is unknown. One potential selective impediment to network structuring into multiple 'communities' in cooperative vertebrates (that lack task partitioning) is that it may reduce nest visit coordination and hence information shared among carers concerning offspring need. On the other hand, if the number of carers in a group is large enough such that they can provide more food than the offspring can consume, the

community-structuring might become adaptive, assuming the sub-groups can coordinate their provisioning visits effectively to each other.

In this paper, I propose and validate a technique to quantify social networks using PIT-tag monitoring systems in a novel context: synchronous provisioning at breeding nests of a cooperatively breeding passerine, the Chestnut-crowned Babbler (*P. ruficeps*). Provisioning offspring is one of the most significant determinants of reproductive success in cooperative vertebrates, but whether and how group visits are coordinated with increasing group size is not known. Despite the advantages of PIT-tags for collecting large quantities of data simultaneously over multiple nests and for days at a time, this approach has a few potential shortcomings. These include: (1) the accuracy with which PIT-tag readings reflect independent nest visits; (2) group sizes of cooperative breeders are often relatively small, leading to analytical difficulties; and (3) analyses based on conventional modelling (fitting one model for one network) can be difficult to interpret as the number of networks increases. Here I demonstrate the use of PIT-tags in social network analyses of provisioning data, as well as how to overcome the problems using an array of supplementary monitoring tools and recently developed regression models for social network data. Our hope is to encourage and provide directions for future investigations of social networks in a context for which data can be easily, and indeed is routinely, collected, but for which analysis of social networks have hitherto been ignored.

Methods

Study species and population

The Chestnut-crowned Babbler is a medium-sized (50 g) passerine bird endemic to semi-arid and arid zones of the southeastern Australia. A population of this species has been studied since 2004 at the University of New South Wales Arid Zone Research Station, Fowlers Gap, New South Wales, Australia (141.39˚E, 31.09˚S). The study site, located in the arid zone of far western NSW, is characterised by open chenopod shrubland, with the few trees being largely limited to short linear stands along drainage zones and (dry) creek beds (Portelli et al. 2009). Over 90% of group members have been captured using mist nets, with each individual banded with one uniquely numbered metal band (Australian Bird & Bat Banding Scheme) and three colour bands, as well as being injected subcutaneously in the flank with a 2x12 mm PIT-tag (Trovan Ltd, UK). The colour band combinations represent a standard method for identifying birds in the field, but are an inappropriate method for quantifying provisioning rates in babblers due to their rapid movements and large group sizes. Use of inserted PIT-tags (similar to those used for the identification of companion animals) offers a long term means of gathering large amounts of accurate data for a range of questions (e.g. Browning et al. 2012a,b; Young et al. 2013), in a way that causes no obvious deleterious effects to the birds (Schroeder et al. 2011). Our observations with this technique suggest that as long as pit-tags are inserted fully in a downward direction, sealed with standard surgical glue and inserted in an area where the pressure between muscle and skin is minimal, PIT-tags can remain in the birds for at most six years.

Evidence to date from the population suggests that during periods of breeding, Chestnut-crowned Babblers live in units of 2-15 individuals (mean = ~6) (Portelli et al.

2009; Russell et al. 2010). A single female typically lays 3-5 eggs in each breeding unit and, she alone, incubates the clutch and broods the young (Russell et al. 2010). Females have 1-4 'partners', although the mode is one (SC Griffith & AF Russell unpubl. results). Breeding males in each attempt were determined molecularly with precision using 14 polymorphic microsatellite loci (see Rollins et al. 2012 for more details). Breeding males and non-breeding helpers of both sexes (generally male) almost always provide care to young of a single breeding female within the social group (Browning et al. 2012a). Each day, nestling provisioning starts at around 06:00 and ends at around 18:00 (approximately the hours of daylight at the field site during the breeding season) and the nestling provisioning period lasts for ~23 days (Russell et al. 2010). With the exception of the breeding female, who frequently visits the nest without food, the vast majority (~90%) of nest visits occur with a single prey item that is fed to offspring in over 97% of occasions (Young et al. 2013). The provisioning rate of non-breeding helpers is greater when provisioning related broods (Browning et al. 2012a), but after controlling for this effect, there is little difference between yearlings and adults or between the sexes (Browning et al. 2012b). However, because females typically immigrate into groups and are therefore unrelated to other group members (Rollins et al. 2012), on average, they tend to contribute significantly less to cooperation than males (Browning et al. 2012a).

Estimating nest visitation synchrony using standard nest observation techniques

Although I advocate the use of PIT-tag systems to generate large amounts of simultaneously collected provisioning data, such data requires instruction from standard observation techniques (see below). In the case of this study, I used external nest observations to define a group of synchronous visits, as this forms the basic ingredient

of social network analyses and is difficult to determine from PIT-tag data in isolation. I used two approaches to arrive at our definition of synchrony. First, I used a single 2-hour long observation data at the nests of 16 breeding units in 2004 when nestlings were 10-15 days old (Russell et al. 2010). As the majority of trees (and hence nests) are located in creek beds, nest observations were conducted by an observer situated at a distance 50 m from the nest tree with a view-angle perpendicular to the creek: closer distances affected the behaviour of the birds. This enabled a clear view of both the nest and approximately 200 m of creek in either direction. Given that babblers almost always approach the nest along the creek line, this enabled the patterns of nest visitation to be determined. Breeding units varied from 2-13 (mean = 6) individuals and a total of 768 individual nest visits were recorded from 253 'group' visits to the nest area. Second, in 2010 I set up a video camera (Sony Handycam HDR-XR150, Sony Corporation, Japan) framed exclusively on the nest-tree from a distance of ~20 m, again positioned with a view perpendicular to the creek. These external video cameras ($N = 3$ nests) monitored the nests for ~14 hours in total over 4 days (brood age 10-16 days). The primary purpose was to determine for each nest visit: (a) the proportion of group members arriving at the nest tree together (i.e. synchronously); and (b) record the time interval between successive entrances by different group members when they arrived at the tree synchronously versus asynchronously. Together, these observations permitted us to determine how synchronous versus asynchronous nest visits arose and differed in terms of inter-visit-intervals; this in turn permitted assignment of synchronous versus asynchronous nest visits in the PIT-tag data. I defined a series of visits in the PIT-tag data and nest-video data as a synchronous group when temporal separation between nest entry times of successive visits were less than 1 minute apart ('chain rule' commonly used to define spatial association (Croft et al. 2008) (See Results).

Nest visit duration and frequency

Provisioning data were collected from July-November in 2007 and 2008. Nest visits were automatically recorded using an LID-650 PIT-tag reader (TROVAN Ltd, UK) placed at the bottom of the nesting tree and attached via a cable to a coil antenna placed around the entrance of the breeding nest. Babblers breed in domed nests with a small (~8 cm diameter) entrance hole, positioned near the top of the nest. Fitting a coil of the same diameter ensured that all birds had to pass through the antenna to access the nest. The readers recorded the identity of all nest visitors, as well as the date and time of nest visitation to the nearest second. A 12V 7.2Ah battery powered the reader and monitored the nest 24 hours a day continuously for up to five days before the data was downloaded and the battery was replaced. However, the duration of the monitoring period varied because of the need to move readers between concurrently active nests. Overall, PIT-tag monitoring durations ranged from 1 to 19 days (mean = 9.4 days, SD = 5.3) across 49 breeding attempts by 32 breeding units).

Interpretation of PIT-tag records is not necessarily straightforward where the data logger records a pass through the nest entrance without the direction of movement being recorded, as was the case in this study using a single antenna for logistical reasons (see also Mariette et al. 2011; Mariette & Griffith 2012). In babblers, multiple records occur for each nest visit, since individuals commonly remain in the proximity of the antenna for a few seconds before entering and/or exiting the nest. Further, the nest of this species is large (~40 cm in depth) and birds are out of range of the antenna while they are feeding young nestlings. To overcome these problems, I used nest cameras in a subset of nests to determine precisely nest visitation durations and frequencies. To this end, MO-S408 pen cameras measuring ~10 mm in diameter (with a 3.1mm pin hole lens) (Misumi Electronics Corporation, Taiwan) were integrated into the PIT-tag reader

system and inserted through the roof of the nest (secured with cable ties) to film the behaviour of birds within (Browning et al. 2012b; Young et al. 2013). Because of the extra battery power required to run the nest-video camera systems, batteries had to be changed daily, reducing the overall amount of data that could be collected with this system. Overall, nest camera systems were established for 1.1 to 13.6 hours per day (mean = 4.6, SD = 3.5), over 1-6 days (mean = 2.6, SD = 1.7) in 22 breeding attempts by 19 breeding units. The data obtained from the integrated system allows us to determine, with a high degree of accuracy, the independent nest visits from the PIT-tag system.

Characterising the social networks

I calculated the number of synchronous visits (as defined above) between all possible dyads of individuals within a breeding unit to explore an individuals' social preference during the synchronous visits and used this data to characterise the social network. The observed number of synchronous visits per dyad was also used as a measure of the strength of connection for each dyad. A class of latent space model was employed to analyse the social network (Hoff et al. 2002). This class of model is able to analyse both binary and weighted networks. In such models, each individual i (or j) has an unobserved position Z_i (or Z_j) in 2-dimensional latent social space (note that $i \neq j$), with synchronicity probability between a pair of individuals decreasing as the distance in the latent social space increases. The number of synchronous visits $Y_{i,j}$ for dyad i, j was approximated using a Poisson distribution, $Y_{i,j} \sim Poisson(\mu_{i,j})$, with $\log(\mu_{i,j}) = \beta + \log(x_{i,j}) - || Z_i - Z_j ||$, where β is intercept, $|| Z_i - Z_j ||$ is a random effect that defines the Euclidean distance in the latent social space for dyad i, j. This term represents transitivity of the networks, which is the degree of local clustering (Krivitsky et al.

2009). The term, $x_{i,j}$ is a function of visit counts of dyad *i*, *j*. This term, $x_{i,j}$, which is often referred to as 'offset', was added to control for the difference in visit rates among individuals, because it is expected that the synchrony count per dyad would be positively influenced by nest visit rate of individuals. In other words, individuals frequently visiting a nest can be synchronous more often by chance than individuals with lower visit rates, even if they have no social motivation to synchronise their visits. I examined three potential ways to capture this effect of individual visit counts and chose $x_{i,j} = \min(N_i, N_j)$, where N_i (or N_j) is visit count of individual *i* (or *j*). I defined $N_{i,j} / \min(N_i, N_j)$ as synchrony frequency and this is considered as the strength of social preference between *i* and *j*. This model structure forms the basis of the analyses below. I added more parameters to this basic model for the analyses of community structure and individuals connectedness. For sample sizes specific to each analysis, see below.

Community structure of social network

The social network of synchronous visits may be sub-divided into multiple communities (also known as clusters), which may lead to changes in the efficiency of provisioning within breeding units. I examined the existence of multi-communities in both nest-video and PIT-tag data. Using the latent space model described above, I attempted to identify network communities of social networks by adding more parameters specifying the positions of the communities in the latent social space and compared the results between nest-video and PIT-tag data. This form of model is called 'latent cluster random-effects model' (Krivitsky et al. 2009). Community structures of networks was explored in the latent social space by assigning individuals to sub-networks at the same time as estimating positions of individuals, Z_i, in the latent social space. Centre (mean) and variance of positions for each community were also estimated simultaneously. The

number of communities were specified before fitting the models rather than estimated. A community that has the largest assignment probability for the focal individuals is judged as the community to which the individuals belong. When more communities than those that actually exist are specified, no individuals will be assigned to the extra communities. Separate models with a different number of communities were fitted until the maximum numbers of non-empty communities were obtained (Krivitsky et al. 2009 for further details).

I used both internal nest-video data and PIT-tag data in latent cluster random-effects models. The analyses were based on data from 18 breeding attempts of 15 breeding units using the nest-video data, and 46 attempts from 29 groups using the PIT-tag data. I did not include breeding units composed of only two individuals as there is no chance of more than one community in such units. Units of three were also removed from PIT-tag data since the data for the breeding females is not available due to difficulties of distinguishing her entrances and exits without video confirmation (i.e. network size for the analysis is only two for all these data). The latent cluster random-effects models were fitted to each breeding attempt separately (64 models in total). Parameters of the models were estimated using MCMC (Markov chain Monte Carlo) algorithm implemented in R package latentnet (Krivitsky & Handcock 2008), with 100,000 iterations, 80,000 burn-in, and 100 thinning interval, resulting 200 samples, which formed posterior distributions of estimated parameters. Convergence of the models was checked by graphically examining the autocorrelation of the estimates following Krivitsky & Handcock (2008).

Estimates of individual connectedness using a hierarchical latent space model

I estimated the connectedness of individuals, and compared relative performance of the

estimates between internal nest-video data and PIT-tag data. For this purpose, I extended the latent space model by incorporating a term called ‘sociality’ (Hoff et al. 2002). I assembled all the networks collected from different broods and fitted a single model to the entire data set for each monitoring method. In this way, I can control for variability in individual connectedness caused by difference among different networks (i.e. individuals in highly connected network are expected to be more connected than those in less connected networks). To achieve this, I added, to the model, brood ID as a random intercept. This type of latent space model is called ‘hierarchical latent space model’ (following Sweet et al. 2012), since it incorporates multilevel structure caused by inclusion of multiple networks in a single model. The model was specified as follows, $Y_{i,j,k} \sim Poisson(\mu_{i,j,k})$, with $\log(\mu_{i,j,k}) = \beta + \log(x_{i,j,k}) + \varphi_k + \delta_{i,k} + \delta_{j,k} - || Z_{i,k} - Z_{j,k} ||$, where $Y_{i,j,k}$ is the number of synchronous visits. The term, φ_k is random intercept and k indexes the brood ID, and $\delta_{i,k}$ and $\delta_{j,k}$ are the ‘sociality’ random term for variation of connectedness at the individual level. The distance in the latent social space, $|| Z_{i,k} - Z_{j,k} ||$, and effect of individual visit rate $x_{i,j,k}$ are the same as the models above. The latter three parameters were subscripted with k so that individuals appear in different breeding attempts have separate parameter estimates for different breeding attempts. The hierarchical latent space models were fitted using WinBUGS 1.4 (Spiegelhalter et al.2003) with three chains of 1,020,000 iterations, 20,000 burn-in, and 20,000 thinning interval, resulting 150 samples (for both nest video data and PIT-tag data). I did not include parameters associated with the community structure since I found no community structure in the analysis of individual networks using separate model above (see Results). Convergence was checked using Gelman-Rubin statistics (Gelman et al. 2004). For nest-video data, I used 205 synchrony frequencies by 87 individuals observed in 22 breeding attempts by 19 breeding units. For PIT-tag data, I used 859

synchrony frequencies by 197 individuals observed in 48 breeding attempts by 31 breeding units. Sample sizes increased compared to the community model above since I included breeding units where only two individuals are available.

Results

Validating nest visit synchronicity: using standard methods

Nest observations conducted by a human observer indicated that while all individuals within a breeding unit tended to visit the nest area (within 100 m of the nest) as a cohesive unit (86% of occasions, $N = 163$ group-visits), individuals uncommonly visited the nest-tree together (33% of occasions). While observing the provisioning ecology of babblers is difficult, the subset of nest-visits successfully recorded suggests that ~49% ($N = 468$) involved individuals arriving at the nest area with food and flying to nest tree or surrounding trees. By contrast, 37% of nest visits involved individuals finding food in the vicinity of the nesting area, the rest involving individuals without food. Individuals arriving in the nesting vicinity with food entered the nest on average 23 s after the preceding bird (95% confidence interval, CI 5-152 s) while those arriving without food did so after 136 s (95% CI 29-305 s). Birds never entered the nest before the previous bird had exited. Finally, on at least 8% of occasions, provisioners fed twice within the same group visiting bout, indicating that those that arrived at the nest tree sometimes obtained more food in the vicinity of the nest after feeding nestlings in the time it took the group to feed the nestlings and depart again.

The data obtained from external video cameras were in broad accordance with those obtained by the first method. In particular, a proportion of group members arrived

in the nest tree (or surrounding trees) together, each with food, and fed the nestlings in quick succession. Thereafter, and following a short delay, other group members arrived at the nest tree, with such visits tending to be less synchronous than the former ones. For example, the median time interval between successive visits by different individuals (entry-entry interval) was 31 s (inter-quartile range; *IQR* = 20 - 46 s), when group members arrived at the nest tree together (Fig.1.1), but was 114 s (*IQR* = 63 - 225 s), when individuals arrived separately. In addition, the inter-visit-interval between different individuals in synchronous visits (i.e. when birds arrived in the nest tree together) was less than 1-min on 83% of occasions, while for asynchronous visits (i.e. when only a single bird was in the nest tree at a time), inter-visit intervals were under a minute in only 24% of occasions. Thus, I defined a series of visits in the nest-video and PIT-tag data below as socially synchronous when temporal separation between nest entry times of successive visits were less than 1 minute apart ('chain rule'), as this most effectively optimised the trade-off between acceptance versus rejection of truly synchronous visits (Fig. 1.1).

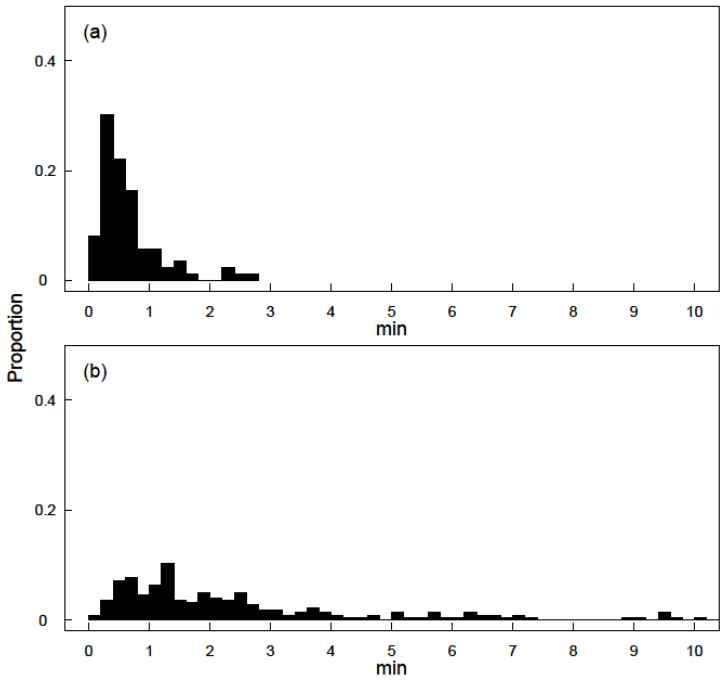

Figure 1.1. (a) The difference in arrival times between different individuals in data from the video camera scanning nesting trees was concentrated to < 60 s for synchronous visits (range 2–162 s, *N* = 86). (b) For asynchronous visits (range 8 s–43 min, *N* = 222) median arrival time was about three times longer (114 *vs*. 31 s). Data for large values were omitted from (b) to aid visualization.

Nest-visit duration and frequency: calibrating PIT-tags

Evidence from the internal nest-videos showed that breeding females remain in the nest for a median duration of 107 s, but that such durations are highly variable (*IQR* = 20.0 s - 14.8 min). This variation precludes either the duration or frequency of nest visits to be determined for breeding females using PIT-tags in isolation. By contrast, all other group members visited the nest for a median of 14 s and were considerably less variable in their visit durations (*IQR* = 6-24 s) (Fig. 1.2a-b, Table 1.1, generalized linear mixed-effects model, GLMM). Nest visit durations by such individuals lasted <30, <60 and <120 seconds (s) on 80%, 92% and 96% of occasions, respectively.

Table 1.1. Summary of the parameters for the generalised linear model for stay duration of individuals across different status (see also Fig. 1.2a-b).

		95% CI	
Parameter	posterior mean	2.5%	97.5%
(Intercept)	5.095	4.902	5.306
Status			
B m - B f	-2.456	-2.758	-2.172
H f o - B f	-2.206	-2.705	-1.675
H f y - B f	-2.229	-2.749	-1.731
H m o - B f	-2.410	-2.711	-2.151
H m y - B f	-2.524	-2.883	-2.139
Brood age	-0.040	-0.063	-0.012
Status × Brood age			
B m - B f	0.082	0.049	0.117
H f o - B f	0.015	-0.075	0.111
H f y - B f	-0.007	-0.084	0.066
H m o - B f	0.101	0.065	0.139
H m y - B f	0.115	0.059	0.165
SD of individuals	0.187	0.121	0.280

Fixed effects are considered significant if the 95% CI's of the parameters do not include zero. Brood ID was removed from the random effects because the estimated variance was close to zero when included.

However, the internal nest-video data also revealed that the time-interval between successive feeds by the same individual, could be as little as 25 s, with 1.2%, 8% and 34% occurring in <60, <120 and <300 s of the previous feed, respectively. The accurate identification of independent nest visits using the PIT-tag data alone will depend on optimising the trade-off between accepting non-independent records and rejecting independent ones. The 1-min cut-off rule appeared optimal (i.e. any records of the same individual within 1-min constituted the same nest visit (excluding breeding females),

while any of longer duration were regarded as independent visits). Applying this cut-off rule to the PIT-tag data revealed close approximations of nest visitation durations (Spearman correlation: $r_s = 0.65$, $p < 0.001$) (Fig. 1.2c, Fig. 1.3) and visit frequencies ($r_s = 0.99$, $p < 0.001$) (Fig. 1.2d) with those obtained from nest-videos. Results were qualitatively similar using a 2-min cut-off rule.

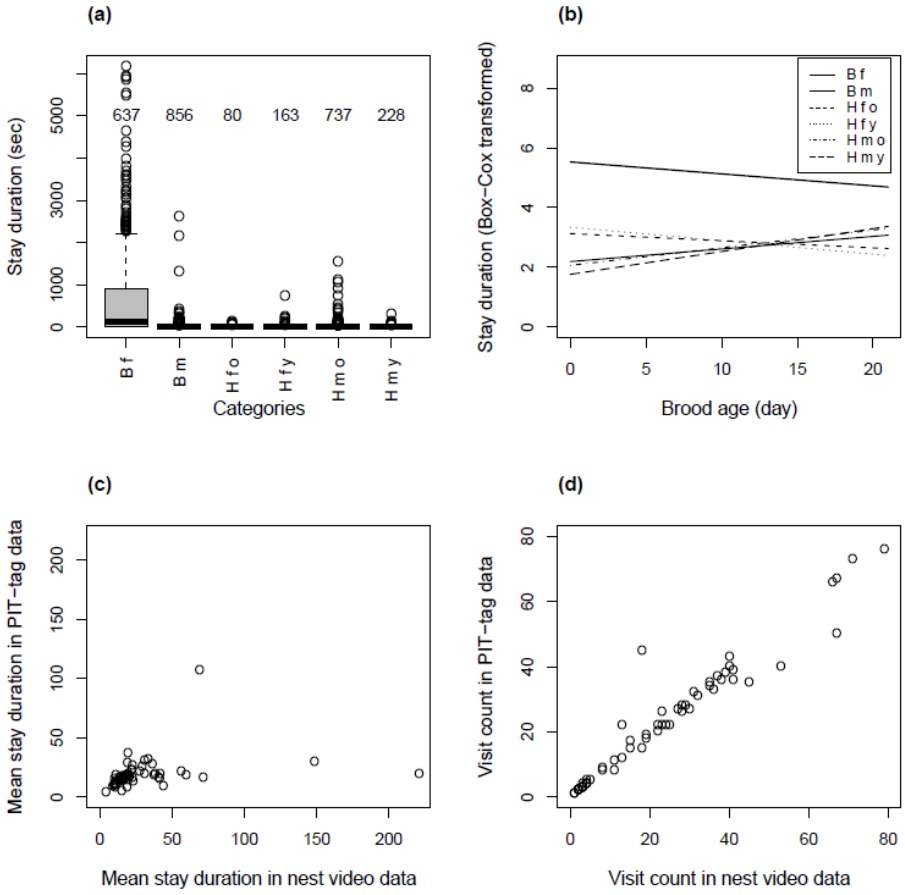

Figure 1.2. (a) Differences in stay duration across different categories: breeding males: median = 13 s, *IQR* = 5-24 s; adult helper females: median = 16 s, *IQR* = 11-24 s; younger helper females: median = 15 s, *IQR* = 7-22; adult helper males: median = 15, *IQR* = 8-24 s; younger helper males: median = 15, *IQR* = 6-23 s; for median and *IQR* for breeding females see text). (b) Estimated effects of brood age and category differences (GLMM, see Table 1.1). Stay duration of breeding females are always higher than others regardless of how old their nestlings are even though they stay for shorter duration when nestlings become older. f: female, m: male, B: breeder, h: helper, a: adult, y: yearling and juvenile. (c) Correlation of mean stay duration, and (d) the number of visits per individual per breeding attempt (both $N = 60$). Breeding females are not included in (c) and (d).

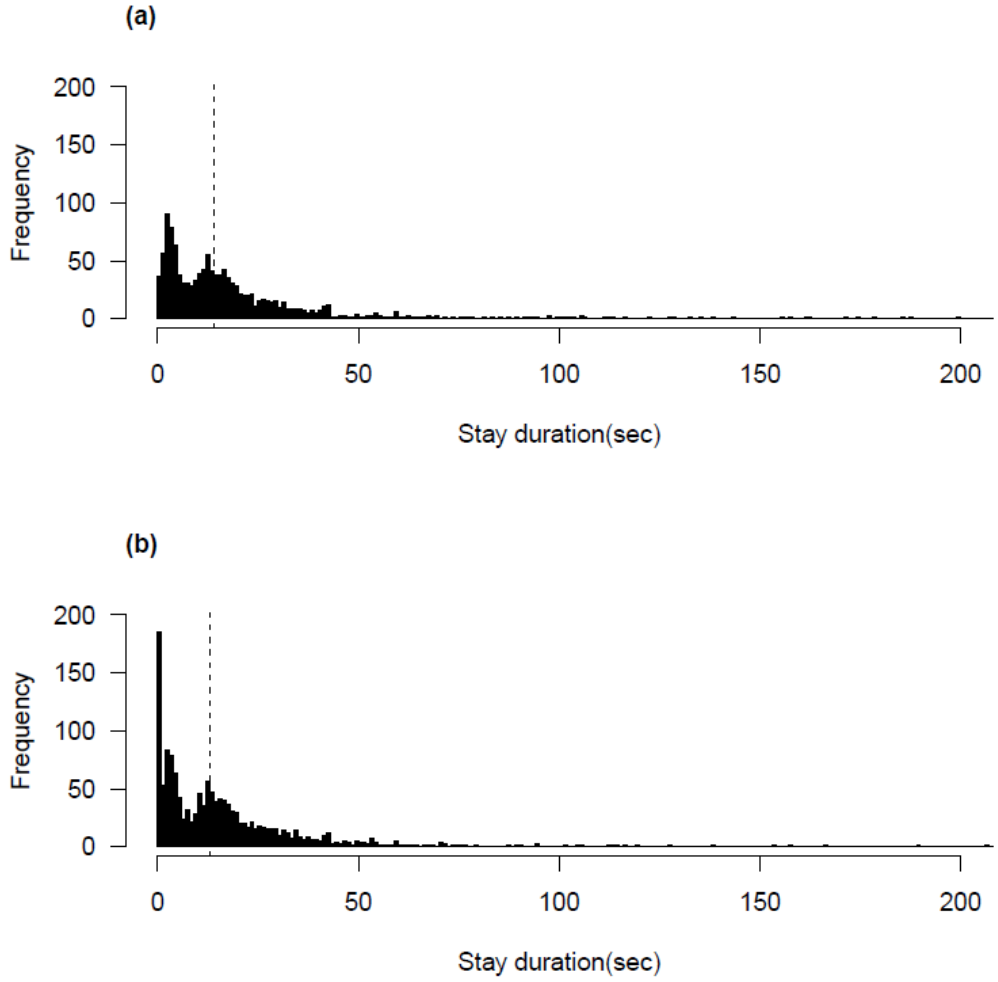

Figure 1.3. Distributions of stay duration matched well between (a) nest visits in nest-video data and (b) nest visits estimated from PIT-tag data recording visits by the same individuals in the same time frame as the nest video data. Vertical dashed lines show median values. Data region for long stay duration in the video is not shown since stay longer than 200 seconds was only 1.7%. Visits of breeding females are not included.

Synchronicity in nest-video data and PIT-tag data

I compared synchronous nest visits in internal nest-video data and PIT-tag data (see Fig. 1.4, Fig. 1.5 for examples). The number of individuals involved in synchronous nest visits ranged from two to nine, but two was the median number in both nest-video and PIT-tag data (nest-video with (N = 585 dyad-brood ID) and without (N = 393) breeding females; PIT-tag data (N = 11,480)). Based on the data from the shared time window, on

average, synchronous nest visits involved 27% of group members in the nest-video data with and without the breeding female (SD = 11%; SD = 12) and 25% in the PIT-tag data (SD = 11%). As expected, there was a negative association between the proportion of group members visiting the nest synchronously and the size of the breeding group (nest video with breeding females: r_s = -0.85, p < 0.001, nest video without breeding females: r_s = -0.79, p < 0.001; PIT-tag data: r_s = -0.85, p < 0.001). Thus, there was little discrepancy in synchronicity between two methods.

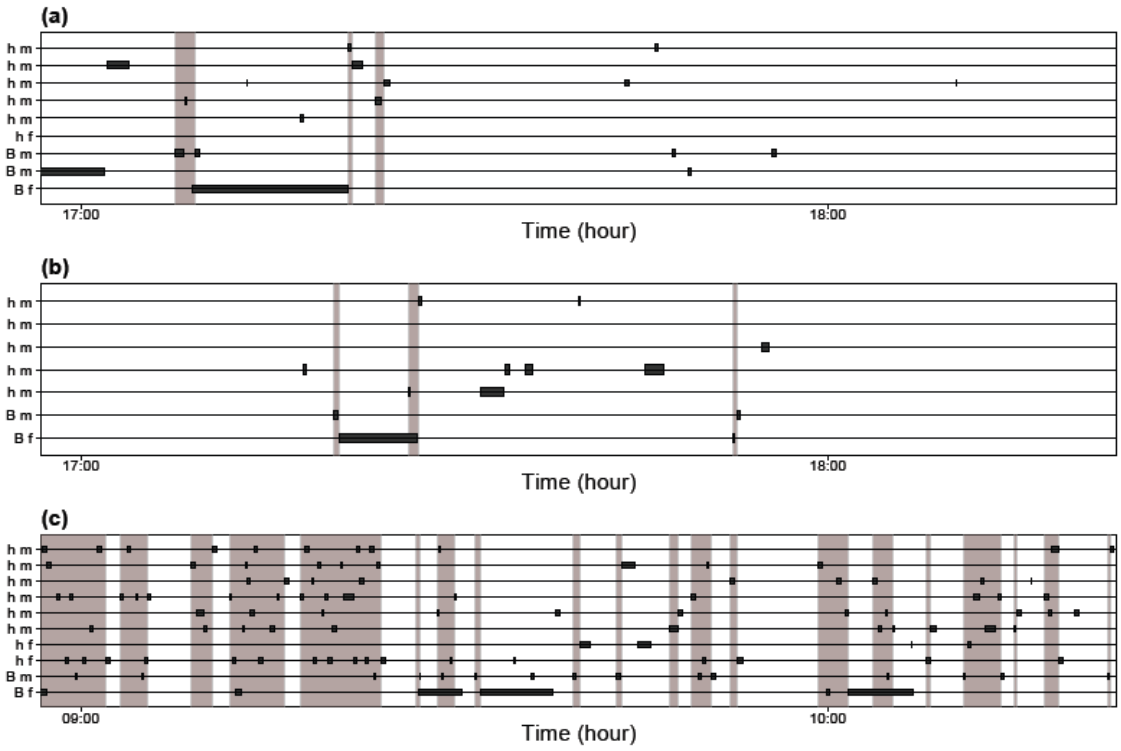

Figure 1.4. Examples of synchronous nest visits observed by nest videos. Horizontal lines correspond to visit record of individuals. Each horizontal black bar represents time when each individual stayed inside the nest (from arrival time to exit time). Each shaded area corresponds to a single synchrony bout, which starts with arrival time of first birds in the synchrony and ends with the arrival time of the last bird. Labels on the y-axis are h: helper, B: breeder, f: female, m: male. Each panel is from three different breeding attempts: (a) cek0702, (b) efg0702, (c) efp0801. Occurrence of synchrony was highly variable across breeding units and time.

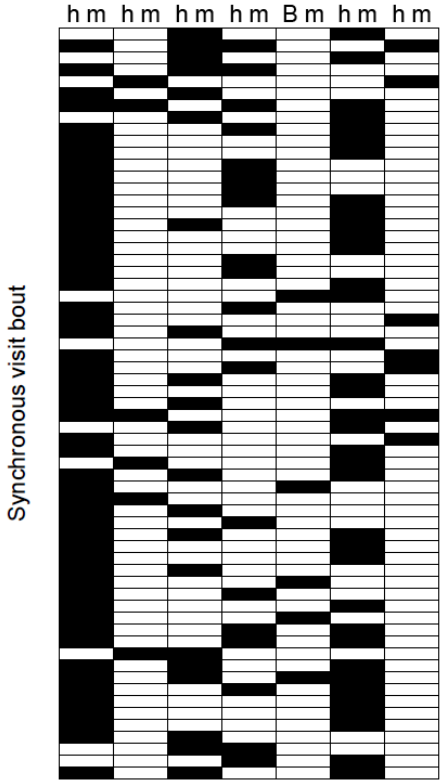

Figure 1.5. An example of sub-grouping of individuals in synchronous visits over time on one whole day of bfd0801 (PIT-tag data). The synchrony events are presented in the order of occurrence (rows). Filled cells indicate synchrony bouts which individuals (columns) were observed to take part in. Individuals have large variation in synchrony rate. Data for the breeding female is not shown due to the problem in the visit reconstruction by PIT-tag (see texts).

Synchrony frequency in nest-video and PIT-tag

The inclusion of the breeding female in the analysis of nest-video data showed a mean frequency of synchronous nest visits (synchrony count divided by $\min(N_i, N_j)$) of 0.3 (SD = 0.22, N = 224 dyad-brood IDs). This frequency was slightly reduced when the breeding female was excluded (mean = 0.29, SD = 0.23, N = 145, Fig. 1.6a, b), and the degree of reduction in the PIT-tag data was similar (mean = 0.26, SD = 0.23, N = 862, Fig. 1.6c, b). It was expected that the frequency of synchronous nest visits would decline with the exclusion of the breeding female because it would automatically lead to

an increased delay between the visits of those individuals 'sandwiching' the breeding female.

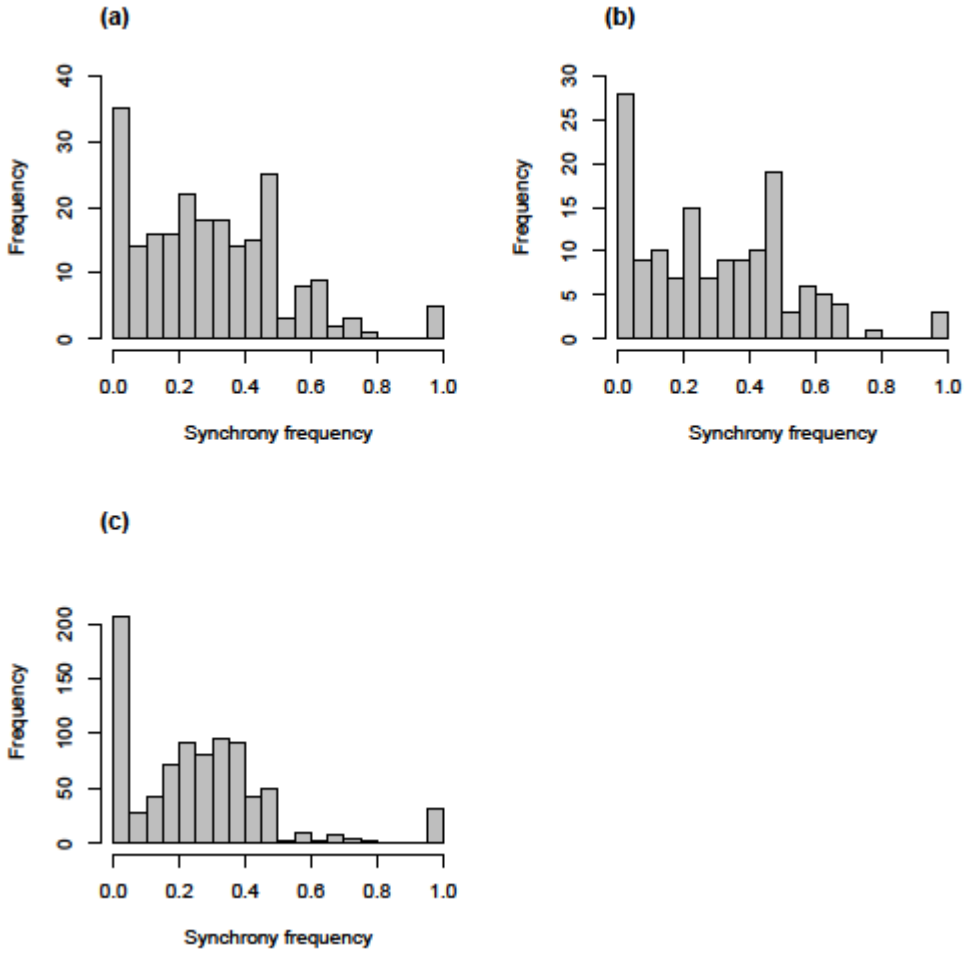

Figure 1.6. Histograms of synchrony frequency per dyad for (a) nest video with breeding females, (b) nest-video without breeding females, and (c) PIT-tag. Full data was used for each.

This explanation was confirmed in direct comparisons of the same dyads across different monitoring methods in the shared time frame. In the direct comparison, both synchrony count per dyad and min(N_i, N_j) per dyad matched well between the three different comparisons: 1) the nest-video with breeding females *vs* the nest-video without breeding females (synchrony count: $r_s = 0.98$, $N = 119$, $p < 0.001$; min(N_i, N_j): $r_s = 0.99$,

$N = 119$, $p < 0.001$), 2) nest-video with breeding female *vs*. PIT-tag data from the same time frames (synchrony count: $r_s = 0.97$, $N = 115$, $p < 0.001$; min(N_i, N_j): $r_s = 0.973$, $N = 115$, $p < 0.001$), and 3) nest-video without breeding females *vs.* PIT-tag (synchrony count: $r_s = 0.98$, $N = 115$, $p < 0.001$; min(N_i, N_j): $r_s = 0.97$, $N = 115$, $p < 0.001$). Synchrony frequency in the direct comparison was also strongly correlated between these three same comparisons: 1) nest-video with breeding females *vs*. nest-video without breeding females ($r_s = 0.95$, $N = 112$, $p < 0.001$, Fig. 1.7a), 2) nest-video with breeding females *vs*. PIT-tag ($r_s = 0.94$, $N = 109$, $p < 0.001$, Fig. 1.7b), and 3) nest-video without breeding females *vs*. PIT-tag ($r_s = 0.97$, $N = 109$, $p < 0.001$, Fig. 1.7c).

The removal of breeding females before the determination of synchronous visits caused the deviation of only a small number of dyads from the linear relationship (Fig. 1.7a-b). These outliers in the correlation plots between the different methods were mainly attributable to the short recording duration over which this comparison was made (only the period where both PIT-tag and nest-video were operating): both min(N_i, N_j) and the synchrony count were small (0-4, 0-3, respectively) for dyads showing rather large differences in synchrony frequency (>0.2) between the three sets of data. Thus, failure to identify even a single synchronous visit due to the removal of the breeding female can cause this magnitude of difference in the synchrony frequency for dyads with a small value for synchrony count and min(N_i, N_j) (i.e. 0-4). This therefore suggests that it is important to gather large amounts of data over an extended period to study dyad-wise nest visit synchrony (as I have done with the PIT-tag data), as this bias will be negligible when the full PIT-tag data across a longer monitoring period are used.

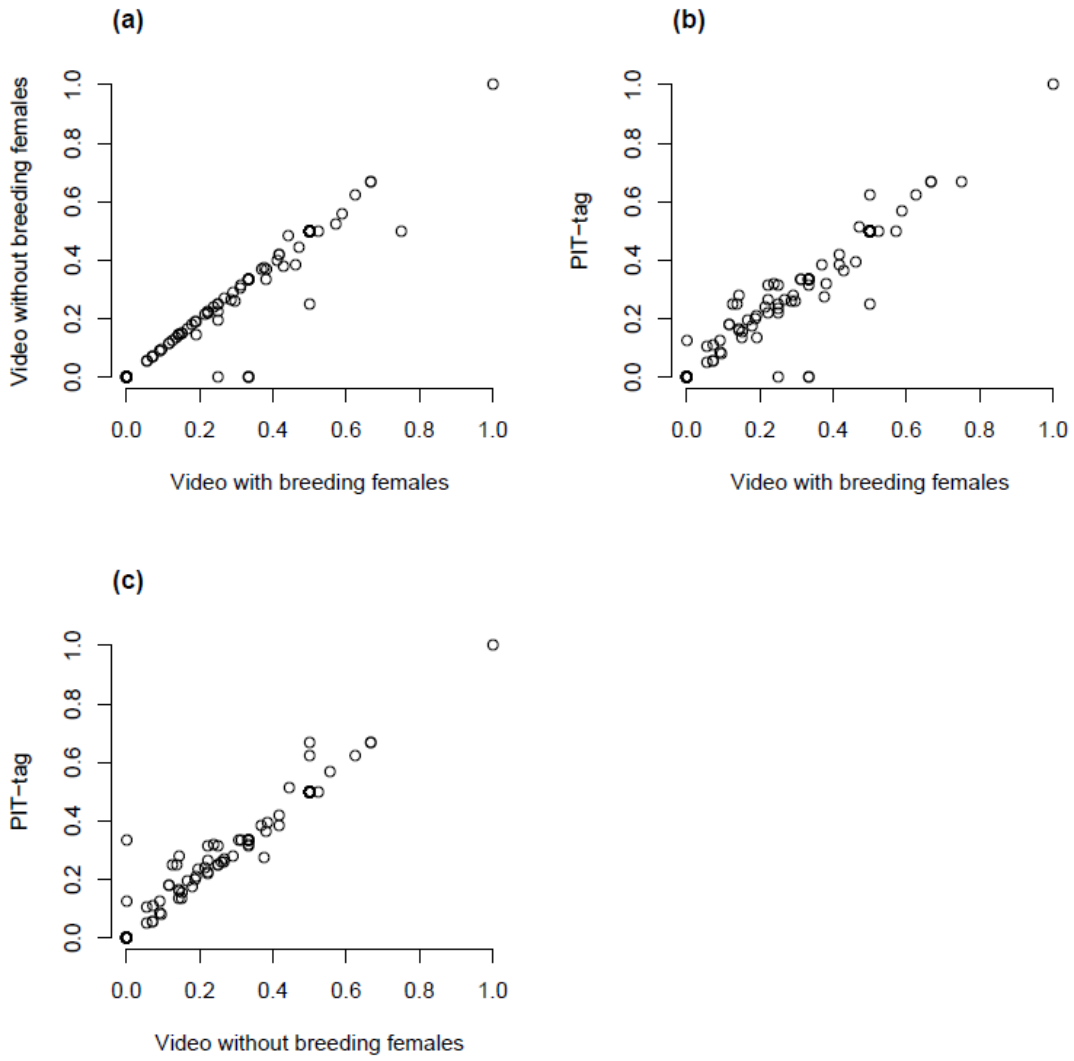

Figure 1.7. Correlations of synchrony frequency between different monitoring methods were strong. (a) nest-video data with breeding females and nest video data without breeding females, (b) nest-video data with breeding females and PIT-tag data, and (c) nest video data without breeding females and PIT-tag data. Only nest visits that occurred in the time frame where both nest videos and PIT-tag readers were recording were used. Note that values for dyad involving breeding females are excluded here.

Community structure

In all of the nest-video data analysed with the latent cluster random-effects model (18 breeding attempts from 15 breeding units), no clear community structure of networks was found. The 2-community models for nest-video data assigned all unit

members into one community leaving the other community empty. Although all breeding units did not form clear communities, the distances between individuals in the latent social space were variable (Fig. 1.8a-b), reflecting the variation of synchrony frequency. The exclusion of breeding females from the nest video data caused no difference in the community structuring (results are not shown).

The 2-community models for more extensive PIT-tag data (46 breeding attempts of 29 breeding units) identified weak division of networks in only two breeding units (Table 1.2, Table 1.3, Fig. 1.9). However, standard deviations of the community positions were largely overlapping (e.g. Fig. 1.9) and community assignment probabilities for individuals assigned to the smaller communities were similar for both communities over both of the two breeding attempts analysed (Table 1.2, Table 1.3). One immigrant female was excluded from the main community in both 2007 and 2008, which hints that the synchrony reflects consistent relationships between individuals. The 3-community model for these two breeding units did not identify a third community. Networks of all other breeding units had only one community (e.g. Fig. 1.8c-f). Overall, network sub-structuring in the form of community of breeding unit during offspring provisioning was weak in this species.

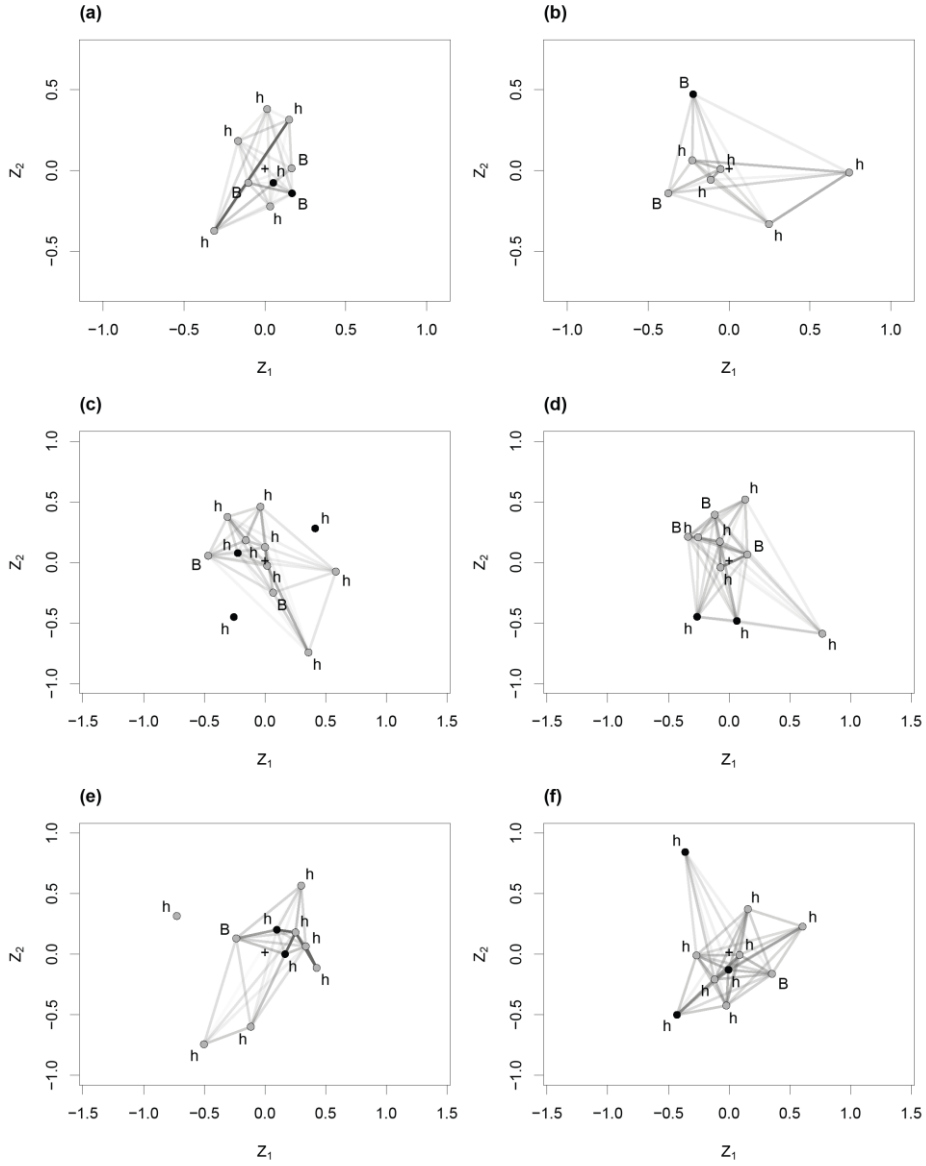

Figure 1.8. Examples of estimated social networks. (a-b) were estimated from nest-video data including breeding females. (c-f) were estimated from PIT-tag data. Nodes of the networks represent individuals, and their positions in the latent social space were estimated by the model. Grey nodes are males and black nodes are females. Darkness of the edge colours is proportional to the observed synchrony frequency. Labels for the nodes are B: breeder, h: helper. Crosses correspond to estimated mean position of networks which are scaled to $Z_1 = 0$, $Z_2 = 0$. (a) cek0702, (b) efg0702, (c) cek0702,(d) ceo0802, (e) efg0702, and (f) efp0801. ID of broods are coded as name of breeding unit (e.g. cek), year, and attempt (first: 01, second: 02, third: 03).

Table 1.2. Community assignment probabilities for individuals in two breeding attempts, sfn0702 and sfn0801 based on PIT-tag data.

	sfn0702					sfn0801				
Sex	Community 1	Community 2	Status	Age	Visit/d	Community 1	Community 2	Status	Age	Visit/d
f	**0.584**	0.416	h	a	1.167	0.251	**0.750**	h	a	0.050
m	0.440	**0.561**	h	a	2.125	**0.909**	0.092	h	a	1.900
m	0.111	**0.889**	h	a	8.625	**0.942**	0.059	h	a	11.950
m	0.084	**0.917**	h	y	3.375	**0.927**	0.073	h	a	8.200
m	0.094	**0.907**	B	a	16.125	**0.940**	0.060	B	a	19.700
m	0.078	**0.923**	h	j	0.792					
m	**0.680**	0.321	h	j	0.792	**0.948**	0.052	h	y	21.150
m						**0.951**	0.050	h	y	7.000
m						**0.891**	0.109	h	y	4.100

Higher assignment probability for each individual was shown in bold. f: female, m: male, B: breeder, h: helper, a: adult, y: yearling, j: juvenile. The membership of the breeding unit changed between 2007 and 2008 and individuals that did not attend the nest in a given attempt were left blank. Results of 2-community models are shown.

Table 1.3 Community assignment probabilities for individuals in an attempt by one breeding unit, ofq0702 based on PIT-tag data.

Sex	Community 1	Community 2	Status	Age	Visit/d
m	0.124	**0.877**	h	a	21.167
m	**0.584**	0.417	B	a	28.167
m	0.213	**0.787**	h	j	0.111

Higher assignment probability for each individual was shown in bold. f: female, m: male, B: breeder, h: helper, a: adult, j: juvenile. Only a result of 2-community model is shown.

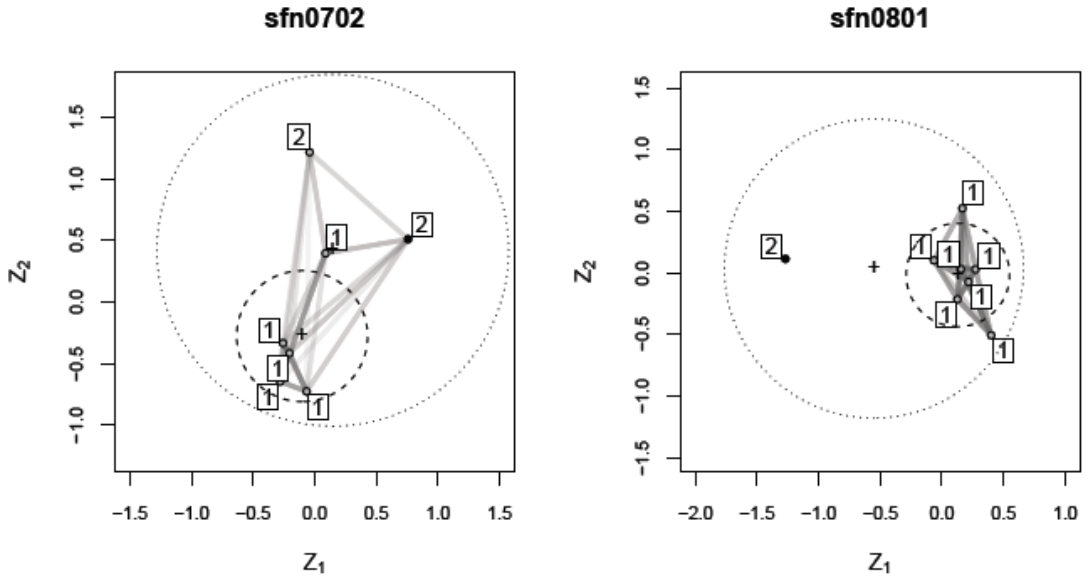

Figure 1.9. Clustering of breeding unit sfn in 2007 and 2008 estimated from the PIT-tag data. Dashed circles are standard deviations of the position of the main communities (community 1), and dotted lines are standard deviations of the position of the communities containing smaller number of individuals (community 2). Community structuring was weak in both years. The number of individuals excluded from the main cluster was only two in 2007 and one in 2008. Crosses show estimated mean positions of individuals within clusters. Nodes were labelled with ID of the clusters (1 or 2) into which they were assigned by the latent cluster random effects models (2-community models). Black nodes are females and grey nodes are males. Other attributes for the individuals in this breeding unit are listed in Table 1.1.

Individual connectedness in the networks

Individual tendencies to form connections with others in the network (measured on the basis of a 'sociality' term) were variable, even after I controlled for the effects of individual visit rate, variability across broods, and the effects of transitivity in the hierarchical latent space model. Individual connectedness estimated using PIT-tag data revealed more variation compared to the estimates based on nest-video data. None out of 96 estimates for nest-video data was significantly different from average level of

connectedness (corresponding to parameter value of zero, N = 96 individual-brood ID, Fig. 1.10, Table 1.4). On the other hand, PIT-tag estimates for both 2007 and 2008 showed lower uncertainty in the estimates (narrower credible intervals, Fig. 1.10, Fig. 1.11), perhaps owing to the larger number of synchronous visit bouts per dyad. Eleven estimates (3.8%) were higher and lower than average (N = 290, Fig. 1.11, Table 1.5). In the PIT-tag data, individuals that had higher 'sociality' than average were not restricted to certain categories. Such individuals included both those natal to the social group to which their breeding unit belongs (6 out of 11) and those whose origin is unknown (5 out of 11). Both of two individuals that had a sociality estimate below average were helpers (one female and one male) born in a social group other than that to which they currently belong. In addition to identifying these rare outliers, lower uncertainty in the estimates suggests analyses based on the larger data is more reliable and will open broader opportunities to explore factors associated with the connectedness of individuals.

Table 1.4. Summary of parameter estimates of the hierarchical latent space model fitted to nest-video data.

Parameters	50%	2.5%	97.5%
Intercept	-1.037	-1.399	-0.685
SD for brood ID	0.342	0.176	0.532
SD for sociality	0.151	0.007	0.260
SD for latent space position	0.156	0.006	0.359

Median and 95% CI of parameter estimates are shown. SD denotes standard deviation.

Table 1.5 Summary of parameter estimates of the hierarchical latent space model fitted to PIT-tag data.

Parameter	50%	2.5%	97.5%
Intercept	-1.017	-1.123	-0.904
SD for brood ID	0.185	0.137	0.289
SD for sociality	0.141	0.107	0.175
SD for latent space position	0.170	0.122	0.230

Median and 95% CI of parameter estimates are shown. SD denotes standard deviation.

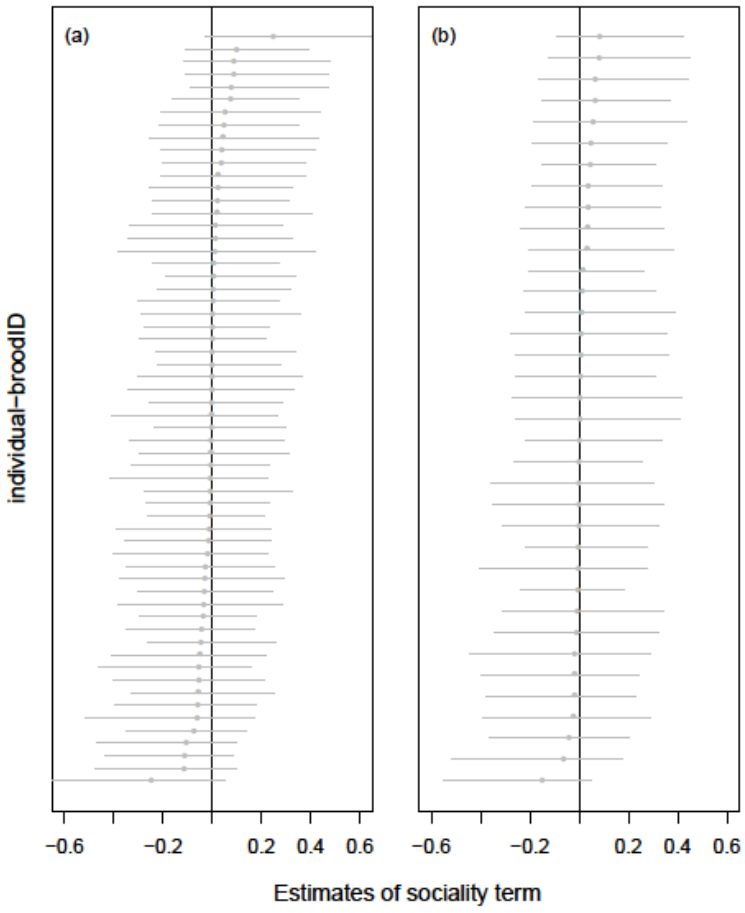

Figure 1.10. Estimates (medians and 95% CIs) of 'sociality' ($\delta_{i,k}$) for all individuals based on the nest-video data (breeding females are included) are presented in the increasing order from the bottom. Zero corresponds to global mean of estimates (both years combined). All estimates included zero in the 95% CI, indicating that no individual showed 'sociality' significantly different from the average. (a) shows estimates for individuals observed in 2007 and (b) shows estimates for 2008.

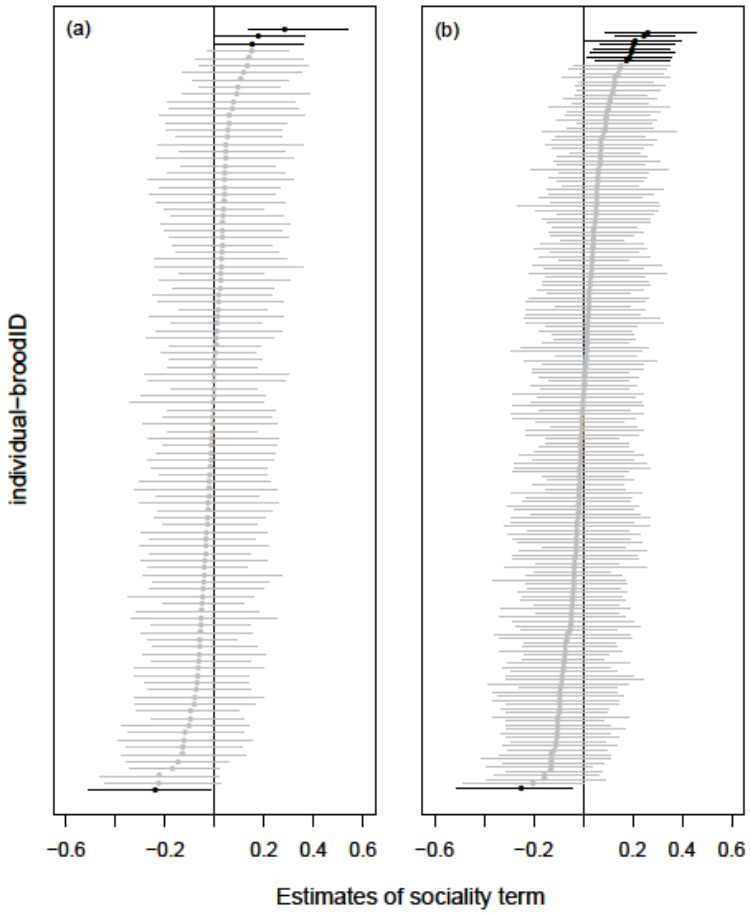

Figure 1.11. Estimates (medians and 95% CIs) of 'sociality' ($\delta_{i,k}$) for all individuals based on the PIT-tag data (breeding females are not included) are presented in the increasing order from the bottom. Zero corresponds to global mean of estimates (both years combined). Several estimates were significantly different from zero, which are shown in black. Estimates that included zero in the 95% CI are shown in grey. (a) shows estimates for individuals observed in 2007 and (b) shows estimates for 2008.

Discussion

I have successfully validated an economical method for quantifying social networks in a novel context, although species-specific validation is likely to be necessary through similar techniques to those used here. Nest visitation duration, and particularly frequency, was obtained with a high degree of accuracy for all group members, other than the breeding female, which spend variable times in the nest. I recommend that in similar circumstances, breeding female visitation is determined with two-way antennae, inexpensive temperature gauges (e.g. Joyce et al. 2001) or sound recording equipment. Two-way antennae are more suitable for nest box species or those visiting a burrow or funnel entrance. However, I were able to estimate both nest visit behaviour and key metrics of social networks with a high degree of confidence.

Although one of the key points of this paper was to provide methodological guidance to the collection and analysis of an otherwise routinely collected behaviour (i.e. individual provisioning behaviour), it is important to note that all social network analyses are constrained in only being able to analyse those individuals that actually contributed to a given behaviour in a given location. For example, Chestnut-crowned Babblers live during periods of non-breeding in large social groups (3-23, mean = 11), which then disband into smaller, discrete units for breeding (2-15, mean = ~6) (Portelli et al. 2009; Russell et al. 2010). Given that these units are virtually wholly distinct during breeding, with each unit member contribution to the nest in which it is associated (Browning et al. 2012a), means that community structuring must occur in babblers at the level of the non-breeding social group. In addition, not all members of a breeding unit contributes to offspring rearing, with non-breeding unrelated unit members (particularly immigrant females) refraining from offspring provisioning (Browning et al.

2012a). Thus multiple communities within breeding units are also likely to occur between carers and non-carers, but again this cannot be analysed when the currency used is provisioning. Indeed, it is noteworthy in this regard that I found that all birds that were significantly less connected than average were immigrants and that an immigrant female repeatedly had peripheral position in one breeding unit in both 2007 and 2008.

Notwithstanding, our methods are wholly appropriate for investigating the question of how social network based on offspring-provisioning behaviour in a cooperatively breeding vertebrate is structured. Our evidence suggests that there were no community structure within breeding unit in this species. Despite the peripheral positions of some individuals, I did not find any clear divisions within the networks of carers, suggesting that, in this species, all carers are linked to each other in the social network. A possible explanation is that by remaining as a single cohesive unit, babblers maintain information of the behaviour of other carers and/or brood need; thereby maintaining efficient provisioning (Johnstone & Hinde 2006). On the other hand, connectedness of individuals within networks based on PIT-tag data showed substantial variation, while further studies are needed to elucidate what factors may produce variation in the individual connectedness. Distribution of individual connectedness in each breeding unit may affect breeding success of the units if well-connected individuals play a role in increasing cohesiveness of the units at a level more subtle than subdivision into communities (Bode et al. 2011).

More generally, the success of any study attempting to construct the social network of interacting individuals is heavily dependent upon gathering a high number of replicated encounters or interactions between all individuals. For animals frequently returning to a central place - such as a breeding nest, burrow, or den - our results

demonstrate that the use of a PIT-tag system can improve monitoring of visits in terms of both the number of groups, the number of dyads and the number of synchronous events recorded, over an extended period. As well as being able to collect large numbers of interactions using an automated monitoring system that can be run for a long time, the data processing is relatively straightforward as well. By contrast, data collected with nest-video cameras is more limited in its scope (currently they are unable to run for as long as the PIT-tag system), and in the cost and efficiency with which the video data can be processed manually. An analysis based on the more extensive data set from the PIT-tag system results in a more reliable measure of network structure, as long as it is validated and coupled with appropriate statistical methods. The PIT-tag system also allowed us to collect behavioural data from a large number of breeding units, resulting in many discrete networks involving different groups. The need of analysing multiple discrete networks appears in studies on both humans (Sweet et al. 2012) and wild animals (Cross et al. 2012) to ensure that conclusions of the studies do not rely on a single network obtained by chance. In this study, multiple discrete networks were analysed with a hierarchical version of the latent space model. More common statistical approach to this kind of data involves conducting a statistical test or fitting a model for one network at a time (e.g. Goodreau et al. 2009; Madden et al.2009). Although such approaches may work well depending on the purpose of the study, the hierarchical modelling approach can provide one way to investigate patterns or effects that are common to all the separate networks (e.g. what factors affect individual connectedness?).

The approach I have demonstrated to characterise social network, is potentially applicable to a wide range of animal societies and behavioural contexts. Mark-recapture studies persist in many taxa, but is generally an ineffective way of accurately

quantifying social networks owing to uncertainty of group/population membership (but see Korslund 2006; Perkins et al. 2009; Streatfeild et al. 2011). Even in the species where observations of social interactions are relatively easy, automated monitoring would substantially contribute to understanding of social network if it helps to increase sample size. An important but little understood aspect of social network structure in animals is their stability across contexts and time (Whitehead 2008; Sih et al. 2009). To begin to gain insight into social relationship dynamics and stability, new studies will need to quantify social networks over long periods and across multiple behavioural contexts to reveal how dynamic the social networks are, and how stability has impacts on population level processes, individual behaviours and fitness (Sih et al. 2009). The efficiency with which the social interactions data are collected is key to being able to address such questions. The PIT-tag system can be applied to study social network if individuals keep returning with other individuals to a closed space with relatively small entrance to which the coil antenna can be installed (e.g. roost sharing of bats, Patriquin et al. 2010) or a feeding station that can be established to monitor the feeding visits of different members of a social group (e.g. Mariette et al. 2011). There should be more situations where the PIT-tag system can be used to quantify social network (e.g. timing of entry and departure at burrows of social mammals or reptiles). Although the applicability and effectiveness of the approach depends on species and study questions, I believe that PIT-tag monitoring will facilitate studies on social networks in many taxa that have not been accessible to this kind of research to date.

Chapter 2

Social prestige benefit and nest visit synchrony

Introduction

In humans, individual contributions to cooperation are commonly influenced by the presence of onlookers. A subtle form of an 'audience', such as a pair of abstract eyes, can be sufficient to reduce defection from the common good (Haley & Fessler 2005; Bateson et al. 2006). Dictator games reveal that individuals donate less of their money to non-endowed players with increasing anonymity (Bonhet & Frey 1999; Burnham 2003; Soetevant 2005; Charness & Gneezy 2008; Alpizar et al. 2008; Engel 2011). Additionally, an employee's work rate can be elevated by being in direct view of an influential co-worker (Bandiera et al. 2005; Mas & Moretti 2009). While the full array of mechanisms accounting for such observations is not fully understood, at least one important contributor is that cooperators gain social benefits (or prestige) from their 'altruistic' actions in the presence of others (Nowak & Sigmund 1998; Wedekind & Milinski 2000; Gintis et al. 2001; Lotem et al. 2003; Mas & Moretti 2009). Despite the significant evidence for a role of social prestige, or image scoring, in explaining human cooperation, whether or not this is true of other animals is more contentious (Nowak & Sigmund 2005; Bshary & Gutter 2006).

One context in which social prestige has been suggested to account for cooperation in animals is in cooperative breeding systems (Zahavi 1974, 1990, 1995; Roberts 1998; Lotem et al. 2003), wherein non-breeding group members provide care to the offspring of breeders. While kin selection has a significant influence on the incidence of cooperative breeding in most cases, it neither presents a universal explanation nor explains all of the variance in helper decisions (Emlen 1991; Cockburn 1998; Cornwallis et al. 2009). The social prestige hypothesis proposes that the evolution

of cooperative breeding, as well as the levels of investment in cooperative care therein, could be accounted for by selection on signalling the ability to invest in parent-like behaviours. The primary assumptions of this hypothesis are typically upheld in cooperative vertebrates: that helping is costly and that the magnitude of such costs vary among individuals; so contributions to cooperation can potentially represent a reliable signal of an individual's ability to invest in offspring. For example, individual contributions to cooperation are typically elevated to varying degrees by supplemental feeding (Boland et al. 1997; Wright & Dingemanse 1999; Clutton-Brock et al. 2002) and those that contribute heavily to cooperation typically suffer reduced growth/mass gains (Russell et al. 2003).

By contrast, evidence in support of critical predictions is scant and inconclusive. Ultimately, the key predictions of the evolution of cooperative breeding through social prestige are that: (1) patterns of helper provisioning reflect an attempt at self-advertising quality; (2) increasing competition through market forces should inevitably lead to increasing individual investment; (3) partner choice should be based on levels of investment; (4) current contributions are a reliable indicator of future contributions; and (5) choosing high contributors leads to a fitness advantage. Testing all such predictions is beyond the scope of a single study, and it seems sensible to tackle them in sequence since the latter predictions become increasingly obsolete as the former are rejected for a given system. Accordingly, the few tests of the social prestige hypothesis in cooperative breeders have specifically addressed the first two predictions only, with conflicting results (Carlisle & Zahavi 1986; Wright 1997, 1998; Doutrelant & Covas 2007; McDonald et al. 2007, 2008a, b).

First, there is inconsistent evidence that helpers behave so as to maximize the chances that their cooperative actions are witnessed by the intended audience. Helpers

in Arabian babblers (*Turdoides squamatus*) were found to utter loud vocalizations and to wait for other group members before approaching the nest with food (Carlisle & Zahavi 1986), but such findings were not corroborated by a follow-up study on the same population (Wright 1997). In the colonial sociable weaver (*Philetairus socius*), helpers were found to hold their prey for longer than parents before provisioning offspring, and did so particularly when rainfall was low and when they had a large load size; suggesting that helpers might be attempting to advertise their investment (Doutrelant & Covas 2007). However, such apparent supporting evidence might be explained by confounding effects. For example, in a study of human observer effects in bell miners (*Manorina melanophrys*), McDonald et al. (2007) found that when observers were close to the nest, group members increased the frequency of 'false feeding', which has been suggested to be an attempt to increase their apparent contribution. In addition, Raihani et al. (2010) showed in pied babblers (*Turdoides bicolour*) that waiting for other group members before visiting the nest could be explained adaptively by birds attempting to reduce nest visit rate when the threat of nest predation is high. Indeed, in the most comprehensive tests, McDonald et al. (2008a) found no evidence that helpers in bell miners attempt to advertise their investment to breeding females, one of the most likely recipients of signalling under social prestige, and removal of the breeders had no influence on the provisioning behaviour of helpers (McDonald et al 2008b). Second, there is little evidence that helpers compete with each other over contributions to cooperation, although Carlisle & Zahavi (1986) reported that dominant helpers attempted to prevent more subordinate helpers from feeding nestlings. However, again this was not corroborated in follow-up studies (Wright 1997, 1998), and as outlined above, this discrepancy might be caused by confounding effects of observer presence (Wright 1997; McDonald et al. 2007).

The broad aim of this study was to test the first two predictions outlined above of the social prestige hypothesis in the Chestnut-crowned Babbler (*P. ruficeps*), a 50 g obligate cooperative breeder endemic to arid and semi-arid regions of southeastern Australia. Several features of this species rendered it particularly apt for this study. First, the sex ratio of babbler groups is significantly male biased (1.7:1.0; Rollins et al. 2012), meaning that males need to compete with each other to secure a breeding female as a mate. Second, along with the breeding male, helper males are commonly unrelated to the current breeding female owing to frequent breeder turnover followed by female immigration (Rollins et al. 2012), meaning that males might be expected not only to benefit from signalling their quality to the breeding female, but also to compete with others to do so. Third, males have rarely been observed to disperse in coalitions (Rollins et al. 2012), meaning that there should be relatively little benefit for males to signal their quality to each other, at least under social prestige (Zahavi 1995). Finally, Chestnut-crowned Babblers are only weakly territorial (Portelli et al. 2009) and nest predation is uncommon (Russell et al. 2010). Consequently, the primary way in which group members can help is through nestling provisioning (Browning et al. 2012a) and the threat of nestling predation is unlikely to influence the pattern of provisioning.

Together, these features of the Chestnut-crowned Babbler suggest that the primary target of any male signalling under social prestige will be the breeding female and that the primary method of signalling will be through strategic contributions to offspring provisioning. These details are important both biologically and statistically: with a single audience and a single currency of advertising, males' efforts to advertise their quality will not be diluted across multiple birds or contexts, substantially increasing any selection on signalling as well as statistical detection thereof. Specific aims here were to test whether those males most likely to benefit through social prestige

provision offspring in a way that maximizes their detection by the breeding female, and compete with potential rivals to do so. These aims were addressed by investigating whether those males most likely to benefit from signalling (i.e. those unrelated to the breeding female) simply contribute more to offspring provisioning and/or whether they attempt to increase the breeding female's perception of their investment by coinciding their feeds with her presence. This latter aim is important for two reasons. First, males that are unrelated to the breeding female will be less related to the brood on average (maximum r = 0.25 through the breeding male) than those that are related to her (minimum r to brood = 0.25). As such, if the kin-selected benefit of helping mothers exceeds the prestige-selected benefit of helping non-mothers, then males helping the latter need not contribute more than those helping the former, but only males helping non-mothers should be under selection to compete with rivals and coincide their visits with the breeding female (Zahavi 1990, 1995). Second, a potential force selecting against signalling is that the costs to the target individual(s) of monitoring the provisioning rates of group members might be prohibitively high (Dawkins & Guilford 1991; Semple & McComb 1996; Roberts 1998). I reduced this problem by effectively investigating whether potential signallers have been selected to reduce the costs to the target of monitoring their contributions. Finally, I used a combination of standard mixed modelling approaches and, where necessary, recently developed social network analyses, with the latter allowing greater control of non-independent data inevitably arising from multiple provisioning birds within the group (see Methods).

Methods

Field methods

Study population and general field methods are described in Chapter 1.Overall provisioning data were collected for 1.1–13.6 h per day (mean ±SD = 4.65 ± 3.46 h) at 23 nests of 19 breeding units over 1–6 days during the 23-day provisioning period (mean ±SD = 2.59 ± 1.68 days). I only included nest visits with food, about 90% of all nest visits (Young et al. 2013), totalling 1,630 nest visits with food by 81 males.

All breeding unit members were categorized according to their relationship to the breeding female; the numbers in each category are provided in the Figures. Males that gained paternity in a given attempt were assigned as either a sole breeder (BMs) or polyandrous breeders (BMp). Paternity was assigned with precision at all nests using 14 polymorphic microsatellite loci (Holleley et al. 2009; Rollins et al. 2012). Helper males that gained no paternity in the brood were categorized as being either related (HMr) to the breeding female or not (HMu). This is because females rarely immigrate into groups as related coalitions (Rollins et al. 2012); so helpers are either offspring of the breeding female or unrelated to her. (Note that HMu are not necessarily unrelated to the brood, as they will commonly be related through the breeding male; Browning et al. 2012a). For helpers, relationships with the breeding female were determined through pedigree data, although 23% were determined through pairwise relatedness values determined using the 'Coancestry' software program (Wang 2011). In the latter case, helpers were assigned as related if they had pairwise relatedness values $R \geq 0.20$, with this cut-off being used since all known offspring and non-offspring of the breeding female have higher and lower relatedness values, respectively (mean known related: $R = 0.49$, range 0.37–0.70, $N = 36$; mean known unrelated; $R = 0.06$, range -0.15–0.18, $N = 7$). Both

genetic relatedness and molecular sexing (Griffiths et al. 1998) were conducted on DNA extracted from blood samples (<100 μl) collected following brachi-venipuncture and stored in 100% ethanol (see Rollins et al. 2012 for further details).

Statistical analyses were conducted using one of three approaches: a generalized linear mixed-effects model, a zero-inflated Poisson model and a social network model (see below for specific details). In all models, parameter estimates were derived using a Bayesian method employing Markov chain Monte Carlo (MCMC) in WinBUGS 1.4 (Spiegelhalter et al. 2003). Continuous explanatory variables, breeding unit size and the number of unrelated males therein were centred in order to facilitate model fitting (Gelman & Hill 2007). Breeding unit size was fitted to control for inter-unit differences in the availability of carers and/or patterns of brood care by the breeding female. The number of males that were unrelated to the breeding female in the breeding unit was used as an indicator of potential competition. Where possible, the male category effect and its interaction with the number of unrelated males were included as random intercepts and slopes, respectively. This allows more conservative inference by estimating a variance associated with the difference of slope across categories: fixed-effect interactions are a special case of the random slope with the variance parameter being fixed to infinity (Gelman & Hill 2007). Estimated parameters are considered significant in the sense of Bayesian statistics when 95% credible intervals (CI) of the posterior distributions do not include zero. The significance of categorical variables and interactions was examined by pairwise comparison of the estimate of each level (post-processing of posterior distributions).

Nestling provisioning rates

Individuals might attempt to signal their quality to the breeding female simply by

provisioning at a high rate. To test this idea I fitted the numbers of feeds by each individual recorded in the total observed time period as the response term in a zero-inflated Poisson (ZIP) mixture model (Martin et al. 2005; Congdon 2010; see also Cockburn et al. 2008). The ZIP mixture model comprised two regression components: a Poisson regression with logarithm link function and binomial regression with logit link function, with the former using counts of feeds and the latter using the probability that a given individual fed. I fitted observation time (h) as an offset term in the Poisson component and as an explanatory variable in the binomial component to control for the variable amounts of times for which nests were observed. Breeding unit size and the number of males unrelated to the breeding female were fitted as fixed terms in both Poisson and binomial components. I also included male category and its interaction with the number of unrelated males as fixed effects rather than random terms because of computational constraint (cf. Bolker et al. 2009). Individual and brood identities were fitted as random terms to account for any biases arising from the few repeated measures in the Poisson component only: 10 of 81 individuals were monitored across two breeding attempts in three of 19 breeding units (N = 23 broods). I was unable to include either random term in the binomial component owing to model non-convergence. Previous analyses in this population of babblers have revealed that male group members contribute similarly to brood provisioning irrespective of whether the brood is related by 0.5 or 0.25 on average (Browning et al. 2012a). The social prestige hypothesis therefore predicts that male babblers that are related to the brood, but unrelated to the breeding female, will provision offspring at a higher rate than those that are related to both, and that the former, but not the latter, will increase their provisioning rates as a function of increasing competition in the group.

Timing nest visits to female brooding periods

Males could attempt to signal their quality to the breeding female by timing their arrival to coincide with periods when the breeding female is brooding nestlings. The proportion of feeding visits that males conducted when the breeding female was brooding was used as the response term in a generalized linear mixed model (GLMM) with a binomial error structure and logit link function. Fixed effects included breeding unit size and the number of unrelated males in the breeding unit, while random terms included individual and brood identities. Male category effect and its interaction with the number of unrelated males were also included as random intercepts and slopes, respectively. This analysis is based on 61 individuals from 19 breeding units (individual–brood ID: N = 67; brood ID: N = 23). The sample size was reduced in this analysis compared with that given above because individuals that did not visit the nest were removed. I predicted that those males that are unrelated to the breeding female should time their visits to coincide with the breeding female brooding chicks and that this should be particularly the case when the potential for competition increases.

Synchronizing nest visits with breeding female

Males under selection to signal their quality to the breeding female may do so by timing their arrival at the nest to coincide with the breeding female's arrival. I defined a series of visits in the nest video data as synchronous when temporal separation between nest entry times were less than 1 min. Individuals were deemed synchronous with the breeding female when they and the breeding female visited the nest within the same group of synchronous visits.. This rather protracted time interval arises because provisioning birds tend to wait for the previous bird to exit the domed nest before entering (Young et al. 2013) and breeding females commonly preen nestlings or repair

the inside of the nest for a brief period before exiting (AF Russell and LE Browning unpublished data). The relevance of this cut-off value was confirmed using hide observations; the distribution of the time separation between nest visits by synchronizing individuals is provided in Fig. 1.3. The measure of synchrony between a breeding female *f* and male *m* was defined as $Y_{f,m}/\nu_f\nu_m$, where $Y_{f,m}$ is the rate of synchronous nest visits by male and the breeding female, ν_f the visit rate by the breeding female and ν_m the visit rate by male. The ratio $Y_{f,m}/\nu_f$ is considered as the female-perceived contribution by males. If males attempt to increase this perceived contribution without raising their actual contribution (ν_m), $Y_{f,m}/\nu_f\nu_m$ is expected to become higher; $Y_{f,m}/\nu_f\nu_m$ was compared across males of the four different categories mentioned previously, with predictions as outlined for (2) above.

However, dyadic data suffer from problems of data independence (Krivitsky et al. 2009; Croft et al. 2011). Dyadic data suffer from problems of data independence (Krivitsky et al. 2009; Croft et al. 2011), leading to at least two sources of bias, as described in Chapter 1. First, individuals may have specific levels of synchrony regardless of the partners with which they synchronize. If a certain individual has a high general tendency of synchrony with group members, synchrony frequencies of that individual with all other breeding unit members will be high. In this case, high synchrony between a breeding female and a given male may be a by-product of the general synchronous tendency of that male. Second, dyadic data can be affected by individuals outside the dyad. For example, if a male has a high level of synchrony with another male, and this latter male has a high preference to synchronize with the breeding female, the focal male would also be observed to have high synchrony with the breeding female even if he does not have a strong preference to synchronize with her. The third-party effect of this form is known as transitivity in the social network literature (Wasserman & Faust

1994). To deal with these potential sources of bias, I used a latent space model in which synchrony between all combinations of breeding unit members was fitted to a Poisson distribution with log link function, and problems of independence were accounted for by fitting 'sociality' and 'distance in latent social space' terms as random effects (Hoff et al. 2002; Hoff 2005; Krivitsky et al. 2009).

To analyse dyadic data effectively, a latent space model (Hoff et al. 2002; Krivitsky et al.2009) was specified as follows: $y_{i,j} \sim$ Poisson ($\lambda_{i,j}$), $\log(\lambda_{i,j}) = \beta_0 + \log(t_{i,j}) + \log(v_i) + \log(v_j) + \beta_1 w_{i,j} + \beta_2 x_{i,j} + \alpha_c + \gamma_c x_{i,j} + \varphi_s + \delta_i + \delta_j - \| Z_i - Z_j \|$, for i (or j) = 1,…, k, c = 1,…, l and s = 1,..., n, where k is the number of individuals, l is the number of dyad types and n is the number of brood ID. $y_{i,j}$ is the number of synchronous visits per dyads i, j, ($i \neq j$), $t_{i,j}$ is observation duration, and v_i (or v_j) is feeding visit rate/h by individual i (or j). β_1 is a slope for the number of provisioning birds in the breeding units (the size of breeding units, $w_{i,j}$). This term was added as a covariate because synchrony is expected to be more frequent in larger breeding units. β_2 is a slope for the number of 'unrelated males' within breeding units ($x_{i,j}$). α_c is the random intercept for dyad types, γ_c is the random slope varying by dyad types for the number of males unrelated to the breeding female (serving as an interaction). The offset terms, $\log(t_{i,j}) + \log(v_i) + \log(v_j)$, were added so that synchronous visit rate ($Y_{i,j} = y_{i,j}/t_{i,j}$) is evaluated relative to $v_i v_j$ in the model. δ_i is a 'sociality' random effect (Hoff 2005). The term $\| Z_i - Z_j \|$ represents Euclidean distance in a two-dimensional latent social space and serves to deal with the transitivity effect. Z_i is a vector of two dimensions representing the positions that individual i has relative to other unit members in the latent social space. Individuals will have closer positions to others when they more frequently synchronize. In this model, the few individuals (see above) that appeared in the data from multiple broods were treated as different individuals for simplicity, because the estimation of transitivity

across different attempts is difficult. However, a random term φ_s was included to account for variation in the level of synchrony across broods. For the latent social space Z_i, a multivariate normal distribution of two dimensions was specified as a prior with uniform distributions of range [0, 100] as hyperpriors. I used 60 individuals from 19 breeding units for this analysis (individual–brood ID: N = 66; brood ID: N = 23). Only individuals that fed the nestlings at least once during monitoring were included.

Feeding before versus after breeding female

Finally, if males try to advertise themselves to the breeding females in their synchronous nest visits, they might be expected to ensure that they are next in line to provision the nestlings following the breeding female. This is because the lack of obvious queuing-to-provision in Chestnut-crowned Babblers and the enclosed nature of their nests mean that the breeding female is most likely to witness a feeding attempt when it immediately follows her own. I therefore examined whether those males most likely to benefit from advertising arrived at the nest before (precede) or after (follow) the breeding female during synchronous visits. I examined the ratio of the number of follows by males to the total number of the synchronous visits between the males and breeding females as a response term of a GLMM with binomial error structure and logit link function. The same fixed and random terms as the model for encounter with the breeding female described above were used in this model. Only dyads that showed synchronous visits during the video recording were used in this analysis: 52 individuals from 18 breeding units (individual–brood ID: N = 58; brood ID: N = 22).

General statistical methods

Normal distributions with mean 0 were used for prior distributions for random effects in each case (Gelman et al. 2004). In addition, hyper-priors for the variance of the prior normal distributions were specified with non-informative uniform distribution with a range [0, 100] (Gelman et al. 2004). Model convergence was confirmed for all parameters, with the Gelman–Rubin statistic for all posterior distributions being less than 1.1 (Gelman et al. 2004). When included as random terms, estimates of the male category and its interaction were standardized following Gelman & Hill (2007), since limited numbers of levels in the factor male category can lead to biased estimates (i.e. non-identifiability, Gelman & Hill 2007).

Results

Nestling provisioning rates

Males included in these analyses provisioned offspring at an average rate of 2.1 times/h (sample mean, SD = 2.3, N = 91). This average provisioning rate was not significantly influenced by the number of individuals in the breeding unit (Table 2.1). Males that bred in competition (BMp) showed no tendency to feed nestlings more often than those breeding without competition (BMs), while non-breeding helper males that were unrelated to the breeding female fed offspring at a similar rate to those males that were related to the breeding female (Fig. 2.1a). Nevertheless, different categories of males appeared to differ in their sensitivity to the number of unrelated males in the breeding unit. Polyandrous males increased their provisioning rate as the number of unrelated males in the unit increased, while monogamous males showed a non-significant

tendency for the reverse pattern (Fig. 2.1b). The increase in the provisioning rate by polyandrous males was largely generated by their high probability of feeding young in the presence of more competitors (i.e. significant interaction in the binomial component of the ZIP mixture model, Table 2.1). Male helpers unrelated to the breeding female showed little difference in their provisioning rate as a function of the number of unrelated males, while related male helpers reduced their provisioning rate (Fig. 2.1b). The reduction shown by the former was again attributed to the lower probability of feeding by this category with increasing competitor number. These precise patterns of results are not predicted by the social prestige hypothesis (see Discussion).

Table 2.1. Summary of the parameter estimates in the zero-inflated Poisson mixture model for male feeding rate (medians and 95% credible intervals)

Parameter	50%	2.5%	97.5%
Poisson (non-zero count)			
Intercept (HMr)	0.70	0.30	1.07
Male category			
HMu	-0.13	-0.65	0.45
BMs	0.22	-0.38	0.87
BMp	0.40	-0.01	0.93
Size of breeding unit	-0.01	-0.13	0.10
Number of unrelated males (HMr)	0.01	-0.41	0.38
Number of unrelated males*Male category			
HMu	0.30	-0.32	0.85
BMs	-0.11	-0.56	0.38
BMp	0.10	-0.29	0.60
σ for individual ID	0.54	0.40	0.72
σ for brood ID	0.58	0.37	0.84
Binomial (probability of zero)			
Intercept (HMr)	-0.49	-1.76	0.62
Male category			
HMu	-0.24	-2.10	1.33
BMs	-0.05	-2.11	1.85
BMp	0.03	-1.46	1.54
Monitoring duration	-0.02	-0.11	0.06
Size of breeding unit	0.22	-0.03	0.48
Number of unrelated males (HMr)	0.84	0.16	1.73
*Number of unrelated males*Male category*			
HMu	-0.31	-1.60	0.64
BMs	0.71	-1.21	2.96
BMp	-2.24	-4.14	-1.13

σ denotes standard deviation of the random effects. The parameters for the male category term show the difference of each category relative to a related male helper (Intercept). Asterisk denotes an interaction (fixed effect) term. HMr: male helper related to breeding female; HMu: male helper unrelated to breeding female; BMs: sole sire; BMp: polyandrous male. Parameters of significant effect are shown in italics. Pairwise comparison was performed to test significance of the categorical variable and its interaction. Tuning parameters of MCMC (Markov chain Monte Carlo): three chains of 901,000 iterations with burn-in of 1,000 and 20,000 thinning intervals (135 iterations were saved). The Spearman rank correlation between breeding unit size and the number of unrelated males was $r_s = 0.40$, $P < 0.001$.

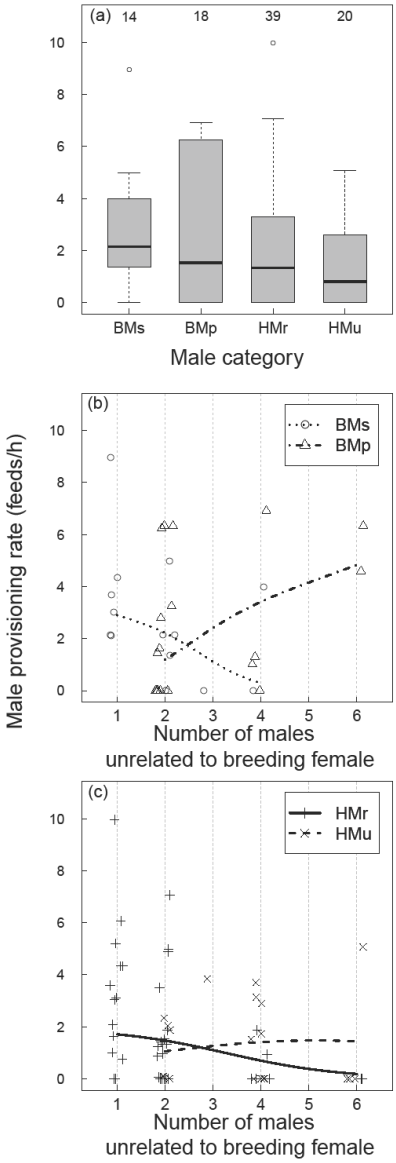

Figure 2.1. Hourly provisioning rate by males of different status. (a) Box plot shows median, interquartile range and approximate 2.5–97.5 percentiles of observed data. Circles represent outliers. Numbers at top denote the sample sizes for each category. (b-c) Effects of the number of males unrelated to the breeding female on provisioning rates of breeding males (b) and non-breeding helper males (c). Lines show values predicted by median estimates of the zero-inflated Poisson mixture model and cover ranges of the number of unrelated males observed for each category. BMs = sole sire; BMp = polyandrous sire; HMr = male helper related to breeding female; and HMu = male helper unrelated to breeding female. Data points are jittered along x axis. Vertical grey dotted lines show the true positions of values on the x-axis.

Timing nest visits to female brooding periods

On average, 40% (sample mean, SD = 26%, N = 67) of male nest entries with food were conducted when the breeding female was brooding young. The probability that males encountered the breeding female in the nest was independent of breeding unit size (Table 2.2). In addition, I found no statistical difference between male categories in the probability that they would encounter a brooding female during a provisioning visit; any apparent trends were not in a direction predicted by social prestige (Fig. 2.2a). On average, the probability that breeding females were encountered in the nest tended to increase as a function of the numbers of male unit members that were unrelated to the female, but the coefficient of the regression slope was not significant (Table 2.2). Furthermore, different categories of male did not respond differently to the number of potential competitors within the breeding unit (Fig. 2.2b, Table 2.2). None of these results is consistent with the predictions of social prestige.

Table 2.2. Summary of the parameter estimates in the generalized linear mixed models for probability of encountering with breeding female on nest (medians and 95% credible intervals)

Parameter	50%	2.5%	97.5%
Intercept	-0.30	-0.96	0.38
Male category			
HMr	0.06	-0.15	0.35
HMu	0.01	-0.28	0.35
BMs	0.01	-0.26	0.29
BMp	-0.07	-0.51	0.12
σ for male category	0.17	0.01	1.25
Size of breeding unit	-0.03	-0.27	0.26
Number of unrelated males	0.35	-0.30	0.99
Number of unrelated males*Male category			
HMr	0.05	-0.05	0.21
HMu	-0.03	-0.22	0.09
BMs	-0.03	-0.26	0.13
BMp	0.02	-0.11	0.23
σ for Number of unrelated males*Male category	0.11	0.01	0.82
σ for individual ID	0.18	0.01	0.50
σ for brood ID	1.51	1.04	2.34

σ denotes standard deviation of the random effects. The parameters for the male category and its interaction term show differences of each category relative to the intercept and the main effect of the continuous variable. Asterisk denotes an interaction term (random slope). HMr: male helper related to breeding female; HMu: male helper unrelated to breeding female; BMs: sole sire; BMp: polyandrous male. Pairwise comparison was performed to test the significance of the categorical variable and its interaction. None of the parameters showed a significant effect. Tuning parameters of MCMC (Markov chain Monte Carlo): three chains of 801,000 iterations with burn-in of 1,000 and 10,000 thinning intervals (240 samples were saved). The Spearman rank correlation between breeding unit size and the number of unrelated males was r_s = -0.23, P = 0.29.

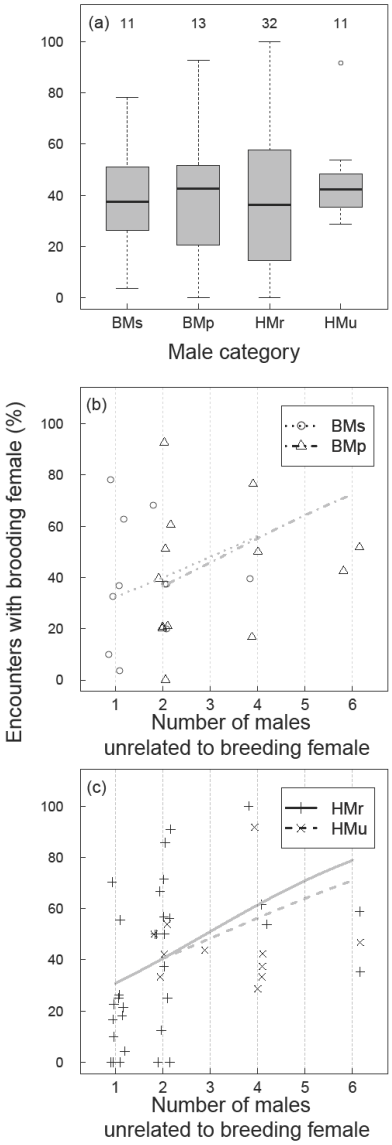

Figure 2.2. Probability of encounter with the breeding female on the nest. (a) Box plot shows median, interquartile range and approximate 2.5–97.5 percentiles of observed data. Circles represent outliers. The numbers at the top denote the sample size for each category. (b-c) Relationships between the encounter probability and the number of unrelated males within a breeding unit for either breeding (b) or helper males (c). Non-significant trend lines predicted by median estimates of the generalized linear mixed model cover ranges of the number of unrelated males observed for each category. Acronyms for male category are provided in Fig. 2.1 legend. Data points are jittered along x axis. Vertical grey dotted lines show the true positions of values on the x-axis.

Synchronizing nest visits with breeding female

The ratio of 'perceived' ($Y_{f,m}/v_f$) to actual (v_m) feeds by males ($Y_{f,m}/v_f\ v_m$) averaged 0.064 (sample mean, SD = 0.04, N = 66). This ratio was uninfluenced by the size of breeding units (β_1, Table 2.3). I found little evidence to suggest that male categories differed in the level of synchrony with the breeding female (comparison of α_c across four dyad types consisting of breeding female and males; Fig. 2.3a). In addition, the number of unrelated males in the breeding units did not influence the overall level of synchrony with the breeding female (Table 2.3). Furthermore, pairwise comparisons of γ_c (estimates of random slope) showed that there was no significant difference in the level of synchrony of males in different categories as a function of the number of unrelated males (Fig. 2.3b). It thus seems unlikely that males advertise their contribution by preferentially synchronizing their feeds with those of the breeding female.

Table 2.3. Summary of the parameter estimates in the latent space model for synchronous provisioning (medians and 95% credible intervals)

Parameter	50%	2.5%	97.5%
β_0	-2.43	-2.66	-2.12
β_1	0.03	-0.01	0.08
β_2	-0.08	-0.21	0.03
σ_α	0.11	0.01	0.30
σ_γ	0.04	0.002	0.12
σ_φ	0.16	0.01	0.36
σ_δ	0.13	0.03	0.24
σ_z	0.08	0.006	0.25
α_c (random intercept)			
HMr-BF	-0.04	-0.23	0.08
HMu-BF	-0.03	-0.28	0.15
BMs-BF	-0.04	-0.33	0.12
BMp-BF	-0.04	-0.27	0.11
γ_c (random slope)			
HMr-BF	0.008	-0.06	0.10
HMu-BF	-0.005	-0.13	0.06
BMs-BF	0.003	-0.08	0.12
BMp-BF	-0.001	-0.09	0.05

β_0: intercept; β_1: slope for the size of breeding unit; β_2: slope for the number of males unrelated to breeding female; σ_α: standard deviation for dyad types; σ_γ: standard deviation for dyad types for the random slope for the number of males unrelated to breeding female varying by dyad types; σ_φ: standard deviation of brood ID; σ_δ : standard deviation of individual ID ('sociality'); σ_z: standard deviation of latent social space position; α_c: estimates of random intercept for dyad types; γ_c: random slope for the number of unrelated males that vary by dyad types. Only dyad types comprising male and breeding female are shown for random intercept α_c and random slope γ_c. HMr: male helper related to the breeding female; HMu: male helper unrelated to the breeding female; BMs: sole sire; BMp: polyandrous breeding male; BF: breeding female. Pairwise comparison was performed to test the significance of the categorical variable and its interaction. None of the parameters showed a significant effect. Tuning parameters of MCMC (Markov chain Monte Carlo): three chains of 200,000 iterations with burn-in of 2,000 and 4,000 thinning intervals (150 iterations were saved). The correlation Spearman rank between breeding unit size and the number of unrelated males was r_s = -0.15, P = 0.048.

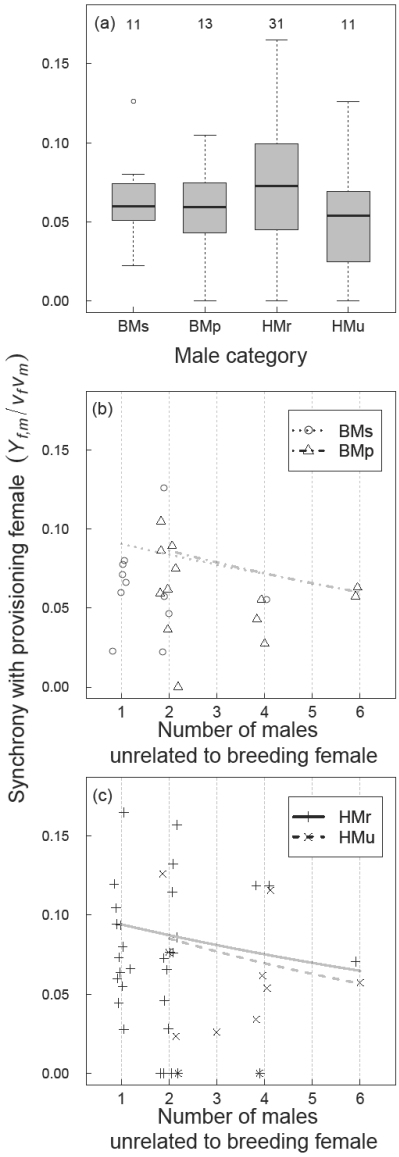

Figure 2.3. Synchrony between males and the breeding female characterized by ratio of perceived ($Y_{f,m}/v_f$) to actual male provisioning rate (v_m). The ratio is low because the synchronous visits/h was divided by hourly visit rates of both males and the breeding female rather than just one of them. This was done to control for the visit rate of both individuals in each dyad. (a) Box plot shows median, interquartile range and approximate 2.5–97.5 percentiles of observed data. Circles represent outliers. The numbers at the top denote the sample size for each male category. (b-c) Relationships between patterns of synchrony and the numbers of males in the breeding unit that were unrelated to the breeding female for breeding (b) and non-breeding (c) males. Non-significant trend lines predicted by median estimates of the latent space model cover ranges of the number of unrelated males observed for each category. Acronyms for male category are provided in Fig. 2.1 legend. Data points are jittered along x axis. Vertical grey dotted lines show the true positions of values on the x-axis.

Feeding before versus after breeding female

On average, males were as likely to precede as follow the breeding female during provisioning bouts, with the percentage of nest visits in which males followed the breeding female in synchronous nest visits being 54% (sample mean, SD = 32%, *N* = 58; Table 2.4). The observed value was not statistically different from the 50% that is expected under random expectation (estimate of intercept was not significantly different from zero; Table 2.4). There was little evidence to suggest that males breeding in the presence (BMp) versus absence (BMs) of reproductive competition attempted to follow the breeding female more often during synchronous feeding visits, although there was a non-significant trend for unrelated helpers to do so more than related helpers (Fig. 2.4a). There was no overall effect of the number of unrelated males in the unit on the probability that males followed the breeding female in synchronous feeding visits (Table 2.4). In addition, although polyandrous males showed a non-significant tendency to follow females more with increasing numbers of unrelated males, this was not the case for either monogamous males or unrelated helpers, and the interaction between male category and the number of unrelated males on this probability was not statistically significant (Fig. 2.4b). Overall, these results fail to provide compelling support for the social prestige hypothesis.

Table 2.4. Summary of the parameter estimates in the generalized liner mixed models for the frequency of following the breeding females by males (medians and 95% credible intervals)

Parameter	50%	2.5%	97.5%
Intercept	0.10	-0.38	0.59
Male category			
HMr	0.03	-0.55	0.51
HMu	0.65	0.003	2.06
BMs	-0.55	-1.71	-0.01
BMp	-0.06	-0.60	0.40
σ for male category	0.79	0.06	4.35
Size of breeding unit	0.02	-0.11	0.17
Number of unrelated males	0.13	-1.82	1.83
Number of unrelated males*Male category			
HMr	0.05	-0.17	0.51
HMu	0.02	-0.42	0.48
BMs	-0.25	-1.13	0.10
BMp	0.14	-0.12	0.63
σ for Number of unrelated males*Male category	0.42	0.01	4.00
σ for individual ID	0.22	0.026	0.72
σ for brood ID	0.30	0.02	0.96

σ denotes standard deviation of the random effects. The parameters for the male category and its interaction term show differences of each category relative to the intercept and the main effect of continuous variable. Asterisk denotes an interaction (random slope) term. HMr: male helper related to the breeding female; HMu: male helper unrelated to the breeding female; BMs: sole sire; BMp: polyandrous male. Italic indicates parameter of significant effect. Pairwise comparison was performed to test the significance of the categorical variable and its interaction. In the male category term, difference was significant only between HMu and BMs. All other parameters were non-significant. Tuning parameters of MCMC (Markov chain Monte Carlo): three chains of 4,001,000 iterations with burn-in of 1,000 and 80,000 thinning intervals (150 iterations were saved). The Spearman rank correlation between breeding unit size and the number of unrelated males was $r_s = 0.20$, $P = 0.13$.

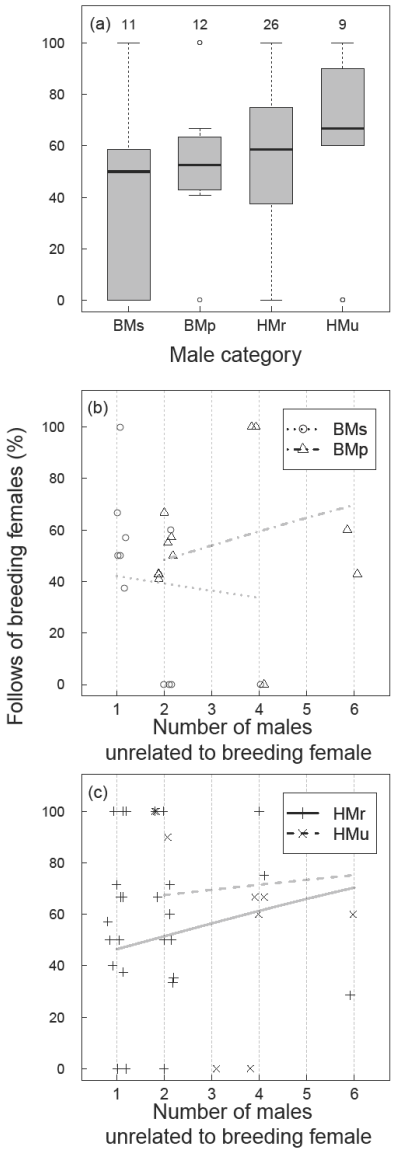

Figure 1.4. Probability of males following the breeding female when they synchronize their provisioning with her. (a) Box plot shows median, interquartile range and approximate 2.5–97.5 percentiles of observed data. Circles represent outliers. The numbers at the top denote the sample size for each category. (b-c) Relationships between 'following' probability and the number of unrelated males within the breeding unit for either breeders (b) or helpers (c). Non-significant trend lines are predicted by median estimates of the generalized linear mixed model and cover ranges of the number of unrelated males observed for each category. Acronyms for male category are provided in Fig. 2.1 legend. Data points are jittered along x axis. Vertical grey dotted lines show the true positions of values on the x-axis.

Discussion

This study represents one of the few attempts to investigate the role of social prestige in explaining the level and patterns of male provisioning behaviour. Males provisioned at a similar rate irrespective of their reproductive status or relatedness status to the breeding female. In addition, there was no significant difference between the four categories of males in their probability of maximizing detection of provisioning by the breeding female. Furthermore, although I found a significant interaction between male status and the number of potential reproductive competitors in the group on offspring provisioning rates, the results were not consistent with the predictions of social prestige (see below). Finally, I found little evidence to suggest that the potential for reproductive competition affected the probability that categories of males most likely to benefit from advertising their parenting ability as a mate increased their probability of coinciding nest visits with the presence of the breeding female. I conclude that the social prestige hypothesis is likely to have limited explanatory power in accounting for the patterns of nestling provisioning in the cooperatively breeding Chestnut-crowned Babbler.

The social prestige hypothesis predicts that any form of cooperation has the potential to act as a signal of individual quality/ability as long as it is costly, the level contributed can be reliably monitored and there is a benefit to basing partner choice on the level observed (Zahavi 1990, 1995; Roberts 1998; Lotem et al. 2003). Two criticisms of this study therefore might be that I considered only a single trait of a single cooperative activity (i.e. nestling provisioning) and assumed the only potential audience to be the current reproductive female of the breeding unit. This apparently restrictive analysis of social prestige was utilized because the present Chestnut-crowned Babblers were shown that the rate at which broods receive food is the primary

determinant of their success (Browning et al. 2012a, b), and that other forms of cooperation are uncommon (e.g. territorial defence: Portelli et al. 2009; nest defence: Russell et al. 2010; sentinel behaviour: Sorato et al. 2012). In addition, adult females are limiting and I have little evidence to suggest alliance formation is an important mechanism of dispersal or group formation (Rollins et al. 2012). Thus, previous evidence suggests that the rate at which group members provision nestlings is the key functional method of cooperation and, if this method of cooperation contains reliable information about future parenting contributions, the most likely target of any signalling will be the single reproductive female in each breeding unit.

Two key predictions of the social prestige hypothesis are that males differing in their reproductive status and relatedness status to the breeding female should be under differing selection to advertise their parenting ability, and that any selection to advertise should increase with within-group reproductive competition (Zahavi 1990, 1995; Roberts 1998; Lotem et al. 2003; Wright 2007). One way that advertising could be achieved is by simply provisioning at a high rate, if those males doing so are more likely to be observed provisioning by the breeding female (Wright 1997; McDonald et al. 2008a). Under this prediction, males in actual reproductive competition (i.e. males in polyandrous pairings) should be under the greatest selection to contribute most to nestling rearing (Zahavi 1990), while male helpers that are related to the breeding female (chiefly her sons) should be under the weakest selection to do so (Koenig & Haydock 2004). That I found no effect of male status on provisioning rates (see also McDonald et al. 2008a) either suggests that males do not use provisioning rates as a reliable indicator of their parenting ability, or that examining provisioning rates represents a prohibitively crude way of estimating attempts at advertising by males. This latter possibility arises because similar provisioning rates might be generated by

different selection pressures (e.g. benefits of advertising to unrelated female versus benefits of rearing offspring of varying relatedness; Wright 2007).

To overcome this problem, I also tested the prediction that individuals that would be expected to benefit most from signalling their parenting ability to the breeding female are expected to maximize the probability that their efforts are witnessed (Endler 1993; Maynard Smith & Harper 1995). This prediction is seldom tested explicitly (Wright 2007), but is important because it averts the potential problem described above and the criticism that signalling is selected against because of prohibitively high costs to the recipient of monitoring signaller behaviour. By investigating whether males attempt to coincide their visits to the presence of the female, I assumed the costs were imposed on the signaller not the receiver (see also Doutrelant & Covas 2007). In Chestnut-crowned Babblers, group members should have relatively precise information regarding the whereabouts of the breeding female because she utters a distinct call during much of the provisioning period both from within the nest and during her time foraging with the group (Russell et al. 2010). In addition, males only reliably have a chance of advertising their provisioning 'effort' by visiting the nest when the breeding female is inside or by synchronizing their nest visit with hers, since the nest of this species is enclosed and individuals forage up to a kilometre from the nest. Nevertheless, males showed no significant differences in their tendency to coincide nest visits with the breeding female's presence according to the potential benefits of doing so under social prestige (see also McDonald et al. 2008a). An absence of attempts to facilitate accurate transmission of information regarding provisioning behaviour strongly suggests that variation in feeding rate among males is generated by factors other than the benefits of signalling (Clutton-Brock et al. 2005; Wright 2007). In combination, I believe that these results counter the first prediction of the social prestige hypothesis that males unrelated

to the breeding female attempt to signal their ability to provide for future offspring by advertising their ability to contribute to current offspring.

The social prestige hypothesis also predicts that those males most likely to benefit from advertising should be under greatest selection to respond to increments to potential reproductive competition by increasing their provisioning rates or the female's perception thereof (Reyer 1986). Nevertheless, I found little supporting evidence: in direct contrast to this prediction, helpers that were unrelated to the breeding female were unresponsive to changes in the numbers of other males in the breeding unit that were unrelated to the breeding female. In addition, although polyandrous males showed the predicted increase in provisioning rates with increasing potential competition, monogamous males showed a trend in the opposite direction. One explanation for these latter results is that they are driven by between-group differences in brood demand, a factor to which all provisioning group members appear to be sensitive (Browning et al. 2012a) contrary to expectations under social prestige (Wright 1997, 1998). For example, high numbers of unrelated males tend to be associated with newly immigrant females, and such females tend to be polyandrous when their work-force is small and monogamous when it is high (S. C. Griffith & A. F. Russell, unpublished data), leading to less need for high contributions by males breeding in the latter compared with the former situation. Finally, I found no evidence to suggest that males most likely to benefit from advertising compete with each other to coincide their visits with the presence of the breeding female. I thus provide no compelling evidence for the second prediction of the social prestige hypothesis; hence the available evidence suggests that contributing to nestling rearing in this species is not currently selected through the benefits of gaining social prestige.

Although some previous studies on cooperatively breeding birds have reported

results consistent with social prestige (Carlisle & Zahavi 1986; Doutrelant & Covas 2007), such results are open to alternative interpretations of observer disturbance effects and/or risks of nest predation. This study is less likely to suffer from either problem because I used an automated recording system and babblers experience little nest predation (Russell et al. 2010). One obvious question arising from this study, and others showing complementary results (Wright 1997; McDonald et al. 2008a, b), is why an apparently costly cooperative activity does not necessarily evolve into a signal? Previous explanations have tended to invoke the costs to the intended audience of accurately monitoring the contributions of multiple individuals to multiple cooperative activities (Roberts 1998; Clutton-Brock et al. 2005; Wright 2007; Raihani & Bshary 2012). While I am not in a position to rule out this explanation for other studies, I propose that it is unlikely to explain the results because contributing to nestling provisioning is the key cooperative activity in babblers. In addition, I investigated whether males attempt to signal to females by coinciding feeds with her presence: not only is coinciding visits likely to be low cost owing to the female's vocalizations in this system, but doing so would remove most of her assessment costs. It also seems unlikely that current provisioning effort is a poor predictor of future effort because contributions are significantly repeatable across attempts in other cooperative species (Clutton-Brock et al. 2002; MacColl & Hatchwell 2003; Russell et al. 2003; Charmentier et al. 2007; Bergmüller et al. 2010; English et al. 2010). Furthermore, it is unlikely that there is little benefit to females choosing mates based on parenting ability, particularly in babblers, because breeding males play a major role in provisioning both the breeding female and her offspring. One potential explanation is that there is little selection on signalling because partner 'choice' is determined by the outcome of male–male competition and/or the number of helpers associated with each male (Wrege & Emlen 1994), with females

having little option of choosing males based on prior contributions to nestling provisioning. Either way, this study adds to a growing consensus that indirect reciprocity, generally, and social prestige, in particular, have minimal scope for explaining patterns of (allo)paternal care in non-human cooperatively breeding vertebrates (Wright 2007). Whether or not such a conclusion is specific to non-humans or simply to (allo)paternal care, requires that future studies investigate the role of social prestige in explaining patterns of (allo)parental care in humans.

Chapter 3

Pay-to-stay hypothesis and nest visit synchrony

Introduction

In cooperatively breeding species, staying at home is a favourable option for young individuals when their prospect of acquiring territory and mate for their own breeding is limited and/or mortality increases while they are floaters (Emlen 1982, 1994; Koenig 1992). The limited opportunity for independent breeding owing to high population density is referred to as ecological constraint (Pruett-Jones & Lewis 1990; Komdeur et al. 1995; Pasinelli & Walters 2002). This explains delayed dispersal of young birds in cooperative breeders. Young birds may also benefit from the delayed dispersal through enhanced probability of inheritance of breeding positions or gaining a share of reproduction within the territory (e.g. Goldstein et al. 1998).

On the other hand, the retention of subordinates in territory imposes costs on breeders of the same sex due to reproductive competition (e.g. Goldstein et al. 1998; Mumme et al. 1983; Magrath & Whittingham 1997), as well as competition over resources in the territory (Gaston 1978). Those subordinates that do not provide care for offspring of the dominants could be evicted from the breeding groups by the dominants of the same sex. In fact, it is known in several species that failure to provide help results in punishment by dominants (Reyer 1980, 1984, 1986; Mulder & Langmore 1993; Boland et al. 1997), or by other subordinates (Balshine-Earn et al. 1998; Bergmüller & Taborsky 2005).

Gaston (1978) proposed the ‘pay-to-stay’ hypothesis that helpers benefit from securing the membership in the current territory by informing the dominant that they provide help for the offspring care and how much they help. If this is the predominant benefit of helping, subordinates who are in reproductive conflict with the dominant breeder provide more care than those who are not (Zöttl et al. 2013). Another prediction

from the pay-to-stay hypothesis is that subordinates do not directly gain fitness increase from successful growth and survival of the young in the breeding groups. Instead, they gain benefit from helping (i.e. they can stay in the group) only when the dominants perceive that the helpers substantially contribute to the brood care. If this is the case, subordinates may benefit from deceiving the dominants by exaggerating their provisioning rate without increasing the actual rate. However, except for one study (Boland et al. 1997), preceding studies failed to show that helpers deceive the breeders they assist (Canestrali et al. 2004, 2010; Clutton-Brock et al. 2005; McDonald et al. 2007, 2008a, b; Young et al. 2012). The lack of evidence suggests that deception is not a stable strategy for subordinates in this system. However, signalling their contribution to offspring care may still be beneficial if it prevents the dominants from underestimating their actual contribution.

This chapter investigates whether provisioning behaviour of subordinate individuals in the cooperatively breeding Chestnut-crowned Babbler are consistent with the pay-to-stay hypothesis. Since helper males of this species have a potential to reduce the fitness of the breeding males by mating with the breeding female when they are unrelated to her (Chapter 2), they may be evicted from the group by the breeding males. For helpers related to offspring, kin-selected benefit might be sufficient to maintain allo-parental care. The theory suggests that helping as a rent payment can evolve mainly in the case where the relatedness between helper and offspring is low (Kokko et al. 2002). Subordinates who are related to the breeding females may also need to pay rent owing to conflict caused by other competitions, for example foraging competition, especially for helpers unrelated to the primary breeding male because the reduction in fitness of unrelated individuals does not translate into the cost of the primary male (Kokko et al. 2002). Therefore, subordinates whose relatedness is low may need to advertise their

contribution to the breeding males to avoid eviction or aggression (Kokko et al. 2002; Reyer 1980, 1984, 1986; Zöttl et al. 2013). In this species, individuals often visit the nest synchronously with other members of breeding groups during chick-rearing period (Chapter 1, Chapter 2). If unrelated subordinate males raise the rate of synchronous visits with the breeding males, they may be able to secure their contribution perceived by the primary breeding males. To test this possibility, the synchronous provisioning between the primary breeding males and all the subordinate individuals was examined.

If unrelated subordinate males try to signal their contribution toward the dominant breeding males, individual feeding rate and synchrony with the dominant males are expected to be higher in unrelated subordinate males compared with those of subordinate males closely related to both breeders and female helpers. In addition, reflecting the reproductive competition, synchrony with the dominant male is expected to be higher in the subordinate males unrelated to both breeders compared with males unrelated only to the male breeders. This is particularly the case when the unrelated subordinates hold paternity in the current breeding attempt (secondary breeding males). Alternatively, a high rate of synchronous visits may occur when individuals have similar behavioural rules, such as responsiveness to begging of nestlings. In fact, individuals having similar behavioural rules are known to synchronise their activities such as foraging in ungulates (Ruckstuhl 2007). In this case, high synchronous visit with the primary breeding male is expected in secondary breeding males and males closely related to the brood since they have similar fitness benefit return from brood care. Synchronous visits between subordinates should become higher when they have similar relatedness to the brood than when they have dissimilar relatedness. In this chapter, this possibility was also examined by comparing the synchrony across all combinations of individuals.

Methods

Field and molecular methods

Field and molecular methods were described in Chapters 1 and 2.

Determination of kinship categories

Parentage of nestlings in each breeding attempt was estimated using the genotypes at 14 microsatellite loci (Rollins et al. 2012). In the estimation, a single female was assigned as a mother of each brood. In 34.7 % of the broods used in this study, more than one male had paternity (N = 49). In these breeding units, I defined males that showed the highest paternity as the primary breeding male (BM) and others as the secondary breeding males (BM2). Helper females (HF) and helper males (HM) were further split according to their kinship to the breeding female and the primary breeding male. Kinship between the breeders and helpers was determined using coefficient of relatedness (R), calculated from microsatellite markers with a software "Coancestry" (Wang 2011) and pedigrees reconstructed from the markers. For individuals whose mothers were not known in the pedigree analyses, relatedness to the breeding females was determined 0 if the marker coefficient was equal to or smaller than 0.2, and 0.5 if the coefficient was greater than 0.2. Individuals were categorised into three classes according to the relatedness to the primary breeding males: (i) $R < 0.2$, (ii) $R \geq 0.2$, and (iii) offspring of the primary males. The value of 0.2 was used to separate 'unrelated dyads' from 'closely related dyads'. Because of the estimation error of relatedness using the pairwise marker, individuals with the true kinship of 0.25 (e.g. half-sibs) could be assigned to both categories, $R < 0.2$ and $R \geq 0.2$. This determination is justified by the low frequency of dyads with the true relatedness of 0.25 (Browning et al. unpublished

data): by this cut-off rule, most individuals were classified into two groups, one with the relatedness less than 0.25 and the other with the relatedness large than 0.25. I set a different category for offspring of the primary males determined by the pedigree analyses, since they had a complete certainty in their relatedness and were larger in sample size than individuals with relatedness of 0 and 0.25. Then, helpers were classified into 6 kinship categories: [0.5 / offs], [0.5 / ≥ 0.2], [0.5 / < 0.2], [0 / offs], [0 / ≥ 0.2], and [0 / < 0.2], where the left of the slash denotes relatedness to the breeding females and the right denotes the relatedness or relation to the primary breeding males. Individuals were classified into 19 categories on the basis of their sex, parentage in the current brood and kinship to the breeding females and the primary breeding males (e.g. HM [0.5 / offs] is helper males closely related to both breeders with certainty). Finally, based on the combination of individual categories, dyads in the breeding units were divided into 91 types. Some types of dyads were not present because some categories of individuals were not present. The dyad types comprised of the same individual categories were also included in the analyses (e.g. HM [0.5 / offs] - HM [0.5 / offs]).

Individual feeding rates

The feeding rate of each individual was estimated from PIT-tag records at the net entrance. I applied a 1-min cut-off to the inter-detection interval of the same individuals in the PIT-tag data to define single visit. A subset of the PIT-tag data was compared to the nest video data for checking correlation between them. Nest visits of the breeding females were excluded from all the analyses, since the reconstruction of the number and timing of their nest visits from PIT-tag data was difficult due to variable duration of their stay at the nest (see Chapter 1 for more details). The feeding rate was compared across individuals from the categories described above using a generalised linear mixed

model (GLMM) with Poisson distribution and log link function. The number of feeding visits was observed during total recording period set as a response variable and logarithm of total recording duration (h) at each nest was set as an offset (exposure). For explanatory variables, I set the size of breeding units and the brood size as fixed effects, and category of individuals and brood ID as random intercepts. The difference of the feeding rate across individual categories was estimated as a random intercept since the number of categories was rather large and the number of individuals in some categories was rather small. The analysis based on 172 individuals from 42 breeding attempts in 32 breeding units.

Synchronous feeding rates

I defined the synchronous visits as nest visits of different individuals that are separated by less than 1 minute (entry-entry time, Chapter 1). The definition of synchrony is given in Chapter 1.

The synchronous visit data had two properties to be notified when modelling them as count data. First, although the data were collected at the level of dyad and cannot be broken down further to smaller units, effects at the level of individual on the occurrence of synchronous visits need to be considered. Second, the 'gambit of group' assumption that all individuals within a synchronous group are synchronised to each other in the data processing may create artificially exaggerated synchrony regardless of individual preference or motivation for synchronisation underlying the pattern of synchronous visits. Such effect can be modelled as 'transitivity' effect in social network models. The latent space model (Krivitsky et al. 2009) was used to estimate variability caused by the individual level effect and the transitivity. The model was specified as follows, $y_{i,j,k} \sim \text{Poisson}(\lambda_{i,j,k})$, $\log(\lambda_{i,j,k}) = \beta_0 + \log(t_k) + \beta_1 \log(v_{i,k} v_{j,k}) + \beta_2 u_k + \beta_3 x_k + \alpha_c +$

$\varphi_k + \delta_{i,k} + \delta_{j,k} - \| Z_{i,k} - Z_{j,k} \|$, where i and j index individual ID, c indexes the dyad types and k indexes brood IDs. The offset term, $\log(t_k)$, was added so that the number of synchronous visits ($y_{i,j,k}$) is evaluated relative to the duration of recording (t_k). $\beta_1 \log(v_{i,k} v_{j,k})$ was also added to control for the effect of individual hourly visit rates ($v_{i,k}$ and $v_{j,k}$) that may confound the individual category effect (Note that the offset term $\log(\min(v_{i,k} v_{j,k}))$ was used in the similar model in Chapter 1, but the term $\beta_1 \log(v_{i,k} v_{j,k})$ showed a better performance in this latent space model). The visit rate here was calculated on the basis of the number of independent visits. β_2 is a slope (fixed effect) of the number of non-juvenile birds in the breeding units (the size of breeding unit, u_k). β_3 is a slope (fixed effect) of brood size (x_k). $\delta_{i,k}$ is 'sociality' random effect (Hoff 2005) that models variation in the dyadic data at the individual level. The other explanations on this model were given in Chapter 1.

Dyads involving individuals that did not visit nests during the PIT-tag recording were not included in this analysis. All individuals except for the breeding females and juveniles were used in this analysis for accurate estimation of the transitivity effects, even though some categories on individuals are not relevant to the hypothesis I attempt to test (e.g. individuals with unknown sex, or relatedness) because they contribute to the estimation of other parameters of the model. In total, this analysis was based on 507 dyads from 49 breeding attempts in 32 breeding units.

Statistical methods

General statistical methods were described in Chapter 1.

Results

Difference of visit rates among individuals of different categories

The median of the feeding frequencies per hour was 4.01 in BM (SD = 1.71, *N* = 45), 2.03 in BM2 (SD = 2.16, *N* = 19), 1.00 in HF (SD = 2.63, *N* = 32), and 1.66 in HM (SD = 1.75, *N* = 162). Thus, the primary breeding males (BM) had higher feeding rates than all other individuals (Fig. 3.1). However, the feeding rate of related helper males, HM [0.5 / offs] estimated by the GLMM was higher than that of the secondary males (Fig. 3.1). The estimated feeding rate was similar between helpers of different sexes if they belong to the same categories of the relatedness to breeders, except for helpers of the category [0.5 / <0.2] in which helper males had significantly higher rates of feeding than helper females (Fig. 3.1). Overall, individuals that gain high indirect fitness from helping tended to have high feeding rates. However, helper males partly related to the brood showed provisioning at the similar rate to the helper males fully related to the brood. Helper males that were unrelated to the breeding females but were offspring of the primary breeding males (HM [0 / offs]) and helpers that were related to the breeding females but not to the primary breeding males (HM [0.5 / 0]) had similar provisioning rate to that of helper males closely related to both breeders (HM [0.5 / offs]). The feeding rate of HM [0 / offs] was tended to be higher than HM [0.5 / offs]. The unit size did not significantly affect the overall level of the feeding rate (i.e. coefficient included 0 in 95% CI: Table 3.1), although the effect was slightly negative. The brood size had a significant positive effect on the overall level of the feeding rate (Table 3.1).

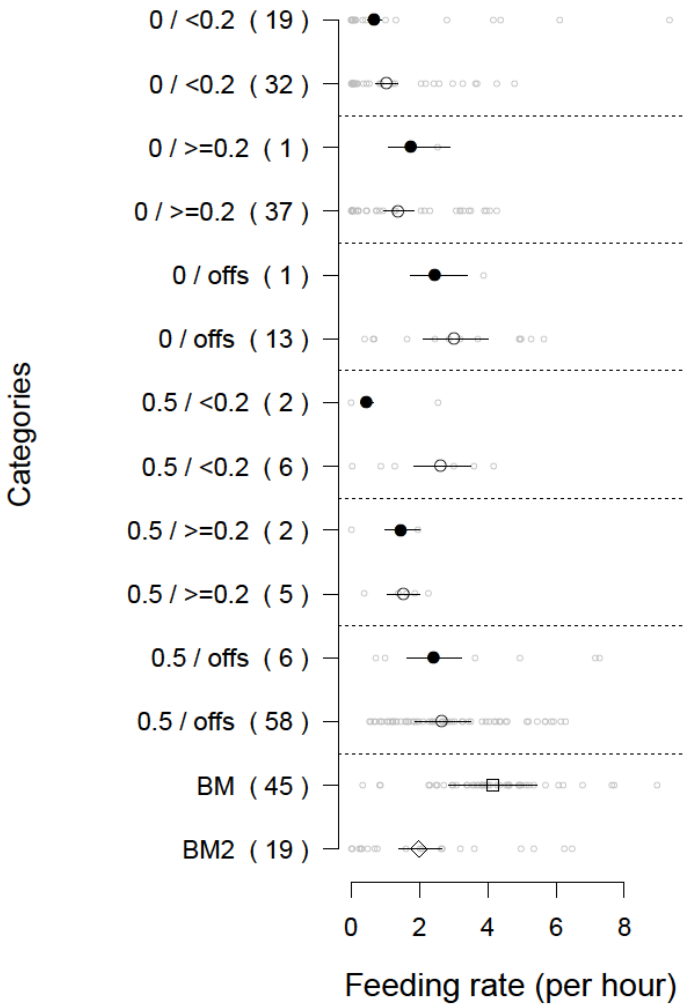

Figure 3.1. Difference of the estimated feeding rates per hour across individuals of different categories. Grey dots are data points. Filled and open circles denote female and male helpers, respectively. Open square and open diamond denote the primary breeding males and the secondary breeding males, respectively. The relatedness to the breeding female (left) and the primary breeding male (right) in each breeding unit was given following the abbreviation of categories (offspring of the primary breeding male was denoted as 'offs' instead of relatedness value). Numbers in the parentheses are sample sizes. Bars indicate 95% credible intervals.

Table 3.1. Summary of parameter of models for the feeding rate.

Parameter	Median	2.5%	97.5%
Intercept	0.44	0.07	0.75
Unit size	-0.04	-0.10	0.03
Brood size	0.15	0.02	0.29
σ for categories	0.68	0.49	0.96
σ for brood ID	0.49	0.41	0.59

σ denotes standard deviation of the random effects.

Synchrony between the primary breeding male and individuals of other categories

The synchronous visits rate (number of synchronous visits per hour) was 0.15 in median (SD = 0.56, N = 672 dyad). The median rates of synchronous visits between the primary breeding males and other individuals was 0.42 (SD = 0.68, N = 137), reflecting the high feeding rate of the primary breeding males. The relationship between synchronous visit rate and the individual visit rate was predicted well by the model (Fig. 3.2, Table 3.3),

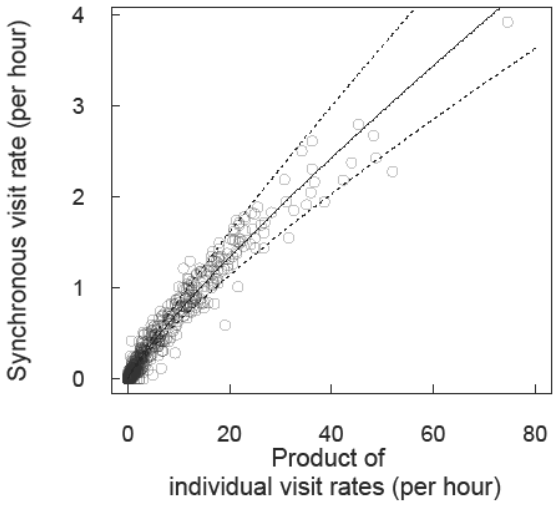

Figure 3.2. Relationship between the synchronous visit rate per dyad ($y_{i,j,k}/t_k$) and the product of visit rates ($v_{i,k}v_{j,k}$). Solid line indicates the prediction based on medians of the parameter estimates in the model, and dotted lines are 2.5% and 97.5% bounds of the estimates.

indicating that the effect of individual visit rate was successfully controlled for when estimating the difference in synchrony across dyad types. Neither unit size nor brood size significantly influenced the synchronous visit rate (Table 3.3). Estimated relative frequency of synchrony with the primary breeding males (subset of α_c) was different across individuals of different categories, but a significant difference observed only between HM [0.5 / offs] and HF [0 / <0.2]. In contrast to the prediction of the pay-to-stay hypothesis, helper males closely related to the brood (HM [0.5 / offs]) had the highest synchrony, and HM [0 / offs] had a comparable level of synchrony (Fig. 3.3). On the other hand, HF [0 / <0.2] had the lowest synchrony with the primary breeding males, and the estimate of its α_c was significantly deviated from the mean of α_c (i.e. 0). Individuals of all other categories had similar levels of synchronous visit rates to each other (Fig. 3.3). Dyads of the same individual categories (assortative dyads) tended to have higher synchrony rates (median α_c for assortative dyad = 0.01, 95% CI = −0.11-0.12) than those of the different categories (median α_c for disassortative dyad = −0.003, 95% CI = −0.05-0.05) (e.g. Fig. 3.4), but the difference was not significant (median difference of the estimates: 0.01, 95% CI = −0.12- 0.14, averages for each of assortative and disassortative dyads were calculated using the MCMC samples for each α_c).

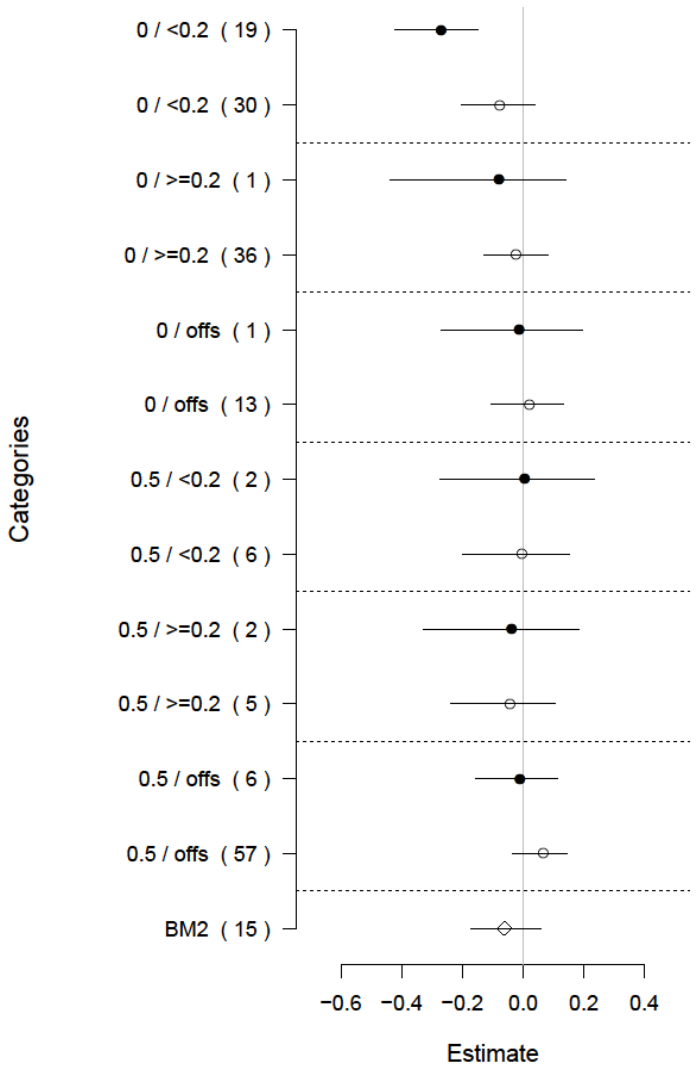

Figure 3.3. Estimates of random intercept (α_c) for dyads including primary breeding male. Filled and open circles denote female and male helpers, respectively. Open diamond denotes the secondary breeding males. For the complete set of estimates of α_c see Fig. 3.4.

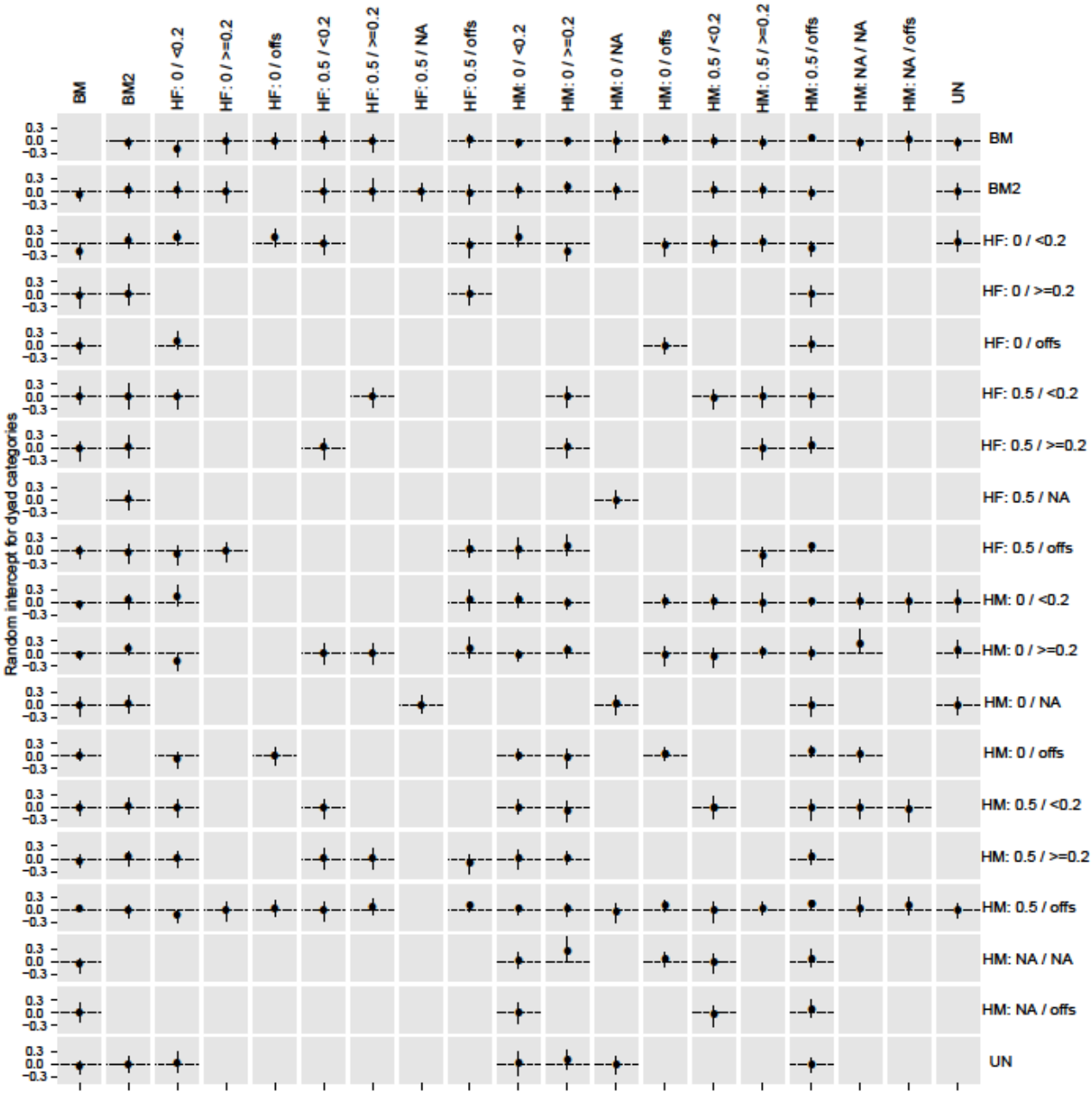

Figure 3.4. Estimates of random intercept (α_c) for all dyad types in the synchronous visit model. All combinations of individual categories were visualised as a square matrix. The upper and lower cells of the diagonal show the same values (symmetric matrix). The point and the bar in each cells show the median estimates and 95% credible intervals (CI), respectively. Horizontal lines denote 0. All dyads include 0 in 95% CI of the estimates. Helper females of low relatedness (HF: 0 / < 0.2) had particularly low synchrony with primary male (BM).

Table 3.3. Summary of parameters of the model for the synchronous visit rate.

Parameter	Median	2.5%	97.5%
β_0	-2.09	-2.20	-2.00
β_1	0.87	0.84	0.89
β_2	0.003	-0.03	0.03
β_3	-0.04	-0.10	0.00
σ_α	0.11	0.07	0.18
σ_φ	0.14	0.07	0.21
σ_δ	0.03	0.00	0.09
σ_z	0.21	0.15	0.25

β_0: intercept, β_1: coefficient for log ($v_{i,k}v_{j,k}$), β_2: the size of breeding unit, β_3: brood size, σ_α: standard deviation for dyad categories, σ_φ: standard deviation for brood ID, σ_δ : standard deviation for individual (sociality), σ_z: standard deviation for latent social space position.

Discussion

The biological signal theory proposes that signal is modified by selection to facilitate the transmission of information that affects the behaviours of the receiver (Maynard-Smith & Harper 1995). For the synchronous feeding to be a pay-to-stay signal, synchrony needs to facilitate the transmission of information on the amount of contribution of helpers to potential receivers. In the Chestnut-crowned Babblers, however, synchrony with primary breeding males by males that are expected to benefit from paying 'rent' were not higher compared with other males. Individuals that had a highest level of the synchronous visit with the primary breeding male was helper males who were closely related to both parents (HM [0.5 / offs]). Subordinates that are expected to pay rent in the pay-to-stay hypothesis synchronised with the primary males only at a rate close to the average synchrony rate in the groups.

The synchronisation between the primary male and other breeding unit members may be achieved as a result of shared behavioural rules (Ruckstuhl 2007). In ungulates, individuals are more likely to synchronise their activities such as resting and foraging with those that have similar optimal scheduling of behaviours. Synchronisation between individuals with different behavioural rules has been suggested to be costly because individuals may sacrifice their optimal timing of foraging (Ruckstuhl 2007). In cooperatively breeding birds, temporal variation of the nestling begging might cause individuals who have similar responsiveness to the need of chicks to return to the nest with similar timing after they received the last begging of the chicks. Further, helpers who gain benefits from offspring care at the level similar to dominants may use the behaviour of dominants to know the level of hunger of nestlings (Johnstone & Hinde 2006). If related helper males infer the chick's hunger from the provisioning rate of the breeding males, higher synchrony is predicted between related helpers and the breeding males. Such matching of provisioning behaviour is adaptive either when helpers are less experienced and less able to adjust their timing of feeding to optimise their investment into feeding by themselves, or when helpers have limited information on chick's need in comparison with the breeding males. However, the similarity in the responsiveness to the begging did not explain the present results; i.e., the rate of synchronous visits of individuals of the same categories did not differ from that of individuals of different categories.

Synchronous visit with the primary male by helper females related to neither dominant pairs was low. This indicates that unrelated females provision offspring when other members are not provisioning. Recent investigations in the cooperative Carrion Crows (*Corvus corone*) found that helpers of low feeding rate increase their helping when helping by other group members was reduced experimentally (Baglione et al.

2010). They maximize their indirect fitness benefit by helping only when their help is needed. However, the compensatory help does not provide kin-selected benefit to unrelated helpers. Although provisioning is low on average in this category, some of the individuals from this category showed provisioning rates as high as related helpers (Fig. 3.1), indicating that unrelated females gain substantial direct fitness benefit from helping under some restricted conditions. I cannot preclude the possibility that unrelated females use their help to avoid aggression from the breeding female.

Another explanation would be that the pattern of synchrony is shaped by the familiarity between breeding unit members. Unrelated females are almost always immigrants from other breeding units (either within or outside of social group). Their low familiarity to the primary male is more likely to explain the low rate of synchrony with him (see also Chapter 1). Indeed, unrelated females have relatively high synchrony with individuals of low relatedness to the dominant pairs (Fig. 3.4). Individuals unrelated to the breeders may be co-disperser from the same breeding unit (Rollins et al. 2012), and therefore, they may be familiar with each other. However, I could not test this possibility owing to the relatively low number of individuals whose dispersal history is known. Collecting the history of movement of individuals across breeding units from more years will enable us to determine the familiarity between subordinates with greater accuracy and to test the effect of familiarity on the synchronous visits.

Among individuals examined in this study, helpers showing the highest relatedness to the brood had higher feeding rates than helpers with low relatedness, suggesting that individuals mainly seek indirect fitness benefit from helping. The feeding visits by the primary males and individuals who are in reproductive conflict did not highly synchronise, suggesting that feeding by unrelated helpers is more likely to be investment to the success of the brood care rather than signal to placate the dominant

males. I also found that male helpers who are partly (by 0.25) related to the brood had provisioning rates similar to male helpers who are fully (by 0.5) related to the brood. This might be interpreted as incomplete recognition of the relatedness. However, paternal half-sibs tended to have higher provisioning rate than maternal half-sibs, even though mother is more easily recognised by helpers than father because of polyandrous mating. This suggests that the high investment into helping by half-sibs may be driven by some direct fitness benefit other than signalling toward dominants, such as group augmentation (Kokko & Johnstone 2001).

In summary, the present results in the Chestnut-crowned Babblers suggest that individual feeding rate was largely consistent with kin selection, and the nest visit synchrony by subordinates does not serve as a signal of contribution to provisioning toward the dominant breeder. Taken together, the pay-to-stay hypothesis is unlikely to explain the variation in the provisioning rate in this species.

General discussion

Animals living in groups often prefer specific individuals as counterparts of social interactions. Social relationship is defined as a collection of such social interactions with specific counterparts, and social structure is a collection of social relationships of society members (Hinde 1976). For understanding of social structure and its effects on fitness, therefore, precise description of social interactions is indispensable. For this purpose, social network analysis is an excellent tool and becoming increasingly popular in the studies on animal societies (Croft et al. 2008). This analysis enables us to examine (1) subdivision or internal clustering of society, (2) temporal patterning of social structure, (3) relationship between individuals indirectly connected via a third individual, and (4) relations of individual position in social network with behavioural, physiological and morphological traits of individuals.

Social network analysis deals with social structure as network of individuals connected via social interactions or relationships. Network is often constructed on the basis of group co-membership through observation on simple association (e.g. how often the two focal individuals occur in close vicinity). In avian species, cooperative breeders are possible targets of the network analysis, but they have not yet been subjected to it. This is partly because observation of the repeated social interactions between every combination of individuals in wild avian species is not easy. So far, observation on their behaviours at breeding nests has been commonly conducted through identification of individuals by colour rings, and this approach has provided important information on their social lives. For further understanding of their social ecology, information on interactions among all group members is needed. Use of video camera and electronic passive integrated transponder (PIT) –tags is one of excellent ways to obtain data on interactions among all group members at least at the nesting sites.

In the present study on social networks in the Chestnut-crowned Babblers using

data on synchronous feeding, I found that this species has heterogeneous social network structure within their breeding unit at the level of network centrality, i.e., individuals that are immigrants and therefore are less familiar with other group members tended to have peripheral positions in the networks. Familiarity has been reported to have profound effects on social network in animals of other taxa (Griffiths & Magurran 1999; Ward & Hart 2003). In the present study species, synchrony could also be dependent on assortativity where individuals with similar attributes, especially responsiveness to the begging of nestlings, associated more closely to each other than individuals that are dissimilar. However, I found no such assortativity in this study (Chapter 3). Further investigation in this population would reveal the importance of familiarity in the social network of synchronous provisioning, and monitoring of dispersals between groups over years would provide better measure of familiarity.

One of important questions on social network is why individuals associate with specific individuals. In cooperatively breeding avian species, the primary breeding males often stay at close proximity of the mates and guard them from cuckoldory by extra-group males (e.g. Komdeur et al. 1999). In addition to the interactions that are associated with such obvious fitness benefit, the 'social prestige' and 'pay-to-stay' hypotheses dealt in this thesis provide another interesting view on the function of social network; i.e., the former predicts that helper males synchronise their nest visits with the breeding females when unrelated to her to advertise their contributions for increasing possibility to mate with her in the future, and the latter predicts that unrelated helper males show high nest visit synchrony with the primary breeding males to advertise their contributions for reducing possibility to be evicted or punished by the primary breeding males. In the present study, however, I found no evidence that unrelated helper males are engaged in such signalling using nest visit synchrony in this species. This result is

consistent with the result of a previous study on the same population (Young et al. 2012).

There are three possible reasons why there is no clear signalling in this species. First, despite their large home rage, individuals may be able to monitor behaviours of others well, so that individuals do not use the synchronous visits as a tool to assess the feeding rate of others. In this species, the breeding units form compact flock most of the time while they are foraging and rarely split into discrete flocks (Sorato et al. 2012), as suggested by the present results that the subsections of networks as community structure are virtually absent (Chapter 1), and therefore the breeding individuals may be able to monitor behaviours of all others. Second, synchronous visits may be costly, since individuals have to adjust their behaviours to synchronise with others possibly by reducing foraging time to gain their own food. However, it is unlikely that the cost of synchrony prevents the emergence of signalling, since the cost of waiting for others after finding a prey is considered to be low. Third, there is no benefit to signal their cooperation in acquiring mates or avoiding punishment or eviction. This scenario is possible, since eviction has not been so far observed in this population and the frequency of aggressive interactions during the nest provisioning is not particularly high (personal observation). Helpers may not have to pay rent to the dominants if they are always valuable workforce for the breeders and there is no threat of aggression. To determine which scenario is likely, individual mating success and dispersal between groups should be monitored for a longer period. The data presented here were obtained from only two years and were quite limited for this purpose.

Another important issue in the study of cooperative breeding is whether and how individuals adjust or change their behaviours in response to behaviours of other group members. Most studies on individual contributions to the nestling care in cooperative breeders assume that the individual decision regarding the amount of

feeding is independent of other carers. However, it is likely that individuals change their feeding rates in response to the feeding rates of others. Only a few studies have investigated whether provisioning of helpers is facilitated by aggression or presence of dominant breeders in vertebrates (Santema & Clutton-Brock 2012; Kutsukake et al. 2012), despite the awareness among researchers on the punishment and coercive process operating between breeders and helpers. In addition, McDonald (2009) showed that, when provisioning rate of the male breeders was experimentally increased in the Bell Miner (*Manorina melaphrys*), the feeding visit rate of unrelated helper males increased. Furthermore, compensatory reduction in investment in the parental care by the breeders in response to the presence of helpers has been highlighted in some cooperative species (load-lightening, Hatchwell et al. 1999; Russell et al. 2007, 2008). Further studies are needed to identify the role of inter-individual dependence in provisioning in determining fitness consequences of the cooperative breeding.

Summary

Chapter 1

Recent developments in social network analyses have confirmed that animal groups are not necessarily collections of panmictically associating individuals, but that group members can interact non-randomly. However, behavioural contexts in which social network structure of wild animals has been described is still relatively limited, perhaps owing to the large amounts of repeated interaction data required, and difficulty in extracting realistic network metrics from the observation data. Here I highlight the use of an automated method, PIT (passive integrated transponder)-tag monitoring system, for collecting sufficient data of a type required for social network analysis and do so in a novel context– individual contributions to nestling provisioning in an avian cooperative breeder, Chestnut-crowned Babbler (*Pomatostomus ruficeps*). I tested the PIT-tag system against standard video camera system and determined appropriate procedures to quantify the synchronous nest visit from the PIT-tag system, and then compared the parameters of social network structure (community structure and individual connectedness) based on pair-wise synchronous visit frequency between PIT-tag and video system. I found that PIT-tag system cannot reconstruct the behaviour of the breeding females owing to the large variability in their nest visit behaviour. Community structure was not found with either method. However, the extensive data set based on PIT-tag system uncovered the significant variability in individual connectedness that video system failed to capture. These results highlight the importance of combining observation methods that complement each other when conducting the social network analyses in wild animals whose social interactions are difficult to study with direct observation. I hope that the methods that I have provided will facilitate the advance of social network analyses in cooperative breeders and other social animals.

Chapter 2

Humans are commonly concerned with social status, and often cooperate in the presence of others in an attempt to signal their potential as a social or reproductive partner. Whether or not cooperation might signal prestige in non-human animals is seldom tested and poorly understood. I investigated whether male Chestnut-crowned Babblers that are unrelated to the breeding female, and hence most likely to benefit from signalling their parenting ability to her, strategically adjust their actual or perceived contributions to nestling rearing. Male contributions to nestling rearing were unaffected by either their reproductive status (breeder *vs*. non-breeder) or, in the case of non-breeding helpers, their relatedness to the breeding female (related *vs*. unrelated). In addition, I found little support for the possibility that current breeders or unrelated helpers adjusted their nestling provisioning rates in the presence of actual or potential reproductive competition in the group, at least in a manner consistent with the social prestige hypothesis. Finally, I found no evidence to suggest that unrelated (breeding or non-breeding) males attempted to increase the breeding female's perception of their provisioning behaviour by timing their feeds to her presence. I conclude that, in Chestnut-crowned Babblers, patterns of male provisioning behaviour are not obviously consistent with advertising their parenting ability, and that social prestige is likely to have limited power in explaining male care in this system.

Chapter 3

In cooperative breeding systems, it has also been proposed that the allo-parental care provided by unrelated subordinates is explained as a ‘rent’ paid to the dominants in the group to be permitted to stay in the territories. Unhelpful subordinates have a risk of eviction and punishment from their dominant breeder. Under this pay-to-stay hypothesis, subordinates are expected to benefit from unambiguously showing that they contribute to the rearing of dominant’s offspring. I tested whether synchronous nest visits can facilitate the communication of the contribution of the subordinates, i.e., whether unrelated helpers and secondary breeders that are expected to need to pay rent according to the pay-to-stay hypothesis have higher rate of synchrony with the primary breeding males than related helpers in the Chestnut-crowned Babbler. I found no evidence of signalling of contributions for rent payment, and that investment to nestling provisioning was high in related helpers as expected from the kin-selected benefit. The results suggest that the synchronous visits were characterised by the individual provisioning rule rather than the signalling from helpers to the breeding males.

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