

The role of social environment on parental care: offspring benefit more from the presence of female than male helpers

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Summary

1. Investment in offspring depends on the costs and benefits to the carer, which can vary with sex and social status. Investment also depends on the effort of others by allowing for compensation (load-lightening), with biparental care studies showing that this depends on the state and type of the other carer. By contrast, studies on cooperative breeders have solely focussed on the effects of group size rather than its composition (i.e. social environment).

2. Here we propose and provide the first test of the ‘Social Environment’ hypothesis, that is, how the characteristics (here the sex) of other helpers present in the group affect parental care and how this in turn affects offspring fitness in cooperatively breeding red-winged fairy-wrens (*Malurus elegans*).

3. Breeders provisioned nestlings at a higher rate than helpers, but there was no sex difference in provisioning rate. Compensation to increasing group size varied little with sex and status, but strongly depended on social environment. All group members reduced their provisioning rates in response to an increasing number of male (load-lightening), but not female helpers (additive care).

4. As a result, nestlings received more food and grew faster in the presence of female helpers. The increased nestling growth did convey a fitness advantage due to a higher post-fledging survival to adulthood.

5. Our study provides the first evidence that parental care can depend on social environment. This could be an important overlooked aspect to explain variation in parental care in cooperative breeders in general and in particular the enormous variation between the sexes, which we reveal in a literature overview.

Key-words: cooperative breeding, helping, load-lightening, provisioning behaviour, red-winged fairy-wren, sex differences

Introduction

Parental investment is energetically costly; hence, parents should balance the cost and benefits influencing the trade-off between current and future reproduction (Williams 1966; Drent & Daan 1980). In systems with biparental care, the investment given by an individual also depends on the amount of care given by the other parent (Johnstone & Hinde 2006). Theory predicts that biparental care is evolutionarily stable when each parent compensates

incompletely for a reduction in care by its partner (Houston & Davies 1985). Importantly, variation between individuals means that the amount of investment can depend on the state or type of the partner (Burley 1988; McNamara & Houston 1996; Sheldon 2000; Rutstein 2005). For example, reducing nest visitation rate by handicapping a bird resulted in an increase in provisioning rates by the unmanipulated partner in European starlings (*Sturnus vulgaris*) (Wright & Cuthill 1989). As another example, female Gouldian finches (*Erythrura gouldiae*) that breed with males of the same colour morph provision at higher rates than those paired to incompatible males (Pryke & Griffith 2009).

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The role of the type, quality or attractiveness of the other carer is a specific research focus of biparental care systems (Sanz 2001; Mazuc 2003; Pilastro, Griggio & Matessi 2003; Limbourg *et al.* 2004; Pryke & Griffith 2009), but it is striking that studies on cooperative breeders have largely ignored this key aspect of parental care. Possibly, the obvious difference in number of carers between biparental and cooperative care systems has led researchers to concentrate on how group size instead of group composition (e.g. sex of other carers) affects parental investment in cooperative breeders (Heinsohn 2004; Johnstone 2011). Such studies have shown that in some cooperative systems, individuals respond in a similar manner as biparental systems by reducing their effort in response to the work done by additional carers (i.e. load-lightening; Hatchwell & Russell 1996; Wright & Dingemanse 1999; Legge 2000b; Balshine *et al.* 2001), which could increase future fitness through both increased survival (Reyer 1984; Russell & Rowley 1988; Cockburn *et al.* 2008b) and a reduced interval between reproductive attempts (Woxvold & Magrath 2005; Blackmore & Heinsohn 2007; Canestrari *et al.* 2008). In other cooperative breeders, the extra help provided by subordinates increases total care (i.e. additive care), which may increase immediate productivity (Heinsohn 1992; Clutton-Brock *et al.* 2001; Doerr & Doerr 2007; Kingma *et al.* 2010).

In cooperative breeding systems, the neglect of the influence of the type of other carers on parental investment lacks a clear scientific justification although sex of the carers is often ignored because in many species just one sex helps and when both sexes help telling them apart was often impossible before the availability of molecular methods (Cockburn 2004). Cooperative breeders vary widely both in the amount of help they provide and in the way they respond to the effort of group members, and our understanding of this variation both within and between species remains poor (Heinsohn 2004; Koenig & Walters 2011). However, in cooperative breeding systems, there are particularly good reasons to expect some type of carers to invest more than others. Benefits from helping are generally expected to be less than benefits from independent reproduction, despite a typically high degree of relatedness between helper and recipient in most species (Cockburn 1998). Thus, helpers are expected to invest less than breeders, a pattern found in numerous species (Brown *et al.* 1978; MacColl & Hatchwell 2003; Doerr & Doerr 2007; Koenig & Walters 2011), but not all cooperative breeders (Reyer & Westerterp 1985; Wright 1998; Woxvold, Mulder & Magrath 2006). The costs and benefits of parental care are also expected to vary with sex because one sex is typically more likely to benefit, for example, from inheriting dominance status (Clutton-Brock *et al.* 2006). Recent theoretical work has shown that sex differences in the cost of care can give rise to sex differences in the compensatory response (Johnstone 2011). Indeed, empirical work shows that compensation can vary between males and females in species where both

sexes are philopatric (Vanderwerf & Strahl 1990; Woxvold, Mulder & Magrath 2006; Meade *et al.* 2010). We propose the 'Social Environment' hypothesis, which states that not only the number of helpers, but also the type of helpers (specified by, e.g. their sex, personality or state) present in the group will affect the investment strategies of the other group members.

Here we investigate whether parental investment varies among individuals of different sex and status and how they respond to their social environment (i.e. number and sex of group members). We quantified parental investment by means of provisioning rates (number of prey items delivered), as well as more subtle differences in prey species delivered and nest-guarding duties. Subsequently, we investigate what the fitness consequences are for the offspring raised in different social environments. We addressed these questions by studying parental care behaviour in the cooperatively breeding red-winged fairy-wren (*Malurus elegans*). This species provides a rich range of opportunities to investigate patterns of investment, since (i) both males and females stay in their natal territory for at least 1 year to help and virtually all group members contribute to nestling provisioning (Russell & Rowley 2000); (ii) the same individuals can be observed in different years with variable group compositions and sizes allowing quantification of behaviourally plastic responses to variable social environments; (iii) the very high level of extra-pair paternity (57% of offspring; Brouwer *et al.* 2011) means that helpers are on average less related to the offspring than are dominant females; and (iv) despite both sexes being strongly philopatric, males more often inherit natal territories, while female helpers disperse at a younger age (i.e. the sexes differ in future prospects, Russell & Rowley 2000). Male helpers would therefore benefit more from recruiting new group members who will later help them (delayed reciprocity, Wiley & Rabenold 1984; Kokko, Johnstone & Clutton-Brock 2001).

Methods

STUDY AREA AND DATA COLLECTION

Data were collected in Smithbrook Nature Reserve in Western Australia (116°10'E, 34°20'S) during four breeding seasons (2008–2011). The 95-ha reserve consists of eucalypt wet forest with a dense understorey (for more details: Rowley *et al.* 1988). The main study area comprised ~70 territories of which >99% of the adult birds were individually colour-banded. Each territory was checked at least fortnightly for group composition and breeding activity throughout the breeding season (October–January). Each group comprised a 'dominant' pair-bonded male and female and anywhere from zero to seven subordinate helpers (mean no. helpers: 1.8 ± 1.4 SD). Since red-winged fairy-wrens are sexually dimorphic, the sex of adult birds can easily be determined using plumage characteristics (Rowley *et al.* 1988). Social status was determined from behavioural observations, plumage variation and age (Russell & Rowley 2000). During the study period, on

average 83% of the territories had one or more subordinates, and on average 40% of subordinates were female. Plural breeding, where more than one female in the group builds a nest, was observed in 7% of the territories (Brouwer *et al.* 2011), and since helpers sometimes divided their effort between multiple nests within a group, these territories were excluded from the analyses. Red-winged fairy-wrens only rarely re-nest in the same season after fledging a brood, but in these cases, the juveniles from the previous attempt have never been observed to help.

Nestling provisioning behaviour was determined on days 8 and 10 after hatching. By this stage, nestlings are no longer brooded by the dominant female, so her contribution can be compared to that of other group members. Practical constraints meant that some nests were observed on day 9 or 11, and due to nest predation, some nests were only watched once. In total, 290 nest-watches on 317 different birds in 66 territories produced 1079 observations of provisioning rates. After the first nest-watch, the nestlings were colour-banded, and their body mass and tarsus length were measured.

Nest-watches were made from a hide that was placed at $5.7 \text{ m} \pm 1.9 \text{ SD}$ from the nest 1 day before the watch. Comparing feeding rates from nest-watches of the same nest performed from variable distances showed that the distance between hide and nest did not affect provisioning rate (correlation Δ distance vs. Δ total feeding rate: $R^2 = 0.0002$, $n = 75$ nests). Nest-watches lasted for at least 1 h, with groups larger than four birds being observed for 1.5 h. The identity of each bird that visited the nest was recorded using binoculars. In a few cases (<1%), the bird visiting the nest could not be identified, and these unknown feeds were equally divided over all group members. Occasionally birds were observed guarding the nest from a nearby bush (<2.5 m from nest), and the time spent nest-guarding was recorded for each bird.

In 2009–2011, the prey items fed to the nestlings were identified whenever possible. Prey items were divided into eight classes: Arachnida, Diptera, Formicidae, Lepidoptera adults, Lepidoptera larvae, Hemiptera and Coleoptera, unidentified larvae and unknown (if the prey was observed, but could not be identified).

STATISTICAL ANALYSES

Provisioning rate of an individual (number of feeds per hour) was transformed using $\log_{10}(x + 1)$ and then fitted as a normal response variable in a linear mixed model (LMM). Territory identity, individual identity and nest-watch identity were included as random intercepts to account for non-independence of the data (e.g. feeding rates of birds in the same territory might be intercorrelated). Age of the brood (days), day of season (counting from October 1) and the number of helper males and females in a group were included as covariates, while status (dominant or helper), sex of the provisioning bird, brood size and year were included as fixed factors.

Many individuals were of unknown age at the start of this study. Restricting analyses to known age helpers showed that provisioning behaviour did not vary with age within the first 3 years of life (LMM: $\chi^2 = 0.47$, d.f. = 2, $P = 0.79$, $n = 297$ feeding rates on 115 helpers). Most helpers are within this age range (82%; Russell & Rowley 2000), and age was henceforth not considered in the analysis.

Since not all individuals nest-guard, the distribution of 'time spent on nest-guarding' includes large numbers of zeros.

Therefore, both the probability that an individual would nest-guard and the proportion of time that individuals that nest-guarded spent on this task were analysed. Territory identity, nest-watch identity and individual identity were included as random effects with the probability of nest-guarding fitted as a binary response variable in a generalized linear mixed model (GLMM) and the proportion of time spent nest-guarding fitted as a normal response variable after \log_{10} transformation in a LMM.

Analyses on prey types delivered were restricted to observations of individuals for which at least 80% of the prey items fed to the nestlings were observed ($n = 743$ feeds in 116 nest-watches), to avoid a possible bias to more easily identifiable prey items. To investigate whether prey types varied with status or sex of the provisioner, the number of prey of a particular prey type was fitted as a binomial response in a GLMM with the denominator set to the total number of prey items determined and individual identity and nest-watch identity included as random effects.

To investigate the fitness consequences of provisioning behaviour, we also considered effects on the total number of feeds received per nestling, nestling mass, tarsus length, fledging numbers and survival after fledging. The number of feeds received, nestling mass and tarsus length were fitted assuming normal errors and using an identity link, with nest identity included as random effect. The number of fledglings produced per group was fitted using a Poisson regression, with the number of male and female helpers included as covariates, year as a fixed factor and territory identity as a random effect. Survival of fledglings until adulthood (first year of life) with respect to mass and tarsus length was analysed by fitting survival as a binary response in a GLMM with territory identity as random effect. Our data did not allow for a direct comparison of how the number of male and female helpers differentially affects offspring survival, as this model would not converge (this analysis focuses on successful nests only, and the associated reduction in sample size probably makes it difficult to estimate the within-territory effect of the number of helpers because there are fewer territories with varying group composition in the data set).

Since we observed the same individuals in multiple years in groups of varying size and composition, our data allow us to distinguish within-subject effects (i.e. plastic behavioural response) from between-subject effects (i.e. a fixed response based on the differences between groups with and without helpers). We quantified within- and between-subject effects of group composition on helping behaviour and offspring fitness using a widely used mixed modelling technique called within-subject centring (van de Pol & Wright 2009). We first tested whether there was any evidence for a difference between the within- vs. between-subject effects and if significant investigated whether it was the within-, between- or both subject effects that were significant (van de Pol & Wright 2009). Model selection was based on stepwise backward elimination of non-significant fixed terms in order of their P -value. Significance of fixed terms was assessed by a likelihood ratio test. Effect sizes come from final models that contain all terms with P -values < 0.10. Standardized values in figures were obtained by calculating the residuals from the observed and the predicted values according to the final model. All statistical analyses were performed in R v.2.14 (R Development Core Team 2012) using package `lme4` (Bates, Maechler & Bolker 2011, p. 4).

Results

PROVISIONING

Average provisioning rate was higher in 2010 than in the other 3 years of study, increased with brood size and tended to increase with nestling age (Table 1). In addition to these effects, average provisioning decreased with increasing number of helpers present in a territory, indicative of load-lightening (Fig. 1a,b). Strikingly, social environment played an important role in provisioning rates: there was a sharp decline in provisioning as the number of male helpers increased, independent of the number of female helpers present in the group (different lines in Fig. 1c). However, there was only a slight (non-significant) reduction in care as the number of female helpers increased (Fig. 1d). The absence of a compensatory response to the number of female helpers was independent of the number of male helpers in the group (Fig. 1d), although the average provisioning rates declined as the number of males increased (different lines in Fig. 1d), as expected from the compensatory response to the number of male helpers (see Fig. 1c). It should be realized that the linear compensatory responses in the \log_{10} -transformed provisioning rates in Fig. 1 imply that real provisioning rates (right y-axes) decline logarithmically with the number of helpers. Dominants provisioned at a higher rate than

helpers (Fig. 2a,b; Table 1), but provisioning rates did not vary between the sexes (Fig. 2c,d; Table 1). Furthermore, there was no evidence that helper males provisioned at a different rate from helper females or, similarly, dominant males at a different rate from dominant females (Table 1: Sex \times Status).

Dominants and helpers exhibited a similar compensatory response to the number of male helpers in the group (Fig. 2a,b; Table 1: Status \times No. helper males). However, dominants and helpers exhibited a slightly different compensatory response to the number of female helpers in the group (Table 1: Status \times No. helper females). Helper provisioning rates remained constant with increasing number of female helpers in the group (Fig. 2b), while there was a slight reduction in provisioning rates of dominants, but still not as strong a compensatory response as to the number of male helpers (Fig. 2a).

The negative association between the number of male helpers and provisioning rate was likely a plastic response, as indicated by the non-significance of between- vs. within-subject effects (Table 1). In other words, there was no indication that the relationship resulted from a consistent between-group difference in provisioning rates that might be associated with larger groups being on superior territories or being better foragers. The differential response to male vs. female helpers was not due to differences in prey items fed to the nestlings by provisioners of different

Table 1. Results from a LMM examining provisioning of nestlings measured as the \log_{10} -transformed number of feeds of a bird per hour ($n = 1079$)

Parameter	Estimate \pm SE	d.f.	χ^2	<i>P</i>
Final model				
Intercept	0.60 \pm 0.07	1		
Year*		3	19	<0.001
β_{2009}	0.023 \pm 0.025			
β_{2010}	0.080 \pm 0.024			
β_{2011}	-0.010 \pm 0.026			
Brood size [†]		2	41	<0.001
$\beta_{\text{brood size } 2}$	0.13 \pm 0.027			
$\beta_{\text{brood size } 3}$	0.20 \pm 0.029			
Age brood	0.012 \pm 0.0069	1	3.1	0.08
Status [‡]	-0.13 \pm 0.024	1	31	<0.001
No. of helper males	-0.075 \pm 0.011	1	43	<0.001
No. of helper females	-0.037 \pm 0.015	1	2.0	0.15
No. of helper females \times status [‡]	0.040 \pm 0.018	1	5.0	0.03
Random effects				
$\sigma^2_{\text{territory}}$	1.2 $\times 10^{-4}$			
$\sigma^2_{\text{individual}}$	0.020			
$\sigma^2_{\text{nestwatch}}$	0.0075			
Rejected terms				
Day of season	-6.6 $\times 10^{-4} \pm 4.9 \times 10^{-4}$	1	1.8	0.18
Sex [§]	-0.024 \pm 0.021	1	1.3	0.26
Sex [§] \times status [‡]	0.0029 \pm 0.039	1	0.006	0.94
No. helper males \times status [‡]	0.025 \pm 0.017	1	1.9	0.16
$\Delta_{(\text{between vs. within})}$ no. helper male	-0.013 \pm 0.020	1	0.42	0.52
$\Delta_{(\text{between vs. within})}$ no. helper female	0.018 \pm 0.019	1	0.92	0.34

Reference categories are as follows: *2008; [†]brood size 1; [‡]dominant; [§]male.

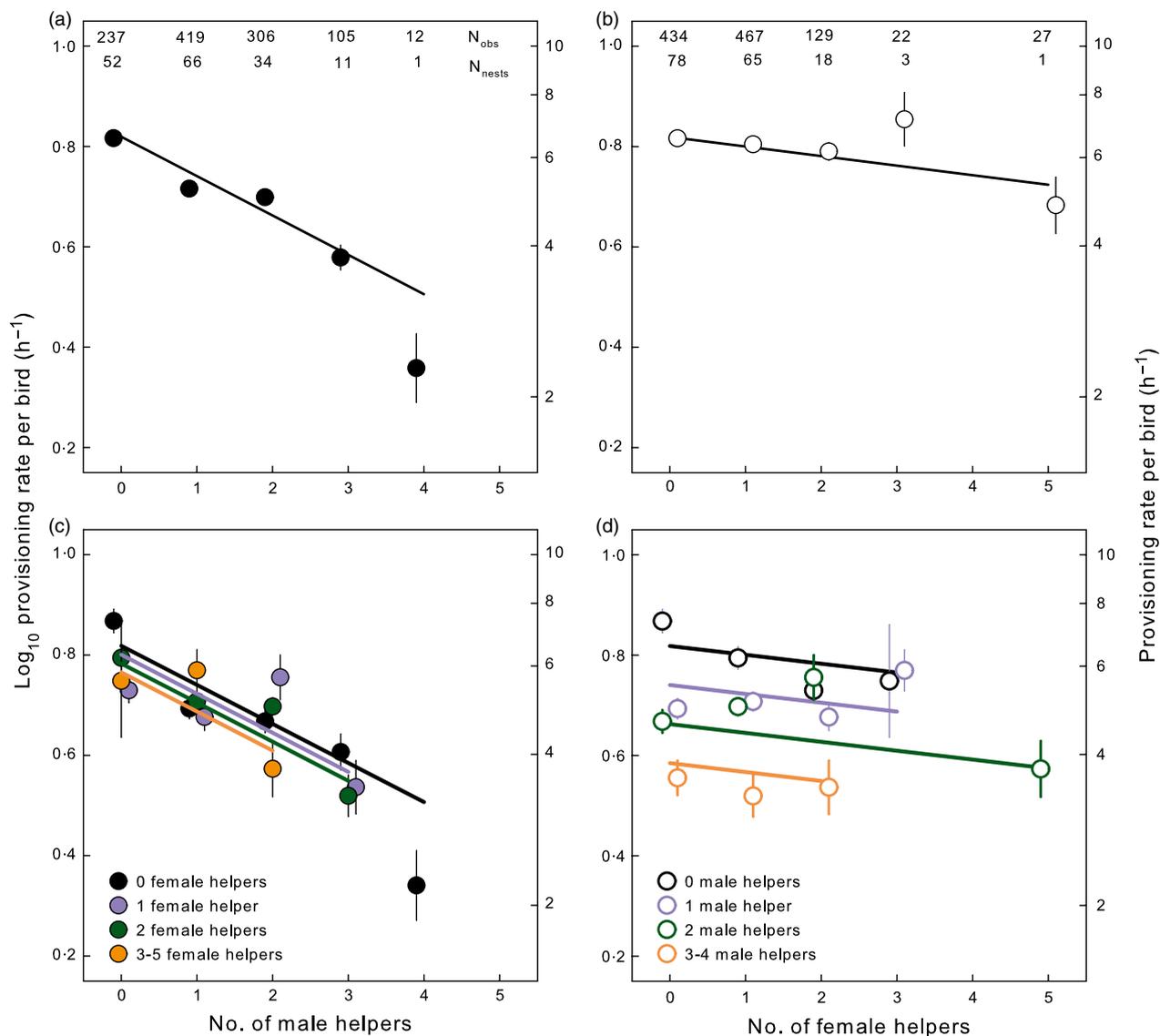


Fig. 1. The standardized average provisioning rate per bird per hour in relation to (a) the number of male helpers in the group in the absence of female helpers, (b) the number of female helpers in the group in the absence of male helpers, (c) the number of male helpers in the group shown for varying number of female helpers and (d) the number of female helpers in the group shown for varying number of male helpers. Provisioning rate is standardized for the effects of year, brood size, age of the brood, status and the number of female (a & c) or male helpers (b & d) according to the final model in Table 1. Numbers on top indicate the number of observations (N_{obs}) and the number of nests (N_{nests}). Error bars are based on SEM.

sex or social status (all prey types GLMM: $\chi^2 < 1.96$, d.f. = 1, $P > 0.16$; Fig. S1, Supporting Information). Finally, restricting analyses to groups where at least one male helper and one female helper are present showed qualitatively the same differential response dependent on sex of the helpers present, indicating that our findings are not due to any unaccounted differences between groups with male vs. groups with female helpers.

NEST-GUARDING

The likelihood that a bird would guard the nest was not associated with its provisioning rate (GLMM: $\chi^2 = 0.64$,

d.f. = 1, $P = 0.42$) or the duration of the nest-watch (GLMM: $\chi^2 = 1.2$, d.f. = 1, $P = 0.26$). However, dominants were more likely to guard the nest than helpers, and females were more likely to nest-guard than males (GLMM status: $\chi^2 = 34.5$, d.f. = 1, $P < 0.01$; sex: $\chi^2 = 5.9$, d.f. = 1, $P = 0.02$). There was no evidence that there was compensation with respect to nest-guarding behaviour. By contrast, the probability that an individual guarded the nest increased with the number of helpers present and only decreased at very large group sizes (Fig. S2, Supporting Information). Furthermore, there was no evidence that the probability that an individual guarded the nest depended on social environment (Fig. S2,

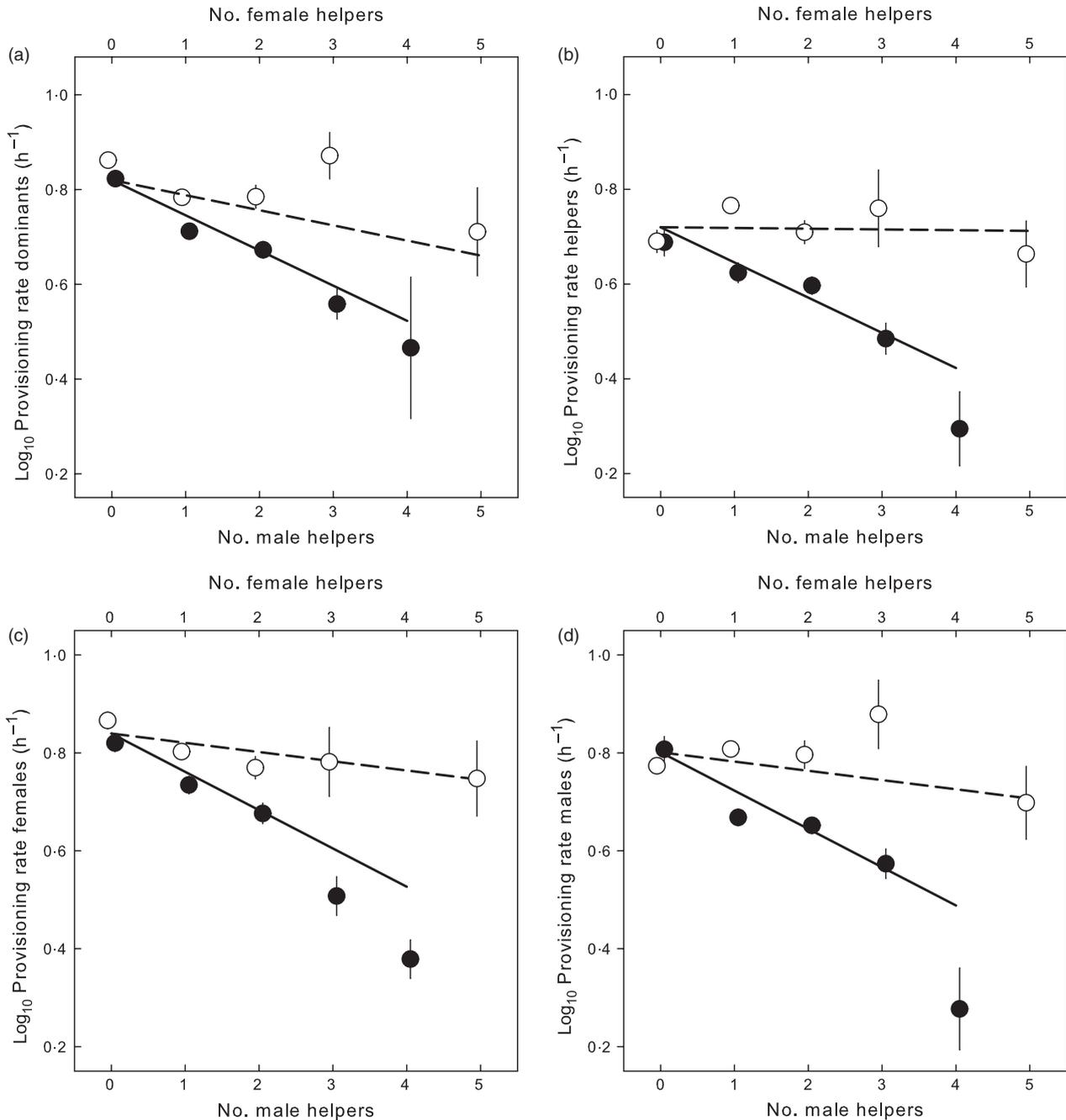


Fig. 2. The standardized average provisioning rate (log₁₀-transformed) for (a) dominants, (b) helpers, (c) females and (d) males shown in relation to the number of male helpers in the absence of female helpers (● bottom x-axis) and female helpers in the absence of male helpers (○ top x-axis). Provisioning rate is standardized for the effects of year, brood size, age brood, status and the number of male or female helpers according to the model in Table 1. See Fig. 1 for sample sizes; error bars are based on SEM.

Supporting Information). The proportion of time spent nest-guarding was not associated with status, sex or social environment (GLMM all: $\chi^2 < 1.4$, $P > 0.24$).

FITNESS CONSEQUENCES

When the number of female helpers increases, the nestlings receive more food because birds do not reduce their provisioning rates (Fig. 3a) and the nestlings were heavier (Fig. 3b; Table 2a) and larger (Fig. 3c; Table 2b). By

contrast, a larger number of male helpers had no effect on the food received by nestlings or their tarsus length, though there was a positive effect on nestling mass (Fig. 3b). However, this effect was due to variation between, not within, territories with helper males (Table 2a).

There was no positive association between fledgling production and the number of female or male helpers (GLMM $\chi^2 < 0.03$, d.f. = 1, $P > 0.86$). Furthermore, despite the higher provisioning rates and larger mass and size of the nestlings in the presence of female

helpers, territories with female helpers did not produce more fledglings than territories with male helpers (Fig. 3d).

Fitness consequences of compensatory responses did become apparent in the post-fledging life stage. Fledgling survival to adulthood improved with nestling tarsus length (Fig. 4), but heavier nestlings did not have a higher survival in their first year of life (Table 3).

Discussion

The role of an individual's social environment on its parental care has not previously been investigated in cooperative breeders. We investigated this for the first time by focussing on the sex of other group members in a system where helpers of both sexes are common. We found that male and female helpers provision at

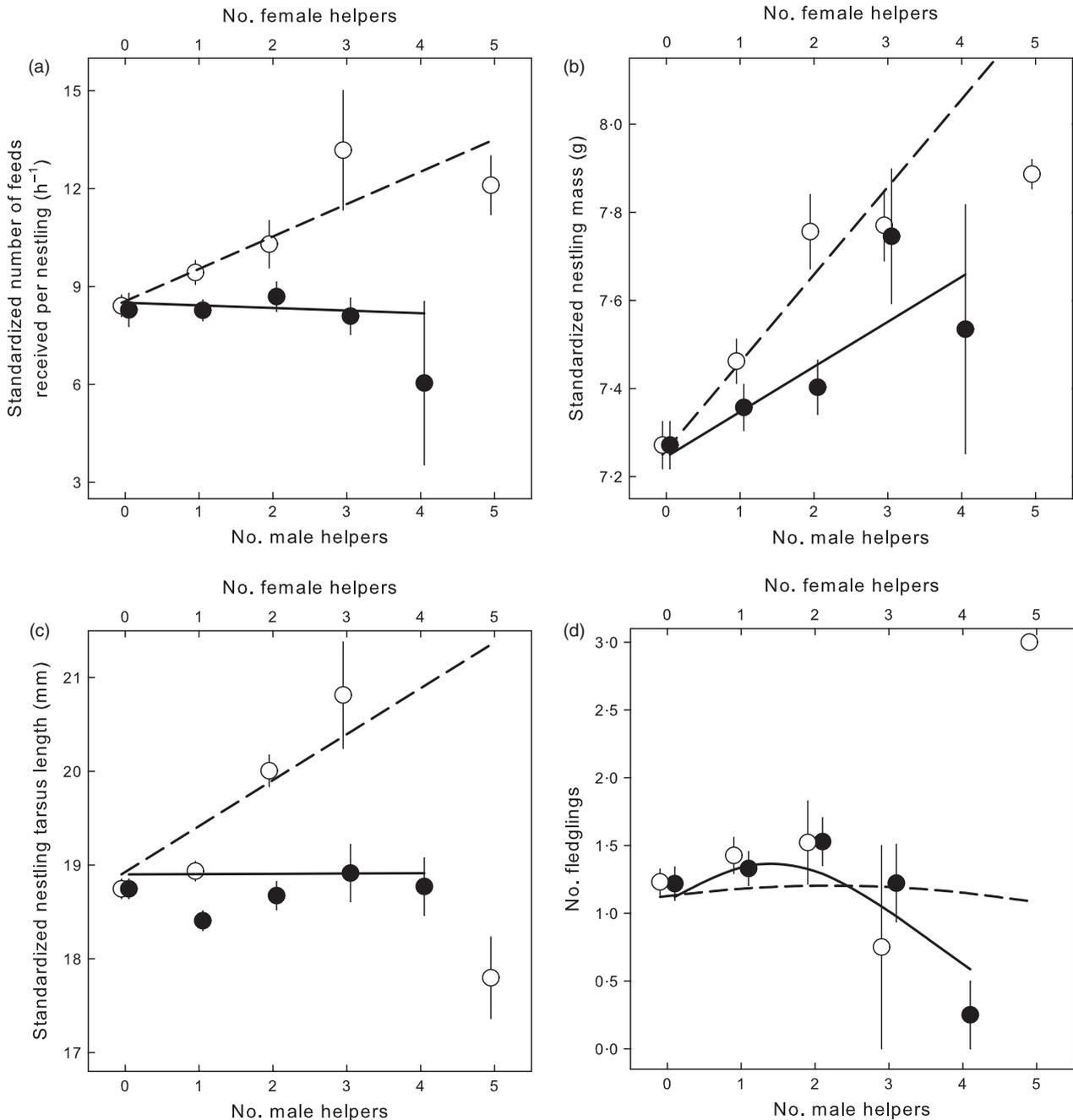


Fig. 3. (a) The number of feeds received per nestling, (b) nestling mass, (c) nestling tarsus length and (d) the number of fledglings produced in relation to the number of male helpers in the absence of female helpers (● bottom *x*-axis) and female helpers in the absence of male helpers (○ top *x*-axis). Feeds received per nestling are standardized for the effects of year, brood size, age brood, status and the number of male or female helpers. Nestling mass is standardized for the effects of year, age brood and number of male or female helpers. Tarsus length is standardized for the effects of year, age, observer and number of male or female helpers according to the models in Table 2. Lines show the predictions according to the final models; error bars are based on SEM.

Table 2. Results from a LMM examining (a) nestling mass and (b) nestling tarsus length ($n = 485$ nestlings)

Parameter	Estimate \pm SE	d.f.	χ^2	<i>P</i>
(a) Final model				
Intercept	-1.34 \pm 1.41	1		
Year*		3	9.2	0.03
β_{2009}	0.26 \pm 0.13			
β_{2010}	0.18 \pm 0.12			
β_{2011}	-0.072 \pm 0.12			
Age brood	1.54 \pm 0.31	1	23	<0.001
Age brood ²	-0.062 \pm 0.016	1	14	<0.001
No. of helper females	0.19 \pm 0.056	1	11	<0.001
No. of helper males _(between-subject)	0.16 \pm 0.052	1	8.8	0.003
Random effects				
σ^2_{nest}	0.31			
Rejected terms				
Day of season	-0.0022 \pm 0.0022	1	1.0	0.32
Brood size [†]		2	3.6	0.17
$\beta_{\text{brood size 2}}$	-0.021 \pm 0.14			
$\beta_{\text{brood size 3}}$	-0.18 \pm 0.15			
No. of helper males _(within-subject)	-0.0037 \pm 0.083	1	0.001	0.96
No. of helper females $\Delta_{\text{(between vs. within)}}$	-0.092 \pm 0.11	1	0.72	0.40
(b) Final model				
Intercept	4.90 \pm 1.03	1		
Day of season	0.0017 \pm 0.005	1	10	0.001
Year*		3	12	0.009
β_{2009}	2.15 \pm 0.56			
β_{2010}	2.39 \pm 0.61			
β_{2011}	1.67 \pm 0.56			
Age	1.31 \pm 0.085	1	157	<0.001
No. of helper females	0.45 \pm 0.13	1	12	<0.001
Observer		5	21	<0.001
Random effects				
σ^2_{nest}	1.68			
Rejected terms				
Age ²	-0.057 \pm 0.037	1	2.4	0.12
Brood size [†]		2	2.9	0.24
$\beta_{\text{brood size 2}}$	0.014 \pm 0.31			
$\beta_{\text{brood size 3}}$	-0.34 \pm 0.34			
No. of helper males	0.025 \pm 0.10	1	0.06	0.80
$\Delta_{\text{(between vs. within)}}$ no. of helper males	0.11 \pm 0.22	1	0.22	0.64
$\Delta_{\text{(between vs. within)}}$ no. of helper females	0.074 \pm 0.24	1	0.09	0.76

Reference categories are as follows: *2008; [†]brood size 1.

comparable rates in the red-winged fairy-wren. However, social environment plays an important role in provisioning behaviour: all individuals show load-lightening in the presence of male helpers, but provide additive care in the presence of female helpers. As a consequence, nestlings gain more food with increasing number of female helpers and grow larger. Provisioning was not associated with the number of offspring, probably because productivity is strongly determined by high rates of predation. However, increased nestling growth did convey a fitness advantage due to a higher post-fledging survival to adulthood.

ROLE OF SOCIAL ENVIRONMENT: INCREASED COMPETITION OR ARE FEMALES UNRELIABLE HELPERS?

Male helpers are more likely to inherit the territory and therefore benefit from active group augmentation (Kokko,

Johnstone & Clutton-Brock 2001), but such differences in fitness benefits of helping were not reflected by differences in provisioning rates between male and female helpers. However, active group augmentation is only expected to be beneficial when the newly recruited helpers improve survival or reproductive success of the group, for which we did not find much evidence, although the influence of helpers on adult survival requires future investigation. On the other hand, living in larger groups can also increase competition (e.g. for food) and thereby reduce survival (Brouwer *et al.* 2006). Intragroup competition is expected to be stronger in the presence of several male helpers, who are more likely to stay in their natal territory than female helpers. Thus, if competition is important, the average value of young decreases more with the number of male helpers than with the number of female helpers, favouring load-lightening to a greater extent in the presence of male helpers. However, if this explanation is true,

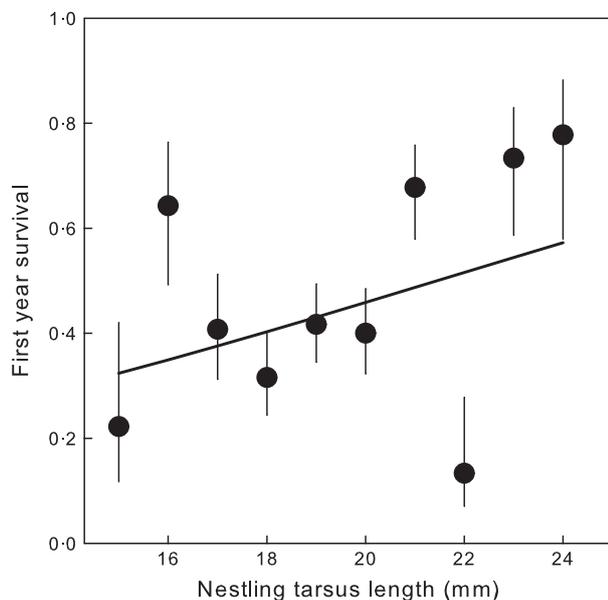


Fig. 4. Average post-fledging first-year survival of red-winged fairy-wrens in relation to their tarsus length as nestling. Line shows the prediction according to the model in Table 3; error bars show SEM.

Table 3. Results from a GLMM examining offspring survival in the first year after fledging ($n = 246$)

Parameter	Estimate \pm SE	d.f.	χ^2	P
Final model				
Intercept	-0.22 ± 0.18	1		
Residual tarsus length	0.16 ± 0.08	1	3.8	0.052
Random effects				
$\sigma^2_{\text{territory}}$	0.80			
Rejected terms				
Brood size*		2	2.7	0.26
$\beta_{\text{brood size 2}}$	-0.16 ± 0.67			
$\beta_{\text{brood size 3}}$	-0.68 ± 0.68			
Cohort [†]		2	1.2	0.56
β_{2009}	0.43 ± 0.39			
β_{2010}	0.12 ± 0.34			
Residual mass	-0.28 ± 0.26	1	1.0	0.31

Residual tarsus is calculated by taking the residuals from a linear regression of age and observer on tarsus length. Residual mass is calculated by taking the residuals from a linear regression of age on mass. Reference categories are: [†]2008, *brood size 1.

it remains unclear why care is additive in the presence of multiple females.

Results from a comparative analysis suggest that care is often compensatory when nestling starvation is rare and that care is usually additive when starvation is frequent (Hatchwell 1999). Nestling starvation in red-winged fairy-wrens is rare, yet in the presence of female helpers, care was additive. Another possibility is that female help may be more unreliable than males, and hence, it may be more risky to make investment decisions predicated on their presence. Although there was no evidence that female helpers fed different prey types or provisioned with a

greater variance (females: $\sigma^2 = 0.03 \pm 0.18$ SD; males: $\sigma^2 = 0.04 \pm 0.19$ SD), subordinate females disperse on average earlier than males and are therefore more likely to leave during any reproductive bout. Indeed, 11% ($n = 16$) of the female and only 3% ($n = 8$) of the male subordinates were observed to disperse during the breeding season. Females can also initiate their own nest (11% of subordinate females) and breed plurally (Brouwer *et al.* 2011), in which case their contribution to provisioning the nest of the dominant female could either be non-existent or end abruptly. One could expect compensation after a group member stops provisioning, but anecdotal evidence shows that this might not happen. Two nests where the dominant male died during the provisioning stage were among the extremely few cases where the nestlings starved to death. In the superb fairy-wren (*M. cyaneus*), which lacks female helpers, the breeding female is extremely sensitive to experimental perturbations of group size just before the fertile period and abandons the reproductive bout if helpers are removed (Dunn & Cockburn 1996). This sensitivity may be because males are cautious feeders, as infidelity reduces their relatedness to the brood for which they care. If female help in red-winged fairy-wrens is intrinsically unreliable, it may be better to make investment decisions without presuming that female help will be available, so the additional benefit becomes a bonus rather than a part of the decision-making that affects the investment by the other birds in the group. This in turn might help us understand the greatly improved productivity in response to female and not male help in the splendid fairy-wren (*M. splendens*, Brooker & Rowley 1995), in which females can be philopatric and plural breeding is moderately common, but where the frequency of both female help and plural breeding varies strongly with respect to ecological circumstances (Rowley *et al.* 1989).

An alternative explanation for our results is that an unobserved variable, such as territory quality, affects both the group composition and provisioning rates. A decline in territory quality could result in reduced provisioning rates of all group members and also make it more likely for females to disperse (or die). In this scenario, the observed within-territory association between the number of female helpers and parental care does not reflect a causal relationship, but is caused by unobserved changes in territory quality. However, this explanation is unlikely for various reasons. First, it can only explain our results when territories strongly vary among each other in their quality between years, because we have shown that the absence of load-lightening in the presence of female helpers was not the result of consistent differences between territories. Secondly, an analysis restricted to groups with at least one female helper and one male helper gave qualitatively similar results, suggesting that our findings are not the result of any unaccounted differences between groups with only male vs. groups with only female helpers. Thirdly, this alternative explanation requires only females, but not male helpers to disperse (or die) when conditions deteriorate.

Table 4. Variation in helping effort with respect to sex of the helper or dominant

	Fairy-wrens (<i>Malurus</i>)	Other bird species	Other vertebrates
Helping effort differs by sex			
♀♀ predominantly philopatric	–	White-throated magpie-jay ¹	–
♂♂ predominantly philopatric	Superb ² , red-backed fairy-wren ³	White-browed scrubwren ⁴ , pied kingfisher ⁵ , western bluebird ⁶ , red-cockaded woodpecker ⁷	–
♀♀ provide more care	–	Brown jay ⁸	Meerkat ⁹ , brown hyena ¹⁰ , African lion ¹¹ , daffodil cichlid ¹²
♂♂ provide more care	Purple-crowned fairy-wren ^{13,14}	Apostlebird ¹⁵ , carrion crow ¹⁶ , laughing kookaburra ¹⁷ , galapagos mocking bird ¹⁸	Banded mongoose ¹⁹ , alpine marmot ²⁰
Helper's compensatory response differs by own sex			
♀♀ load-lighten exclusively or more than ♂♂	–	Apostlebird ¹⁵	Cotton-top tamarin ²¹
♂♂ load-lighten exclusively or more than ♀♀	–	–	–
Dominant's compensatory response differs by own sex			
♀♀ load-lighten exclusively or more than ♂♂	Splendid fairy-wren ²²	Chestnut-crowned babbler ²³ , hoatzin ²⁴	Cotton-top tamarin ²¹
♂♂ load-lighten exclusively or more than ♀♀	–	White-banded tanager ²⁵ , long-tailed tit ²⁶ , European bee-eater ²⁷	–
♀♀ gain survival advantage, ♂♂ do not	Superb ^{28,29} , splendid fairy-wren ³⁰	–	–
♂♂ gain survival advantage, ♀♀ do not	–	Long-tailed tit ²⁶ , acorn woodpecker ³¹	–
Dominant's fecundity response differs by sex of helpers			
Fecundity increases with no. of ♀♀, but not ♂♂ helpers	Splendid fairy-wren ³²	–	–
Fecundity increases with no. of ♂♂, but not ♀♀ helpers	–	Grey-crowned babbler ³³ , acorn woodpecker ³¹	Daffodil cichlid ³⁴
Fecundity decreases with no. of ♀♀, but not ♂♂ helpers	–	Laughing kookaburra ³⁵	–
Fecundity decreases with no. of ♂♂, but not ♀♀ helpers	–	–	–
Dominant's and helper's response differs by sex of helpers			
Load-lighten to ♂♂, additive response to ♀♀	Red-winged fairy-wren ^{this study}	–	–
No sex differences in effort or compensatory response			
–	–	Bell miner ³⁶ , Florida scrub-jay ³⁷ , Arabian babbler ³⁸ , white-fronted bee-eater ^{39,40} , stripe-backed wren ⁴¹ , Seychelles warbler ^{42,43} , pied babbler ⁴⁴	Dwarf mongoose ⁴⁵ , Damaraland mole-rat ⁴⁶

¹Berg *et al.* (2009), ²Cockburn *et al.* (2008a), ³Varian-Ramos *et al.* (2010), ⁴Magrath & Yezerinac (1997), ⁵Reyer (1980), ⁶Dickinson, Koenig & Pitelka (1996), ⁷Walters, Doerr & Carter (1988), ⁸Williams & Hale (2007), ⁹Clutton-Brock *et al.* (2002), ¹⁰Owens & Owens (1984), ¹¹Packer, Scheel & Pusey (1990), ¹²Stiver *et al.* (2005), ¹³Kingma, Hall & Peters (2011), ¹⁴Margraf & Cockburn (2013), ¹⁵Woxvold, Mulder & Magrath (2006), ¹⁶Canestrari, Marcos & Baglione (2005), ¹⁷Legge (2000b), ¹⁸Curry & Grant (1989), ¹⁹Hodge (2007), ²⁰Allain *et al.* (2000), ²¹Sánchez *et al.* (1999), ²²Rowley (1981), ²³Browning *et al.* (2012), ²⁴Vanderwerf & Strahl (1990), ²⁵Manica & Marini (2012), ²⁶Meade *et al.* (2010), ²⁷Lessells (1990), ²⁸Russell *et al.* (2007), ²⁹Cockburn *et al.* (2008b), ³⁰Russell & Rowley (1988), ³¹Koenig, Walters & Haydock (2011), ³²Brooker & Rowley (1995), ³³Blackmore & Heinsohn (2007), ³⁴Heg (2006), ³⁵Legge (2000a), ³⁶Wright *et al.* (2010), ³⁷Woolfenden & Fitzpatrick (1984), ³⁸Wright (1997), ³⁹Emlen & Wrege (1988), ⁴⁰Emlen & Wrege (1991), ⁴¹Rabenold (1985), ⁴²Eikenaar *et al.* (2010), ⁴³Dugdale *et al.* (2010), ⁴⁴Ridley, A. R. (pers. comm.), ⁴⁵Rood (1990), ⁴⁶Gaylard, Harrison & Bennett (1998).

ROLE OF SOCIAL STATUS

Dominant red-winged fairy-wrens provisioned at a higher rate than helpers, suggesting that dominants gain more benefits from raising offspring than helpers or that the costs of parental care are higher for helpers. This cannot be explained by relatedness since the high levels of EPP

(Brouwer *et al.* 2011) mean that helpers are on average less related to the offspring than the dominant female, but not the dominant male. Helpers could also invest less in parental care since they spent time on other behaviours such as searching for breeding vacancies (Young, Carlson & Clutton-Brock 2005) or displaying to extra-group females to gain extra-pair matings, although dominant

males might be even more likely to be involved in display behaviour (Green *et al.* 1995).

Variation in parental investment is expected to result in variation in compensation. Johnstone (2011) predicted that if costs of parental care increases steeply, and thereby causes individuals to provide less care, they should also become less responsive to helper effort (i.e. show little compensation). This implies that in red-winged fairy-wrens where helpers invest less than breeders, they should also show less compensation than breeders. Indeed, in the presence of female helpers, the compensation was less strong for helpers than for breeders, although only slightly, and there was no difference in the presence of male helpers. Several other studies have shown that helpers invest less and show less compensation than breeders (Hatchwell & Russell 1996; Gilchrist & Russell 2007), although helpers are also expected to show less compensation if a large reproductive skew means that they gain less from saving resources for future reproduction (Gilchrist & Russell 2007). Furthermore, patterns in the opposite direction, with helpers compensating more than breeders, have also been shown (Legge 2000b), and even an absence of a difference in compensation despite differential investment (Koenig & Walters 2011).

MALE AND FEMALE PHILOPATRY IN FAIRY-WRENS

Possibly, our results can explain why female red-winged fairy-wrens are allowed to stay in their natal territory, even though that increases the risk of incestuous mating. All fairy-wrens (*Malurus genus*) are cooperative breeders with extreme levels of male philopatry, the highest known from year-round territorial birds (Cockburn *et al.* 2008a). By contrast, female helpers are rare or absent in most fairy-wrens, except for the red-winged fairy-wren (Rowley & Russell 1997; Cockburn *et al.* 2008a). Here we have shown that offspring fitness increases as a result of the presence of female helpers. Possibly, these fitness benefits outweigh any costs associated with the presence of female helpers, which together with any environmental conditions allowing for larger group sizes, might be why females are allowed to stay in their natal territory in this species.

SEX DIFFERENCES IN PARENTAL CARE IN COOPERATIVE BREEDERS

Previous studies of cooperatively breeding species have revealed considerable variation in the way that males and females provide care as helpers and receive care as dominants (Table 4). One sex can be more likely to help because of differences in philopatry, but when both sexes are present, investment can also vary with gender. The response by male and female dominants to the presence of helpers also shows strong variation, with in some species the dominant male and in others the female showing load-lightening. Unsurprisingly then, survival advantages in the presence of helpers might be

largely monopolized by just one sex, though sometimes in complex ways (Russell *et al.* 2007). More unusually, in some cases, immediate fecundity responds more to the presence of one sex, with both increased and decreased productivity being reported. In the splendid fairy-wren (*M. splendens*), where fecundity increased with more female helpers, the underlying mechanism remained obscure (Brooker & Rowley 1995), while in the laughing kookaburra (*Dacelo novaeguineae*), Legge (2000a) interpreted the reduced fecundity as failure of other group members to compensate adequately for the indifferent effort from females.

General patterns regarding sex differences between birds and mammals are not obvious; other than that in mammals, it is the dominant female (who invests most) that is expected to benefit most from help. In contrast to birds, in both mammals and fish, there is often a strong division of labour. In mammals, only females can help with lactation, and in fish, there are often large differences in helper size. This division of labour might explain why in the daffodil cichlid (*Neolamprologus pulcher*), only the presence of large males results in higher fecundity despite female subordinates having higher helping rates (Stiver *et al.* 2005; Heg 2006). Here we add further to the existing complexity by reporting a novel form of response to help in the red-winged fairy-wren. Possibly, focusing on the social environment of individuals might improve our knowledge of the enormous variation in helping behaviour. However, our study also illustrates that even though social environmental effects can explain much of the variation in parental investment, they can take quite unexpected forms that require adaptive explanations.

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References

- Allain, D., Brondex, F., Graziani, L., Coulon, J. & Till-Bottraud, I. (2000) Male-biased sex ratio in litter of alpine marmots support the helper repayment hypothesis. *Behavioural Ecology*, **11**, 507–514.
- 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., Maechler, M. & Bolker, B. (2011) lme4: Linear mixed-effects models using Eigen and S4 classes.
- Berg, E.C., Eadie, J.M., Langen, T.A. & Russell, A.F. (2009) Reverse sex-biased philopatry in a cooperative bird: genetic consequences and a social cause. *Molecular Ecology*, **18**, 3486–3499.

- Blackmore, C.J. & Heinsohn, R. (2007) Reproductive success and helper effects in the cooperatively breeding grey-crowned babbler. *Journal of Zoology*, **273**, 326–332.
- Brooker, M. & Rowley, I. (1995) The significance of territory size and quality in the mating strategy of the splendid fairy-wren. *Journal of Animal Ecology*, **64**, 614–627.
- Brouwer, L., Richardson, D.S., Eikenaar, C. & Komdeur, J. (2006) The role of group size and environmental factors on survival in a cooperatively breeding tropical passerine. *Journal of Animal Ecology*, **75**, 1321–1329.
- 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*, **20**, 4796–4807.
- Brown, J.L., Dow, D.D., Brown, E.R. & Brown, S.D. (1978) Effects of helpers on feeding of nestlings in the grey-crowned babbler (*Pomatostomus temporalis*). *Behavioral Ecology and Sociobiology*, **4**, 43–59.
- Browning, L.E., Young, C.M., Savage, J.L., Russell, D.J.F., Barclay, H., Griffith, S.C. et al. (2012) Carer provisioning rules in an obligate cooperative breeder: prey type, size and delivery rate. *Behavioral Ecology and Sociobiology*, **66**, 1639–1649.
- Burley, N. (1988) The differential-allocation hypothesis: an experimental test. *The American Naturalist*, **132**, 611.
- Canestrari, D., Marcos, J. & Baglione, V. (2005) Effect of parentage and relatedness on the individual contribution to cooperative chick care in carrion crows *Corvus corone corone*. *Behavioral Ecology and Sociobiology*, **57**, 422–428.
- Canestrari, D., Chiarati, E., Marcos, J.M., Ekman, J. & Baglione, V. (2008) Helpers but not breeders adjust provisioning effort to year-round territory resource availability in carrion crows. *Animal Behaviour*, **76**, 943–949.
- Clutton-Brock, T., Russell, A.F., Sharpe, L.L., Brotherton, P.N.M., McIlrath, G.M., White, S. et al. (2001) Effects of helpers on juvenile development and survival in meerkats. *Science*, **293**, 2446–2449.
- 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**, 253–256.
- Clutton-Brock, T.H., Hodge, S.J., Spong, G., Russell, A.F., Jordan, N.R., Bennett, N.C. et al. (2006) Intrasexual competition and sexual selection in cooperative mammals. *Nature*, **444**, 1065–1068.
- Cockburn, A. (1998) Evolution of helping behavior in cooperatively breeding birds. *Annual Review of Ecology and Systematics*, **29**, 141–177.
- Cockburn, A. (2004) Mating systems and sexual conflict. *Ecology and Evolution of Cooperative Breeding in Birds* (ed. W. D. Koenig & J. L. Dickinson), pp. 81–101. Cambridge University Press, Cambridge, UK.
- Cockburn, A., Osmond, H.L., Mulder, R.A., Double, M.C. & Green, D.J. (2008a) Demography of male reproductive queues in cooperatively breeding superb fairy-wrens *Malurus cyaneus*. *Journal of Animal Ecology*, **77**, 297–304.
- Cockburn, A., Sims, R.A., Osmond, H.L., Green, D.J., Double, M.C. & Mulder, R.A. (2008b) Can we measure the benefits of help in cooperatively breeding birds: the case of superb fairy-wrens *Malurus cyaneus*? *Journal of Animal Ecology*, **77**, 430–438.
- Curry, R.L. & Grant, P.R. (1989) Demography of the cooperatively breeding Galapagos Mockingbird, *Nesomimus parvulus*, in a climatically variable environment. *Journal of Animal Ecology*, **58**, 441–463.
- Dickinson, J.L., Koenig, W.D. & Pitelka, F.A. (1996) Fitness consequences of helping behavior in the western bluebird. *Behavioral Ecology*, **7**, 168–177.
- Doerr, E.D. & Doerr, V.A.J. (2007) Positive effects of helpers on reproductive success in the brown treecreeper and the general importance of future benefits. *Journal of Animal Ecology*, **76**, 966–976.
- Drent, R.H. & Daan, S. (1980) The prudent parent: energetic adjustments in avian breeding. *Ardea*, **68**, 225–252.
- Dugdale, H., Richardson, D.S., Komdeur, J. & Burke, T. (2010) *Fitness Consequences of Helping in the Cooperatively Breeding Seychelles Warbler*. CEES report, University of Groningen, Groningen, the Netherlands.
- Dunn, P.O. & Cockburn, A. (1996) Evolution of male parental care in a bird with almost complete cuckoldry. *Evolution*, **50**, 2542–2548.
- Eikenaar, C., Brouwer, L., Komdeur, J. & Richardson, D.S. (2010) Sex biased natal dispersal is not a fixed trait in a stable population of Seychelles warblers. *Behaviour*, **147**, 1577–1590.
- Emlen, S.T. & Wrege, P.H. (1988) The role of kinship in helping decisions among White-fronted Bee-eaters. *Behavioral Ecology and Sociobiology*, **23**, 305–315.
- Emlen, S.T. & Wrege, P.H. (1991) Breeding biology of White-fronted Bee-eaters at Nakuru: the influence of helpers on breeder fitness. *Journal of Animal Ecology*, **60**, 309–326.
- Gaylard, A., Harrison, Y. & Bennett, N.C. (1998) Temporal changes in the social structure of a captive colony of the Damaraland mole-rat, *Cryptomys damarensis*: the relationship of sex and age to dominance and burrow-maintenance activity. *Journal of Zoology*, **244**, 313–321.
- Gilchrist, J.S. & Russell, A.F. (2007) Who cares? Individual contributions to pup care by breeders vs non-breeders in the cooperatively breeding banded mongoose (*Mungos mungo*). *Behavioral Ecology and Sociobiology*, **61**, 1053–1060.
- Green, D.J., Cockburn, A., Hall, M.L., Osmond, H.L. & Dunn, P.O. (1995) Increased opportunities for cuckoldry may be why dominant male fairy-wrens tolerate helpers. *Proceedings of the Royal Society B: Biological Sciences*, **262**, 297–303.
- Hatchwell, B.J. (1999) Investment strategies of breeders in avian cooperative breeding systems. *The American Naturalist*, **154**, 205–219.
- 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, Series B: Biological Sciences*, **263**, 83–88.
- Heg, D. (2006) Cichlids do not adjust reproductive skew to the availability of independent breeding options. *Behavioral Ecology*, **17**, 419–429.
- Heinsohn, R.G. (1992) Cooperative enhancement of reproductive success in white-winged choughs. *Evolutionary Ecology*, **6**, 97–114.
- Heinsohn, R.G. (2004) Parental care, load-lightening, and costs. *Ecology and Evolution of Cooperative Breeding in Birds* (ed. W. D. Koenig & J. L. Dickinson), pp. 67–80. Cambridge University Press, Cambridge, UK.
- Hodge, S.J. (2007) Counting the costs: the evolution of male-biased care in the cooperatively breeding banded mongoose. *Animal Behaviour*, **74**, 911–919.
- Houston, A.I. & Davies, N.B. (1985) The evolution of cooperation and life history in the dunnoek. *Prunella Modularis. Behavioural Ecology* (eds R. Sibly & R.H. Smith), pp. 471–487. Blackwell Scientific Publications, Oxford, UK.
- Johnstone, R.A. (2011) Load lightening and negotiation over offspring care in cooperative breeders. *Behavioral Ecology*, **22**, 436–444.
- Johnstone, R.A. & Hinde, C.A. (2006) Negotiation over offspring care—how should parents respond to each other's efforts? *Behavioral Ecology*, **17**, 818–827.
- Kingma, S.A., Hall, M.L. & Peters, A. (2011) Multiple benefits drive helping behavior in a cooperatively breeding bird: an integrated analysis. *The American Naturalist*, **177**, 486–495.
- Kingma, S.A., Hall, M.L., Arriero, E. & Peters, A. (2010) Multiple benefits of cooperative breeding in purple-crowned fairy-wrens: a consequence of fidelity? *Journal of Animal Ecology*, **79**, 757–768.
- Koenig, W.D. & Walters, E.L. (2011) Brooding, provisioning, and compensatory care in the cooperatively breeding acorn woodpecker. *Behavioral Ecology*, **23**, 181–190.
- Koenig, W.D., Walters, E.L. & Haydock, J. (2011) Variable helper effects, ecological conditions, and the evolution of cooperative breeding in the acorn woodpecker. *The American Naturalist*, **178**, 145–158.
- Kokko, H., Johnstone, R.A. & Clutton-Brock, T. (2001) The evolution of cooperative breeding through group augmentation. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **268**, 187–196.
- Legge, S. (2000a) The effect of helpers on reproductive success in the laughing kookaburra. *Journal of Animal Ecology*, **69**, 714–724.
- Legge, S. (2000b) Helper contributions in the cooperatively breeding laughing kookaburra: feeding young is no laughing matter. *Animal Behaviour*, **59**, 1009–1018.
- Lessells, C.M. (1990) Helping at the nest in European bee-eaters: who helps and why? *Population Biology of Passerine Birds. An Integrated Approach Series G: Ecological Sciences 24* (eds J. Blondel, A. Gosler, J.D. Lebreton & R. MacCleery), pp. 357–368. Springer, Berlin.
- Limbourg, T., Mateman, A.C., Andersson, S. & Lessells, C.M. (2004) Female blue tits adjust parental effort to manipulated male UV attractiveness. *Proceedings of the Royal Society B: Biological Sciences*, **271**, 1903–1908.
- MacColl, A.D.C. & Hatchwell, B.J. (2003) Sharing of caring: nestling provisioning behaviour of long-tailed tit, *Aegithalos caudatus*, parents and helpers. *Animal Behaviour*, **66**, 955–964.
- Magrath, R.D. & Yezerinac, S.M. (1997) Facultative helping does not influence reproductive success or survival in cooperatively breeding white-browed scrubwrens. *Journal of Animal Ecology*, **66**, 670.

- Manica, L.T. & Marini, M.Â. (2012) Helpers at the nest of white-banded tanager *Neothraupis fasciata* benefit male breeders but do not increase reproductive success. *Journal of Ornithology*, **153**, 149–159.
- Margraf, N. & Cockburn, A. (2013) Helping behaviour and parental care in fairy-wrens (*Malurus*). *Emu*, **113**, 294–301.
- Mazuc, J. (2003) No evidence for differential maternal allocation to offspring in the house sparrow (*Passer domesticus*). *Behavioral Ecology*, **14**, 340–346.
- McNamara, J.M. & Houston, A.I. (1996) State-dependent life histories. *Nature*, **380**, 215–221.
- Meade, J., Nam, K.-B., Beckerman, A.P. & Hatchwell, B.J. (2010) Consequences of “load-lightening” for future indirect fitness gains by helpers in a cooperatively breeding bird. *Journal of Animal Ecology*, **79**, 529–537.
- Owens, D.D. & Owens, M.J. (1984) Helping behaviour in brown hyenas. *Nature*, **308**, 843–845.
- Packer, C., Scheel, D. & Pusey, A.E. (1990) Why lions form groups: food is not enough. *The American Naturalist*, **136**, 1–19.
- Pilastro, A., Griggio, M. & Matessi, G. (2003) Male rock sparrows adjust their breeding strategy according to female ornamentation: parental or mating investment? *Animal Behaviour*, **66**, 265–271.
- van de Pol, M. & Wright, J. (2009) A simple method for distinguishing within- versus between-subject effects using mixed models. *Animal Behaviour*, **77**, 753–758.
- Pryke, S.R. & Griffith, S.C. (2009) Maternal adjustment of parental effort in relation to mate compatibility affects offspring development. *Behavioral Ecology*, **21**, 226–232.
- R Development Core Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rabenold, K.N. (1985) Cooperation in breeding by nonreproductive wrens: kinship, reciprocity and demography. *Behavioral Ecology and Sociobiology*, **17**, 1–17.
- Reyer, H.U. (1980) Flexible helper structure as an ecological adaptation in the Pied Kingfisher (*Ceryle rudis rudis* L.). *Behavioral Ecology and Sociobiology*, **6**, 219–227.
- 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.
- Reyer, H.U. & Westerterp, K. (1985) Parental energy expenditure: a proximate cause of helper recruitment in the Pied Kingfisher (*Ceryle rudis*). *Behavioral Ecology and Sociobiology*, **17**, 363–369.
- Rood, J.P. (1990) Group size, survival, reproduction, and routes to breeding in dwarf mongooses. *Animal Behaviour*, **39**, 566–572.
- Rowley, I. (1981) The communal way of life in the splendid fairy wren, *Malurus splendens*. *Zeitschrift für Tierpsychologie*, **55**, 228–267.
- Rowley, I. & Russell, E. (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 *Malurus elegans*. *Emu*, **88**, 161.
- Rowley, I., Russell, E.M., Payne, R.B. & Payne, L.L. (1989) Plural breeding in the Splendid Fairy-wren, *Malurus splendens* (Aves: *Maluridae*), a cooperative breeder. *Ethology*, **83**, 229–247.
- Russell, E. & Rowley, I. (1988) Helper contributions to reproductive success in the splendid fairy-wren (*Malurus splendens*). *Behavioral Ecology and Sociobiology*, **22**, 131–140.
- Russell, E. & Rowley, I. (2000) Demography and social organisation of the red-winged fairy-wren, *Malurus elegans*. *Australian Journal of Zoology*, **48**, 161–200.
- 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.
- Rutstein, A.N. (2005) Experience counts: lessons from studies of differential allocation. *Behavioral Ecology*, **16**, 957–960.
- Sánchez, S., Peláez, F., Gil-Bürmann, C. & Kaumanns, W. (1999) Costs of infant-carrying in the cotton-top tamarin (*Saguinus oedipus*). *American Journal of Primatology*, **48**, 99–111.
- Sanz, J.J. (2001) Experimentally reduced male attractiveness increases parental care in the pied flycatcher *Ficedula hypoleuca*. *Behavioral Ecology*, **12**, 171–176.
- Sheldon, B.C. (2000) Differential allocation: tests, mechanisms and implications. *Trends in Ecology & Evolution*, **15**, 397–402.
- Stiver, K.A., Dierkes, P., Taborsky, M., Lisle Gibbs, H. & Balshine, S. (2005) Relatedness and helping in fish: examining the theoretical predictions. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 1593–1599.
- Vanderwerf, E.A. & Strahl, S.D. (1990) Effects of unit size and territory defense on communal nest care in the hoatzin (*Opisthocomus hoazin*). *The Auk*, **107**, 626–628.
- Varian-Ramos, C.W., Karubian, J., Talbott, V., Tapia, I. & Webster, M.S. (2010) Offspring sex ratios reflect lack of repayment by auxiliary males in a cooperatively breeding passerine. *Behavioral Ecology and Sociobiology*, **64**, 967–977.
- Walters, J.R., Doerr, P.D. & Carter, J.H. (1988) The cooperative breeding system of the red-cockaded woodpecker. *Ethology*, **78**, 275–305.
- Wiley, R.H. & Rabenold, K. (1984) The evolution of cooperative breeding by delayed reciprocity and queuing for favorable positions. *Evolution*, **38**, 609–621.
- Williams, G.C. (1966) Natural selection, the cost of reproduction, and a refinement of Lack’s principle. *American Naturalist*, **100**, 687–690.
- Williams, D.A. & Hale, A.M. (2007) Female-biased helping in a cooperatively breeding bird: female benefits or male costs? *Ethology*, **113**, 534–542.
- Woolfenden, G.E. & Fitzpatrick, J.W. (1984) *The Florida Scrub Jay: Demography of a Cooperative-Breeding Bird*. Princeton University Press, Princeton, NJ.
- Woxvold, I.A. & Magrath, M.J.L. (2005) Helping enhances multiple components of reproductive success in the cooperatively breeding apostlebird. *Journal of Animal Ecology*, **74**, 1039–1050.
- Woxvold, I.A., Mulder, R.A. & Magrath, M.J.L. (2006) Contributions to care vary with age, sex, breeding status and group size in the cooperatively breeding apostlebird. *Animal Behaviour*, **72**, 63–73.
- Wright, J. (1997) Helping-at-the-nest in Arabian babblers: signalling social status or sensible investment in chicks? *Animal Behaviour*, **54**, 1439–1448.
- 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.
- Wright, J. & Cuthill, I. (1989) Manipulation of sex differences in parental care. *Behavioral Ecology and Sociobiology*, **25**, 171–181.
- Wright, J. & Dingemans, N.J. (1999) Parents and helpers compensate for experimental changes in the provisioning effort of others in the Arabian babbler. *Animal Behaviour*, **58**, 345–350.
- Wright, J., McDonald, P.G., te Marvelde, L., Kazem, A.J.N. & Bishop, C.M. (2010) Helping effort increases with relatedness in bell miners, but “unrelated” helpers of both sexes still provide substantial care. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **277**, 437–445.
- Young, A.J., Carlson, A.A. & Clutton-Brock, T. (2005) Trade-offs between extraterritorial prospecting and helping in a cooperative mammal. *Animal Behaviour*, **70**, 829–837.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Proportion of different prey items fed to nestling red-winged fairy-wrens by dominant females, dominant males, helper females and helper males.

Fig. S2. The standardized average probability that a bird guards the nest in relation to the number of male helpers (● bottom x-axis) and female helpers (○ top x-axis).