Social context dependent provisioning rules in red-winged fairy-wrens do not vary with signals of increased chick need

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Abstract

Individuals should adjust investment in parental care in order to maximize current and future reproductive success. In cooperative breeders, where helpers assist with raising offspring, larger groups may allow for a reduction in investment (load-lightening) of each individual. Additionally, the type of individual and thus the social context can play an important role in individual investment. Less attention has been paid to how provisioning rules vary across ecological contexts, though theory suggests that individuals can only afford to reduce their investment when nestling starvation is unlikely, thus under mild conditions. Here, we test whether previously reported provisioning rules based on social context vary with ecological conditions, by experimental manipulation of signals of chick need, in the cooperatively breeding red-winged fairy-wren (*Malurus elegans*). Previous work in this species has shown that all group members load-lighten with additional male helpers, whereas effort remains constant in response to the number of female helpers in the group. We show that experimental begging playback resulted in all individuals increasing their provisioning rates, indicating that our treatment was perceived as increased chick need. However, in contrast to our prediction, increased chick need did not stop individuals from reducing their investment with an increasing number of male helpers in the group. These results suggest that despite some flexibility in parental effort, individuals use strict rules with respect to group composition, suggesting that individual provisioning effort is based on multiple integrated cues, and responses to changes in the environment are highly context-dependent.

<u>Keywords</u>: parental investment, helping behaviour, cooperative breeding, load-lightening, additive care, playback, *Malurus*

Introduction

In species that provide care to offspring, individuals should adjust their investment in costly care behaviour, such as provisioning of food to offspring, in order to maximize current and future reproductive success (Stearns 1992). In biparental species, investment decisions are not only conditional upon the demands of the young (Kilner & Drummond 2007), but also on the investment or characteristics of one's partner (Sheldon 2000). In cooperatively breeding species, not only the breeding pair, but also the helpers that assist with raising offspring, should strategically adjust their investment in care behaviours, as alloparental care incurs significant costs (Taborsky 1984; Heinsohn & Cockburn 1994). If individuals reduce their own investment according to the investment of their group members, there is a "load-lightening" effect ("compensation"); in contrast, if there is no adjustment to the care provided by others, or if compensation is incomplete, an individual's care has an "additive" effect (Hatchwell & Davies 1990; Hatchwell 1999). Accordingly, investment decisions by breeders and helpers in cooperative groups can vary according to the number (Balshine *et al.* 2001; Savage, Russell & Johnstone 2015) and effort (Wright 1998) of group members. Individual effort itself might depend on the type of individual, for example, parental investment might depend on whether or not an individual is likely to breed in the near future, which may vary among the sexes (Clutton-Brock *et al.* 2002). However, until recently the role of social context (e.g. the number and sex of the helpers) on breeder and helper investment patterns received little attention (but see Brouwer, Van de Pol & Cockburn 2014; Adams *et al.* 2015).

Various aspects of the ecological environment can also influence parental investment. For example, parental provisioning rate has been shown to decrease with increasing risk of predation in 10 bird species (Ghalambor, Peluc & Martin 2013) and low food availability decreases maternal sensitivity to offspring signals in stitchbirds (*Notiomystis cincta*; Low, Makan & Castro 2012). Not surprisingly, harsh conditions might result in food deprivation, which will result in higher begging intensity (Drummond & Garcia Chavelas 1989; Lotem 1998; Leonard *et al.* 2000). Because ecological conditions often determine the value of extra parental care (Davies & Hatchwell 1992), ecological context will also interact with social context to determine parental investment. Thus the compensatory or additive nature of parental investment may vary according to the harshness of the environment. Indeed, a comparative study showed that investment is more likely to be compensatory when the likelihood of nestling starvation is low (Hatchwell 1999). However, how flexible investment decisions are with respect to social and ecological context has received little attention. Recently, a study on long-tailed tits (*Aegithalos caudatus*) showed that adjustment of provisioning effort to others varied among years, suggesting that provisioning rules are dependent on environmental variables (Adams *et al.* 2015). In addition, female superb fairy-wrens (*Malarus cyaneus*) with helpers were able to reduced their investment (load-lightening, by reducing egg size), but only under good conditions (Langmore *et al.* 2016). Whether the interaction of parental investment between social and ecological context is a general pattern remains unknown, yet this could improve our understanding of cooperative systems and how they may plastically respond to environmental change.

In this study, we investigate provisioning behaviour of dominant breeders and helpers across varying social contexts by experimental manipulation of the perceived ecological conditions, through simulating increased chick need with a nestling playback experiment. We use the facultative cooperatively breeding red-winged fairy-wren (*Malurus elegans*) as a model system. Parental investment has been shown to depend on social environment in this species, with both additive care and load-lightening occurring depending on group composition. All group members decrease their provisioning rates with an increasing number of male helpers (load-lightening), but not female helpers (additive care) (Brouwer *et al.* 2014). This is in spite of male and female helpers feeding at similar rates, and not differing in the type of food they provide (Brouwer *et al.* 2014). Second, high rates of extra-pair paternity (Brouwer *et al.* 2011) and a difference in future prospects between male and female helpers, indicate likely variation in the benefits of investing in offspring care.

We predict that simulated increased chick need through playback of chick begging will result in increased provisioning rates, but that the response will depend on group composition and vary among different type of group members. Load-lightening should only occur when group members can afford to reduce their investment, thus when the likelihood of nestling starvation is low (Hatchwell & Russell 1996). Thus, we predict that in response to perceived increased chick need, the previously reported load-lightening pattern with an increasing number of male helpers should disappear and become additive care, similar to the response to the number of female helpers (Brouwer *et al.* 2014).

Furthermore, we predict that, irrespective of group composition, dominant females will show a stronger response to increased chick need than dominant males and helpers, because high rates of extra-pair paternity (57%) (Brouwer *et al.* 2011) mean that they are most highly related to the offspring and thus gain most benefits from successfully raising the brood. In addition, we predict that male helpers show a stronger response than female helpers, because males are more likely to inherit the natal territory and would therefore benefit more from recruiting new group members who will later help them (Russell & Rowley 2000; Brouwer *et al.* 2014), in line with group augmentation theory (Kokko, Johnstone & Clutton-Brock 2001).

Methods

Study area and data collection

Data were collected during the 2015 breeding season in a population of red-winged fairy-wrens at Smithbrook Nature Reserve, near Manjimup, Western Australia (34°20'S, 116°10'E) that has been studied since 2008 (Brouwer *et al.* 2011). This reserve is a 95-ha area of state-owned karri forest (*Eucalyptus diversicolor*) (for more details on habitat see Rowley et al. 1988). The main study area comprised around 65 territories in which >99% of the adult birds were colour-banded with unique combinations. Territories were regularly checked to determine breeding activity and to confirm group composition. . In each group, a 'dominant' pair raise young with the help of subordinate helpers of both sexes. Social status was based on behavioural observations, plumage variation, and age

(Russell & Rowley 2000). Adult birds are sexually dimorphic, so breeder and helper sex is easily determined visually (Rowley *et al.* 1988).

Nests, once discovered, were checked at least twice a week to monitor the progress of nest building, egg laying, and chick hatching. Nests are incubated by the dominant female for approximately 15 days and clutch size variation is limited (98% of nests have 2 or 3 eggs, Lejeune et al. 2016). Broods are provisioned by group members until fledging at around 12 days (Rowley *et al.* 1988). Nestlings can be accurately aged based on characteristics like colour and the presence of wing buds (Rowley & Russell 1997). Plural breeding, where more than one female in the group builds a nest (Brouwer *et al.* 2011), were excluded from our experiments given that in these rare instances helpers may divide their efforts between the nests of the primary and the secondary breeder.

Recording of playback stimuli

Experimental playbacks were created from recordings of natural begging at nests. To obtain these recordings, a camouflaged dummy recorder was placed 20-30 cm from the nest opening the day before recording was to take place. The dummy was swapped for the camouflaged recording device (Zoom Handy Recorder H5, Zoom Corporation, Tokyo, Japan) at least fifteen minutes before recording began. Nests were recorded when nestlings were aged 8 and 10 days old (day 1 being the day of hatching), for at least one hour. Sound files were recorded as broadcast wave files at 48kHz sampling rate. Times of day when begging may be reduced, such as very early morning or in the middle of the day when temperatures were highest, were avoided.

Playback sound files were created using the free software AudacityR ("Audacity(R): Free Audio Editor and Recorder" 2014). Each playback contained only begging calls from a single nest, recorded on a single day. The first 5 minutes of every raw recording were deleted to remove noises associated with, and in case chicks were momentarily disturbed by, placement of the recorder. Periods of chick begging were identified, excised from the recording, and copied into a separate file. From these excerpts, segments including adult calls, calls from other birds, or other significant background noises such as traffic, were removed. The edited excerpts were run together, with any gaps of silence removed, so that the resulting playback was continuous natural begging with no other stimuli (mean playback duration 126s). Three recordings/playbacks were made for each chick age (8 and 10 days old), at five different nests, all of which contained two chicks.

As a control, recordings of background noise from the study area were used for playback (*sensu* Burford et al. 1998). Control recordings and playback files were created in the same way as above, using recordings that were made at least 30m from any known nests. Control recordings were free of calls of red-winged fairy-wrens, predatory birds or birds that should cause alarm (any such calls were excised from the recording in Audacity). Three control playbacks were made at three different locations (mean recording duration 37mins 15s).

Playback experiment

The first experiment was performed when chicks were 7 or 8 days old. By this stage nestlings are no longer brooded by the female, so her contribution can be compared to that of other group members. Each experiment consisted of two treatments per nest (control and experimental playback in random order), which lasted for at least 1 hour (with groups larger than four birds being observed for 1.5 hours), separated by a break of 30 min during which time no noise was played to allow all birds to feed with no additional stimuli. To increase sample sizes the experiment (again, a control and an experimental playback in random order) was performed at each nest two days later, thus when chicks were 9 or 10 days old. Due to nest predation, we were not able to perform a second test on all nests, but our set-up with both experimental and control playback performed within the same group on the same day ensures there is no bias due to variation between days and chick ages.

As with the recording equipment, a camouflaged dummy speaker was placed directly behind the nest at least one day before the experiment. At least fifteen minutes before the experiment commenced, the dummy speaker was replaced by a camouflaged rechargeable portable Bluetooth speaker (Trek Micron: TDK Corporation, Tokyo, Japan), connected to an iPhone 4s (Apple Inc, USA). The presence of a speaker did not alter provisioning rates (average provisioning rates were in the same range as those previously reported without auditory playback or playback equipment: Brouwer et al. 2014). The first feeding visit to the nest after the initial fifteen minutes had elapsed marked the start of the experiment; similarly, the first feed after the half hour break between treatments marked the start of the second part of the experiment. Treatment order (control/experimental) was determined by coin toss to minimise effects of time of day, and within treatment, which of the recordings was used was determined using a random number generator (www.random.org). Nests were never played playbacks created using recordings of their own nestlings or those of their neighbours. Playback volume was matched to natural amplitude of background noise and the natural average volume of chick begging respectively. The volume of chick begging was determined by measuring volume at 4 nests prior to the start of the experiment using a sound meter application [Decibel X, SkyPaw Co. Ltd, Vietnam, used on iPhone 4s, Apple Inc, USA]). In day 7 & 8 trials, playbacks were subsequently played at 60-65 dBA, while in day 9 & 10 trials, playbacks were played at the higher volume of 75-80 dBA (variation due to natural fluctuation in volume in recordings). Measurements of average background noise were measured in the same way (standing at least 20m from any known nest) and control playbacks were subsequently played at 40-50 dBA, mimicking the natural range, in order to adequately control for speaker noise while also not providing a potential deterrent (which playing background noise at unnaturally high volumes might be).

To mimic the natural situation, birds were only subjected to playback when approaching the nest. During each treatment, playbacks were started when a bird was <10cm from the nest opening, and continued for 5 seconds (average length of a begging bout in fairy-wrens; MacGregor & Cockburn 2002). Observations and control of the playback were done from a hide placed between 6 and 8m from the nest, which was put up at least one day before the experiment to minimize disturbance. The identity of each bird that brought food to the nest was recorded, allowing calculation of each individual's provisioning rate, and the total number of feeds provisioned to chicks by the whole group. In a few cases where the vegetation surrounding the nest was dense, the identity of the provisioning bird could not be identified (<1% of feeds), in which case these feeds were included in the count of group feeds and equally distributed among all members of the group.

In total, we observed 290 feeding visits from 78 individuals, in 42 trials of 22 groups with varying group composition (0-3 male helpers, 0-2 female helpers). Mean group size was 3.7 ± 0.9 S.D. (range 2-6). Group sex ratio (proportion male) was on average 0.54 ± 0.2 S.D. (range 0.25 to 0.8). Group size was not correlated with brood size (Spearman's rho = 0.23, $P = 0.31$).

Statistical analyses

In order to determine whether the experimental playback treatment was successfully perceived as increased chick need, we first analysed whether the total feeding rate of a group per hour was significantly higher with the experimental treatment compared to the control playback treatment on the same day, using a paired t-test.

To test whether ecological context (perceived chick need) influenced individual provisioning decisions, the number of feeds per bird per hour (transformed using $\log_{10}(x+1)$ to normalize data) was fitted as a normal response variable in a LMM. Identity of the group, trial (control and experimental observations of a group within same day) and individual were included as nested random intercepts to control for repeated observations. In addition, we fitted the number of feeds using a Poisson distribution with the duration of the observation (on log scale) as an offset. Our data was over-dispersed and to account for this, subject identity was added as a random intercept (Harrison 2014). The results from the Poisson provided qualitatively similar results (Table S1). To investigate whether load-lightening in the presence of male helpers became additive in response to the experimental treatment, the covariate number of male helpers, fixed factor playback treatment and their interaction were included in the analysis. To test our prediction that dominant females would respond stronger to the playback treatment than other group members, status of the individual (dominant male, dominant female, helper male, helper female) and its interaction with playback treatment were also included as fixed factors. Subsequently this interaction allowed us to test whether helper males responded more strongly than helper females by investigating the contrasts using a post-hoc test. We also accounted for brood size (2 or 3 chicks), chick age, and the number of helper females by including them as covariates.

Statistical analyses were performed in R (version 2.4.2) (R Core Team 2015) using packages lme4 (Bates *et al.* 2015) and phia (De Rosario-Martinez 2015). All effects were mean centred before including them in the model, allowing for interpreting main effects in the presence of (non-significant) interactions in a full model (Schielzeth 2010). Significance was based on comparing the final model with a reduced model without the predictor of interest using likelihood ratio tests. Feeding rates in Fig. 1b were corrected for the number of helper males in the group by calculating the difference between the observed values and the predictions from the male helper effect (Table 1). Means are reported ± standard error throughout except where otherwise stated.

Ethical Note

Although fairy-wrens are highly tolerant of human disturbance around the nest site, we minimized the time at the nest setting up equipment and made sure the birds returned to provision after this was done. The Western Australian Department of Biodiversity, Conservation and Attractions gave permission for fieldwork and the ANU Animal Experimentation Committee licensed our field research. Permission for colour-banding was given by the Australian Bird and Bat Banding Scheme (ABBBS).

RESULTS

Response to experimental treatment

Groups responded to our begging playback treatment as would be expected if it was perceived as a signal of increased chick need: experimental begging playback treatment significantly increased total feeding rates to the chicks compared to control playback treatment at both chick ages (control vs experimental: 7-8 days old, 15.7±1.37 vs. 23.2 ± 2.12 feeds/hr, paired $t = -3.79$, df = 22, $P = 0.001$; 9-10 days old, 23.1 ± 2.14 vs. 31.4 ± 3.20 feeds/hr; paired $t = -4.58$, df = 17, $P < 0.001$).

Response to social and ecological context

As previously reported (Brouwer et al 2014), individual provisioning rates of all group members decreased with an increasing number of male helpers (load-lightening), but not with the number of female helpers (additive care), (Fig. 1, Table 1). However, in contrast to our prediction increased chick need did not result in load-lightening in the presence of male helpers to become additive care: provisioning rates declined with an increasing number of helper males in both the control and playback treatments (Fig. 1; Table 1: Treatment × number of ♂ helpers).

Variation in response due to type of group member

Dominants responded stronger to the begging playback than helpers (Fig. 2), however, in contrast to our prediction, dominant females did not respond more strongly to the experimental playback than other group members (Fig. 2a; interaction treatment × status). In addition, our prediction that helper males would invest more compared to helper females was also not supported (Fig. 2a; post-hoc $\chi^2_1 = 0.001$, $P = 0.92$). Finally, the patterns were similar when considering the relative change in investment of different type of group members (Fig. 2b).

Table 1. Results of a linear mixed model (LMM) examining provisioning rates measured as the $\log_{10}$-transformed number of feeds of a bird per hour in response to control and experimental (begging) playback at the nest (N = 290 observations).

	Estimate ± S.E.	***d.f.***	***X^2***	***P***
Intercept	0.80 ± 0.03			
Treatment*	0.11 ± 0.02	1	24.4	<0.01
Number of ♂ helpers	-0.09 ± 0.04	1	6.2	0.01
Number of ♀ helpers	-0.002 ± 0.04	1	0.002	0.97
Status§		3	15.4	<0.01
♂ Dominant	0.05 ± 0.05			
♂ Helper	-0.07 ± 0.05			
♀ Helper	-0.17 ± 0.06			
Brood size	0.16 ± 0.06	1	6.7	<0.01
Chick age	0.06 ± 0.02	1	6.8	<0.01
Treatment × number of ♂ helpers	-0.02 ± 0.03		0.62	0.43
Treatment*×status§		3	5.7	0.13
Treatment × ♂ Dominant	0.04 ± 0.05			
Treatment × ♂ Helper	-0.07 ± 0.06			
Treatment × ♀ Helper	-0.08 ± 0.06			
Random effects				
σ^2_{Group}	<0.001			
σ^2_{Trial}	0.02			
$\sigma^2_{\text{Individual}}$	0.02			

Reference categories are as follows: *control; § ♀ Dominant

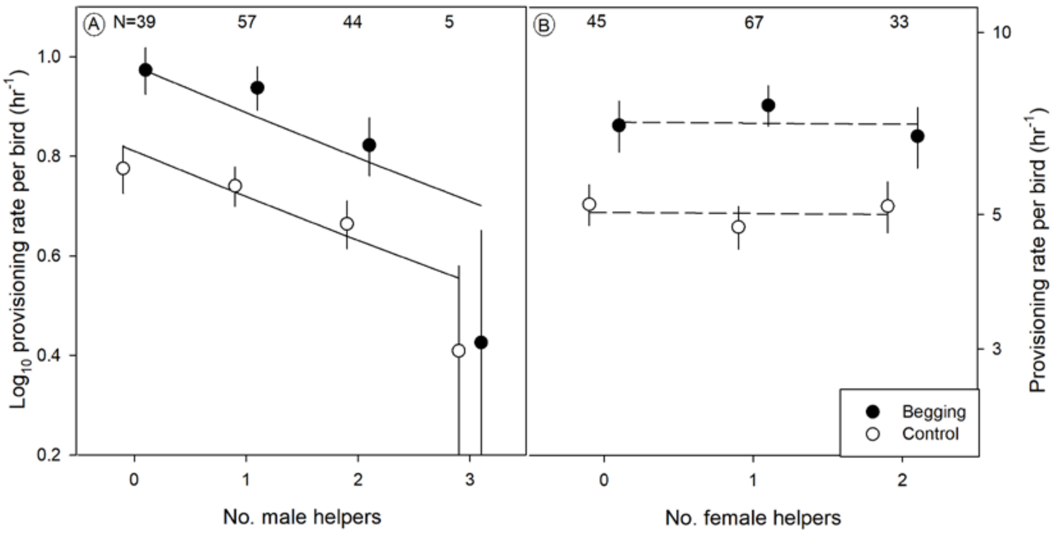

Fig. 1. The average provisioning rates per bird per hour in relation to a) the number of male helpers in the group and b) the number of female helpers in the group (corrected for the number of male helpers a). Numbers on top indicate the number of observations. Error bars represent standard errors. Trendlines show the predictions according to the model (Table 1), with solid lines indicating significant and dashed lines indicating a non-significant association.

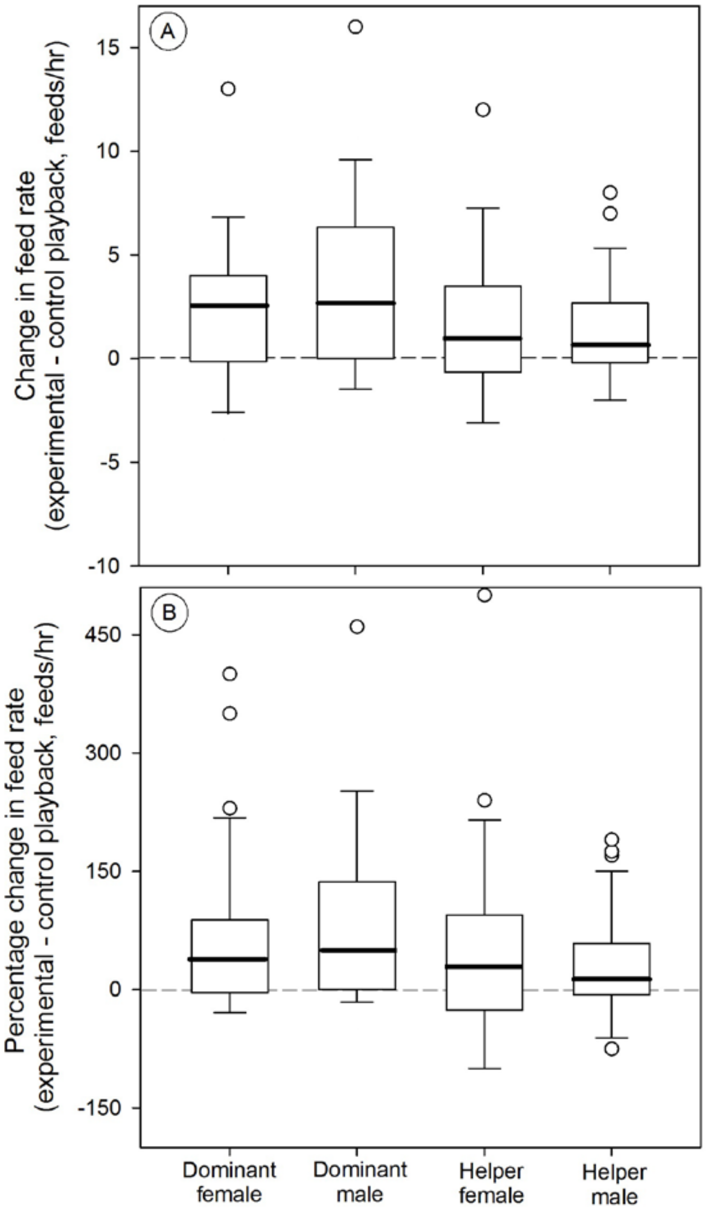

Fig. 2. Boxplots showing the a) absolute and b) relative increase in provisioning rates in response to begging playback (experimental – control) for dominants and helper red-winged fairy-wrens of both sexes.

DISCUSSION

Understanding how key behaviours, such as parental care, might vary based on social and ecological context could improve our understanding of how species may plastically respond to environmental changes. Although considerable plasticity has been demonstrated in parental investment of cooperative breeders in response to a variety of ecological conditions, little attention has been paid to how responses to social and ecological contexts (Adams *et al.* 2015). In this study, we experimentally manipulated chick begging signals through begging playback thereby mimicking harsh conditions, in the cooperatively breeding red-winged fairy-wren. We found that individual provisioning rate decreased according to the number of male helpers, independent of whether signals of perceived chick need were at normal or experimentally elevated levels, thus differences in offspring provisioning depending on social environment were consistent across ecological contexts. In addition, there was no evidence that individuals likely to gain more from future benefits showed a stronger response to increased chick hunger. Together these results enforce the importance of the social environment for investment decisions in cooperative breeders; individuals of different status and sex showed consistent patterns in provisioning behaviour even when overall feeding rates were increased in accordance with chick need.

Increased chick need did not result in additive care

Our experimental treatment resulted in increased provisioning rates, indicating that the begging playback was perceived as a signal of hunger. However, in contrast to our prediction, there was still load-lightening in the presence of male helpers, whereas a reduction in investment is only expected when individuals can afford to do so. Yet, although a comparative analysis of 27 cooperatively breeding species showed that, across species, the occurrence of additive care is significantly associated with a higher rate of nestling starvation (Hatchwell 1999), evidence for plasticity in provisioning rate based on cues related to nestling starvation is mixed. Luck (2002) demonstrated that compensatory and additive investment strategies may be exhibited in the same species depending on landscape characteristics that are linked to food availability: rufous treecreepers (*Climacteris rufa*) in a fragmented, disturbed landscape with decreased food availability did not reduce feeding rates as the number of nest attendants increased, while load-lightening was observed in an undisturbed landscape, where food was more abundant (Luck 2002). Conversely, in the ground tit (*Parus humilis*), investment by breeders varies according to the presence/absence of helpers regardless of the quality of the foraging environment (Lu, Yu & Ke 2011).

This lack of consistency suggests that parental investment in addition to being sensitive to cues of chick need or other environmental cues relating to the likelihood of chick starvation, might also be dependent on other factors, such as the relative costs of plastically increasing investment. Such costs may be reduced in temperate or tropical habitats, where the costs for parents of increasing their feeding effort is relatively low due to greater food abundance and mild environmental conditions (Lu *et al.* 2011). There may also be temporal variation in cue sensitivity. For example, a long-term study of how breeders respond to group size in the acorn woodpecker (*Melanerpes formicivorus*) demonstrated that load-lightening becomes more likely when chicks are older (> 7 days) and the likelihood of brood reduction decreases (Koenig & Walters 2012). Although group members were responsive to experimentally elevated chick begging in our study, the relatively short time-window in which we conducted the experiment may not have been sufficient to result in a change in provisioning rules. If each individual carefully considers its investment compared to others and the need of the brood, more time might be needed to change care from load-lightening to additive care.

Investment did not vary with current and potential future benefits

As typical for many species of the fairy-wren genus, many offspring are sired by males from outside the social group (Brouwer *et al.* 2017). As a result, dominant females have the highest relatedness to the offspring and thus benefit most from raising young. However, in contrast to our prediction, dominant females did not respond more strongly to increased chick need compared to other group members. Possibly the extra costs of increasing provisioning even more do not outweigh the benefits of increased offspring production, particularly because dominant females already incur the costs of egg production, incubation and brooding of the chicks. Alternatively, these additional costs to breeding females may mean that females lack the flexibility of care that males have because they may be working closer to their maximum capacity (Low *et al.* 2012).

Surprisingly, we found that dominant males too showed a strong response to increased chick need, despite the fact that the offspring they care for are often unrelated, and future helpers are costly for them as they compete for extra-group matings (Brouwer et al 2011). A study in closely-related superb fairy wrens (*Malarus cyaneus*) also showed that dominant males, but not females, responded strongly to increased chick begging (MacGregor & Cockburn 2002). This sex difference was attributed to differences in time spent at the nest: breeding female superb fairy-wrens spend more time at the nest than their male counterparts, and therefore potentially are better able to accurately assess chick condition (in other words, they were "not fooled" by the playback experiment) (MacGregor & Cockburn 2002). In their study, dominant males may have increased their feeding rates in order to compensate for the dominant females' lack of response (MacGregor & Cockburn 2002). However, this is an unlikely explanation for the strong male response in our study, because all group members, including dominant females, increased feeding rates in response to increased begging. Alternatively, the costs of not responding to nestlings (e.g. nestling starvation) may outweigh the benefits, such as reduced workload or increased opportunities to solicit for extra-pair copulations. Dominant males might be able to cope well with the costs of working harder and the opportunities for increasing their chances of more extra-pair copulations might be few since extra-pair mate choice seems to be based on moult date long before the breeding season starts (Brouwer et al. 2011).

Despite the fact that male helpers are more likely to inherit the territory than females (Russell & Rowley 2000) and thus would benefit more from recruiting new group members who will later help them (Kokko *et al.* 2001; Clutton-Brock 2002), we did not find that helper males responded to increased chick need more strongly than female helpers. Such a pattern was shown in cooperative meerkats (*Suricata suricatta*), where philopatric females fed proportionally more than males in response to begging playback (English *et al.*

2008). As for other group members, however, further increasing investment might not outweigh the costs this incurs, because future group members might also be costly as being in a group with more female helpers reduces survival (Lejeune *et al.* 2016).

Cues for investment decisions

The consistent provisioning patterns across contexts that we found suggest that group composition is an important cue that is used by individuals as a basis for provisioning decisions. However, in red-winged fairy-wrens it remains unclear what information group composition actually provides. Why is the number of helper males an important cue to individuals in red-winged fairy-wren groups, particularly given that the number of helper females does not appear to be an important cue? Previously, we hypothesised that helper males may be perceived as being more reliable, given that they are less likely to disperse mid-season than helper females (Russell & Rowley 2000; Brouwer *et al.* 2014). Based on this idea group members should base their investment decisions without presuming that female help will be available.

Alternatively, males and females might use different cues on which to base their investment decision. For example, in the closely related superb fairy-wren it was shown that dominant females did not respond to increased nestling begging, whereas both dominant and helper males did (MacGregor & Cockburn 2002). In contrast, both helpers and dominants did use the same provisioning rules in Arabian babblers (*Turdoides squamiceps*) (Wright 1998). In red-winged fairy-wrens there is no indication that males and females use different cues, since all group members respond in a similar way to the number of helper males and there is no difference in overall investment among the sexes (Brouwer *et al.* 2014) and the response to increased chick begging does not vary consistently among males and females (Fig. 2). It is thus likely that both chick need and investment of others are important cues, although when individuals show load-lightening and thus have lower nest visitation rates, the signals of chick need might become less important and individuals might rely more on what other group members do. Nevertheless, although unlikely, we cannot rule out the possibility that males and females use different cues, as this would require playback experiments targeting focal individuals (e.g. one sex) only rather than the whole group simultaneously. Here, we did not use such a design since we were specifically interested in differences in responsiveness to chick cues within the context of the group, not to the responses other individuals. Future experiments targeting begging playback to helper males and females separately might shed light on whether males and females use different cues, though in practice such experiments are very difficult to perform for larger group sizes and when birds arrive at the nest simultaneously or shortly after another.

Conclusions

Red-winged fairy-wrens show considerable complexity in provisioning rules, displaying status-dependent differences in provisioning rates and a mix of additive and load-lightening care according to group composition, which was independent of chick need. The combination of responsiveness to group composition, but individual and across-context consistency in provisioning rules, reinforces the importance of considering social environment when investigating resource investment in offspring. Furthermore, the quick response to increased chick need indicates some flexibility in investment decisions. A fuller understanding of the cues used by individuals (and how those cues may interact) will further illuminate how we might expect key behaviours (such as parental care), and cooperative species more generally, to respond to patterns of global environmental change (Sih, Ferrari & Harris 2011).

References

Adams, M.J., Robinson, M.R., Mannarelli, M.-E. & Hatchwell, B.J. (2015) Social genetic and social environment effects on parental and helper care in a cooperatively breeding bird. *Proceedings of the Royal Society B: Biological Sciences*, **282**, 20150689.

Arnold, W. (1990) The evolution of marmot sociality: I. Why disperse late? *Behavioral Ecology and Sociobiology*, **27**, 229–237.

Audacity(R): Free Audio Editor and Recorder. (2014)

Balshine, S., Leach, B., Neat, F., Reid, H., Taborsky, M. & Werner, N. (2001) Correlates of group size in a cooperatively breeding cichlid fish (Neolamprologus pulcher). *Behavioral Ecology and Sociobiology*, **50**, 134–140.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, **1**, 1–48.

Brouwer, L., van de Pol, M., Aranzamendi, N.H., Bain, G., Baldassarre, D.T., Brooker, L.C., Brooker, M.G., Colombelli-Négrel, D., Enbody, E., Gielow, K., Hall, M.L., Johnson, A.E., Karubian, J., Kingma, S.A., Kleindorfer, S., Louter, M., Mulder, R.A., Peters, A., Pruett-Jones, S., Tarvin, K.A., Thrasher, D.J., Varian-Ramos, C.W., Webster, M.S. & Cockburn, A. (2017) Multiple hypotheses explain variation in extra-pair paternity at different levels in a single bird family. *Molecular Ecology*, **26**, 6717–6729.

Brouwer, L., Van De Pol, M., Atema, E. & Cockburn, A. (2011) Strategic promiscuity helps avoid inbreeding at multiple levels in a cooperative breeder where both sexes are philopatric. *Molecular Ecology*, 4796–4807.

Brouwer, L., Van de Pol, M. & Cockburn, A. (2014) The role of social environment on parental care: Offspring benefit more from the presence of female than male helpers. *Journal of Animal Ecology*, **83**, 491–503.

Burford, J., Friedrich, T. & Yasukawa, K. (1998) Response to playback of nestling begging in the red-winged blackbird, Agelaius phoeniceus. *Animal behaviour*, **56**, 555–561.

Clutton-Brock, T. (2002) Breeding Together: Kin Selection and Mutualism in Cooperative Vertebrates. *Science*, **296**, 69 LP-72.

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 Behavior in Meerkats. *Science*, **297**, 253 LP-256.

Crick, H.Q.P. (1992) Load-lightening in cooperatively breeding birds and the cost of reproduction. *Ibis*, **134**.

Davies, N.B. & Hatchwell, B.J. (1992) The Value of Male Parental Care and its

Influence on Reproductive Allocation by Male and Female Dunnocks. *Journal of Animal Ecology*, **61**, 259–272.

Drummond, H. & Garcia Chavelas, C. (1989) Food shortage influences sibling aggression in the blue-footed booby. *Animal Behaviour*, **37**, 806–819.

English, S., Kunc, H.P., Madden, J.R. & Clutton-Brock, T.H. (2008) Sex differences in responsiveness to begging in a cooperative mammal. *Biology Letters*, **4**, 334 LP-337.

Ghalambor, C.K., Peluc, S.I. & Martin, T.E. (2013) Plasticity of parental care under the risk of predation: how much should parents reduce care? *Biology Letters*, **9**.

Harrison, X.A. (2014) Using observation-level random effects to model overdispersion in count data in ecology and evolution (ed C Miao). *PeerJ*, **2**, e616.

Hatchwell, B.J. (1999) Investment Strategies of Breeders in Avian Cooperative Breeding Systems. *The American Naturalist*, **154**, 205–219.

Hatchwell, B.J. & Davies, N.B. (1990) Provisioning of nestlings by dunnocks, Prunella modularis, in pairs and trios compensation reactions by males and females. *Behavioral Ecology and Sociobiology*, **27**, 199–209.

Hatchwell, B.J. & Russell, A.F. (1996) Provisioning Rules in Cooperatively Breeding Long-Tailed Tits Aegithalos caudatus: An Experimental Study. *Proceedings of the Royal Society of London B: Biological Sciences*, **263**, 83–88.

Heinsohn, R. & Cockburn, A. (1994) Helping is costly to young birds in cooperatively breeding white-winged choughs. *Proceedings of the Royal Society of London B: Biological Sciences*, **256**, 293–298.

Kilner, R.M. & Drummond, H. (2007) Parent–offspring conflict in avian families.

Journal of Ornithology, **148**, 241–246.

Koenig, W.D. & Walters, E.L. (2012) Brooding, provisioning, and compensatory care in the cooperatively breeding acorn woodpecker. *Behavioral Ecology*, **23**, 181–190.

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

Langmore, N.E., Bailey, L.D., Heinsohn, R.G., Russell, A.F. & Kilner, R.M. (2016) Egg size investment in superb fairy-wrens: helper effects are modulated by climate. *Proceedings of the Royal Society B: Biological Sciences*, **283**, 20161875.

Lejeune, L., van de Pol, M., Cockburn, A., Louter, M. & Brouwer, L. (2016) Male and female helper effects on maternal investment and adult survival in red-winged fairy-wrens. *Behavioral Ecology*, **27**, 1841–1850.

Leonard, M.L., Horn, A.G., Gozna, A. & Ramen, S. (2000) Brood size and begging intensity in nestling birds. *Behavioral Ecology*, **11**, 196–201.

Lotem, A. (1998) Differences in begging behaviour between barn swallow,Hirundo rustica, nestlings. *Animal Behaviour*, **55**, 809–818.

Low, M., Makan, T. & Castro, I. (2012) Food availability and offspring demand influence sex-specific patterns and repeatability of parental provisioning. *Behavioral Ecology*, **23**, 25–34.

Lu, X., Yu, T. & Ke, D. (2011) Helped ground tit parents in poor foraging environments reduce provisioning effort despite nestling starvation. *Animal Behaviour*, **82**, 861–867.

Luck, G.W. (2002) The Parental Investment Strategy of an Avian Cooperative

Breeder Differs between a Fragmented and an Unfragmented Landscape. *The American Naturalist*, **160**, 809–814.

MacGregor, N.A. & Cockburn, A. (2002) Sex differences in parental response to begging nestlings in superb fairy-wrens. *Animal Behaviour*, **63**, 923–932.

R Core, T. (2015) R: A language and environment for statistical computing.

Reyer, H.-U. (1984) Investment and relatedness: a cost/benefit analysis of breeding and helping in the pied kingfisher (Ceryle rudis). *Animal Behaviour*, **32**, 1163–1178.

De Rosario-Martinez, H. (2015) phia: Post-Hoc Interaction Analysis. R package version 0.2-1.https://CRAN.R-project.org/package=phia

Rowley, I. & Russell, E.M. (1997) *Fairy-Wrens and Grasswrens*. Oxford University Press, Oxford, UK.

Rowley, I., Russell, E., Brown, R. & Brown, M. (1988) The Ecology and Breeding Biology of the Red-winged Fairy-wren <I>Malurus elegans</I>. *Emu*, **88**, 161–176.

Russell, A.F., Langmore, N.E., Cockburn, A., Astheimer, L.B. & Kilner, R.M. (2007) Reduced Egg Investment Can Conceal Helper Effects in Cooperatively Breeding Birds. *Science*, **317**, 941–944.

Russell, A.F., Langmore, N.E., Gardner, J.L. & Kilner, R.M. (2008) Maternal investment tactics in superb fairy-wrens. *Proceedings. Biological sciences / The Royal Society*, **275**, 29–36.

Russell, E. & Rowley, I. (2000) Demography and social organisation of the red-winged fairy-wren, *Malurus elegans*. *Australian Journal of Zoology*, **48**, 161–200.

Savage, J.L., Russell, A.F. & Johnstone, R. a. (2015) Maternal allocation in cooperative breeders: should mothers match or compensate for expected helper contributions? *Animal Behaviour*, **102**, 189–197.

Schielzeth, H. (2010) Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, **1**, 103–113.

Sheldon, B.C. (2000) Differential allocation: Tests, mechanisms and implications. *Trends in Ecology and Evolution*, **15**, 397–402.

Sih, A., Ferrari, M.C.O. & Harris, D.J. (2011) Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications*, **4**, 367–387.

Stearns, S.C. (1992) *The Evolution of Life Histories.* Oxford University Press, Oxford, UK.

Taborsky, M. (1984) Broodcare helpers in the cichlid fish Lamprologus brichardi: their costs and benefits. *Animal Behaviour*, **32**, 1236–1252.

Wright, J. (1998) Helpers-at-the-nest have the same provisioning rule as parents: Experimental evidence from play-backs of chick begging. *Behavioral Ecology and Sociobiology*, **42**, 423–429.