The behaviours of sentinels and benefits of philopatry in helpers of the

cooperatively breeding chestnut-crowned babbler (*Pomatostomus ruficeps*)

Submitted by **Richard Hollis**, to the University of Exeter as a thesis for the degree of **Masters by Research** in **Biological Sciences**, **March 2019**.

This thesis is available for library use on the understanding that it is copyrighted material and that no quotation from this thesis may be published without proper acknowledgment.

I certify that all material in this thesis which is not my own work has been identified and that any material that has been previously submitted and approved for the award of a degree by this or any other University has been acknowledged.

Signed:……………………………………….

Richard S. Hollis

Abstract

Numerous studies have shown that an understanding of cooperative breeding requires a thorough knowledge of the processes promoting family living and the key driving benefits behind seemingly cooperative behaviours displayed by groups. Sentinel behaviour is an important behaviour to study as it does not necessarily direct care towards kin, but to the group as a whole and so understanding the benefits attained from this behaviour are imperative to understanding social and cooperative behaviours as a whole. There is some debate as to whether sentinel behaviour is indeed cooperative or selfish and this is explored in chapter 1 by investigating the sentinel behaviour and its associated benefits in chestnut-crowned babblers (*Pomatostomus ruficeps*), an obligate cooperatively breeding bird of south-eastern Australia. One way in which cooperative breeders can focus their help towards kin is to remain philopatric. The benefits of philopatry hypothesis suggests that it is not ecological constraints on outside territories that promotes delayed dispersal but that some territories are worth remaining on and provide greater benefit than dispersing. To provide evidence for this, we investigate the differences between territories with differing habitat features and the effect this has on group provisioning. The territories and the habitats did not significantly affect provisioning behaviour of chestnut-crowned babblers, and did not significantly impact group sizes. Thus, we found little evidence for the benefits of philopatry as a process behind delayed dispersal in chestnut-crowned babblers and discuss this in chapter 2.

Acknowledgements

List of Contents

List of Figures and Tables

Chapter 1   **Page**

Figures

Tables

Chapter 2

Tables

Author's Declaration

Data for Chapter 1 was collected by Richard S. Hollis between September and November 2015. Data for Chapter 2 were collected by Lucy E. Browning in 2007 and 2008, amalgamated and edited by Richard S. Hollis and Professor Andrew F. Russell for the purposes of this study in 2018. Literature searches, data processing, data analysis and thesis preparations were undertaken by Richard S. Hollis. For Chapter 1, data analysis was co-supervised by Dr. Deborah J. F. Russell.

Professor Andrew F. Russell provided supervision to Richard S. Hollis for the entirety of data collection, processing and analysis and thesis preparation across the studies.

General Introduction

Evolution by natural selection posits that individuals carrying genes that offer a reproductive advantage over competitors will be favoured (Williams 1966; Dawkins 1976). Despite this, apparently mal-adaptive behaviours are common-place. One of the most widespread and common of such behaviours is cooperative breeding, where individuals refrain from breeding currently, in favour of helping others to do so. This behaviour poses the obvious question: if behaviour is governed by genes and genes are propagated to future generations through reproduction, how can genes for helping be favoured in populations? Despite the apparent evolutionary paradox presented by such behaviours, it is both common and widespread. For example, cooperative breeding is found in all ants, as well as 10% of bees, wasps, birds and mammals, as well as a small percentage of other insects, crustaceans, spiders and fish (Wilson 1971; Choe and Crespi 1997; Koenig & Dickinson 2016). Thus, the evolution of cooperative breeding clearly requires explanation.

Hamilton (1963) solved the paradox of cooperative breeding through his formulation of inclusive fitness theory. Briefly, cooperative breeding can be selected where helpers increase the productivity of breeders with which they share genes by descent. Evidence is overwhelming. First, cooperative breeding tends to evolve from monogamous common ancestors, in which helpers tend to be related to the offspring to which they direct care (Hughes 1998; Cornwallis et al. 2009; Lukas & Clutton-Brock 2012). Second, where helpers have a choice of helping varying degrees of kinship in the group, they invariably direct their care to the most related individuals (Cornwallis et al. 2009). Finally, helpers typically increase the productivity of recipient breeders, as expected under Hamilton's rule, allowing them to increase representation of related genes in the

following generation (Cornwallis et al. 2009; Koenig & Dickinson 2016). Satisfying Hamilton's rule requires that helpers have the opportunity to direct their care towards more related individuals in the population on average. This can be achieved in a number of ways. For example, individuals can delay dispersal and help in their natal territory where relatives are more likely. This is particularly beneficial to species such as red-cockaded woodpeckers (*Picoides borealis*) where dispersing in your first year has a low rate of success, as does breeding at early ages and thus can improve your lifetime fitness level (Walters et al. 1992). Alternatively, individuals can direct their care towards kin over non-kin through recognition. Long-tailed tits (*Aegithalos caudatus*) are facultative cooperative breeders, and in the event that their nest fails, will direct care towards neighbours with a preference towards their relatives which are identifiable through vocalisations learned during the nesting period (Hatchwell et al. 2001). Nevertheless, kin are not always the receivers of help, suggesting that some cooperative systems and/or behaviours therein are not easily explained by kin selection (Cockburn 1998).

One hypothesis is that, by helping, individuals improve their future direct fitness (Brown 1983). For example, helping might be a form of rent payment, if offspring benefit from remaining on their natal territory beyond nutritional independence, but need to help in order to offset the cost of their presence to breeders (Gaston 1978). Alternatively, helpers might gain experience from contributing to a current breeding attempt (Selander 1964; Brown 1983; Komdeur 1994), or by helping, they might signal their quality to potential mates (Zahavi 1995). Finally, if helpers increase the survival of other group members, and group size is important for future breeding success, then by helping, individuals might gain future benefits when they obtain the future breeding role in a large

group (Kokko et al. 2001). Testing whether kin selected benefits or future direct benefits select for cooperative behaviour is challenging, but necessary to our understanding of the evolution of cooperative societies.

A key component to understanding the evolution of cooperative breeding is to understand the forms of help provided and the fitness consequences that behaviours can confer to donor and recipient. For example, whether or not helpers gain immediate indirect kin-selected benefits or delayed direct benefits might be biased by the cooperative behaviour studied; with attributing selective pressure on the cooperative behaviour (and system) largely down to measurable cost: benefit ratio for that behaviour. Where the costs incurred and benefits provided are high, kin selected benefits might be more operational, assuming kin are being helped. While where both are low, direct benefits are more likely to be achieved. The problem is that the costs and benefits can be hard to measure and many measures might be confounded by factors such as habitat quality (Brown 1982).

One of the most contentious cooperative behaviours is sentinelling. Sentinel behaviour, defined as coordinated vigilance by group members, may be explained through indirect fitness benefits of helping through increasing the anti-predatory success of collateral kin, but has been argued by Bednekoff (1997), to be a selfish behaviour. Whether or not sentinelling is cooperative or selfish hinges on whether or not it is costly. On the one hand, it would appear costly because sentinels often adopt vulnerable positions and refrain from feeding during their bout. On the other hand, if sentinels are satiated, adopt a position close to cover and are the first to spot and take cover from predators, then sentinelling would be more consistent with selfish behaviour (Bednekoff 1997). In

support of direct benefits, a study by Clutton-Brock et al. (1999) found that meerkat (*Suricata suricatta*) sentinels were the first group member to escape to the safety of bolt holes. Reducing predation risk to self over group mates is not the only way in which to achieve direct benefits from sentinelling, further studies provide more evidence of this as sentinels improve hierarchical position (Dattner et al. 2015), secure paternity (Walker et al. 2016) and is used in prospecting (Clutton-Brock et al. 2002) across habitats. However, studies into pied babbler (*Turdoides bicolor*) sentinel behaviour found that sentinels allowed the group to forage more efficiently, but were suggested to be at a greater, not lesser, risk of predation than the remaining group members (Hollén et al. 2008; Ridley et al. 2013). This supports the idea that sentinel behaviour is kin selected and leads to indirect benefits through improved survivorship of kin.

Given that models of kin selection versus direct benefits typically predict differences in the helper impacts on breeding success, any confounder of such helper impacts will necessarily cloud our interpretation of selection on cooperative breeding (Brown 1982; Cockburn 1998). One of the most problematic confounders is territory quality. This is because improved habitat quality is likely to yield improved reproductive output of breeders regardless of helper number, either through better food supply or reduced nest predation risk, leading to a spurious association between helper number and reproductive success. For example, Eguchi et al. (2002) found that territory quality, rather than helper number was responsible for variation in breeding success in rufous vanga (*Shetba rufa*). Further, as intimated above, habitat structure might also confound associations between helper number and breeding success, but less work has been conducted on the potential issue. There are two ways habitat structure might influence breeding success. First, if sentinelling is costly in terms of reducing foraging time and

the need for sentinelling in open habitat is high, open habitat might be associated with sub-optimal provisioning behaviour – leading to reduced breeding success in such habitats. Second, alternatively, open habitats might have a direct effect on provisioning behaviour, and through doing so compromise optimal patterns of provisioning from the perspective of maximising breeding success.

This thesis uses the cooperatively breeding chestnut-crowned babbler (*Pomatostomus ruficeps*) to two ends. First, I provide a detailed examination of the prevalence and status of sentinels, before going on to investigate the effects of group size, the presence of offspring and habitat structure on sentinel behaviour (Chapter 2). Here I predict that sentinelling is a cooperative behaviour most commonly adopted in the presence of offspring and in open habitat. Second, I investigate the effect that the quality of natal habitat has on nest provisioning and what this means for delayed dispersal in babblers (Chapter 3). Patterns of provisioning focus on the inter-visit interval and its variance in intervals between providing food for offspring in the nest as well as the proportion of prey items that are dug versus gleaned. It is anticipated that open habitat will require more food to be obtained by digging in the ground, which is more time-consuming and risky – leading to increased inter-visit intervals and/or reduced visitation synchrony which would lead them to be of lower quality for breeding and closed habitats favoured. Also, that closed habitats would themselves allow for group augmentation through delayed dispersal by providing more food and/or cover from predation.

The chestnut-crowned babbler is an obligate cooperatively breeding bird of arid and semi-arid south-eastern Australia, occupying a region with low annual rainfall (~200mm). The habitat is dominated by open chenopod shrubland with the dominant tree species,

belah (*Casuarina pauper*) restricted to linear stands in typically dry drainage lines and creeks, and patches of denser prickly wattle (*Acacia victoriae*) in other areas. These 50g passerines live in large, extended kin groups with some non-relatives, typically females which emigrate to new groups in their first year, of up to 27 individuals which fragment into 1-4 semi-independent breeding groups of up to 15 individuals (mean 6) (Russell 2016). The open areas which they inhabit, of sparsely populated trees and bushes, have a high predation risk, primarily from medium sized birds of prey, and the closed areas which have dense thickets of bushes and trees and have low predation risk (Sorato et al. 2015). Little work into sentinels in this species has been carried out, however we know that groups do have sentinels, particularly during foraging bouts and that groups are at risk from several aerial predator species which the sentinels alarm call when observed (Sorato et al. 2012). Provisioning in this species is directed preferentially towards kin however this does not wholly explain the variation in provisioning by helpers, with provisioning characteristics changing further with age of helper and role within the group (Browning et al. 2012). We also know that offspring are fed a variety of invertebrates and that this does change over the course of the nesting phase, however we do not know the role that habitat plays in this behaviour.

Chapter 1

Sentinel behaviour in the cooperatively breeding chestnut-crowned babbler: frequency, form and function

Richard S. Hollis[1], Andrea L. Liebl[1], Alex G. Cones[1], Deborah J. F. Russell[2], Andrew F. Russell[1,2*]

[1] Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Penryn Campus, Penryn, Cornwall TR10 9FE, U.K.

[2] Fowlers Gap Arid Zone Research Station, University of New South Wales, Sydney NSW 2033, Australia

* Corresponding author: a.russell@exeter.ac.uk

Running title: sentinelling in chestnut-crowned babblers

Keywords: cooperation; group-living, raised guarding; selfish sentinels; vigilance

Word count: 4854

Abstract: 277

Abstract

Understanding the evolution of group-living requires quantification of the associating benefits and costs. A common cost is the increased detectability of groups to predators. One potential means of mitigating such costs is through the evolution of sentinel behaviour, where a minority of group members at a time spend a protracted period scanning for predators while the rest of the group forages. However, whether or not sentinelling represents a selfish or cooperative behaviour remains contentious, largely owing to the paucity of detailed studies on such behaviour. Here we report on the frequency, form and function of sentinelling in the cooperatively breeding chestnut-crowned babbler (*Pomatostomus ruficeps*) of inland south-eastern Australia where the threat of aerial predation is high. Sentinelling typically occurred from elevated, exposed positions at a frequency of ~2 bouts per hour and lasted an average of ~3 min. The primary contributors were those over 1 year, except for breeding females which contributed equivalently to juveniles; we never witnessed competition over sentinelling. Both the frequency and duration of sentinelling were elevated in open habitat and in large groups, while the frequency was also greater early in the morning, when the group was actively foraging on the ground and in the presence of fledglings. First, our results are consistent with the hypothesis that sentinelling has evolved to enhance predator detection in this species, and we found no evidence to suggest that it is performed to detect neighbouring groups. Second, on balance, that it typically occurred without competition, in open habitat without obvious access to cover, and when individual-level costs and group-level benefits are likely to be high suggests that it primarily serves as a cooperative rather than selfish function.

Introduction

Living socially is associated with well-documented benefits and costs (Macdonald 1983). For example, improved foraging efficiency (Herbert-Read et al. 2016), acquisition of foraging skills (Thornton & McAuliffe 2006) and food sharing (Rebout et al. 2017) are common benefits of group living. On the other hand, groups are more conspicuous to predators than individuals (Jackson et al. 2008). Although this cost of group living to a given individual can be mitigated passively through confusion effects (Neill & Cullen 1974; Hogan et al. 2016), dilution effects (Foster & Treherne 1981; Lehtonen & Jaatinen 2016) and selfish herd theory (Hamilton 1971; De Vos & O'Riain 2013), these seldom compensate the need for direct vigilance (Vainikka et al. 2005). However, vigilance itself can be costly due to a loss of foraging time (Bachman 1993). One option to alleviate this cost is to evolve coordinated vigilance, whereby a minority of the group take turns to scan for predators while the remainder of the group forage. Despite this theoretical expectation (Wickler 1985; Rasa 1986; Bednekoff 1997), the number of social species known to show coordinated vigilance, or sentinelling, is limited, and the selective pressures remain controversial.

Sentinelling (also termed sentry or watchman behaviour) differs from more general vigilance behaviour in at least two key ways. First, it is coordinated, in that a small proportion of the group, often only a single individual, performs sentinel duty at any one time; while the rest of the group forages (Clutton-Brock et al. 1999). Second, sentinels remain vigilant against threats for a protracted period (defined as ≥ 30 seconds), often from an elevated position and can also advertise their behaviour through the use of a specific accompanying vocalisation (Rasa 1986; Manser et al.

1999; Wright et al. 2001; Ridley et al. 2013). Although documented in rather few species to date, sentinelling appears to be widespread, both taxonomically and socio-ecologically. For example, apparent sentinelling has been documented in pair living rabbitfish species (*f. Siganidae*) inhabiting coral reefs (Brandl & Bellwood 2015), group living rock hyrax (*Procavia capensis*) and klipspringer (*Oreotragus oreotragus*) (Kotler et al. 1999; Tilson 1979), as well as in socially monogamous, polygynous and polyandrous bird species (Mainwaring & Griffith 2013; Burton & Yasukawa 2001; Malan & Jenkins 1996). Perhaps the system with the greatest incidence of sentinels is the cooperative breeders, which might be because they tend to live in relatively stable groups comprising of kin and/or because they habitually show other forms of cooperation (Russell 2004; Koenig & Dickinson 2016). However, even in these systems, our knowledge of the incidence of sentinelling and the selective forces are biased by the accounts of a few select species.

Current estimates of the number of cooperatively breeding birds and mammals are at least several hundred in each taxon (Cockburn 2003; Russell 2004; Jetz & Rubenstein 2011; Griesser et al. 2017). However, sentinelling has only been documented in 18 bird and 2 mammalian cooperatively breeding species to date (Bednekoff 2015), and few of these have been subject to detailed study. In addition, contention exists as to whether the behaviour is primarily selfish or cooperative. In a mathematical model, Bednekoff (1997) suggested that sentinelling could be selfish if sentinels are in good condition or have recently foraged successfully, and by spotting predators first, they have a survival advantage. In support, Clutton-Brock et al. (1999) found that in cooperative meerkats (*Suricata suricatta*), sentinel behaviour was most commonly performed by those that had recently foraged successfully (and

could be induced to sentinel through supplemental feeding), and that sentinels were the first group members to escape to bolt holes. However, in a subsequent study, Santema and Clutton-Brock (2013) found that sentinelling was more common when groups had pups present with detriments to the sentinel's foraging time; hinting that sentinelling might function as a cooperative behaviour. Further, whilst sentinels in pied babblers (*Turdoides bicolor*) allowed the group to forage more efficiently, they were suggested to be at a greater, not lesser, risk of predation due to their greater distance than foraging group members from cover (Hollén et al. 2008; Ridley et al. 2013). Finally, Wright et al. (2001) found little evidence to suggest that individuals in Arabian babblers (*Turdoides squamiceps*) compete over sentinelling, which might be expected if sentinelling is selfish, although more recently Dattner et al. (2015) reported dominant males competing with subordinates over sentinelling duty in the same population. In order to make more sense of the distribution of sentinel behaviour, as well as the socio-ecological associates and selective forces, more studies are required.

As such, our aims in this study are to investigate the incidence, patterns and socio-ecological predictors of sentinelling in the cooperatively breeding chestnut-crowned babbler (*Pomatostomus ruficeps*). Although Australian avifauna is rich in cooperatively breeding birds (Cockburn 2003), sentinelling has been rarely documented. Yasukawa and Cockburn (2009) found evidence of sentinel behaviour in the cooperatively breeding superb fairy-wren (*Malurus cyaneus*), although it occurred at the nest, rather than during foraging, and served to improve provisioning efficiency. Previous work on the chestnut-crowned babbler has shown sentinelling to occur during foraging, but its biology and predictors are poorly understood (Sorato et

al. 2012). Occupying inland, south-eastern Australia, chestnut-crowned babblers typically frequent open (semi) arid areas in extended family groups and forage for invertebrates and small vertebrates (Portelli et al. 2009; Browning et al. 2012). Although invertebrates can be gleaned from trees and shrubs, foraging primarily occurs on the ground, often by digging. Thus, their habitat and foraging technique makes them highly vulnerable to aerial attack. Indeed, in a previous study, encounters with aerial predators was shown to reduce time spent foraging on the ground (Sorato et al. 2012), while the extent of arboreal cover was shown to influence a group's response to encounters with neighbours (Sorato et al. 2015). Finally, while sentinelling has sometimes been suggested to facilitate extra-group mating opportunities or detection of intruders (Walker et al. 2016), neither is likely in chestnut-crowned babblers because extra-group paternity is exceptional (Russell 2016) and this species is weakly territorial (Sorato et al. 2015), with any intrusions being detected aurally rather than visually. As such, we expect sentinelling behaviour in this species to serve a primarily anti-predator function, although whether it is self-serving or cooperative is not known.

We have two broad aims. First, we outline the ecology of sentinelling, including its incidence and duration, where it is conducted, as well as whether or not there is any evidence that individuals compete to sentinel which would be consistent with selection on selfish sentinelling (Wright et al. 2001). Second, we investigate its socio-ecological predictors, including: the time of day; the group size, activity and current location; the presence of fledglings and the local habitat in which they occupy. These predictors permit a test of the common assumptions that sentinelling serves an anti-predation function (Clutton-Brock et al. 2002; Kern & Radford 2014, see Discussion),

and subsequently contrasting predictions concerning whether or not the behaviour is driven by selection on benefits to self or collateral kin (Bednekoff 1997; Russell 2004). For example, in addition to expected competition over sentinelling, the hypothesis that sentinelling is selfish will be further supported if: (a) sentinel behaviour is independent of where the group is currently foraging (e.g. ground versus tree), since the vulnerability of the group should be independent of decisions to sentinel under this hypothesis; (b) show lower incidence and duration early in the morning, since individual condition will be lower immediately following the ~10h night without food; and (c) sentinels are taking positions which are close to or already provide cover to conform with the hypothesis that sentinels are in the safest position of the group.

Materials and Methods

Study site and population

Data were collected between September and November 2015 at the University of New South Wales Arid Zone Research Station, Fowlers Gap, in far-western New South Wales, Australia (31°05′ S 141°43′ E). The climate is arid with low annual rainfall (~200mm), daytime air temperature during the study period ranged from 6–37^{0}C. The habitat is dominated by open chenopod shrubland with the dominant tree species, belah (*Casuarina pauper*) and prickly wattle (*Acacia victoriae*), restricted to short linear stands in association with drainage lines and creeks which remained dry during the study. The study population of chestnut-crowned babblers was established in 2004, and the vast majority of birds in each group are identifiable in the field from their unique combination of colour leg bands, further details of the

study site and population are provided in Portelli et al. 2009; Sorato et al. 2012 and Russell 2016.

Babblers are not strong fliers and are vulnerable to aerial attack in the open habitat, and the only predators observed during the study were aerial. Brown falcon (*Falco berigora*) and nankeen kestrel (*& F. cenchroides*) as well as collared sparrowhawk (*Accipiter cirrocephalus*) and brown goshawk (*& A. fasciatus*) were all observed approaching or attempting predation on babblers during observations, while Australian magpie (*Cracticus tibicen*) was also seen attacking fledglings. Aerial predation events and attempts witnessed during this study typically involved an ambush from low flying predators onto foraging babblers on the ground or shrubs, but predation events in trees also occur. Although aerial predators were observed at the study site, predation events were too infrequent for formal analysis.

Data Collection

The study was conducted on 19 breeding units (mean unit size ± SD = 7.7 ± 3.8, range 3 – 16 birds in adult plumage, which is attained by 6 months post-fledging). Observations on each group were carried out for 1 – 6 hours, between 06:15hrs – 17:15hrs (total = 116 h, mean = 3.6 h per observational period, total observation periods = 33). The study population was not tame, but the presence of sentinels and their sentinelling duration were easily determined in the sparsely vegetated habitat, while the identity of the individual on sentinel could be determined in about 50% of occasions using photographs taken with a camera using a 300 mm lens. A sentinel

was defined as an individual in an elevated position, relative to the ground and foraging group, actively scanning for predators (Hollén et al. 2008) for a duration of at least 30 s (Ridley et al. 2012).

The behavioural ecology of sentinelling and potential predictors were recorded in two ways. First, we used scan sampling every 5 min to determine whether or not a sentinel was present. This frequency of scan sampling was based on preliminary observations of the frequency and duration of sentinelling (see also Results). During each scan, we recorded time of day, group size (excluding any individuals in pre-adult plumage) and group activity (which was the activity of the group at the start of the scan i.e. whether or not they were actively foraging, nest building or provisioning or resting which included preening). Further, we recorded whether the majority of the group was positioned on the ground or in trees; with the latter divided into tree edge versus centre. If the group were moving this was noted, but removed from analysis as potential sentinels were never in position for the required 30s when the group was travelling. Group location was categorised based on the majority of the group's position, but generally included the whole group. Second, whenever a potential sentinel was observed, we recorded the start and end time *ad libitum* although only those bouts exceeding 30 s were defined as sentinels. Again we defined the group behaviour and location (see above). Finally, we recorded the stage of breeding attempt and whether or not the habitat was open or closed. The stage of the breeding attempt for each group was recorded in Julian days from the first egg, and was known with precision owing to on-going studies. Whether or not the habitat was open or closed was based on the extent of vegetative cover of chenopods (shrubs of 15-120 cm high) and trees (typically 3-15 m). The habitat was defined as open when

the size and cover of chenopods were below median and trees were below median numbers, while habitats were defined as closed when the above were greater than the median across the territories (for further details, see Portelli et al. 2009; Sorato et al. 2012 2015).

Statistical analysis

Statistical analyses were performed in R for Microsoft Windows version 3.0.1 (R Core Team 2013, http://www.R-project.org/). Two statistical models were created, one pertaining to the initiation of sentinelling and the other to the duration of sentinelling. In each case, the explanatory terms were: time of day (to the nearest hour); group behaviour (active or resting) and location (ground, tree centre or tree edge); group size (number of independent adults in the group); stage of breeding (Julian day); habitat state (open and closed). Potential explanatory terms (see below) were removed from the model when they failed to explain significant variance based on log-likelihoods when the term was included versus excluded from the model (Zuur et al. 2009) using the anova function in R ($\alpha < 0.05$).

To investigate the factors associated with the initiation of sentinelling, we divided our observation periods into 5 min time-blocks (see above), and asked what factors influence the probability that a sentinelling bout will be initiated (1) or not (0) in each time block using a binomial generalised estimating equation generalised linear model (GEE GLMs) in the R package geepack with the geeglm function (Højsgaard, Halekoh & Yan 2006). This analysis allows for temporal autocorrelation across time-

blocks by clustering the data by observation day for each group (N=913 time blocks, mean blocks/group=48.1, range=8 - 86, N=19 breeding groups). Whether or not an individual was already on sentinel at the onset of each time-block was fitted as a covariate. Scaled Pearson's residuals were used to check assumptions of the model. *P* values were calculated when the explanatory variable is set as the final tem due to the hierarchical regression of GEE as terms are processed sequentially within the model. Predictions used to produce graphical representations in the figures are derived from a glm as per R's package ggplot2 requirement (Wickham 2009).

To investigate the factors associated with sentinel durations, mixed-effects models were fitted using the lme4 package (Bates et al. 2014) with the lmer function following natural logarithm transformation. All sentinel bouts exceeded 30 s (Ridley et al. 2009). Two outlying durations were removed: one occurring as the group left the communal roost and the other as a nestling was fledging (N = 219 sentinel durations). Observation group (breeding unit) was fitted as a random effect in all models as focal groups received repeat observations leading to statistical non-independence. Scatterplots of residuals and predicted values were generated to check model assumptions.

Results

Incidence, duration, position and identity of sentinels

A total of 219 sentinel bouts were recorded during the 116 hours of observations in the 19 breeding units. Sentinelling was recorded at least once in all of the 19 units,

although rates of sentinelling varied by an order of magnitude from a low of 0.2 bouts/h to a high of 4.7 bouts/h among units (overall mean bouts/h ± SD = 2.0 ± 1.1) (Figure 1a). Sentinels adopted a range of positions, but were at least three times more likely to be found on highly exposed dead tree 'stags', usually ~ 5m above the ground, than on live trees or shrubs (Figure 1b). The individual on sentinel was identified for 112 of the 219 bouts, comprising of 62 different individuals in 18 of the units. Of these 62 18% were juveniles (1 – 6 months post-fledging), 32% were 1st year birds, 40% were 2 - 9 years old and 10% were breeding females. Based on the numbers of each category present in the 18 units, fewer juveniles and breeding females were identified on sentinel than would be expected given their proportional representation (Figure 1c).

Factors affecting the initiation of sentinelling bouts

Sentinels were never observed replacing each other directly and individuals never competed for a sentinel position or interfered with another's sentinel bout. The average latency between sentinels when replaced within 15 min was 3.4 min (± SD = 2.6). Further, the probability that a new sentinel arose within a 5 min time-block was halved when a sentinel was already on duty in the time-block or in the last minute of the previous time-block (Figure 2a). After controlling for this effect, we found that the probability of sentinelling being initiated in a given 5 min time-block was influenced by time of day and habitat openness, as well as by group size, location, activity and breeding stage (Table 1). Sentinelling was initiated twice as often in the early morning than it was in the middle of the day, although it showed a non-significant tendency to increase again in the late afternoon (Figure 2b). It was also twice as

likely to be initiated in those groups living in relatively open habitat, where the risk of aerial predation is presumably greater (Sorato et al. 2012 2015) (Figure 2c). Finally, it was approximately twice as likely in large versus small groups (Figure 2d), when groups were active, particularly when foraging on the ground (Figure 2e) and in the presence of fledglings compared with at the onset of breeding (Figure 2f).

Factors affecting sentinelling duration

The duration of sentinel bouts averaged 3.4 mins (± 2.4 mins SD; range = 0.5 – 17 mins, N= 219 bouts), and the mean duration of sentinelling varied by up to fivefold across the units observed (Figure 3a). Chestnut-crowned babblers are highly active and have home ranges of around 1km². As such it is unsurprising that at least 20% of all sentinel bouts were terminated because the group moved off. Probably for the same reason, there was little association between the frequency and duration of sentinelling during observations (r = -0.189, N = 19). The only factors to predict sentinelling duration were habitat structure and group size (Table 2). Sentinelling durations were 44% longer in open habitat than in closed habitat (Figure 3b). Group size showed a significant quadratic relationship with sentinelling duration, with durations increasing by 65% between groups of 2 and 9, before declining by 40% to groups of 16 (Figure 3c). Time of day, breeding stage, group activity or group location failed to predict sentinelling duration significantly (Table 2).

Discussion

In chestnut-crowned babblers, bouts of sentinelling averaged 2 /h and lasted an average of 3.4 min. Sentinels were most often adults (other than the breeding female) that adopted a highly exposed position near the top of a dead tree stag (5 m above the ground). Sentinelling was most often initiated in the morning, when the group was actively foraging on the ground in open habitat, in large groups and in the presence of fledglings. We found no evidence to suggest that group members competed to sentinel and whether or not a sentinel was on duty in a given 5 min time-block had a strong bearing on initiation of a new sentinelling bout. Sentinelling was often terminated by group movement away from the current location, and its duration was predicted by habitat structure and group size. Together, our findings suggest that sentinel behaviour primarily functions to reduce the threat of aerial predation, and is a costly cooperative activity aimed at improving the survival of group members to which sentinels are typically related.

Sentinelling is typically suggested to evolve in order to reduce the threat of predation and so improve the foraging efficiency of group members. In support, meerkats, for example, scan for predators from elevated positions, utter a "watchman's song" whilst doing so (Manser et al. 1999) and are invariably the first to spot potential predators (Clutton-Brock et al. 1999). However, an alternative possibility is that it serves to detect threats from, or opportunities with, conspecifics. For example, in white-browed sparrow weavers, sentinel behaviour by dominant males is suggested to function to reduce the probability of cuckoldry, while in dominant females, it might facilitate extra-group matings, which are relatively common in this system (Walker et

26

al. 2016). Our evidence in chestnut-crowned babblers is that it primarily serves to reduce the threat of aerial predation. While one could doubtlessly argue that any of our results could be explained by the hypothesis that sentinelling serves to detect conspecifics rather than predators, we find this possibility unlikely. First, we have shown previously that the incidence of sentinelling increases following an aerial threat (Sorato et al. 2012). Second, extra-group paternity is exceptional in chestnut-crowned babblers (Russell 2016), and breeding females seldom initiated sentinelling, suggesting that it does not function to influence extra-group mating opportunities. Third, this species is weakly territorial and neighbouring groups are easily located aurally, negating the need to sentinel in order to detect any 'intrusions', particularly as breeding groups are fragmented social groups, and which helpers can assist with provisioning at multiple nests (Russell 2016). There is one possible exception however: juveniles were surprisingly likely to initiate sentinelling, and one explanation is that sentinelling by this age class might facilitate maintaining contact with the group, for they commonly lag. This possible caveat notwithstanding, the findings presented in this study in conjunction with our understanding of the socio-ecology of this species (Sorato et al. 2012 2015; Russell 2016) lead us to suggest that the primary function of sentinelling is to reduce predation.

Nevertheless, we acknowledge that the rate of sentinelling observed, averaging just 2 bout /h, is low compared with other species, such as meerkats which had a near permanent rotation of sentinels during foraging bouts (Clutton-Brock 1999). The low rate of sentinelling in chestnut-crowned babblers is unlikely to be due to the low risk of predation, for aerial predators are common and cover is limiting in the open habitat in which that reside. There are several explanations which would explain this

low average. In small groups (≤ 5 adults) where sentinelling was very infrequent, we found that they would often be recorded foraging for long periods with heterospecific arboreal passerines of a similar size, for example spiny-cheeked honeyeater, *Acanthagenys rufogularis,* which fulfilled a similar role to that of a sentinel by producing aerial predator alarm calls to which the babblers responded; taking over the position of a previous babbler sentinel and mobbing nest predators. Large groups, however, did not use this tactic and would disassociate from heterospecifics (positive/negative heterospecific associations for small vs. large groups: X^2=8.4, *df*=1, *P*<0.005), but is a similar strategy to that observed by Ridley and Raihani (2006) with small pied babbler groups utilising heterospecific sentinels. Secondly, the relatively large (overlapping) home ranges of this species coupled with their relatively fast movement might preclude sentinelling which requires groups to remain in one place for a sufficient duration. For example tracking studies showed that this species of babbler have home ranges during breeding averaging 38 ha and move at a rate of 4 ha / h (Portelli et al. 2009; Sorato et al. 2016). Indeed, this hypothesis might contribute to explaining the greater incidence of sentinelling in the presence of fledglings, which reduce the mobility of the group, although their increased vulnerability is also a likely factor and the duration of sentinelling bouts were not elevated in the presence of fledglings. Second, babbler groups are highly clumped (AF Russell unpubl.) and they have a distinctive, far-reaching alarm call (Crane et al. 2016). Indeed, the presence of an aerial threat sets off a cascade of aerial alarm calling across groups. As a consequence, the need to sentinel in order to spot predators in this species might be diminished, but further work is required to test the validity of this hypothesis.

In contrast to the relatively low rate of sentinelling, the average bout duration of 3.4 min accords well with those of other studies. For example, sentinelling bouts in pied babbler average 3.7 min, meerkat average 3.6 min, dwarf mongoose (*Helogale pavula*) 3.2 and white-browed sparrow weaver 2.9 minutes (Hollén et al. 2011; Clutton-Brock 1999; Kern & Radford 2014; Walker et al. 2016). In our study, sentinelling bouts were terminated 47 times due to group movement, and no incidences of sentinel replacement were observed. When successive bouts of sentinelling were initiated within 15 min of each other, the mean latency between bouts was 3.4 min. The factors responsible for predicting variation in sentinel bout duration are not wholly understood, but some studies suggest food or dominance to be a factor (Clutton-Brock 1999; Dattner et al. 2015). In this study, sentinel bout duration was predicted by habitat structure and group size. Bouts were longer in open habitat, presumably because the risks of predation are greater, and in medium-sized groups. Why group size should show a quadratic relationship with sentinel duration is not currently known. However, relatively short bouts of sentinelling might arise in small groups because they are less often targeted by predators (Sorato et al. 2012) and can associate with heterospecific sentinelling species, and large groups may benefit from passive antipredator tactics which come from group augmentation ('many eyes theory', Lima 1995 & 'confusion effect' Neill & Cullen 1974). Further work is required to better understand the duration of sentinelling and the variation therein.

Irrespective of the incidence and duration of sentinelling or whether it is performed as an anti-predation strategy, contention remains as to whether it is self-serving or 'altruistic' (Russell 2004). For example, in a game-theoretic model, Bednekoff (1997)

showed it could be self-serving, when being on sentinel duty is the safest place to be for satiated group members. In support, Clutton-Brock et al. (1999) showed that in cooperative meerkats, sentinels had recently foraged successfully (or had received supplementary food), adopted positions close to bolt holes and were the first to detect predators. Although in a more recent study of meerkats it was suggested that sentinelling might also be cooperative, based on the primary finding that it was more common in the presence of pups (Santema & Clutton-Brock 2013), dependent young might also attract predators, as is the case in chestnut-crowned babblers (Sorato et al. 2012). As a consequence, increases in the rate of sentinelling in the presence of dependent young does not clarify whether or not its function is primarily self-serving or cooperative. By contrast, sentinelling was suggested to be cooperative in pied babblers, based on the finding that sentinels were often further from cover than other group members (Ridley et al. 2013), and in Arabian babblers, based on the finding that group members seldom competed to sentinel, as might be expected if self-serving (Wright et al. 2001).

At least four of our findings on chestnut-crowned babbler, which is unrelated to the aforementioned Turdoides babblers, suggest a primarily cooperative function of sentinelling. First, like pied babblers, sentinels most often adopted highly exposed positions on dead tree stags far from cover, and initiated sentinelling more often in open habitat where the threat of predation is higher (Sorato et al. 2012). Second, like Arabian babblers, we found no evidence to suggest that group members competed over sentinelling. In particular, we never witnessed disruption of a sentinelling bout, which would be expected under the self-serving hypothesis given that sentinels are expected to be the safest and will lose condition relative to foragers. Third,

sentinelling was most often initiated early in the morning, when body condition following a ~10 h night would be at its lowest, even after controlling for whether or not the group was active. Finally it was also more often initiated when the group was foraging on the ground, where they are known to be more vulnerable (Sorato et al. 2012).

If sentinelling is cooperative in chestnut-crowned babblers, the final question is what benefits do they gain in return? We are not yet in a position to answer this question definitively, owing to the fact that the population is not habituated to close observation and so precise measures of costs and benefits are challenging. Nonetheless, some possibilities seem unlikely and others probable. Given the low incidence and lack of competition, hypotheses based on direct reciprocity (Trivers 1971), pay to stay (Gaston 1978) or social prestige (Zahavi 1995) seem unlikely candidates. This leaves two alternatives, group augmentation (Kokko et al. 2001) and kin selection (Hamilton 1963). Chestnut-crowned babblers live in extended family groups and varying numbers of unrelated immigrant females. As such, if group members benefit from the presence of a sentinel, which seems likely given that it most often occurs when groups are actively foraging on the ground, in open habitat and in the presence of fledglings, kin selected benefits are inescapable. By contrast the scope for group augmentation benefits are less obvious. On the one hand, because group benefits are generalised by sentinelling, there is scope for relatives and non-relatives to benefit similarly, which might suggest a role for group augmentation in selecting for sentinelling in this system. On the other hand, increasing the survival of unrelated immigrant females will provide kin selected benefits because such females will breed with males to which natal sentinels will

invariably be related. Although we are not in a position to test between these competing hypotheses formally, it is at least noteworthy that breeding females, which are unrelated to all immigrant females and many of the adult males, contributed little to sentinelling. Further studies are required in this, and other systems, in order to clarify the forces selecting for their evolution of sentinelling.

Figures
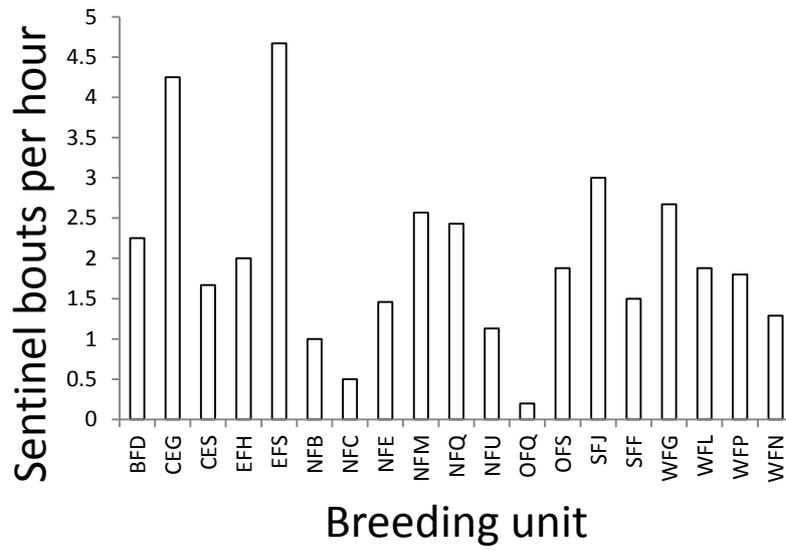
a)
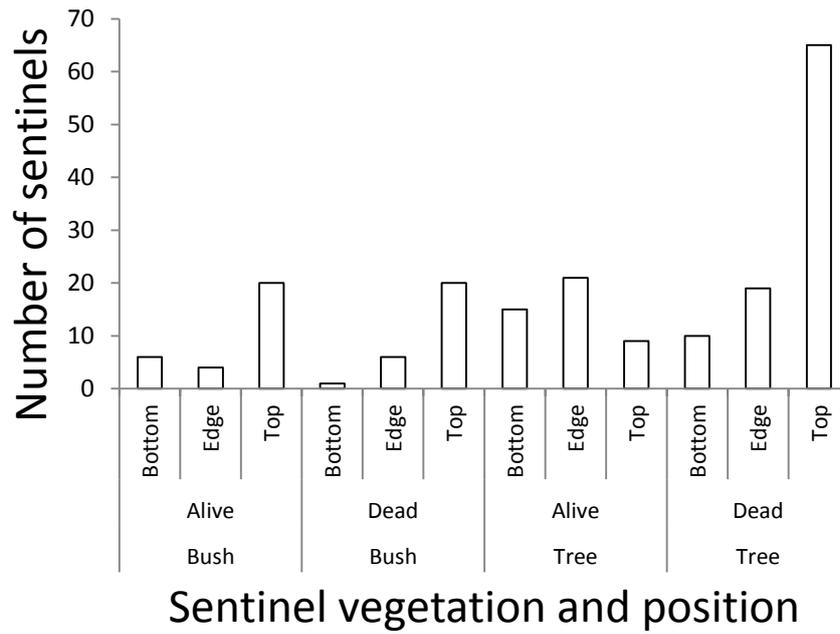
b)
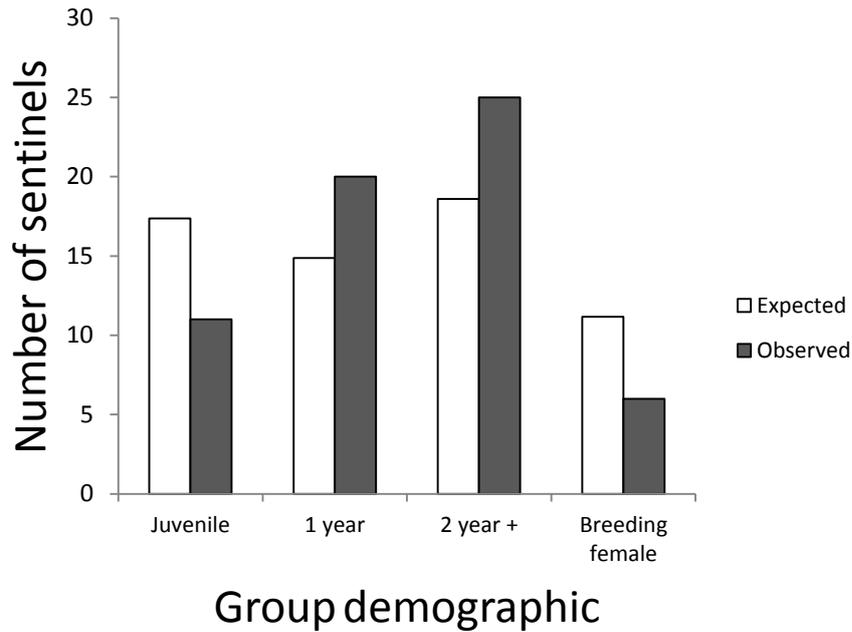
c)

Figure 1: a) Mean sentinel bouts per hour expressed by each group throughout the study (September – November 2015) (N = 33). Groups are divided into active breeding groups ranging in size from 3 – 16 adult plumaged birds. b) The number of sentinels across all groups which took up different positions within their habitat (N = 219). Bushes represent vegetation with a height of up to 50cm, trees up to a height of approx.. 3m. Dead vegetation was devoid of leaves and consequently represented a position with reduced cover. c) The expected and number of sentinels across groups which were identified to a group demographic using unique colour rings on legs (N = 112). The expected number of sentinels for a given demographic was calculated on the number of that demographic within the group sentinelling, if all demographics sentinelled equally in number of bouts.

a)

b)

$y = 0.590466 + -0.129099\ x + 0.004376\ x^2$

c)

d)

$y = 0.67268 + 0.04745\ x + -0.00231\ x^2$

e)

f)

$y = 0.109528 + 0.00228\ x$

35
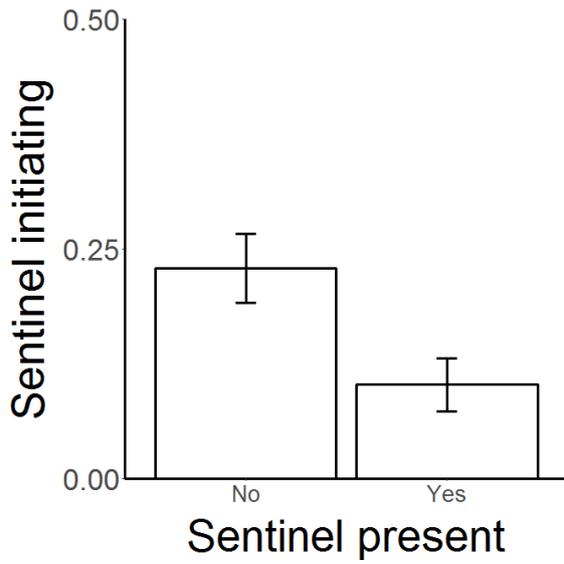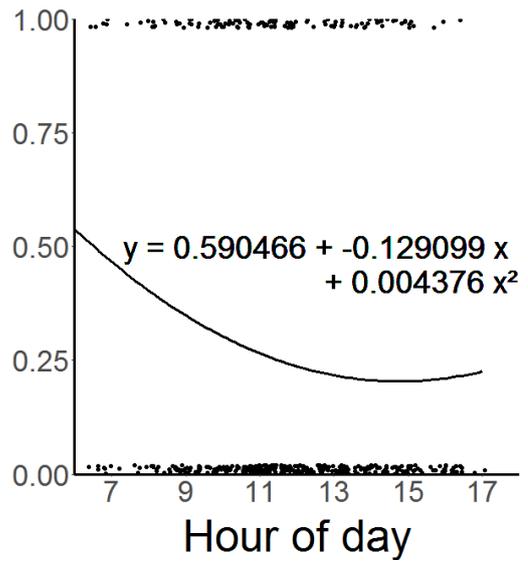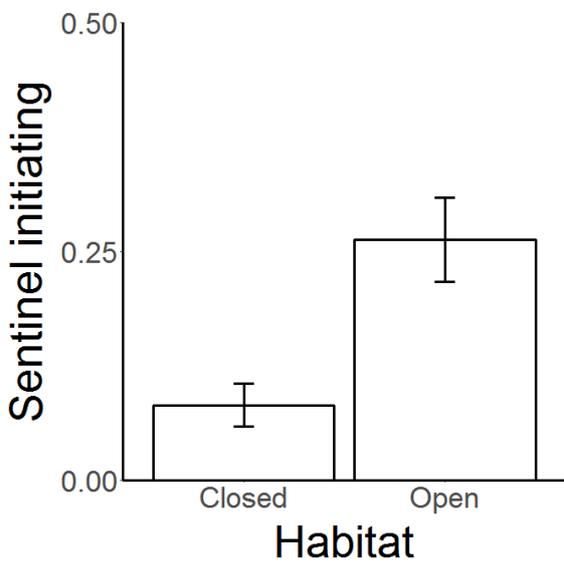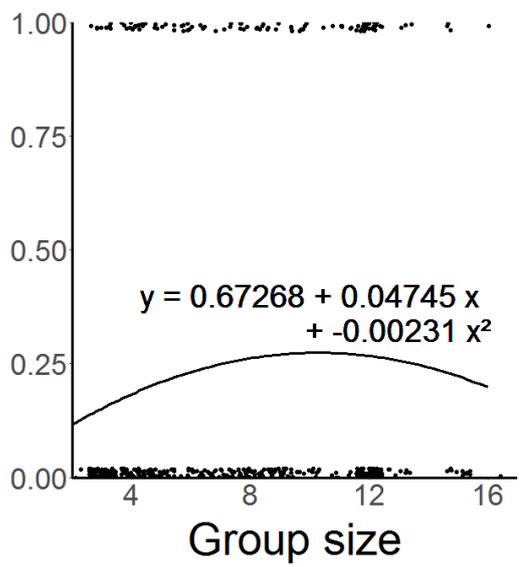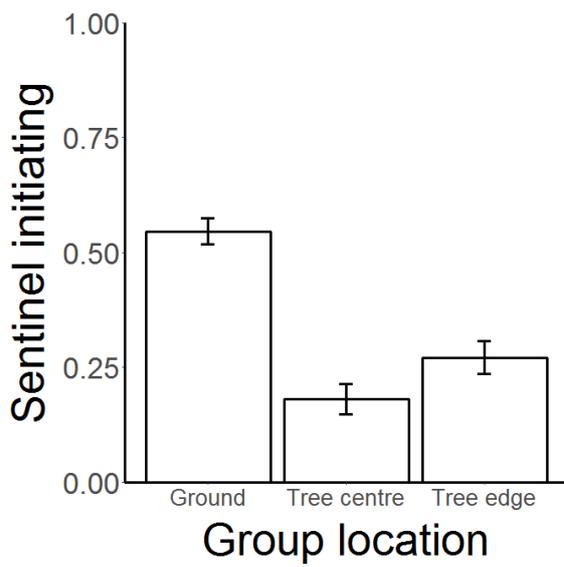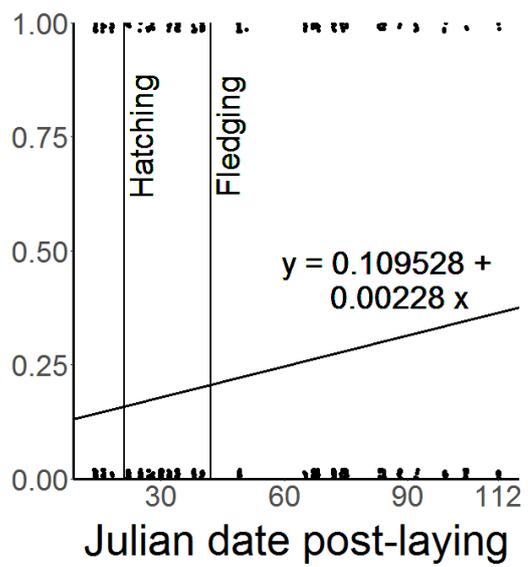
Figure 2: Shows the probability of a sentinel initiating on a given 5 minute time-block dependent on a) there being a sentinel already observed within that time-block or within a minute before it commenced. b) The hour in the day in which the time-block is located which was observed between 06:15hrs and 17:15hrs. c) The habitat in which the group occupied divided into closed or open (see Methods). d) The group size which is determined by the number of adult plumaged birds within the group (see Methods). e) The group's location determined by the location of the majority if not all of the group at the start of the 5 minute time-block. f) Julian date post-laying, calculated by 1 being the first lay date, and continuing consecutively in days.
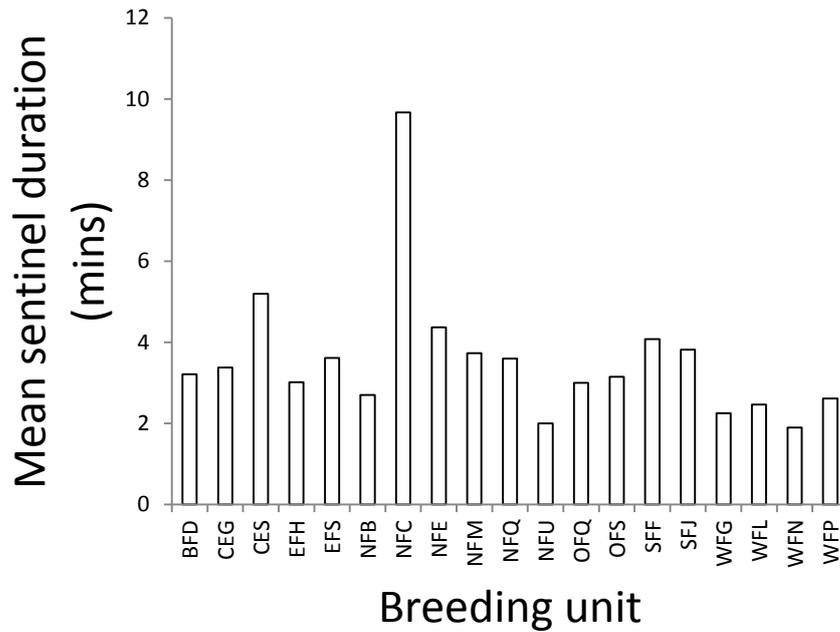
a)

b)
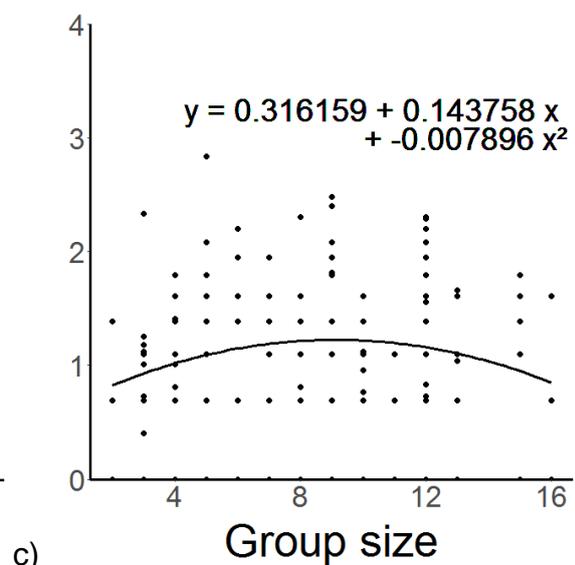
c)

Figure 3: a) The mean sentinel duration for each group across the study in minutes (N = 19). The groups represent breeding units which ranged in size from 3 – 16. b) The logged sentinel durations as predicted by Model 2 (see Table 2) for closed and open habitats (see Methods for habitat details). c) The logged sentinel durations as predicted by Model 2 (see Table 2) for the varying group sizes across the study. Group size is determined by the number of birds in adult plumage (see Methods).

Tables

Table 1: GEE model on sentinel initiations in a given 5 minute block, clustered by observation group. Model of best fit includes terms "hour of day squared" and "group size squared" as hour of day and group size are both non-linear. Presented outputs are retrieved from GEE glm model. "Group active vs. resting" does not have a corresponding plot as the prediction glm model produces a non-significant outcome for this term.

Term	Estimate	SE	χ^2 Statistic	df	p value
Intercept	1.02	2.13	0.23		
Group location: fig 1a			29.48	2	**<0.001**
Tree edge vs. tree centre	0.70	0.33	4.47	1	**<0.035**
Ground vs. tree centre	2.24	0.43	27.63	1	**<0.001**
Julian date (days post-laying)	0.01	0.005	8.26	1	**0.004**
Habitat: closed vs. open	1.14	0.41	7.62	1	**0.006**
Sentinel present	-1.07	0.41	6.87	1	**0.009**
Hour of day	-0.76	0.34	5.11	1	**0.024**
Group active vs. resting	-0.53	0.26	4.05	1	**0.044**
Group size	0.44	0.22	3.90	1	**0.048**
Hour of day squared	0.02	0.01	2.82	1	0.093
Group size squared	-0.02	0.01	3.27	1	0.070
Observation duration	-0.14	0.17	0.65	1	0.421

Table 2: Mixed effects model on logged sentinel durations, random effects are observation group and Julian date due to the repeated observation on groups and dates. "Group size squared" and "Hour of day squared" are presented as both of these terms were non-linear.

Term	Estimate	SE	T value	df	P value
Intercept	0.32	0.21	1.48		
Habitat: closed vs. open	0.25	0.09	2.79	1	**0.007**
Group size	0.14	0.06	2.5	1	**0.013**
Group size squared	-0.008	0.003	-2.36	1	**0.019**
Observation duration	-0.07	0.05	-1.41	1	0.160
Group location (tree centre)				2	0.210
Tree edge vs. tree centre	0.26	0.15	1.74		
Ground vs. tree centre	0.15	0.11	1.34		
Hour of day squared	<0.001	<0.001	0.87	1	0.386
Group active vs. resting	-0.09	0.11	-0.81	1	0.421
Hour of day	0.01	0.02	0.67	1	0.503
Julian date (days post-laying)	<0.001	<0.001	0.02	1	0.981

Chapter 2

No evidence for the benefit of philopatry hypothesis in the chestnut-crowned babbler

Richard S. Hollis[1], Lucy E. Browning[1], Andrew F. Russell[1,2*]

[1] Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Penryn Campus, Penryn, Cornwall TR10 9FE, U.K.

[2] Fowlers Gap Arid Zone Research Station, University of New South Wales, Sydney NSW 2033, Australia

* Corresponding author: a.russell@exeter.ac.uk

Running title: benefits of philopatry in chestnut-crowned babblers

Keywords: benefits of philopatry, delayed dispersal, cooperation, family-living

Word count: 3,362

Abstract: 222

Abstract

The puzzle of cooperative breeding has recently been shown to require an understanding of the factors that drive delayed dispersal by offspring and family-living. One hypothesis, the benefits of philopatry, proposes that the answer lies with variance in territory quality; with offspring benefitting more from staying at home in a high quality territory than moving to a low quality territory. Tests of this hypothesis are hampered by the challenges of measuring variance in territory quality. I circumvent this problem with a general observation that biologically meaningful variance, if it exists, should manifest in predictable variation in group provisioning behaviour. To this end, I investigate among-group variation in patterns of group provisioning in the chestnut-crowned babbler (*Pomatostomus ruficeps*) wherein helpers are delayed dispersers. Contrary to the predictions of the benefits of philopatry, after controlling for the expected effects of helper number, brood age and size, I found no evidence to suggest that groups varied predictably in their provisioning rate, variance of prey delivery or prey size. Nor did I find evidence to suggest that group size, which is primarily determined by the number and survival of delayed dispersers, is associated with known correlates of food availability or cover from aerial predators. My results suggest that the benefits of philopatry, at least as measured, is not a major predictor of delayed dispersal in this system.

Introduction

Family-living is now recognised to be a key step in the evolutionary transition to cooperative breeding, wherein individuals in addition to parents provide care for offspring (Emlen 1995; Drobniak et al. 2015). One hypothesis proposed to explain family-living in cooperative breeders is the benefits of philopatry hypothesis (Stacey & Ligon 1987; Koenig et al. 1992; Shen et al. 2017). Under this hypothesis, delayed dispersal by offspring, and so families, are promoted when the quality of available territories is variable, and offspring are selected to remain on higher quality natal territories (Stacey & Ligon 1987; Stacey & Ligon 1991). Testing this hypothesis is challenging, but is required to elucidate forces selecting for evolutionary transitions to complex societies (Maynard Smith & Szathmary 1997).

A key challenge in testing the benefits of philopatry hypothesis lies with identifying and measuring salient metrics of territory quality. For example, cooperative breeders only seldom rely on critical habitat features, such as cavities for protection or breeding that can be quantified and manipulated (Du Plessis 1992; Walters et al. 1992; Heg et al. 2008). Similarly, while food availability can be measured with sufficient accuracy in some species (Komdeur 1992) and/or manipulated in others (Baglione et al. 2006; Dickinson & McGowan 2006), for most species neither is feasible. This difficulty is compounded by the fact that it might not be the availability of food *per se* that defines a territory's quality, but the different foraging niches available and the energetic costs of obtaining food (Ens et al. 1992; Hansen et al. 2009) and the risks of predation (Peluc et al. 2008). Thus, for many species, if not most, it is likely that territory quality can neither be simply measured in terms of critical resource abundance nor measures of food availability.

A more feasible alternative approach might be to test the role that benefits of philopatry play in influencing family-living indirectly. For example, under a benefit of philopatry model, we would expect patterns of offspring provisioning to vary systematically across groups after controlling for known predictors. In particular, after controlling for differences in helper number, brood age and brood size among nests, support for benefits of philopatry will be provided if food is delivered at systematically different rates or constancy among groups, or of systematically differing size or type. Further, variation in patterns of prey delivery would also be expected to vary predictably with vegetation features known to predict both food availability and cover from predators. Finally, the benefits of philopatry hypothesis predicts a relationship between group size and habitat features known to correlate with food availability and/or cover from predation. This is both because offspring are more likely to delay dispersal on high quality territories and the survival of all group members are expected to be higher on such territories (Stacey & Ligon 1987). By contrast, none of the above patterns are expected by alternative resource-based ecological constraints hypotheses in the absence of philopatric benefits, since it is factors external to the territory that promote family-living under such alternative models and these should be independent of internal benefits (Koenig et al. 1992).

Here I use the above rationale to test for the role of benefits of philopatry in setting the scene for kin directed cooperative breeding in the chestnut-crowned babbler (*Pomatostomus ruficeps*). This 50 g cooperative breeder of inland south-eastern Australia breeds in extended family-groups varying in size from 2-15 individuals (mean = 6), with non-breeding helpers contributing primarily to feeding the nestlings

(Browning et al. 2012a, b). The habitat is open shrubland with substantial bare ground, and babblers forage under a high risk of aerial predation on a range of invertebrates and small vertebrates using techniques from digging in the ground to gleaning substrates (Portelli et al. 2009; Sorato et al. 2012). No evidence for resource-based ecological constraints has been provided in this species: previously occupied territories remain vacant for years in this species, suggesting that dispersal is not constrained (Russell 2016). Habitat structure is expected to have a significant impact both on prey availability and cover from predators in babblers. For example, territories with greater densities of shrubs and trees will offer more foraging substrate and protection from predators than those that have low densities of each (Portelli et al. 2009; Sorato et al. 2015). In addition, we have shown previously that areas with more shrubs have more invertebrate prey than areas devoid of shrubs. I would thus expect that under benefits of philopatry, territories with greater shrub and arboreal cover are superior, and are associated with higher and more uniform patterns of food distribution to growing offspring, as well as with larger group sizes.

Methods and Materials

The study was conducted at the University of New South Wales Arid Zone Research Station, Fowlers Gap, in far-western New South Wales, Australia (31°05′ S 141°43′ E). The climate is arid with an annual rainfall of ~215 mm. The habitat is dominated by open chenopod shrubland with variable cover of low shrubs, and with tall shrubs and trees confined to linear stands of variable lengths along creek beds and drainage zones (Portelli et al. 2009; Sorato et. at. 2012 2015; Hollis Chapter 2). Bare ground of sand, gibber and rock outcrops dominate. Short woody shrubs of 15-50

cm, which offer foraging opportunity, shelter and protection from predators, consist mainly of saltbush (*Rhagodia* and *Atriplex spp*) and bluebush (*Maireana spp.*). Tall shrubs up to 2-4 m high with thick foliage from base are mainly of prickly wattle (*Acacia victoriae*) and dead finish (*A. tetragonophylla*), while trees with bare trunks are mainly belah (*Casuarina pauper*), with some mulga (*A. aneura*) and wild apricot (*Pittosporum angustifolium*). It is important to note that even in the most shrub-rich territories, bare ground predominates, while the extent of cover by low shrubs versus the number of tall shrubs/trees is unassociated. Increases in low shrub cover and numbers of tall shrubs/trees are associated with more areas for foraging, more shelter and more protection from falcons and Accipiter hawks (Sorato et al 2012, 2015).

The present study uses data collected on up to 22 groups breeding in the 2007 and 2008 seasons (n = 28 group years), although sample sizes vary (see below). Groups were captured using mist-nets with constituent members being uniquely banded and having a 2 x 12 mm Trovan transponder tag inserted subcutaneously in their flank (see Nomano et al. 2014 for further details). We then determined the total number of feeds provided by each group member to growing offspring during a set amount of time, along with the size and type of item delivered where possible. To these ends, we fitted a copper coil antenna to the mouth of each breeding nest that was linked to a Trovan LC650 decoder designed to record the identity, along with date and time, of each transponder passing through the antenna. Further, by linking a pen camera system from the back of the nest to the same decoder system, we could film each bird for a set time as it passed through the antenna. Overall, we recorded 2622 feeding events by 101 individuals during 256 h over 53 days (mean = 4.7 h / d, range

= 1-12 h) in the 22 groups. The time stamps from the decoder and camera allowed us to calculate the latency between the recorded feeding events which we term intervisit interval. Brood size varied from 1-5 (mean = 3), while brood age varied from 1-21 (mean = 10 days). In addition, we were able to identify the relative size of prey items delivered (in terms of bill volumes) as well as their taxonomic Order for 1649 of the 2622 prey items delivered (see Browning et al. 2012 for further details) which we were able to organise into food which had been dug for in the substrate (N = 939), for example Coleoptera larvae and wolf spiders, or gleaned from vegetation (N = 710), for example adult insects and caterpillars. Finally, for 15 of the 22 territories we provided an index for shrub and tree cover (see Sorato et al. 2015 for further details). Briefly, we used daily group tracking sessions during breeding to generate home ranges for each group and vegetation surveys over 400 m^2 through the fieldsite to provide an index on a 0-4 point scale for shrub and tree cover in each block. By superimposing each home range onto the 400 m^2 grids, and weighting the contribution of each grid to the home range, we could derive an overall index of the vegetation scores for each home range.

Statistical analyses

Statistical analyses were performed in R for Microsoft Windows version 3.0.1 (R Core Team 2013, http://www.R-project.org/). Model assumptions regarding the normal distribution of residuals was confirmed. The significance of explanatory terms to overall model deviance were determined by comparing models with and without terms of interest. Those terms that did not improve the explanatory power of the model were removed from the final model.

First, I performed a series of mixed models to investigate the effects of habitat on: (i) the mean interval between provisioning events per group per day (hereafter inter-visit interval); (ii) the mean variance in variance in these intervals in each group on each day; (iii) the mean size of prey items delivered in each group on each day; and (iv) the proportion of prey items delivered in each group on each day that were identified as likely to have been dug versus gleaned. The first three mixed models were performed using the lme4 package with the lmer function, in which response terms were fitted to a normal error structure following a squared transformation in the case of Model ii on the variance of inter-visit intervals. The final model used a Generalised Linear Mixed Model (GLMM) using the glmer function of the glm package in which the number of food items delivered that were dug was fitted as the response term and the total number of items delivered was fitted as the binomial denominator. In all four models, group identity was fitted as a random effect to account for repeated sampling of the same groups using the "rand" function in the "lmertest" package (Kuznetsova et al. 2017). In addition, indices of shrub and tree cover were fitted as the primary terms of interest, while brood age, brood size and helper number were fitted as covariates. For further details see Tables 1-4.

Second, to examine the association between habitat type and helper number, a generalised linear model was run due to non-normal distribution of helper number data (N = 25) using the lme4 package (Bates et al. 2014) with the glm function. The habitats were each divided into a tree score (mean number of trees per unit area) and a shrub score (mean number of shrubs per unit area) based on the extent of vegetative cover of chenopods (shrubs of 15-120 cm high) and trees (typically 3-15 m).

Results

Habitat effects on brood provisioning

Broods were provisioned at an average rate of 13 prey items per hour (SD = 9.5), equating to an intervisit-interval of 6.1 (SD = 3.8) min. Brood intervisit intervals were predicted by brood age, brood size and helper number, with intervisit interval declining as each increased (Table 1). Further, there were also significant negative effects of the mean prey size and the proportion of items delivered that were dug versus gleaned on the mean inter-visit intervals. By contrast, indices of shrub cover or tree cover failed to predict mean inter-visit intervals. Finally, there was little evidence to suggest that intervisit intervals varied among the groups after controlling for significant fixed effects (based on a random term with low variance, see Table 1).

An advantage of analysing intervisit interval rather than provisioning rate is that the variance in delivery rates can be analysed. There was a highly significant positive effect of the mean intervisit interval on its variance, with high intervals associating with a high variance in delivery rate (Table 2). After controlling for this effect, I found that only brood size had a further impact on variance at which prey was delivered to the brood, with larger broods provisioned at reduced variance than expected given their provisioning rate. By contrast, I found no evidence to suggest that indices of shrub or tree cover influenced the variance at which prey items were delivered, or independent effects of helper number, average prey size, or the proportion of items delivered that were dug versus gleaned. Finally, again, I found no suggestion that groups varied in their pattern of prey delivery (Table 2).

The average size of prey items delivered by groups on a given day averaged the equivalent of a babbler bill volume, but varied from 0.5 to 1.3 equivalents (SD = 0.2).

The size of prey items delivered increased with brood age and correspondingly declined with the proportion of dug items delivered (which are also known to decline with brood age) (Table 3). However, again there was no effect of indices of habitat on the size of prey items delivered and no suggestion that the size of prey items delivered varied systematically among groups.

Finally, 60% of prey items delivered were likely dug on average on a given day, but this percentage varied from 10-100% (SD = 21%) (Table 4). The proportion of dug items delivered declined as broods aged and increasing brood size, but did not vary with helper number. In this case, the proportion of dug items delivered also declined with increasing shrub index, although not tree index.

Habitat and helper number

In chestnut-crowned babblers, all helpers are recruits and immigrants do not help. The number of helpers in groups for which habitat characteristics were estimated varied from 0-8, with an average of two (SD = 2, N = 17 groups). I found no evidence to suggest that indices of either the cover of low shrubs (estimate = -1.69 ± 1.26 (SE), P= 0.20) or the number of tall shrubs/trees (estimate = 2.57 ± 1.90 (SE), P= 0.20) predicted the number of helpers. These results suggest that for occupied territories, broad habitat characteristics known to correlate with prey availability and cover from predators, do not predict the recruitment of offspring and/or their subsequent survival.

Discussion

I found little support for the hypothesis that benefits of philopatry explain variation in delayed dispersal or group size in chestnut-crowned babblers, at least as tested. First, after controlling for variation in helper number, brood age and size I found no evidence to suggest that the random term group identity examined significant in the four provisioning parameters measured. These results suggest there is no systematic variation in provisioning parameters associated with the territory. Second, there was little evidence to suggest that vegetation characteristics known to correlate with both prey abundance and cover from predators accounted for significant variation in provisioning parameters, although groups in territories with less shrubs delivered a greater proportion of dug items as expected. Finally, there was little evidence for the expected positive association between indices of shrub or tree abundance on group size, suggesting that offspring recruitment and/or survival are not obviously associated with variation in territory quality.

The benefits of philopatry hypothesis predicts that family-living is selected when the benefits of remaining at home with parents outweigh the costs of dispersal (Stacey & Ligon 1987). This hypothesis, therefore, has often been regarded as the opposite side of the same coin from classic, resource-based ecological constraints models, which advocate the role of high dispersal costs in generating families in cooperative breeders (Koenig et al. 1992; Emlen 1994). However, this is not strictly the case, as the benefits of philopatry, but not resource-based ecological constraints, requires that the variance in territory quality is such that offspring benefit from delaying dispersal on some territories but not others, independently of the constraints on dispersal (Stacey & Ligon 1991). Consequently, some classic tests of the two hypotheses are ambiguous. For example, while family dissolution following the

artificial creation of suitable habitat elsewhere might be interpreted as supporting resource-based ecological constraints models (Du Plessis 1992; Walters et al. 1992), because doing so reduces the variance in territory quality, such results might also support benefits of philopatry (but see Pruett-Jones & Lewis 1990). Conversely, one cannot conclude a significant role of the benefits philopatry if the variance in territory quality has not been measured.

Arguably the best evidence for a significant role of the benefits of philopatry come from studies where dispersal has been shown to depend, at least partly, on the relative quality of the natal versus available non-natal territories. For example, Komdeur (1992) showed that dispersal of offspring Seychelles warblers (*Acrocephalus sechellensis*) was a function of both the availability of vacant territories (supporting ecological constraints) and the relative quality of natal and non-natal territories (supporting benefits of philopatry). In addition, Baglione et al (2006) showed that delayed dispersal could be induced in carrion crows (*Corvus corone*) in food supplemented territories, while Dickinson and McGowan (2006) showed that it could be reduced through removal of key food sources in western bluebirds (*Sialia mexicana*). Such manipulations are rarely achievable, however, because they rely on key food resources to be open to manipulation. Here I identified an alternative, more general, approach to testing the role of philopatric benefits in underpinning delayed dispersal in a cooperative breeder based on the predicted patterns of food delivery to offspring and the role of key habitat features therein and to variation in group size.

My approach is based on the simple, generalisable assumption that variation in territory quality required under the benefits of philopatry will manifest in patterns of offspring provisioning. Most notably, if groups inhabit territories of significantly

variable quality in terms of the ability to acquire food, as expected, then significant differences are expected in the prey delivery rates, the variance of such delivery, the size of prey provided and the modes of prey acquisition. On the contrary, after controlling for expected impacts of helper number, brood age and size, I found no compelling evidence for any of these predictions. Nor did I find any firm evidence for the prediction that the extent of shrub or tree cover, which are known to correlate with prey availability (Portelli et al. 2009) and cover from predators (Sorato et al. 2015), was associated with variation in group size, which itself is primarily a function of offspring recruitment and survival (Russell 2016). That the number of recruits varied from 0-8 in this study, these results might be viewed as surprising. Most importantly, these results are not confounded by load-lightening, since it has already been show in this population that nestling starvation is a primary mode of brood reduction (Browning et al. 2012) and that helper care is fully additive (Liebl et al. 2016). One explanation is that foraging in more open habitat, and the increased need for digging therein, is mitigated by sentinelling (Chapter 2). Another is that the variation in vegetation cover across the field site in not biologically meaningful. Either way, the evidence presented suggests that the benefits of philopatry hypothesis does not easily account for delayed dispersal in this cooperative system, although further work might be required.

Given this, coupled with evidence that resource-based ecological constraints through a lack of vacant territories or mates are apparently absent (Russell 2016), the obvious question is what drives delayed dispersal in this system? The results of this study add indirect credence to the idea that delayed dispersal in highly fluctuating environments is driven, at least in significant part, by the difficulty of dispersing to a vacant territory without help (Emlen 1990; Koenig et al. 2016; Russell 2016; Shen et

al. 2017). For example, in chestnut-crowned babblers, successful breeding typically requires help (Browning et al. 2012) suggesting that delayed dispersal in this population is favoured over dispersal to vacant territories when help is unavailable. Although pairs did breed in this study, they were always factions of a larger group which budded part of the social group territory rather than dispersers to a new territory. Thus, while further study is required to fully test the benefits of philopatry hypothesis, the current evidence based on the analyses here suggest this not to be a major driver of delayed dispersal in this system.

Tables

Table 1: Mixed effects model of the mean intervisit interval per group per day (N = 53). Calculated from the latency between feeding visits to the nest. Tree score and shrub score are calculated by the mean number of trees and shrubs (respectively) per unit area (see Methods). Average prey size is in relation to bill length of provisioner (see Methods). Proportion dug is the number of food items which were likely dug to have been foraged versus those which were gleaned off of vegetation. Random effect of Group ID in the model of best fit, containing all and only significant terms (highlighted), showed a variance = 0.049, SD = 0.22, $P = 0.1$.

Term	Estimate	SE	T value	df	P value
Intercept	5.82	0.62	9.41		
Helper number	-0.24	0.04	-5.89	1	**<0.001**
Brood size	-0.20	0.06	-3.27	1	**0.002**
Average prey size	-0.95	0.35	-2.76	1	**0.008**
Chick age	-0.04	0.02	-2.31	1	**0.025**
Proportion dug	0.90	0.40	-2.22	1	**0.030**
Tree score (mean)	0.28	0.26	1.09	1	0.283
Shrub score (mean)	-0.14	0.18	-0.78	1	0.443

Table 2: Mixed effects model of the variance within intervisit interval per group per day (N = 53). Tree score and shrub score are calculated by the mean number of trees and shrubs (respectively) per unit area (see Methods). Average prey size is in relation to bill length of provisioner (see Methods). Proportion dug is the number of food items which were likely dug to have been foraged versus those which were gleaned off of vegetation. Random effect of Group ID during model of best fit, significant terms highlighted, variance = 0.00, SD = 0.00, $P = 1$.

Term	Estimate	SE	Statistic	df	P value
Intercept	3.07	0.79	3.88		
XIVI	1.09	0.06	17.89	1	**<0.001**
Brood size	-0.45	0.18	-2.44	1	**0.017**
Helper no.	-0.17	0.16	-1.09	1	0.279
Chick age	-0.05	0.05	-0.95	1	0.345
Tree score (mean)	-0.79	1.05	-0.75	1	0.454
Produg	-0.46	1.03	-0.44	1	0.657
Average prey size	0.14	1.11	0.13	1	0.901
Shrub score (mean)	0.07	0.66	0.10	1	0.918

Table 3: Mixed-effects model on the average prey size of provisioned food brought in to the nest in proportion to bill length of provisioner. i.e. prey size of 0.5 is equal to half of one bill length, prey size of 1 is equal to one bill length determined by footage captured by pen camera in the back of nest (see Methods) (N = 53). Tree score and shrub score are calculated by the mean number of trees and shrubs (respectively) per unit area (see Methods). Proportion dug is the number of food items which were likely dug to have been foraged versus those which were gleaned off of vegetation. Chick age model output is separate from main model as this term was seen to conflict with the proportion of dug food that was brought into the nest, but still showed significance. Random effect of Group ID in the model containing both significant terms (highlighted) showed variance = <0.001, SD = 0.02, P = 0.8.

Term	Estimate	SE	Statistic	*df*	*P* value
Intercept	1.12	0.12	9.13		
Prop. Dug	-0.42	0.13	-3.23	1	**0.002**
Tree score (mean)	-0.20	0.13	-1.50	1	0.158
Brood size	0.01	0.02	0.27	1	0.791
Shrub score (mean)	0.05	0.08	0.63	1	0.536
Helper no.	-0.003	0.14	-0.20	1	0.846
Term					
Intercept	0.76	0.06	13.77		
Chick age	0.02	0.005	4.00	1	**<0.001**

Table 4: Generalised linear mixed effects model of the proportion of food which was brought into the nest which had likely been dug per group per day (see Methods). Tree score and shrub score are calculated by the mean number of trees and shrubs (respectively) per unit area (see Methods). Average prey size is in relation to bill length of provisioner (see Methods). Calculated by the number of dug items brought into the nest per day, divided by the total number of food items brought into the nest on aforementioned day (N = 37). Random effect of Group ID in model of best fit had variance = 0.17, SD = 0.41.

Term	Estimate	SE	Statistic	*df*	*P* value
Intercept	4.60	0.82	5.63		
Chick age	-0.16	0.02	-7.13	1	**<0.001**
Brood size	-0.40	0.09	-4.45	1	**<0.001**
Shrub score (mean)	-0.80	0.37	-2.18	1	**0.029**
No. Provisioners	-0.10	0.07	-1.53	1	0.127
Tree score (mean)	-0.70	0.52	-1.34	1	0.179

General discussion

Habitat structure and quality is important for many cooperatively breeding species, increasing group size with additional shelter in some species (Balshine et al. 2001), or lack of shelter in others (Du Plessis 1992), groups may increase with improved food availability (Baglione et al. 2006) or lack of unclaimed habitat (Komdeur 1996). Changes in habitat feature can be important in understanding the behaviours of cooperative breeders, for example why individuals delay dispersal in favour of cooperative breeding and why they might sentinel. In Chapter Two we investigated the benefits of philopatry by comparing the provisioning behaviour of groups to understand if some territories were of higher quality than others depending on the vegetation in the area, although we found little evidence to support this hypothesis. In the first chapter we investigated sentinel behaviour, and this was mostly observed in open habitats, where there are few trees and bushes. This may be due to an increase in predator encounters in these habitats (Sorato et al. 2012) and as such, the group are responding by increasing the sentinel effort. It may also be that sentinels are most effective in these areas as their view of the surrounding area is less obscured, allowing them to spot incoming predators sooner, and in other systems allowed sentinels and groups to be better able to remain in contact without distortion or needing to produce contact calls (Kern & Radford 2013), which could alert predators to the group's position. Although we were able to observe a difference between habitats for sentinels, this does not define the benefits the group members receive through sentinelling and this is important to understand sentinelling as a whole, and we still have not been able to understand what pressure encourages individuals to remain at their natal home.

Studies investigating the benefits of sentinel systems suggest that sentinels are benefitting directly from this behaviour. In instances where sentinels do receive a direct benefit, the behaviour allows the acting group member to improve or reaffirm their hierarchical dominance, secure paternity and prospect for other groups in which to emigrate to, as well as allowing them to escape predation before their groupmates (Dattner et al. 2015; Walker et al. 2016; Clutton-Brock et al. 2002; Clutton-Brock et al. 1999). In chestnut-crowned babblers we found no evidence to support this idea. Evidence for these theories in chestnut-crowned babblers could have been provided had any competition in order to sentinel been observed, a skew in sentinel behaviour directed towards dominant individuals or prospectors been recorded, or even a quick succession of sentinels and their replacements to suggest that this is a particularly desirable position to be in. Our study showed that the instances where sentinel behaviour was at its greatest were when groups had the highest risk of predation, for example in open habitats and during ground foraging bouts. Furthermore, sentinel behaviour can incur heavy trade-offs with the potential risks.

Although primarily an antipredatory behaviour, sentinels can find themselves being the target of attacks, particularly if in an exposed position. Bednekoff's theory of selfish sentinels (1997) suggested that sentinels were the safest individual in the group, however Ridley et al. (2013) found that in pied babblers (*Turdoides bicolor*), sentinels were the furthest group member from cover and the target for predators in 13 out of 16 predation events. Further, Rasa (1987) found that 67% of predated adult dwarf mongoose (*Helogale parvula*), were acting as sentinel at the time, leading to dispute about its safety. Had the sentinels been more safe than the group in our study of chestnut-crowned babblers, we would have expected them to be near cover

rather than favouring exposed positions. For example, we would expect a safe sentinel to be located on top of a dense bush or tree, instead babblers favoured to be on top of dead tree stags with no cover. Further trade-offs to self-preservation are also evident in sentinels.

Sentinel behaviour is often recorded while groups are foraging, improving the efficiency of foragers (Radford et al. 2009). The role of the sentinel is to remain vigilant which means that this individual cannot forage and therefore reduces its potential foraging time. This is disputed by Bednekoff's theory (1997) which states that sentinels are satiated individuals, however we found that this may not be the case, with peak sentinel activity early in the morning and the longest duration recorded as the group left the roost nest, therefore the babbler group had had no time to forage before beginning that bout, and for many of the following bouts. Further on from this idea, a reduction in foraging time could also lead to a reduction in ability to provide for the group offspring. In chestnut-crowned babblers, sentinel duty is spread across the group, primarily amongst second year and adult birds, and although the sentinel may be unable to provision at that time, the remaining group members likely benefit from improved provisionable foraging efficiency, outweighing the issue of having one less provisioner by improving the quality and quantity of food brought into the nest.

In chestnut-crowned babblers, provisioners did take longer to forage for dug food than gleaning off of vegetation. However, we found no evidence that group provisioning behaviour was affected by habitat features which could have shown a

predation risk effect as some habitats provide more cover than others which may warrant greater antipredatory behaviour and lead to a reduced quality habitat. Following a lack of uptake in dispersal to previously successful and currently uninhabited territories and habitats by the chestnut-crowned babbler groups (Russell 2016), it had seemed plausible that the babblers were delaying dispersal and assisting at the natal nest in line with the benefits of philopatry hypothesis. Chestnut-crowned babblers build their own shelter and group sizes were not affect by habitats which may have given indication to the predation pressure, so we investigated how provisioning varied across the groups and territories to see how their quality differed, which would then provide support for benefit of philopatry hypothesis and explain why groups did not disperse to new territories. In this scenario, we would have expected variation in provisioning behaviour, in terms of latency between feeds or variance within the latency to be greater in some habitats than others after controlling for the expected variates of helper number and brood age and size. This evidence was not provided and habitat was only seen to affect how provisioned food was foraged. Which then poses the question, what benefits are the babblers receiving in order to remain and help at the nest?

Chestnut-crowned babblers are most heavily constrained by group size, particularly as helpers provision maximally (Liebl et al. 2016) and helper number over any other factor, excluding nest demands, affected provisioning quantity and synchrony. However, it is difficult to understand how vacant available habitat was not utilised if group size is the only limiting factor, especially as outside of the breeding season, breeding groups amalgamate and then divide up the following year for breeding again which could allow for novel territories to be taken over by the dividing groups

(Russell 2016). The climate and environment where the babblers live is extreme and has many predators. This may add to the risk of starting new groups when successful groups already exist, where one can improve the breeding success of kin by remaining in that safe group, and can improve the group's stability and safety further, and as a consequence breeding success, through antipredatory sentinel behaviour. Whether this provides enough benefit to stay is difficult to ascertain. However, Griesser and Ekman (2004) found that sentinels in Siberian jays *Perisoreus infaustus* were showing nepotistic tendencies by preferentially directing their alarm calls towards kin over non-kin, which in itself would provide a direct benefit of philopatry to young inexperienced individuals.

Chestnut-crowned babbler sentinels and philopatric helpers may not receive direct benefits from their help, however both can benefit from indirect fitness benefits and delayed direct benefits to provide enough reward to sustain the behaviours within the population. Anti-predatory sentinel behaviour allows sentinels to aid in group augmentation by reducing the losses incurred to the group. This in turn can help with tasks such as territory defence, but in cooperative breeding species such as chestnut-crowned babbler, also means that the communal nest receives more food, as more individuals help with provisioning, reducing the latency between feeding visits. We know from earlier studies that helpers do not load-lighten (Liebl et al. 2016), so from these behaviours can further maximise the nesting output, and coupled with their philopatric tendencies helps positive feedback further aiding the breeding unit and their kin.

Like many behaviours identified within cooperative breeding species, such as the key component of provisioning for offspring other than your own, sentinel behaviour in the chestnut-crowned babbler relies on delayed direct and indirect fitness benefits, and is an additional cooperative behaviour. Further investigation into the relatedness of individuals that are acting as sentinel would benefit this study greatly, unfortunately it was not currently feasible, but would go a long way to improving our understanding of the benefits achieved by sentinels as different demographics within the groups may benefit in different ways (Walker et al. 2015; Clutton-Brock et al. 2002). It was not possible to provide support for the benefits of philopatry in the delayed dispersal of chestnut-crowned babblers; however it has furthered our understanding of the role and significance that the group as a unit plays in the life history of chestnut-crowned babblers. This could be furthered still with the study of which group members are provisioning and how they do so and it would be invaluable to understand how the sentinel behaviour of individuals affects their provisioning behaviour and whether direct or indirect fitness benefits has a role on those individuals.

References

Stats

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014). Lme4: linear mixed-effetcs models using Eigen and S4. R package version 1.1-7.

Højsgaard, S., Halekoh, U. & Yan, J. (2006). The R package geepack for generalised estimating equations. Journal of Statistical Software. 15: 1-11.

K. Pearson. (1900) On the criterion that a given system of deviations from the probable in the case of a correlated system of variables is such that it can be reasonably supposed to have arisen from random sampling. Philosophical Magazine Series 5,50:157-175 1900.

Kuznetsova A, Brockhoff PB, Christensen RHB (2017). "lmerTest Package: Tests in Linear Mixed Effects Models." Journal of Statistical Software, 82(13) 1–26. doi: 10.18637/jss.v082.i13.

Wickham, H. (2009). Ggplot2: elegant graphics for data analysis. Springer-Verlag New York 2009.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. & Smith, G. M. (2009). GLM and GAM for Count Data. Mixed Effects Models and Extensions in Ecology with R. 209-243.

Literature

Bachman, G. C. (1993). The effect of body condition on the trade-off between vigilance and foraging in Belding's ground squirrels. Animal Behaviour 46: 233-244.

Baglione, V., Canestrari, D., Maros, J. M. & Ekman, J. (2006). Experimentally increased food resources in the natal territory promote offspring philopatry and helping in cooperatively breeding carrion crows. Proceedimgs of the Royal Society B. 273: 1529-1535.

Bednekoff, P. A. (2015).Chapter four – sentinel behaviour: a review and prospectus. *Advances in the Study of Behaviour* 47: 115-145.

Bednekoff, P. A. & Woolfenden, G. L. (2003). Florida Scrub-Jays (Aphelocoma coerulescens) are Sentinels More When Well-Fed (Even with no Kin Nearby). Ethology 109: 895-903.

Bednekoff, P. A. (1997). Mutualism among safe, selfish sentinels: a dynamic game. The American Naturalist 150: 373-392.

Beerman, A., Ashe, E., Preedy, K. & Williams, R. (2016). Sexual segregation when foraging in an extremely social killer whale population. Behavioural Ecology and Sociobiology 70: 189-198.

Bell, M. B. V., Radford, A. N., Smith, R. A., Thompson, A. M. & Ridley, A. R. (2010). Bargaining babblers: vocal negotiation of cooperative behaviour in a social bird. Proceedings of the Royal Society B 277: 3223-3228.

Bender, L. C., Lomas, L. A. & Kamienski, T. (2007). Habitat effects on condition of doe mule deer in arid mixed woodland-grassland. Rangeland Ecology & Management 60: 277-284.

Blumstein, D. T. (1999). Selfish sentinels. Science 284: 1633-1634.

Brandl, S. J. & Bellwod, D. R. (2015). Coordinated vigilance provides evidence for direct reciprocity in coral reef fishes. Scientific Reports 5: 14556.

Brown, J. L. (1983). Cooperation – A Biologist's Dilemma. In. Rosenblatt J. S. Advances in the study of behaviour . Volume 13. *Academic Press*. London.

Brown, J. L., Brown, E. R., Brown, S. D. & Dow, D. D. (1982). Helpers: effects of experimental removal on reproductive success. *Science* 215: 421-423.

Browning, L. E., Patrick, S. C., Rollins, L. A., Griffith, S. C. & Russell, A. F. (2012). Kin selection, not group augmentation, predicts helping in an obligate cooperatively breeding bird. *Proceedings of the Royal Society B*. doi:10.1098/rspb.2012.1080.

Browning, L. E., Young, C. M., Savage, J. L., Russell, D. J. F., Barclay, H., Griffith, S. C. & Russell, A. F. (2012). Carer provisioning rules in an obligate cooperative breeder: prey type, size and delivery rate. Behavioural Ecological Sociobiology 66: 1639-1649.

Burton, N. & Yasukawa, K. (2001). The "predator warning system" of red-winged blackbirds. Journal of Field Ornithology 72: 106-112.

Choe, J. C. & Crespi, B. J. (1997). The evolution of social behaviour in insects and arachnids. Cambridge University Press. Cambridge.

Clutton-Brock, T. H., O'Riain, M. J., Brotherton, P. N. M., Gaynor, D., Kansky, R., Griffin, A. S. & Manser, M. (1999). Selfish Sentinels in Cooperative Mammals. *Science* 284: 1640-1644.

Clutton-Brock, T. H., Russell, A. F., Sharpe, L. L., Young, A. J., Balmforth, Z. & McIlrath, G. M. (2002). Evolution and development of sex differences in cooperative behaviour in meerkats. *Science* 297: 253-256.

Cockburn, A. (1998). Evolution of helping in cooperatively breeding birds. *Annual review of ecology and systematics* 29: 141-177.

Cockburn, A. (2003). Cooperative breeding in oscine passerines: does sociality inhibit speciation? Proceedings of the Royal Society B 270: 2207-2214.

Cornwallis, C. K., West, S. A. & Griffin, A. S. (2009). Routes to indirect fitness in cooperatively breeding vertebrates: kin discrimination and limited dispersal. *Journal of Evolutionary Biology*. 22: 2445-2457.

Crane, J. M. S., Savage, J. L. & Russell, A. R. (2016). Diversity and function of vocalisations in the cooperatively breeding chestnut-crowned babbler. Emu – Australian Ornithology. 116: 241-253.

Dattner, A., Zahavi, A. & Zahavi, A. (2015). Competition over guarding in the Arabian babbler (turdoides squamiceps), a cooperative breeder. *F1000 Research* 4: 618.

Dawkins, R. (1976). The selfish gene. Oxford University Press. Oxford.

De Vos, A. & O'Riain, M. J. (2013). Movement in a selfish seal herd: do seals follow simple or complex movement rules? Behavioural Ecology 24: 190-197.

Dickinson, J. L. & McGowan, A. (2005). Winter resource wealth drives delayed dispersal and family-group living in western bluebirds. Proceedings of the royal society B. 272. https://doi.org/10.1098/rspb.2005.3269

Drobniak, S. M., Wagner, G., Mourocq, E., Griesser, M. (2015). Family living: an overlooked but pivotal social system to understand the evolution of cooperative breeding. Behavioural Ecology. 26: 805-811.

Du Plessis, M. A. (1992), Obligate cavity-roosting as a constraint on dispersal of green (red-billed) woodhoopoes: consequences for philopatry and the likelihood of inbreeding. Oecologia. 90: 205-211.

Eguchi, K., Yamagishi, S., Asai, S., Nagata, H. & Hino, T. (2002). Helping does not enhance reproductive success of cooperatively breeding rufous vanga in Madagascar. *Journal of Animal Ecology.* 71: 123-130.

Emlen, S. T. (1990). White-fronted bee-eaters: helping in a colonially nesting species. In: Stacey. P. B. & Koenig, W. D. eds. Cooperative breeding in birds: long term studies of ecology and behaviour. Cambridge University Press. 487-526.

Emlen, S. T. (1994). Benefits, Constraints and the evolution of the family. Trends in Ecology & Evolution. 9: 282-285.

Emlen, S. T. (1995). An evolutionary theory of the family. PNAS. 18: 8092-8099.

Ens, B. J., Kersten, M., Brenninkmeijer, A. & Hulscher, J. B. (1992). Territory quality, parental effort and reproductive success of oystercatchers (Haematopus ostralegus). Animal Ecology. 61: 703-715.

Foster, W. A. & Treherne, J. E. (1981). Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. Nature 293: 466-467.

Gaston, A. J. (1978). The evolution of group territorial behaviour and cooperative breeding. *The American Naturalist.* 112: 1091-1100.

Gill, B. J. & Dow, D. D. (1984). Waking and roosting of grey-crowned babblers Pomatostomus temporalis in south-east Queensland during spring. Emu. 85: 97-105.

Griesser, M., Drobniak, S. M., Nakagawa, S. & Botero, C. A. (2017). Family living sets the stage for cooperative breeding and ecological resilience in birds. PLoS Biology 15: e2000483.

Griesser, M. & Ekman, J. (2004). Nepotistic alarm calling in the Siberian jay, *Perisoreus infaustus. Animal Behaviour.* 67: 933-939

Griffin, A. S., Pemberton, J. M., Brotherton, P. N. M., McIlrath, G., Gaynor, D., Kansky, R., O'Riain, J., Clutton-Brock, T. H. (2003) A genetic analysis of breeding success in the cooperative meerkat (Suricata suricatta). Behavioural Ecology 14: 472-480.

Hamilton, W. D. (1963). The evolution of altruistic behaviour. *The American Naturalist.* 97: 354-356.

Hamilton, W. D. Geometry of the selfish herd. Journal of Theoretical Biology 31: 295-311.

Hansen, B. B., Herfindal, I., Aanes, R., Saether, B.E. & Henriksen, S. (2009). Functional response in habitat selection and the trade-offs between foraging niche components in a large herbivore. Oikos. 118: 859-872.

Hatchwell, B. J., Ross, D. J., Fowlie, M. K. & McGowan, A. (2001). Kin discrimination in cooperatively breeding long-tailed tits. *Proceedings of the Royal Society B*. <u>268</u>: 885-890.

Hatchwell, B. J., Gullet, P. R. & Adams, M. J. (2014). Helping in cooperatively breeding long-tailed tits: a test of Hamilton's rule. *Philosophical Transactions of the Royal Society B* <u>369</u>: 20130565.

Heg, D., Heg-Bachar, Z., Brouwer, L. & Taborsky, M. (2008). Experimentally induced helper dispersal in colonially breeding cooperative cichlids. Environmental Biology of Fishes. 83: 191-206.

Herbert-Read, J. E., Romanczuk, P., Krause, S., Strömbom, D., Couillaud, P., Domenici, P., Kurvers, R. H. J. M., Marras, S., Steffensen, J., F., Wilson, A., D., M. & Krause, J. (2016). Proto-cooperation: group hunting sailfish improve hunting success by alternating attacks on grouping prey. Proceedings of the Royal Society B 283: 20161671.

Hogan, B. G., Scott-Samuel, N. E. & Cuthill, I. C. (2016). Contrast, contours and the confusion effect in dazzle camouflage. Royal Society Open Science 3: 160-180.

Hollén, L. I., Bell, M. B. V. & Radford, A. N. (2008). Cooperative sentinel calling? Foragers gain increased biomass intake. *Current Biology*. <u>18</u>: 576-579.

Hollén, L. I., Bell, M. B. V., Wade, H. M., Rose, R., Russell, A., Niven, F., Ridley, A. R. & Radford, A. N. (2011). Ecological conditions influence sentinel decisions. Animal Behaviour. 82: 1435-1441.

Hughes, C. (1998). Integrating molecular techniques with field methods in studies of social behaviour : a revolution results. *Molecular Techniques in Ecology*. <u>79</u>: 383-399.

Jackson, A. L., Brown, S., Sherratt, T. N. & Ruxton, G. D. (2008). The effects of group size, shape and composition on ease of detection of cryptic prey. Behaviour 142: 811-826.

Jetz, W. & Rubenstein, D. R. (2011). Environmental uncertainty and the global biogeography of cooperative breeding birds. Current Biology 21: 72-78.

Kern, J. M. & Radford, A. N. (2013). Call of duty? Variation in use of the watchman's song by sentinel dwarf mongooses, Helogale parvula. Animal behaviour 85: 967-975.

Kern, J. M. & Radford, A. N. (2014). Sentinel dwarf mongooses, Helogale parvula, exhibit flexible decision making in relation to predation risk. Animal Behaviour. 98: 185-192.

Koenig, W. D. & Dickinson, J. L. (2016). Introduction. In: Koenig, W. D. & Dickinson, J. L. eds. Cooperative breeding in vertebrates. Padstow: Cambridge University Press.1-5.

Koenig, W. D., Pitelka, F. A., Carmen, W. J., Mumme, R. L. & Stanback, M. T. (1992). The evolution of delayed dispersal in cooperative breeders. The Quarterly Review of Biology. 67: 111-150.

Koenig, W. D. & Dickinson, J. L. (2004). Introduction. In: Koenig, W. D. & Dickinson, J. L. eds. Ecology and Evolution of Cooperative Breeding Birds. Cambridge: Cambridge University Press. Pages 1-2.

Kokko, H., Johnstone, R. A. & Clutton-Brock, T. H. (2001). The evolution of cooperative breeding through group augmentation. Proceedings of the Royal Society B. 268: 187-196.

Komdeur, J. (1996). Influence of helping and breeding experience on reproductive performance in the Seychelles warbler: a translocation experiment. *Behavioural Ecology.* 7: 326-333.

Komdeur, J. (1992). Importance of habitat saturation and territory quality for evolution of cooperative breeding in Seychelles warbler. Nature. 358: 493-495.

Kotler, B. P., Brown, J. S. & Knight, M. H. (1999). Habitat and patch use by hyraxes: there's no place like home? Ecology Letters 2: 82-88.

Lehtonen, J. & Jaatinen, K. (2016). Safety in numbers: the dilution effect and other drivers of group life in the face of danger. Behavioural Ecology and Sociobiology 70: 449-458.

Liebl, A. L., Nomano, F. Y., Browning, L. E. & Russell, A. F. (2016). Experimental evidence for fully additive care among male carers in the cooperatively breeding chestnut-crowned babbler. Animal Behaviour. 115: 47-53.

Lima, S. L. (1995). Back to basics of anti-predatory vigilance: the group-size effect. *Animal Behaviour*. 49: 11-20.

Lukas, D. & Clutton-Brock, T. (2012). Cooperative breeding and monogamy in mammalian societies. *Proceedings of the Royal Society B.* doi:10.1098/rspb.2011.2468

Macdonald, D. W. (1983). The ecology of carnivore social behaviour. Nature 301: 379-384.

Mainwaring, M. C. & Griffith, S. C. (2013). Looking after your partner: sentinel behaviour in a socially monogamous bird. PeerJ DOI 10.7717/peerj.83

Malan, A. R. & Jenkins, G. (1996). Territory and nest defence in polyandrous pale chanting goshawks: do co breeders help? African Zoology 31: 170-176.

Manser, M. B. (1999). Response of foraging group members to sentinel calls in suricates, Suricata suricatta. Proceedings of the Royal Society B 266: 1013-1019.

Maynard Smith, J & Szathmary, E. (1997). 16.5 The division of labour in animal societies. In: The Major Transitions in Evolution. Oxford University Press. 268-270.sza

Mumme, R. L. (1992). Do helpers increase reproductive success? Behavioural Ecology and Sociobiology 31: 319-328.

Neill, St S. R. J. & Cullen, J. M. (1974). Experiments on whether schooling by their prey affects the hunting behaviour of cephalopods and fish predators. Journal of Zoology 172:549-569.

Nomano, F. Y., Browning, L. E., Savage, J. E., Rollins, L. A., Griffith, S. C. & Russell, A. F. (2015). Unrelated helpers neither signal contributions nor suffer retribution in chestnut-crowned babblers. Behavioural Ecology 26: 986-995.

Nomano, F, Y., Browning, L. E., Nakagawa, S., Griffith, S. C. & Russell, A. F. (2014). Validation of an automated data collection method for quantifying social networks in collective behaviours. Behavioural Ecology and Sociobiology. 68: 1379-1391.

Peluc, S. I., Sillett, T. S., Rotenberry, J. T. & Ghalambor, C. K. (2008). Adaptive phenotypic plasticity in an island songbird exposed to a novel predation risk. Behavioural Ecology. 19: 830-835.

Portelli, D. J., Barclay, H., Russell, D. J. F., Griffith, S. C. & Russell, A. F. (2009). Social organisation and foraging ecology of the cooperatively breeding chestnut-crowned babbler (Pomatostomus ruficeps). Emu. 109: 153-162.

Pruett-Jones, S. G. & Lewis, M. J. (1990). Sex ratio and habitat limitation promote delayed dispersal in superb fairy-wrens. Nature. 348: 541-542.

Radford, A. N. Hollén, L.I. & Bell, M. B. V. (2009). The higher the better: sentinel height influences foraging success in a social bird. Proceedings of the Royal Society B. 276: 2437-2442.

Rasa, O. A. E. (1986). Coordinated Vigilance in Dwarf Mongoose Family Groups: The 'Watchman's Song' Hypothesis and the Costs of Guarding. Ethology 71: 340-344.

Rasa, O.A.E., (1987). Vigilance behavior in dwarf mongooses - selfish or altruistic? South African Journal of Science 83: 587-590

Rebout, N., Desportes, C. & Thierry, B. (2017). Resource partitioning in tolerant and intolerant macaques. Aggressive Behaviour 9999: 1-8.

Ridley, A. R. & Raihani, N. J. (2006). Facultative response to a kleptoparasite by the cooperatively breeding pied babbler. Behavioural Ecology. 18: 324-330.

Ridley, A. R., Raihani, N. J. & Bell, M. B. V. (2010). Experimental evidence that sentinel behaviour is affected by risk. Biology Letters 6: 445-448.

Ridley, A. R., Nelson-Flower, M. J. & Thompson, A. M. (2013). Is sentinel behaviour safe? An experimental investigation. Animal Behaviour 85: 137-142.

Rollins, L. A., Browning, L E., Holleley, C. E., Savage, J. L. Russell, A. F. & Griffith, S. C. (2012). Building genetic networks using relatedness information: a novel approach for the estimation of dispersal and characterisation of group structure in social animals. Molecular Ecology. 21: 1727-1740.

Russell, A. (2016). Cooperative breeding in vertebrates. Chestnut-crowned babblers: Dealing with climatic adversity and uncertainty in the Australian arid zone. In: Koenig, W. D. & Dickinson, J. L. eds. *Cooperative breeding in vertebrates.* Padstow: Cambridge University Press. 150-164.

Russell, A. (2004). Mammals: comparisons and contrasts. In: Koenig, W. D. & Dickinson, J. L. eds. Ecology and Evolution of Cooperative Breeding in Birds. Cambridge: Cambridge University Press. 210-227.

Russell, A. F., Portelli, D. J., Russell, D. J. F. & Barclay, H. (2010). Breeding ecology of the chestnut-crowned babbler: a cooperative breeder in the desert. Emu 110: 324-331.

Santema, P. & Clutton-Brock, T. (2013). Meerkat helpers increase sentinel behaviour and bipedal vigilance in the presence of pups. Animal Behaviour 85: 655-661.

Selander, R. K. (1965). On mating systems and sexual selection. *The American Naturalist.* 99: 129-141.

Shen, S-F., Emlen, S. T., Koenig, W. D. & Rubenstein, D. R. (2017). The ecology of cooperative breeding behaviour. Ecology Letters 20:708-720.

Sorato, E., Gullett, P. R., Creasey, M. J. S., Griffith, S. C. & Russell, A. F. (2015). Plastic territoriality in group-living chestnut-crowned babblers: roles of resource value, holding potential and predation risk. *Animal Behaviour* 101: 155-168.

Sorato, E., Gullett, P. R., Griffith, S. C. & Russell, A. F. (2012). Effects of predation risk on foraging behaviour and group size: adaptations in a social cooperative species. *Animal Behaviour.* 84: 823-834.

Sorato, E., Griffith, S. C. & Russell, A. F. (2016). The price of associating with breeders in the cooperatively breeding chestnut-crowned babbler: foraging constraints, survival and sociality. Journal of Animal Ecology. 85: 1340-1351.

Sorato, E., Gullett, P. R., Creasey, M. J. S., Griffith, S. C. & Russell, A. F. (2015). Plastic territoriality in group-living chestnut-crowned babblers: roles of resource value, holding potential and predation risk. Animal Behaviour 101: 155-168.

Stacey, P. B. & Ligon, J. D. (1991). The Benefits-of-Philopatry hypothesis for the evolution of cooperative breeding: variation in territory quality and group size effects. The American Naturalist. 137: 831-846.

Stacey, P. B. & Ligon, J. D. (1987). Territory quality and dispersal options in the acorn woodpecker, and a challenge to the habitat saturation model of cooperative breeding. The American Naturalist. 130: 654-676.

Thornton, A. & McAuliffe, K. (2006). Teaching in wild meerkats. Science 313: 227-229.

Tilson, R. L. (1980). Klipspringer (Oreotragus oreotragus) social structure and predator avoidance in a desert canyon. Madoqua 11: 303-314.

Trivers, R. L. (1971). The evolution of reciprocal altruism. The Quaterly Review of Biology. 46: 35-57

Vainikka, A., Jokelainen, T., Kortet, R. & Ylönen, H. (2005). Predation risk allocation or direct vigilance response in the predator interaction between perch (Perca fluviatilisL.) and pike (Esox lucius L.)? Ecology of Freshwater Fish 14: 225-232.

Vehrencamp, S. L. (1977). The adaptive significance of communal nesting in Groove-billed

Walker, L. A., York, J. E. & Young, A. J. (2016). Sexually selected sentinels? Evidence of a role for intrasexual competition in sentinel behaviour. *Behavioural Ecology* 27: 1461-1470.

Walters, J. R., Doerr, P. D. & Carter III, J. H. (1992). Delayed dispersal and reproduction as a life-history tactic in cooperative breeders: fitness calculations from red-cockaded woodpeckers. *The American Naturalist.* 139: 623-643.

Walters, J. R., Copeyon, C. K. & Carter, J. H. (1992). Test of the ecological basis of cooperative breeding in red-cockaded woodpeckers. The Auk. 109: 90-97.

Wickler, W. (1985). Coordination of vigilance in bird groups: the "Watchman's Song" hypothesis. Ethology 69: 250-253.

Williams, G. C. (1996). Natural selection, the costs of reproduction, and a refinement of Lack's principle. *The American Naturalist.*100: 687-690.

Wilson, E. O. (1971). The insect societies. Belknap Press. Harvard University.

Wright, J. Maklavok, A. A. & Khazin, V. (2001). State-dependent sentinels: an experimental study in the Arabian babbler. *Proceedings of the Royal Society of London, B.* 268: 821-826.

Wright, J., Berg, E., De Kort, S. R., Khazin, V. & Maklakov, A. A. (2001) (a). Cooperative sentinel behaviour in the Arabian babbler. Animal Behaviour 62: 973-979.

Wright, J., Berg, E., De Kort, S. R., Khazin, V., Maklakov, A. A. (2001) (b). Safe, selfish sentinels in a cooperative bird. Animal Ecology 70: 1070-1079.

Wright, J., Maklakov, A. A. & Khazin, V. (2001) (c). State-dependent sentinels: an experimental study in the Arabian babbler. Proceedings of the Royal Society B 268: 821-826.

Yasukawa, K. & Cockburn, A. (2009). Antipredator vigilance in cooperatively breeding superb fairy-wrens (Malurus cyaneus). The Auk 126: 147-154.

Zahavi, A. (1995). Altruism as a handicap: the limitations of kin selection and reciprocity. *Journal of Avian Biology*. 26: 1-3.