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Male and female helper effects on maternal investment and adult survival in red-winged fairy-wrens

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Despite its importance for the evolution of cooperative breeding, it has proven difficult to determine whether helpers improve their recipients' fitness. Helpers affect fitness in multiple ways, both positive and negative, but their effects can also be concealed through reduced maternal investment. Furthermore, determining the direction of causation is difficult, as helper presence may indicate a productive territory, rather than high productivity indicating an effect of help. In cooperatively breeding red-winged fairy-wrens (*Malurus elegans*) groups reduce care when they have male helpers, but groups with female helpers do not, so nestlings receive more food. Thus our predictions vary with helper sex rather than helper number, and by studying within-group changes with regard to group composition we separate phenotypically plastic responses from among-group correlations. Females did not reduce egg size in response to an increasing number of female helpers. However, more male or female helpers allowed females to lay larger clutches and more female helpers reduced re-nesting intervals. There was mixed support for a benefit of load lightening: Helpers, but not breeders, gained survival benefits with increasing number of male helpers. However, helper survival decreased with the number of female helpers, suggesting that increased competition counterbalanced these male helper benefits. We also found consistent among-group differences, which would have erroneously been interpreted as helper effects had we not disentangled the within-group changes with regard to group composition. This study highlights the importance of assessing carers' benefits in relation to both group composition and size, and of investigating the within-individual plastic response of helper effects.

Key words: **cooperative breeding, egg size, *Malurus elegans*, maternal investment, survival.**

INTRODUCTION

Cooperative breeding is often considered paradoxical because some individuals assist others to rear offspring instead of breeding on their own (Brown 1987). Much focus has been on determining how helpers improve the fitness of their beneficiaries, because such a positive effect is necessary to explain cooperative breeding through kin selection (Emlen 1995) or group augmentation (Kokko et al. 2001). Breeders may compensate for the presence of helpers by reducing their investment (load lightening; e.g., Hatchwell and Russell 1996; Legge 2000; Balshine et al. 2001),

which can increase their subsequent survival (Russell and Rowley 1988; Cockburn et al. 2008; Paquet et al. 2015) or reduce intervals between reproductive attempts (Woxvold and Magrath 2005; Blackmore and Heinsohn 2007). In the absence of load lightening, or when compensation is incomplete, helpers will increase overall parental effort so that offspring receive greater total care (additive care; e.g., Clutton-Brock et al. 2001; Doerr and Doerr 2007), which can increase offspring growth (Hodge 2005) or productivity of the dominant breeders (Emlen and Wrege 1991; Kingma et al. 2010; Meade et al. 2010). Overall, there is thus ample potential for helpers to not only have short-term effects on current reproduction but also long-term effects on future reproduction (Brouwer et al. 2012).

Despite the potential for great benefits, helper effects on offspring growth and survival are often weak or absent (Griffin and West 2003;

Woxvold and Magrath 2005; Canestrari et al. 2008). To explain this paradox, it has been suggested that helper benefits can also be concealed by compensatory maternal investment (Russell et al. 2007). Females adjusting the size or quality of their eggs can save energy without necessarily reducing their reproductive success, because helper investment is likely to compensate for the "bad start" suffered by the offspring (Russell and Lummaa 2009). Females could reallocate energy from immediate reproduction to future survival or reproductive success, thus improving long-term fitness, and recent findings suggest that this phenomenon is widespread among cooperative breeders (Russell et al. 2007; Taborsky et al. 2007; Canestrari et al. 2011; Santos and Macedo 2011; Paquet et al. 2013; but see: Koenig et al. 2009).

Despite intense focus on the potential benefits of helpers for carers and offspring, there might also be costs associated with the presence of helpers, for example due to intraspecific competition for resources (Newton 1992). Such density dependence could cause individuals living in larger groups to survive worse than individuals in small groups (Brouwer et al. 2006). Theory has long recognized that living with kin can be costly (Hamilton 1964; Taylor 1992; West et al. 2001), but the possibility that costs imposed by helpers have important fitness consequences has been neglected empirically.

The costs and benefits of helper presence can vary with the sex or state of the helpers. For example, one sex may invest more in care than the other, if it is more likely for them to survive and inherit dominance status (Clutton-Brock et al. 2006). The amount of care an individual provides varies not only with the state of the individual itself but also depends on the investment of the other group members. Group composition (i.e., the type of individuals) can thus have important fitness consequences for each group member in addition to the effects of group size. This aspect has only recently be emphasized (Brouwer et al. 2014a, Adams et al. 2015), although some studies have shown that reproductive success is positively associated with only one sex of helpers (Brooker and Rowley 1995; Legge 2000; Koenig et al. 2011) and therefore suggest that the effect of helpers on fitness components should be estimated for each type (e.g., sex) of helper separately.

In this study, we investigate whether and how helpers benefit their group members in the cooperatively breeding red-winged fairy-wren (*Malurus elegans*), a species in which both males and females are highly philopatric and usually stay in their natal territory for at least 1 year to assist the dominant breeders (Rowley et al. 1988). More specifically we investigate 1) whether breeding females show load lightening via egg investment, 2) whether helpers allow females to re-nest more rapidly after nest failure, and (3) whether helpers affect the survival of breeders and of other helpers present in the group.

A difficulty with determining helper effects is that experimental manipulation of group size is complicated. This is not just because enlarging group size is usually impossible, but also because reducing group size might lead to undesirable side effects, like social disruption or abandonment of the current reproductive attempt by the dominant female (Cockburn 1998). Observational data have the disadvantage that it is difficult to determine causality of positive correlations between helper number and fitness components such as reproductive success. High-quality breeders or breeders living in high-quality territories might also produce high-quality offspring and be more likely to have helpers because of past reproductive success (Cockburn 1998). Two features of our study system help us to determine causation. First, in red-winged fairy-wrens, previous work has shown that all group members reduced their provisioning rates in response to an increasing number of male helpers (load lightening), while the total amount of food per nestling remained unchanged. However, an increase in the number of female helpers within the group did not reduce the *per capita* investment of the group members and led to a higher number of feeds received per nestling (additive care, Brouwer et al. 2014a). As a result, with an increasing number of female helpers, nestlings received more food, grew larger, and had a higher postfledging survival. In contrast, an increasing number of male helpers was not associated with offspring growth or survival. These findings mean that our predictions of helper effects vary with the sex of the helpers, while the alternative hypothesis of confounded intercorrelations between territory quality and group size predicts that results are independent of the sex of the helpers. Second, by studying the same individuals over multiple seasons with variable group composition, we are able to separate whether effects are due to a phenotypically plastic response due to a change in helper number within groups rather than noncausal correlations due to large groups being associated with high territory quality. Comparisons of the same group with and without helpers have been criticized as groups where helper numbers change might be a biased sample of the population (Dickinson and Hatchwell 2004), as changes in helper number are the result of high reproduction or low survival. However, here we do not only compare groups with and without helpers but rather analyze the change in number of helpers of each sex within the same group in addition to between-group differences.

Consequently, we predict that 1a) breeding females should decrease the size of their eggs in response to an increasing number of female but not male helpers, because any negative effects of egg size on offspring will be compensated for by the extra care received in the presence of female helpers (Figure 1a); 1b) an increase in male and female helpers should allow breeding females to lay larger clutches, because the increased total care allows more chicks to be provisioned (Figure 1b); 2) the time interval between nest failure and a replacement clutch should be smaller with more male helpers if the previous nest reached the nestling stage, because breeding females will have been able to reduce their provisioning rates in the presence of males (Figure 1a); 3a) survival of all adult members of the group should be higher with an increasing number of male, but not female, helpers due to load lightening at the nestling stage (Figure 1c); 3b) survival of female breeders should also be higher with an increasing number of female helpers, if breeding females decrease their egg size in the presence of female helpers as predicted under 1a (Figure 1e). It should be noted that the overall survival response to the number of helpers needs not be positive, as intra-group competition may outweigh any benefits of load lightening (i.e., we only predict that the association between the number of female helpers and survival is more negative (or less positive) than between the number of male helpers and survival) (Figure 1d,f).

METHODS

Data collection

Data were collected in Smithbrook Nature Reserve in Western Australia (116°10′E, 34°20′S) between 2008 and 2015 under ethics licence A2011/48 and A2014/21 from the Australian National University. The main study area comprises ~65 territories in which >99% of the adult birds were individually color-banded with permission from the Australian Bird and Bat Banding Scheme (authority: 2853). Those territories were checked at least fortnightly for group composition, survival, and breeding activity throughout the breeding season (October to January). Once nests were found, they were checked at least twice a week to collect data on egg-laying
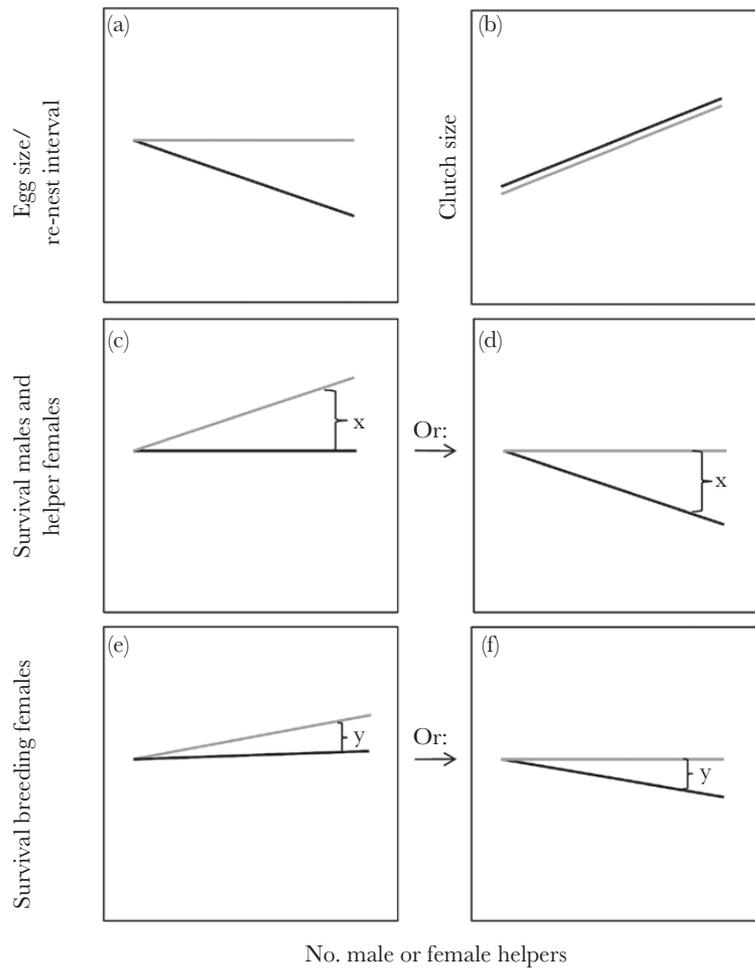
Figure 1
Predictions of the effects of male (gray line) and female (black line) helpers on (a) egg volume and re-nest interval, (b) clutch size, (c and d) survival of males and helper females, and (e and f) survival of breeding females. Note that we predict that $x > y$ if breeder females reduce their egg size and thus benefit from having female helpers too.

date, number of eggs, hatchlings and fledglings and in order to color-band all offspring. Female fairy-wrens re-nest after failure and can initiate as many as four clutches, but only in exceptional cases rear two broods to independence in a season (Russell and Rowley 2000). Starvation of nestlings is negligible, but nest predation is high (Brouwer et al. 2014a).

Eighty-eight percent of the border of the reserve is bounded by unsuitable habitat (farmland), but three narrow corridors lead away from the reserve allowing for dispersal to the surrounding state forests (Brouwer et al. 2014b). From 2009 onwards, each year 50–220 territories in the areas surrounding the main study area were monitored and checked for dispersers (up to 2-km radius). Long-distance dispersal is extremely rare (median distance = 150 m, mean territory width = 103 ± 27 SD, $N = 20$), and considering the spatial configuration of our main study area, this indicates that we can accurately estimate survival consequences for both males and females.

The sex of adult red-winged fairy-wrens can easily be determined using plumage characteristics (Rowley et al. 1988). Social status was determined from behavioral observations, plumage variation, and age (Russell and Rowley 2000; Brouwer et al. 2011), with each group comprising a "dominant" pair-bonded male and female and from zero to eight subordinate male and/or female helpers

(mean group size = 3.8 ± 1.3 SD, $N = 65$). Both males and females stay and help their parents for at least 1 year, but females disperse on average earlier than males (median age at dispersal females: 2 years, males: 3 years; Russell and Rowley 2000), which means that 32–42% of helpers were female each year. Nest watches have shown that both male and female helpers provision the young at a similar rate (Brouwer et al. 2014a). Occasionally an individual joins another group and does not provision (~1.5% of all birds, usually females); these birds were not considered helpers here.

During the seasons 2009–2013, length and width of eggs were measured using calipers with an accuracy of 0.01 mm. Egg size, quantified as the egg volume, was estimated as length × width² × 0.51 (Hoyt 1979). We estimated the interval between clutches after clutch failure (= date of check when nest was observed as failed) using the following method: when a nest was found during the laying phase the date the first egg was laid (= lay date) was estimated assuming that one egg is laid per day; when a nest was found during the incubation phase lay date was back-calculated once the eggs hatched to produce nestlings, assuming an incubation period of 15 days with incubation starting when the last egg was laid (Rowley et al. 1988); when a nest was found incubating but was depredated before nestlings were observed, we estimated the average lay date from the earliest and latest possible lay date, taking the number of

days the nest had been incubated, clutch size, and the incubation period into account.

Statistical analyses

We investigated helper effects on the four response variables: egg volume, clutch size, re-nest interval after nest failure, and annual adult survival probability. For the egg volume, clutch size, and re-nest interval analyses, we used general(ized) linear mixed models (GLMMs), in which a breeder female's identity was fitted as a random effect (intercept) to account for nonindependence of the data, as we collected data on the same birds over different years. In the survival analysis, we included the territory identifier as a random intercept, as the survival of birds from the same territory might not be independent.

Repeated observations of the same breeder female or territory with varying group size and composition allow us to disentangle within- (i.e., plastic behavioral response to changing number of helpers) from between-subject effects of group composition, using a widely used mixed modeling technique called within-subject centering (van de Pol and Wright 2009). In short, this method splits up the effect of helper numbers into two helper number predictor variables: the within-subject centered (within-subject effect) and mean number (between-subject effect) of female and male helpers. In the analyses of egg volume, clutch size, and re-nest interval, the number of (fe)male helpers is centered around the mean number of (fe)male helpers a dominant female had during the study period, whereas for the survival analysis it is centered around the mean per territory. In all analyses, the centered and mean effects were included as continuous covariates.

We analyzed the effects of helpers on the survival of all group members (males, females, breeders, and helpers) in a single model and hence the sex and social status (breeder/helper) of the birds and their interactions were included as fixed categorical covariates in this analysis. To test whether the effect of the number of male and female helpers differed from each other, we did a post-hoc test: The number of male and female helpers were substituted for group size, after which the Akaike Information Criteria (AIC) values of both of these nonnested models were compared (Akaike 1973; Burnham and Anderson 2003). Annual adult survival was estimated for all 671 individuals in the main study area between November 2008 and November 2015. A preliminary capture-mark-recapture survival analysis in program MARK (White and Burnham 1999) showed that for individuals in the main study area, the detection probability is 100% (i.e., there were no individuals that were not seen in 1 year that were observed in later years). Consequently, for final analysis we switched to known fate analysis in which survival to the next year was fitted as a binary variable using a logit link function and binomial error.

Mean egg volume and clutch size were fitted using a multivariate mixed model to account for covariance between egg and clutch size, because a trade-off between egg and clutch size is common in birds (Williams 2001). Clutch and egg size data were available for 292 clutches from 108 females. Because there is limited variation in clutch size (98% were 2 or 3 egg clutches), clutch size was transformed into a binary variable, with small clutches (1–2 eggs) being coded as 0 and large clutches (3 eggs) coded as 1. Clutch size was fitted using a logit link function and binomial error distribution, whereas egg volume was fitted using an identity link function and Gaussian error distribution. The re-nest interval was determined for 267 replacement clutches, in 119 females, and calculated as the number of days it took for a new nest to be initiated and clutch to be laid after nest failure, and fitted using an identity link function and Gaussian error distribution.
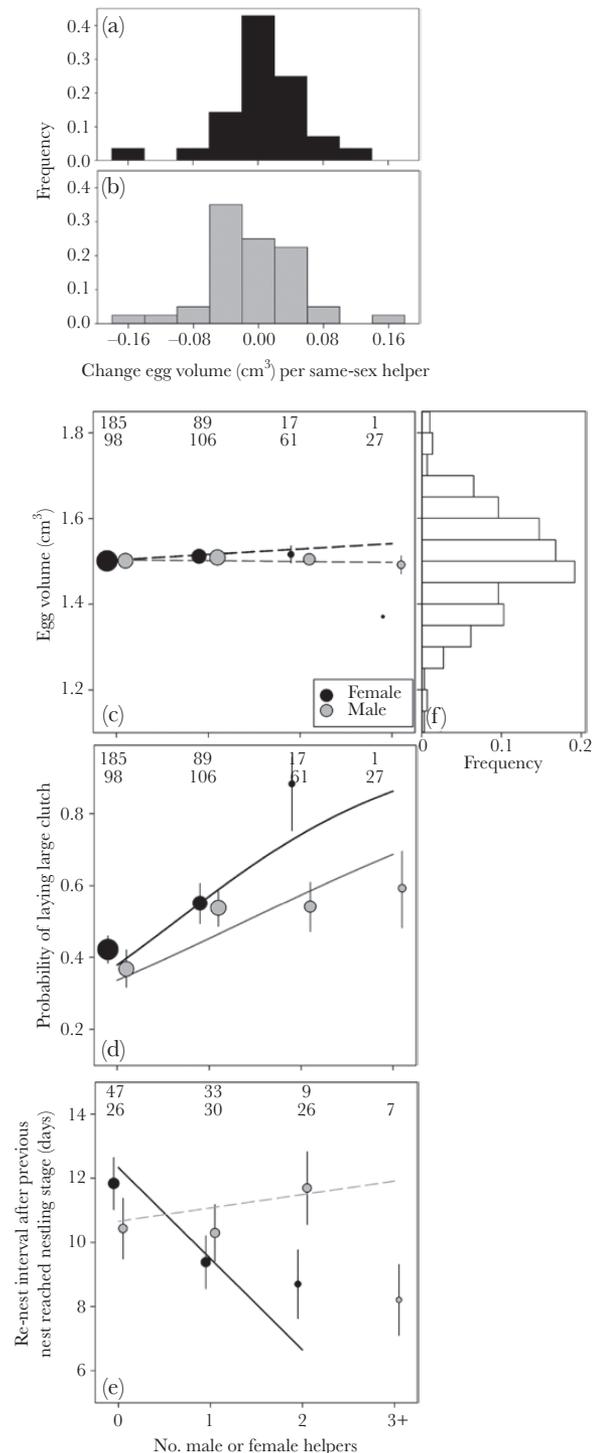
Figure 2.
The distribution of the within-female change in egg volume shown for a change in the number of (a) female and (b) male helpers. The relation between the number of female (black) and male (gray) helpers for (c) egg volume, (d) clutch size, and (e) the re-nest interval after nest failure for groups where the previous nest reached the nestling stage corrected for effects of year and helpers of the other sex. Also shown is (f) the observed distribution of egg volumes. Numbers indicate the sample sizes for the number of female (upper) and male (lower) helpers with symbol sizes adjusted accordingly. Lines show the predictions of the within-subject effects of the models from Table 1 (Figure 1c,d) and Table 2 (Figure 1e). Error bars are the SEM.

Several additional variables were included in some or all the models to account for their separate confounding effect on the fitness-related traits, or to investigate whether they modified the effect of the number of helpers by including their interaction terms. Specifically, year and prior breeding experience of the breeder female (coded yes/no) were included as fixed categorical variables in the analyses on egg volume, clutch size, and re-nest interval. Whether the previous nest reached the nestling phase (coded yes/no) was included as a fixed factor in the re-nest interval analysis. Egg and clutch size typically show seasonal trends in birds (Crick et al. 1993). Therefore, rainfall and day of season were also included in the egg and clutch size analysis. In order to determine the time periods during which mean daily rainfall significantly explained these traits, we used a sliding-window approach implemented in R package climwin (van de Pol and Cockburn 2011; Bailey and van de Pol 2015). We found that the critical time window for rainfall fell between 60 and 12 days before laying, and thus calculated the amount of rainfall over this period for each clutch. Because larger females may lay larger eggs, we included tarsus size of the breeding female. To correct for possible observer biases, the identity of the observer measuring the eggs was also included in the analysis.

Except for the multivariate analysis on egg volume and clutch size (see above), statistical analyses were performed in R3.1.2 (R Development Core Team 2016) using package lme4 (Bates et al. 2016). We used AIC, corrected for the sample size (AICc), to select the most parsimonious model. Models that are better supported by the data result in lower AICc values. We used an all-subset approach in which all possible models with the parameters of interest were run using package MuMIn (Bartoń 2015), but we report the eight top models within ΔAICc of two units of the best supported model only. The fact that the analysis of egg volume and clutch size was multivariate with two different link functions imposed a technical constraint that did not allow us to follow the same procedure as above. Hence, model selection was performed through stepwise backward elimination of nonsignificant fixed terms (α = 0.10) based on likelihood ratio tests in MLWin2.02 (Rasbash et al. 2005). All terms were added to the final model to confirm nonsignificance, and reported effect sizes are derived from final models.

RESULTS

Helper effects on maternal egg investment

In contrast to prediction 1a, there was no evidence that female breeders load lighten during the egg phase: They did not decrease their egg volume in response to a change in the number of female helpers (Figure 2a,c and Table 1), although groups with more female helpers tended to have smaller eggs (Table 1, mean no. ♀ helpers). As predicted, we found no evidence that female breeders decrease their egg volume with a changing number of male helpers (Figure 2b,c and Table 1). In line with prediction 1b, females laid larger clutches with an increasing number of helpers of both sexes (Figure 2d), and this was likely a plastic response (Table 1, within-subject effect no. helpers was significant). The effect of the number of helpers on clutch size and egg volume did not vary among years, with rainfall, or between inexperienced and experienced females (Table 1).

Helper effects on future prospects: re-nest interval and annual survival

In contrast to prediction 2, there was no evidence that re-nest intervals were shorter as the number of males that helped provisioning the preceding nest increased (Table 2, model 2 vs. model 1;

Table 1

Results of a multivariate GLMM examining egg volume and clutch size

Parameter	Egg volume (identity link)					Clutch size (logit link)				
	Estimate	SE	χ^2	df	P	Estimate	SE	χ^2	df	P
Fixed effects										
Intercept	**−0.305**	**0.494**	—	**1**	—	**2.122**	**0.494**	—	**1**	—
No. ♂ helpers	−0.041	0.059	0.50	1	0.48	**0.488**	**0.155**	**9.87**	**1**	**0.002**
Mean no. ♂ helpers	0.046	0.113	0.17	1	0.68	−0.167	0.331	0.26	1	0.61
No. ♀ helpers	0.046	0.067	0.43	1	0.51	**0.776**	**0.240**	**10.5**	**1**	**0.001**
Mean no. ♀ helpers	**−0.312**	**0.163**	**3.65**	**1**	0.056	0.238	0.471	0.25	1	0.62
Tarsus length of breeding ♀	0.159	0.128	1.55	1	0.21	−0.018	0.234	0.01	1	0.92
Day of season	**0.0045**	**0.0019**	**5.70**	**1**	**0.017**	**−0.047**	**0.007**	**41.0**	**1**	**<0.001**
Rainfall	**−0.126**	**0.058**	**4.83**	**1**	**0.028**	−0.145	0.279	0.27	1	0.60
Breeding experience dominant ♀	**0.205**	**0.100**	**4.19**	**1**	**0.041**	**0.694**	**0.383**	**3.29**	**1**	**0.070**
Year	—	—	9.11	4	0.58	—	—	4.36	4	0.36
No. ♂ helpers × rainfall	0.013	0.029	0.19	1	0.66	−0.024	0.135	0.03	1	0.86
No. ♀ helpers × rainfall	0.028	0.055	0.25	1	0.62	0.143	0.392	0.13	1	0.72
No. ♂ helpers × breeding experience ♀	0.067	0.075	0.80	1	0.37	0.008	0.199	0.01	1	0.92
No. ♀ helpers × breeding experience ♀	0.113	0.249	0.21	1	0.65	1.503	1.007	2.23	1	0.14
No. ♂ helpers × year	—	—	2.92	4	0.57	—	—	0.78	4	0.94
No. ♀ helpers × year	—	—	2.55	4	0.64	—	—	2.23	4	0.69
Observer	—	—	4.93	5	0.42	—	—	—	—	—
Random effects										
Variance among breeding ♀♀	**0.797**	**0.124**	—	**1**	—	**0.590**	**0.329**	—	**1**	—
Residual variance	**0.213**	**0.022**	—	**1**	—	—	—	—	—	—
Covariance breeding ♀ level	**−0.166**	**0.163**	—	**1**	—	**−0.166**	**0.163**	—	**1**	—
Correlation residual level	**−0.143**	**0.032**	—	**1**	—	**−0.143**	**0.032**	—	**1**	—

Egg volume was standardized into z-scores before analysis (mean = $1.50 \pm 0.12 \, cm^3$ SD, $N = 292$). The no. of (fe)male helpers indicates the within-subject effect whereas the mean no. of (fe)male helpers represents the between-subject effect. The effects included in the final model are in bold.
Covariance estimates are given in columns of both dependent variables. The covariance equals the correlation multiplied by the product of the square roots of the residual variances of egg volume and clutch size.

Table 2
Summary of model selection on the re-nest interval after nest failure ($N = 263$) showing the coefficients with SE

Model	Intercept	Hatched[a]	No. ♀ helpers	Mean no. ♀ helpers	No. ♂ helpers	Mean no. ♂ helpers	Hatched × no. ♀ helpers	Hatched × no. ♂ helpers	Experience dominant ♀[b]	No. parameters	Deviance	ΔAIC$_c$
1	10.1±1.31	1.55±0.62	1.36±1.58	—	—	−0.65±0.35	−4.20±1.93	—	—	13	1582.3	0
2	10.2±1.31	1.57±0.62	1.39±1.57	—	−0.41±0.93	−0.65±0.35	−4.55±1.92	1.85±1.20	—	15	1578.6	0.9
3	10.1±1.31	1.56±0.62	1.27±1.58	—	0.68±0.61	−0.64±0.35	−4.27±1.92	—	—	14	1581.0	1.0
4	9.54±1.28	1.57±0.62	1.26±1.59	—	—	—	−4.10±1.94	—	—	12	1585.6	1.1
5	9.52±1.46	1.52±0.62	1.35±1.57	—	—	−0.61±0.35	−4.20±1.92	—	0.69±0.73	14	1581.4	1.3
6	9.48±1.49	1.53±0.62	1.38±1.57	—	—	−0.61±0.35	−4.56±1.92	1.88±1.20	0.82±0.73	15	1577.4	1.9

The no. of (fe)male helpers indicates the within-subject effect whereas the mean no. of (fe)male helpers represents the between-subject effect. Year is included as a fixed categorical factor in all models.
[a]Reference category is unhatched.
[b]Reference category is inexperienced.

Figure 2e). There was some evidence that groups with more male helpers generally have shorter re-nest intervals than groups with fewer males, although this effect was rather small (0.6 days; Table 2, model 1 vs. model 4). Interestingly, an increase in female helpers that helped provision the previous nest allowed breeder females to reduce the re-nest interval (Figure 2e), and including the interaction between the number of female helpers and whether the previous nest hatched was supported by the data ($\Delta AIC_c = +2.8$). There was no evidence that either male or female helpers had different effects on experienced and unexperienced mothers ($\Delta AIC_c = +3.6$), or that the effects of helpers varied among years ($\Delta AIC_c > +12$).

Helper but not breeder survival decreased with an increasing number of female helpers (Figure 3, Table 3, interaction status × no. ♀ helpers), but there was no evidence that the number of male helpers affected survival of either helpers or breeders (Figure 3, Table 3, model 5 vs. model 1). To test whether the effects of male and female helpers on survival were different, the number of male and female helpers in model 1 was substituted by group size. However, this model was not better supported by the data ($\Delta AIC_c = +8.4$). This indicates that helper survival was affected differentially by the number of male and female helpers, thus supporting prediction 3a.

DISCUSSION

The questions of whether and how helpers improve the fitness of their recipients are of crucial importance for a complete understanding of the evolution of cooperative breeding. However, it has proved difficult to determine helper effects, because of the difficulty in determining causation when larger group sizes might be associated with better quality territories. Here we made an attempt to disentangle helper effects from possible confounds of group size and quality. First, due to differences in provisioning behavior (load lightening which did not change the amount of food received per nestling in groups with male helpers, additive care which resulted in more food received per nestling in groups with female helpers), our predictions varied with the sex of the helpers rather than overall group size. Second, by having multiple measurements per individual, our dataset allowed us to separate effects due to changes in group composition from consistent differences between groups. We found no evidence for concealed helper effects via reduced maternal investment in egg size. An increase in the number of helpers did allow females to lay larger clutches, and an increase in female helpers was associated with quicker re-nesting. However, helper survival decreased as the number of female helpers increased. Our results also indicate that there are differences among groups. Groups with more female helpers tended to lay smaller eggs, whereas groups with more male helpers had slightly shorter re-nest intervals and survived better.

Absence of concealed helper effects on maternal investment

We did not find evidence for concealed helper effects: Breeding females did not adjust the size of their eggs in response to the number of female helpers, not even in some specific years (as suggested by Koenig et al. 2009). The absence of egg size adjustment was surprising because nestlings receive more food in the presence of female helpers (Brouwer et al. 2014a), thus any negative effects of reduced egg investment would be compensated during the nestling phase. Interestingly, egg size was associated with other
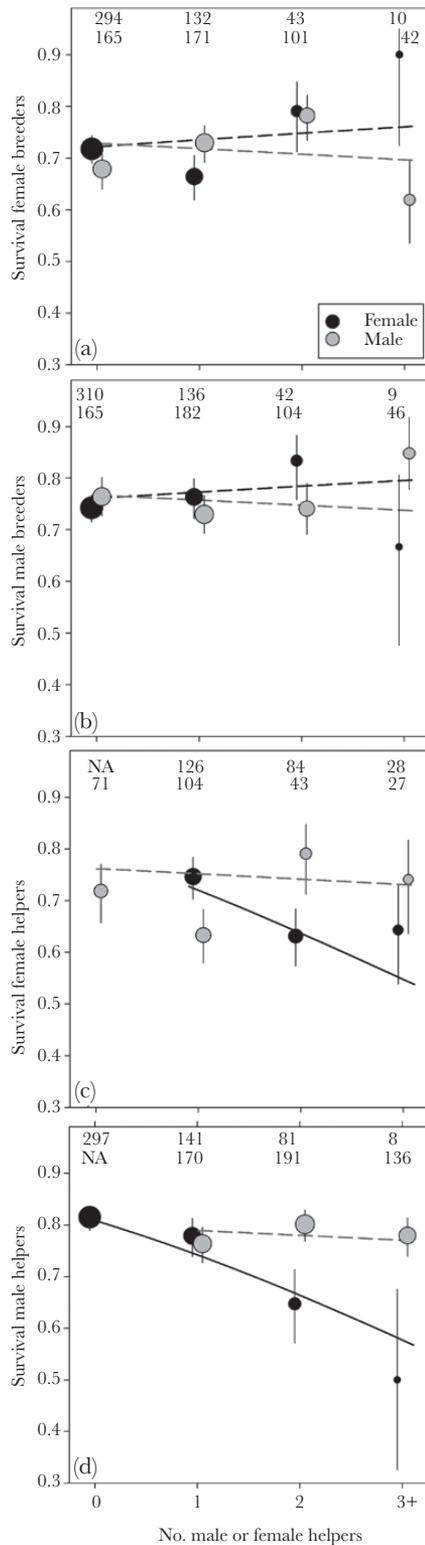
Figure 3
Annual survival in relation to the number of female and male helpers in the group for (a) female breeders, (b) male breeders, (c) female helpers, and (d) male helpers. Numbers indicate the sample sizes for the number of female (upper) and male (lower) helpers with the symbol sizes adjusted accordingly. Lines show the predictions of model 1 from Table 3. Error bars are the SEM.

environmental conditions like rainfall (likely reflecting food availability; Table 1), although this might not be active adjustment by females, but rather a consequence of inferior conditions. A possibility remains that other unmeasured components of egg quality (e.g., nutritional content) were strategically adjusted by the female in response to the number of female helpers.

In their model, Savage et al. (2015) showed that mothers are expected to reduce prebirth investment whenever prebirth investment and postbirth are substitutable, as this reduction can be compensated by the carers later. However, maternal tactics will be less important when group size or helper helpfulness is unpredictable at the time when the mother produces the offspring. Brouwer et al. (2014a) previously hypothesized that lower reliability of female helpers might explain the absence of load lightening in their presence, and the same could be true for investment in egg size. Because female helpers disperse on average earlier than males and can also initiate their own nest, help delivered by females might be less predictable. Therefore, it may be more risky to make investment decisions predicated on their presence (Brouwer et al. 2014a).

Load lightening during the egg phase seems to be common in cooperative breeders. In five of the six species studied so far (including the congener species Malurus *cyaneus*), egg size was reduced in the presence of helpers (Russell et al. 2007; Taborsky et al. 2007; Canestrari et al. 2011; Santos and Macedo 2011; Paquet et al. 2013; but see Koenig et al. 2009). It is interesting to note that had we not specifically investigated whether changes in helper number resulted in changes in egg volume within the same female, we would have erroneously concluded that, as predicted, egg volume was reduced in the presence of female helpers, because groups with more female helpers tended to be associated with smaller egg size.

Helper effects on current reproduction

As predicted, breeding females did lay larger clutches in response to an increasing number of helpers. Although clutch size has been shown to increase with an increase in exclusive male carers in the cooperatively polyandrous dunnock (Davies and Hatchwell 1992) and with the number of helpers in the cooperatively breeding apostlebird (Woxvold and Magrath 2005), such increases have not been commonly reported among cooperative breeders with philopatric helpers at the nest. We have shown that this association was a plastic response in red-winged fairy-wrens. Increased offspring production by females is expected when production costs are cheap relative to those of the rearing period (Savage et al. 2013). Because moving from two to three eggs potentially represents a 50% increase in annual fecundity, this suggests strong fitness benefits from helping. However, the association between fledgling production and the number of female or male helpers was quite weak (Figure 3d; Brouwer et al. 2014a), almost certainly because productivity is strongly determined by high rates of predation.

Helper effects on future prospects

In contrast to our predictions, female but not male helpers allowed breeding females to reduce the re-nest interval after the preceding nest reached the nestling stage before failing. Despite the increased workload experienced during the previous attempt, breeding females reduced their re-nest interval with the prospect of raising a brood with extra female help at hand. Reducing the re-nest interval by more than 3 days per additional helper female could enable breeding females to have an extra nesting attempt within the same

Table 3
Summary of model selection on annual adult survival of red-winged fairy-wrens (N = 1715) showing the coefficients with SE on the logit scale

Model	Intercept	Status[a]	Sex[b]	No. ♀ helpers	Mean no. ♀ helpers	No. ♂ helpers	Mean no. ♂ helpers	Sex[b] × no. ♀ helpers	Status[a] × no. ♀ helpers	Sex[b] × status[a]	Sex[b] × no. ♀ helpers × status[a]	No. parameters	Deviance	ΔAIC_c
1	1.27±0.22	−0.10±0.13	−0.19±0.12	−0.36±0.11	—	—	0.20±0.09	—	0.43±0.16	—	—	13	1911.4	0
2	1.26±0.23	−0.07±0.16	−0.31±0.24	−0.51±0.16	—	—	0.20±0.09	0.33±0.24	0.83±0.24	0.08±0.28	0.79±0.34	16	1905.8	0.5
3	1.20±0.21	−0.14±0.12	—	−0.41±0.11	—	—	0.21±0.09	—	0.48±0.16	—	—	12	1913.9	0.5
4	1.32±0.23	−0.11±0.13	−0.18±0.12	−0.36±0.11	−0.09±0.13	—	0.20±0.09	—	0.42±0.16	—	—	14	1910.9	1.6
5	1.29±0.22	−0.11±0.13	−0.20±0.12	−0.36±0.11	—	−0.05±0.08	0.20±0.09	—	0.43±0.16	—	—	14	1910.9	1.6
6	1.27±0.23	−0.15±0.12	—	−0.40±0.11	−0.12±0.13	—	0.21±0.09	—	0.46±0.16	—	—	13	1913.1	1.8
7	1.25±0.23	−0.07±0.16	−0.14±0.16	−0.38±0.12	—	—	0.20±0.09	—	0.44±0.17	−0.08±0.25	—	14	1911.3	1.9
8	1.28±0.22	−0.11±0.13	−0.18±0.12	−0.34±0.14	—	—	0.20±0.09	−0.04±0.16	0.43±0.16	—	—	14	1911.3	2.0

The no. of (fe)male helpers indicates the within-subject effect whereas the mean no. of (fe)male helpers represents the between-subject effect. Year is included as a fixed categorical factor in all models.
[a]Reference category is helper.
[b]Reference category is male.

breeding season and thus potentially increase their annual repro-ductive success.

Our results were consistent with a survival benefit caused by load lightening at the nestling stage, although only for helpers. However, this positive effect of load lightening is counterbalanced by a survival cost due to increased competition, as the net effect of an increasing number of male helpers is zero. The number of female helpers was negatively associated with helper survival, which is consistent with an absence of survival benefits of female help-ers in combination with a negative effect of increased competition in larger groups (Figure 1d). Intra-group competition could result from increased competition for food (Brouwer et al. 2006; Brouwer et al. 2009), and helpers might incur a higher cost of competition than dominants because breeders are better foragers or in better condition. Helpers may also suffer more from additive care because they undergo more energetic costs than breeders when helping (Heinsohn and Legge 1999, Hatchwell et al. 2014). An alternative explanation for our result would be that there is no measureable survival benefit from load lightening, instead, helpers suffer from increased competition from female helpers. However, we do not have any indication why intra-group competition would increase with more female, but not male helpers.

In superb fairy-wrens, breeding females benefit from helping by having higher survival as a result of egg size reduction (Russell et al. 2007; Cockburn et al. 2008), but there is no evidence that breeding males benefit from helping and it is unknown what the effects on other helpers are. In red-winged fairy-wrens, females increase clutch size with the number of helpers, which can result in increased current reproductive success and therefore also benefits males, although to a lesser extent due to the presence of high rates of extrapair paternity (Brouwer et al. 2011). The reduced helper survival with an increasing number of female helpers will also affect group size the next season and therefore future reproductive suc-cess of the group. Future work integrating the different fitness com-ponents will have to show whether the increased benefits through increased reproductive success (and thus group size) will outweigh the negative effects female helpers have on helper survival.

Disentangling helper effects from possible confounds of group size

Our results indicated that there are differences among groups that were not a plastic response to a changing group composition. Differences among groups of varying sizes could be the result of underlying quality differences when certain high-quality individu-als/territories are more likely to be successful and thus are also more likely to have larger groups. We found that groups with more males survived better and re-nested slightly sooner, whereas groups with more females tended to lay smaller eggs. Unfortunately, we do not have a good idea what determines territory quality, because insect abundance does not predict reproductive success (Brouwer L, unpublished data). Nevertheless, if our results were simply due to differences in quality, then the associations would be expected to occur for both sexes, unless certain conditions result in the accu-mulation of female, but not male helpers and vice versa. Because females disperse on average earlier than males, an accumulation of males could be the result of locally adverse dispersal conditions. Because the role of habitat fragmentation on dispersal within the main study area is limited (Brouwer L, unpublished data), adverse dispersal conditions must be associated with high breeder survival, suggesting good conditions, which are then expected to result in accumulation of female helpers as well.

An alternative explanation for our findings is that because males disperse on average later than females, groups with more males are more stable than groups with fewer males. This could result in higher group survival and allow females to re-nest sooner. Why female breeders with more female helpers lay smaller eggs remains unknown, possibly such an effect could be the result from sex ratio biases due to females hatching from smaller eggs. Whether this is true and whether there are any other biases in offspring sex ratio related to the sex of the helpers present on the territory remain to be investigated.

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