

# Females increase reproductive investment in response to helper-mediated improvements in allo-feeding, nest survival, nestling provisioning and post-fledging survival in the Karoo scrub-robin *Cercotrichas coryphaeus*

Penn Lloyd, W. Andrew Taylor, Morné A. du Plessis and Thomas E. Martin

P. Lloyd (correspondence), W. A. Taylor and M. A. du Plessis, Percy FitzPatrick Inst., DST/NRF Centre of Excellence, Univ. of Cape Town, Private Bag X3, Rondebosch, 7701, South Africa. E-mail: Penn.Lloyd@gmail.com. – T. E. Martin, USGS Montana Coop. Wildl. Res. Unit, Univ. of Montana, Missoula, MT 59812, USA.

In many cooperatively-breeding species, the presence of one or more helpers improves the reproductive performance of the breeding pair receiving help. Helper contributions can take many different forms, including allo-feeding, offspring provisioning, and offspring guarding or defence. Yet, most studies have focussed on single forms of helper contribution, particularly offspring provisioning, and few have evaluated the relative importance of a broader range of helper contributions to group reproductive performance. We examined helper contributions to multiple components of breeding performance in the Karoo scrub-robin *Cercotrichas coryphaeus*, a facultative cooperative breeder. We also tested a prediction of increased female investment in reproduction when helpers improve conditions for rearing young. Helpers assisted the breeding male in allo-feeding the incubating female, increasing allo-feeding rates. Greater allo-feeding correlated with greater female nest attentiveness during incubation. Nest predation was substantially lower among pairs breeding with a helper, resulting in a 74% increase in the probability of nest survival. Helper contributions to offspring provisioning increased nestling feeding rates, resulting in a reduced incidence of nestling starvation and increased nestling mass. Nestling mass had a strong, positive effect on post-fledging survival. Controlling for female age and habitat effects, annual production of fledged young was 130% greater among pairs breeding with a helper, and was influenced most strongly by helper correlates with nest survival, despite important helper effects on offspring provisioning. Females breeding with a helper increased clutch size, supporting the prediction of increased female investment in reproduction in response to helper benefits.

Cooperative breeding describes social systems in which one or more helpers combine with a primary breeding pair to rear offspring as a social group (Clutton-Brock 2002). Helpers are generally offspring from a previous breeding event that assist their parents after deciding to delay dispersal, usually because of one or more constraints on dispersal and independent breeding (Emlen 1991, Hatchwell and Komdeur 2000). Helpers thus bear two potential costs: (1) loss of direct reproductive benefits by deferring reproduction, although helpers in some systems may gain a direct share in reproduction (Richardson et al. 2002), and (2) costs of providing care (Clutton-Brock et al. 1998, Heinsohn and Legge 1999). Measuring the benefits of helping to both the donor and the recipient is therefore crucial for testing the conceptual models that have been proposed to explain the evolution of cooperative breeding (Cockburn 1998, Dickinson and Hatchwell 2004). Helpers can improve the performance of recipient breeders, and potentially their own inclusive fitness (Hamilton 1964), by: (1) increasing the number or quality of offspring produced

(Woxvold and Magrath 2005), and (2) reducing the costs of reproduction to breeders, thereby increasing breeder condition (Anava et al. 2001), breeder survival (Heinsohn 2004, Cockburn et al. 2008) or number of breeding attempts (Langen and Vehrencamp 1999). However, it is insufficient to infer helper effects merely on the basis of correlations between group size and a measure of productivity or survival, because group size may covary with territory and/or breeder quality that may both influence productivity or survival independently of any helper effects. Because helpers are typically retained offspring of successful breeders, group size can be a consequence rather than a cause of higher productivity on higher quality territories (Cockburn 1998, Dickinson and Hatchwell 2004, Cockburn et al. 2008).

Distinguishing helper effects from breeder and territory quality effects can be problematic. Helper removal or addition experiments provide the most rigorous framework for manipulating helper number while controlling for individual and territory quality effects, but may disrupt

the experimental group, thereby reducing its success (Cockburn 1998). Paired comparisons of pairs in sequential years with and without helpers can also control for individual and territory quality effects, but may be flawed by changes in experience levels or helpers being associated only with successful pairs (Dickinson and Hatchwell 2004, but see Cockburn et al. 2008). Furthermore, unless helper contributions are actually measured, distinguishing direct effects of help from more indirect benefits of larger group size, such as shared vigilance that might increase feeding rates, remains problematic. Among birds, helper contributions can take many different forms, including territory defence (Walters 1990, Komdeur 1994), allo-feeding (Poiani 1992, Radford 2004), offspring provisioning (Cockburn 1998, Hatchwell 1999, Dickinson and Hatchwell 2004, Woxvold and Magrath 2005, Ridley 2007), and various predator defence behaviours, such as sentinel and mobbing behaviours (Woolfenden and Fitzpatrick 1990, Maklakov 2002). Yet, most studies have focussed on single forms of helper contribution, particularly offspring provisioning, and few have evaluated the relative importance to group reproductive success of a broader range of helper contributions (Komdeur 2006).

We examined helper contributions to multiple components of breeding performance in the Karoo scrub-robin *Cercotrichas coryphaeus*, including: (1) allo-feeding of the incubating female, and its influence on female nest attentiveness, (2) nest survival, (3) nestling provisioning, and its influence on nestling growth and the incidence of starvation, and (4) survival of fledglings to independence. We evaluate the relative importance of these various contributions to overall annual productivity of breeding pairs. To separate the effect of helpers from the effect of territory and breeder quality, we measure helper versus breeder contributions to allo-feeding and offspring provisioning, and compare pairs in successive years with and without helpers. We also test whether females increase their investment in clutch size in response to helper benefits, a response that is predicted by theory (Charnov and Krebs 1974, Winkler 1987), but that has rarely been demonstrated (Woxvold and Magrath 2005).

## Methods

The Karoo scrub-robin is a socially monogamous, territorial, resident passerine, endemic to arid and semi-arid regions of southern Africa (Oatley 2005). It is a relatively long-lived bird with annual adult survival of  $78.6 \pm 1.7\%$  (P.L. unpubl. data). Apart from observations of helpers at several nests, in one case known to be yearling offspring from a previous brood, little is known about the ecology of cooperative breeding in this species (Oatley 2005). We studied a colour-banded population occupying up to 104 territories within a 260 ha area of the 2,900 ha Koeberg Nature Reserve ( $33^{\circ}41' S$ ,  $18^{\circ}26' E$ ), on the west coast of South Africa. It has a Mediterranean climate with hot, dry summers and cool, wet winters. Annual rainfall over the period 1980–2007 has averaged  $375 \pm 77$  mm (range 242 to 640 mm). The vegetation is coastal shrubland, comprising a mosaic of two distinct vegetation types: dune thicket and sand-plain fynbos (Low and Rebelo 1996), covering

30% and 70% of the study area respectively. Dune thicket has a taller and denser shrub layer, with much less open ground, so is potentially less suitable for a ground-feeding insectivore such as the Karoo scrub-robin. We also expected nest predation to differ between habitats based on earlier work on 17 other species at this study site (e.g. Martin et al. 2007).

## Field data collection

Field work was conducted during the breeding season, August to early November 2000–2007, with more focussed research during 2004–2007. Banding of adults with a unique combination of three colour bands and a numbered metal band commenced in 2001, with 331 banded by the end of 2007. For the analysis of age effects on reproduction, any unbanded female that replaced a previously-banded female on a territory was assumed to be a first year bird, because 27 of 29 female recruits bred in their first year, and breeding dispersal was uncommon (9% of banded breeding females moved territories between years).

The open-cup nest is sited from ground level to a height of 0.5 m (Nalwanga et al. 2004). Nests were located using parental behaviour, usually during the building stage, and checked every 2–4 d to determine status and predation events, but daily near stage-changing events such as laying, hatching and fledging. Eggs were numbered according to their laying sequence using a non-toxic permanent marker. We recorded clutch size, nest mortality rates, and nest productivity. Nest depredation was assumed when nest contents disappeared with no evidence of parents feeding fledged young. During the nestling stage, nests were considered to have failed only if all chicks died or disappeared; incidents of individual chick starvation were treated separately.

Nestlings were individually marked on the tarsus using a non-toxic permanent marker and weighed on a portable digital scale (Acculab PP2060D, precision 0.001 g) at approximately the same time at 1- to 2-d intervals from hatching until they reached an age of 9 d (hatch date = 0 d). Handling of nestlings ceased at this point because premature fledging becomes a risk beyond this age. The nestling period is normally 14–15 d. A small blood sample (20–60  $\mu$ l) was taken from nestlings via brachial venipuncture once they had reached age 3 d. All nestlings reaching age 9 d ( $n = 616$  over seven years) were weighed and banded with a numbered metal band and either: (1) a single coloured plastic band (2001–2004), or (2) a unique combination of three colour bands (2005–2007). From 2003, all territories in a sub-area (2003–2004) or within the whole study area (2005–2007) were monitored with sufficient attention to record annual productivity per female as the total number of young raised to fledging age. In 2005–2007, we recorded the survival of all fledged young at 21–24 d after fledging, when fledglings were still receiving regular feedings from adults, but also foraging competently on their own. We were not confident of separating mortality from natal dispersal beyond four weeks post-fledging.

To monitor parental care behaviours at the nest, nests were video-taped continuously for the first 6–8 h of the day,

beginning within 0.5 h of sunrise, using Sony Hi8 video cameras mounted on low tripods. This protocol standardized both time of day and sampling duration (Martin et al. 2007). Nests were video-taped at three standardized stages of the nesting cycle: (1) 2–3 d after the last egg of a clutch was laid, (2) 2 d after the hatching of the last chick in the brood, and (3) on the day the primary wing feathers of the last-hatched chick broke through their pin sheaths, generally at age 9 d. Female nest attentiveness during incubation (the female incubates alone) was measured as the percent time spent on the nest over the recording period. Allo-feeding rates were measured as the average number of feeding visits (food delivered by a male and accepted by the female) per hour of incubation time (i.e. restricted to times the female was on the nest). Nestling provisioning rates were measured as the average number of feeding visits per hour.

Rainfall data were obtained from a weather station located within the study site. Rainfall has important influences on the breeding parameters of southern hemisphere birds (Lloyd 1999, Spottiswoode 2007, Cockburn et al. 2008). We therefore tested the influence of total rainfall during both the three winter months preceding the breeding season (May–July), and during the spring breeding season (Aug.–Oct.) on breeding parameters.

## Analyses

We examined relationships between dependent variables of interest and potential explanatory variables using LMMs (linear mixed models) or GLMMs (generalised linear mixed models), which allow repeated measures to be fitted as random terms, thus controlling for their effects on the distribution of the data. We fitted these models using the software R 2.4.1 (Ihaka and Gentleman 1996), following the methods of (Crawley 2002). LMMs were fitted using restricted maximum likelihood (REML), and GLMMs were fitted using penalized quasi-likelihood (PQL). We employed a zero-inflated Poisson (ZIP) modelling approach (Welsh et al. 1996, Cockburn et al. 2008) for the analysis of annual productivity data; because most females fledged no young, the distribution of these data was strongly zero-inflated. As the mixed-model formulation of ZIP models is still under development, we used the standard `zeroinfl()` function in R 2.4.1 to build ZIP models (Zeileis et al. 2007). A ZIP model involves: (1) modelling factors associated with reproductive failure using a GLMM with a logit link and binomial error, (2) modelling factors associated with the total number of young fledged in cases where some reproductive success occurred using a GLMM with a log link and truncated Poisson error, and (3) combining the predictions of the two models.

Model simplification using backward-elimination of non-significant explanatory variables and interaction terms was adopted. Terms were systematically removed from the model and only put back in if their removal resulted in a significant loss of model explanatory power, determined by comparing the log-likelihood of the full model to the log-likelihood of the reduced model using the  $G^2$  test, whose sampling distribution approximates a  $\chi^2$  distribution with one degree of freedom (Quinn and Keough 2002). The

significance of each explanatory variable was similarly determined by comparing the log-likelihood of the full minimal model including the variable of interest to the log-likelihood of the reduced model excluding it. All meaningful interactions (only two-way interactions) were included in the saturated model, but only significant interactions are presented. Residual plots and normal probability plots were used to check for deviations from normality in the final model. Throughout the text, means are expressed  $\pm 1$  SD, unless otherwise stated.

We used the nest survival module of Program MARK (White and Burnham 1999) to estimate daily nest survival rates separately during the egg stage (laying and incubation) and nestling stage because we expected patterns of nest mortality to differ between these two stages. Program MARK allows the inclusion of individual and group- and time-specific covariates to build detailed models that investigate the influence of biological factors of interest on nest survival (Dinsmore et al. 2002). Covariates we investigated included: (1) the presence or absence of helpers, (2) nest initiation date in the breeding season, to examine seasonal variation (T) as either a linear, exponential or quadratic term, (3) nest age through the nest attempt as either a linear or exponential term, (4) habitat (sand-plain fynbos or dune thicket, coded 0 and 1 respectively), (5) brood size (for nestling stage only, as a dummy variable coded 0 for brood size 1–2 and coded 1 for brood size 3 because the ratio of brood size 1, 2, 3 was roughly 7:33:60), and (6) year (3 years 2004–2006, entered as dummy variables). Model support was evaluated using Akaike's information criterion (AIC) model selection (Burnham and Anderson 2002).

## Results

Most Karoo scrub-robin pairs breed without the assistance of helpers, with only  $15 \pm 2\%$  (range 12–20%,  $n = 5$  years) of the groups breeding cooperatively. Cooperative groups were roughly evenly distributed between the two habitat types, occupying 15% of territories in sand-plain fynbos and 14% of territories in dune thicket. The number of helpers per cooperative group ranged between one and three, with the following frequencies: 84% with one helper, 14% with two helpers, and 2% with three helpers ( $n = 64$  groups). All individuals that became breeders after initially serving as helpers were males ( $n = 43$ ). Among 36 helpers first ringed as nestlings of colour-marked parents, 31 helped on their natal territory in their first year, always with their social father but not necessarily their social mother present. The remainder dispersed to a neighbouring territory following the death of the social father, to help either a full brother up to five years senior ( $n = 4$ ), or the dispersing mother ( $n = 1$ ). Among known first-year males (i.e., ringed as nestlings), the majority were helpers rather than breeders in their first year; the ratio of first-time breeders to helpers being 1:1.4 overall ( $n = 51$ ). Helpers that survived to recruit as breeders served as helpers for an average of  $1.2 \pm 0.4$  breeding seasons (range 1–2,  $n = 24$ ) before becoming breeders. Females, unlike males, did not appear to help; 27 of 29 females that were ringed as nestlings and subsequently recruited within the study area bred in their

first year, and the remaining two were not sighted in their first year.

### Helper contributions to allo-feeding and effect on nest attentiveness

Female Karoo scrub-robins are the sole incubators, and leave the nest at regular intervals to forage. Males, including helpers, allo-fed the female both on and off the nest during this time. Helpers were also observed allo-feeding the breeding male on occasion. We measured the allo-feeding rates to females on the nest only based on video-sampling of the nest. Allo-feeding rate was not related to group size after controlling for repeated measures on the same territory and a decrease in allo-feeding rate with date (Table 1a, Fig. 1). Using only data for a pair and group filmed on the same day to control for date, the rate of allo-feeding at the nest was greater among cooperative groups ( $4.06 \pm 3.27$  feeds/h incubation) than among pairs ( $1.73 \pm 1.46$  feeds/h incubation; paired t-test on ln-transformed data:  $t = -2.46$ ,  $df = 19$ ,  $P = 0.014$ ). Within cooperative groups, breeding males had a higher allo-feeding rate than helpers ( $2.19 \pm 1.66$  vs.  $1.33 \pm 1.48$  feeds/h incubation; paired t-test on ln-transformed data:  $t = 2.43$ ,  $df = 12$ ,  $P = 0.032$ ). Both date and allo-feeding rate had a positive effect on female nest attentiveness during early incubation (Table 1b).

### Helper contributions to nestling care and correlates with offspring fitness

Hatching was partially asynchronous, being either staggered through a single day or over two consecutive d (24 h). The food delivery rate (feeding visits/nestling/h) to nests decreased with date, but increased with nestling age, in broods of two versus three nestlings, in co-operative groups versus pairs, and was greater in sand-plain fynbos habitat than dune thicket (Table 1c, Fig. 2). Similar results were found when we restricted analysis to known age breeders and included female and male age as predictors (Table 1d). The food-delivery rate of the breeding male increased with nestling age, but was not related to brood size or group size (Table 1e, Fig. 3). The food-delivery rate of the breeding female was related to brood size, nestling age, group size and an interaction between nestling age and group size (Table 1f). When breeding in a cooperative group, females reduced their feeding rate to 2-d-old nestlings, but not to 9-d-old nestlings (Fig. 3). The reduction in nestling feeding to 2-day-old nestlings by females breeding in groups was not accompanied by an increase in nestling brooding (paired t-test:  $t = 0.13$ ,  $df = 12$ ,  $P = 0.9$ ).

The incidence of nestling starvation, which occurred mostly before the nestlings reached nine days of age, was significantly reduced among broods of cooperative groups (Table 1g). Nestling mass at nine days after hatching decreased with hatching order (i.e., controlling for age, nestlings hatching earlier were heavier), was greater for cooperative groups versus pairs breeding alone, and was greater in sand-plain fynbos territories than dune thicket territories (Table 1h, Fig. 4). Similar results were found when we restricted analysis to known age breeders and included female and male age as factors (Table 1i). Among

pairs for which we had data for the pair breeding on the same territory both with and without a helper, average nestling mass at nine days was greater when the pair bred with a helper ( $17.54 \pm 1.22$  g) than without a helper ( $15.86 \pm 1.92$  g; paired t-test:  $t = -2.41$ ,  $df = 13$ ,  $P = 0.031$ ). Among nests where both nestling mass (brood average) and food delivery rate (nestling feeds/nestling/h) were measured nine days after hatching, average nestling mass correlated positively with the nestling feeding rate ( $r = 0.44$ ,  $df = 48$ ,  $P = 0.017$ ).

Post-fledging survival through the first three weeks post-fledging (38 mortalities among 167 individuals) was related to nestling body mass at nine days, with heavier nestlings surviving better (Table 1j, Fig. 5). Controlling for the effect of nestling mass, there was no effect of group size or fledging brood size on post-fledging survival (Table 1j).

### Helper correlates with nest survival

We obtained nest survival data in relation to group size for 467 nests at the egg stage (laying and incubation) and 207 nests at the nestling stage over three years (2004–2006). In an initial analysis of nest survival during the egg stage, using only nests of females known to be either: 1) 1 year old, or 2)  $\geq 2$  years old, the most parsimonious model did not include female age, and was 2.50  $\Delta AIC_c$  units better than the model that included female age. Any model with a  $\Delta AIC_c$  value  $< 2$  between it and the best model is thought to be a reasonable model given the data (Burnham and Anderson 2002). We therefore excluded female age in the analyses of the full dataset reported below. In the analysis of nest survival during the egg stage, the model that included all individual covariates (seasonal trend T, nest age, habitat, year, group size) was the most parsimonious (Table 2). The logistic regression equation for this best survival (S) model during the egg stage (SE in parentheses below) was:

$$\begin{aligned} \text{Logit}(S) = & 2.047 - 0.00012 (T) + 0.324 (\text{nest age}) \\ & + 0.051 (\text{group size}) \\ & (0.163) (0.00003) \quad (0.179) \quad (0.016) \\ & + 0.773 (\text{thicket habitat}) + 0.406 (\text{year 2005}) \\ & - 0.098 (\text{y 2006}) \\ & (0.144) \quad (0.162) \quad (0.162) \end{aligned}$$

The most influential factor was habitat; average daily nest mortality ( $\pm$ SE) was greater in sandplain fynbos ( $10.3 \pm 0.6\%$ ) than in dune thicket ( $4.9 \pm 0.5\%$ ). There was more support for an exponential seasonal trend than a linear or quadratic trend (Table 2), and average daily nest mortality during the egg stage increased through the breeding season, from  $6.6 \pm 0.6\%$  to  $18.8 \pm 4.1\%$ . Daily nest mortality decreased with nest age, from  $10.1 \pm 0.5\%$  to  $4.3 \pm 0.8\%$ . Although group size was the least influential factor, the model that included group size was 1.51  $\Delta AIC_c$  units better than the second-best model that excluded it. Thus, average daily nest mortality during the egg stage was lower at nests of cooperative groups ( $6.4 \pm 1.0\%$ ) than at nests of pairs ( $8.5 \pm 0.5\%$ ). The probability of an average nest surviving the 2-d laying and 14-d incubation period was therefore  $(1 - 0.064)^{16} = 0.347$  for cooperative groups and  $(1 - 0.085)^{16} = 0.241$  for nests of pairs breeding without helpers.

Table 1. Summary of model terms and statistics for minimal linear mixed effects models (models a-f, h-i, l) generalized linear mixed effects models (models g, j-k) and zero-inflated Poisson (ZIP) models (model m) used in this study. Only significant interaction terms are presented. Dichotomous factors included habitat (dune thicket, sand-plain fynbos), group type (pair, group), nestling age (2 d, 9 d), brood size (1–2, 3) and male and female age (1 y,  $\geq 2$  y).

Predictor terms	$\chi^2$	P	Effect size $\pm$ SE
Allo-feeding visits per h (ln-transformed).			
Model a: n = 76 observations/46 territories.			
Constant:			1.179 $\pm$ 0.276
Date	13.12	<0.001	-0.019 $\pm$ 0.005
Habitat	2.40	0.12	
Group type	1.76	0.18	
Rainfall (winter)	0.88	0.35	
Rainfall (breeding)	0.04	0.85	
Nest attentiveness (arcsine-transformed).			
Model b: n = 76 observations/46 territories.			
Constant:			0.625 $\pm$ 0.033
Date	8.89	0.003	0.002 $\pm$ 0.001
Ln (allo-feeds)	4.62	0.032	0.025 $\pm$ 0.012
Rainfall (breeding)	2.53	0.11	
Habitat	1.16	0.28	
Rainfall (winter)	1.13	0.29	
Group type	0.42	0.52	
Nestling provisioning: total feeds per nestling per h (ln-transformed).			
Model c: all nests, n = 105 observations/77 nests/51 territories.			
Constant:			1.78 $\pm$ 0.07
Nestling age	76.77	<0.001	9 d: 0.47 $\pm$ 0.04
Group type	18.03	<0.001	Group: 0.20 $\pm$ 0.05
Brood size	14.07	<0.001	Three: -0.19 $\pm$ 0.05
Date	9.79	0.002	-0.003 $\pm$ 0.001
Habitat	6.40	0.011	Sand-plain: 0.11 $\pm$ 0.05
Rainfall (winter)	1.57	0.21	
Rainfall (breeding)	0.54	0.46	
Nestling provisioning: total feeds per nestling per h (ln-transformed).			
Model d: nests of known-age birds, n = 66 observations/46 nests/31 territories.			
Constant:			1.80 $\pm$ 0.09
Nestling age	39.96	<0.001	9 d: 0.41 $\pm$ 0.05
Brood size	11.65	<0.001	Three: -0.22 $\pm$ 0.06
Group type	10.33	0.001	Group: 0.19 $\pm$ 0.06
Date	5.71	0.017	-0.003 $\pm$ 0.001
Habitat	5.26	0.022	Sand-plain: 0.13 $\pm$ 0.06
Rainfall (breeding)	3.12	0.08	
Rainfall (winter)	2.67	0.10	
Female age	1.88	0.17	
Male age	0.58	0.45	
Male provisioning: feeds per nestling per h (ln-transformed).			
Model e: breeding males, n = 63 observations/41 nests/51 males.			
Constant:			1.37 $\pm$ 0.06
Nestling age	7.30	0.007	9 d: 0.18 $\pm$ 0.06
Brood size	3.04	0.08	
Group type	0.44	0.51	
Date	2.23	0.14	
Female provisioning: feeds per nestling per h (ln-transformed).			
Model f: breeding females, n = 63 observations/41 nests/51 females.			
Constant:			1.20 $\pm$ 0.08
Nestling age	77.89	<0.001	9 d: 0.53 $\pm$ 0.08
Group type	24.14	<0.001	Group: -0.54 $\pm$ 0.10
Group type $\times$ nestling age	3.98	<0.001	Group, 9 d: 0.48 $\pm$ 0.13
Brood size	13.81	0.046	Three: -0.13 $\pm$ 0.07
Date	0.28	0.60	
Incidence of nestling starvation (binomial distribution).			
Model g: n = 80 nests/53 territories.			
Constant:			28.26 $\pm$ 11.90
Group type	14.77	<0.001	Group: -2.39 $\pm$ 1.08
Rainfall (breeding)	8.97	0.003	-0.16 $\pm$ 0.07
Rainfall (winter)	6.30	0.012	-0.04 $\pm$ 0.02
Date	0.47	0.49	
Brood size at hatching	0.37	0.54	
Habitat	0.29	0.59	
Nestling mass at age 9 d			
Model h: all breeders, n = 256 nestlings/101 nests/63 territories.			
Constant:			17.15 $\pm$ 0.41
Order	129.92	<0.001	-1.57 $\pm$ 0.11

Table 1 (Continued)

Predictor terms	$\chi^2$	P	Effect size $\pm$ SE
Group type	24.81	<0.001	Group: 2.45 $\pm$ 0.47
Habitat	4.48	0.034	Sand-plain: 0.88 $\pm$ 0.42
Brood size at 9 d	0.93	0.34	
Rainfall (winter)	0.70	0.40	
Rainfall (breeding)	0.41	0.52	
Date	0.17	0.68	
Nestling mass at age 9 d			
Model i: known age breeders, n = 165 nestlings/62 nests/42 territories.			
Constant:			17.96 $\pm$ 0.41
Order	68.88	<0.001	-1.51 $\pm$ 0.15
Group type	11.61	<0.001	Group: 1.91 $\pm$ 0.54
Brood size at 9 d	3.03	0.082	
Rainfall (winter)	1.23	0.27	
Habitat	0.27	0.61	
Female age	0.22	0.64	
Male age	0.21	0.65	
Date	0.20	0.66	
Rainfall (breeding)	0.04	0.84	
Post-fledging survival to 3 weeks (binomial distribution).			
Model j: n = 167 fledglings/74 nests/53 territories.			
Constant:			-4.72 $\pm$ 2.11
Nestling mass (9 d)	11.04	<0.001	0.39 $\pm$ 0.13
Rainfall (breeding)	2.41	0.12	
Habitat	1.80	0.18	
Brood size at fledging	0.45	0.50	
Group type	0.25	0.62	
Date	0.11	0.74	
First nest date (Poisson distribution).			
Model k: n = 119 observations/78 females.			
Constant:			3.18 $\pm$ 0.09
Female age	28.3	<0.001	Age $\geq$ 2 y: -0.65 $\pm$ 0.11
Group type	0.63	0.43	
Habitat	0.01	0.92	
Clutch size.			
Model l: n = 609 clutches/156 females.			
Constant:			2.89 $\pm$ 0.02
Group type	13.67	<0.001	Group: 0.16 $\pm$ 0.04
Rainfall (breeding)	2.82	0.09	
Habitat	2.80	0.09	
Date	2.76	0.10	
Rainfall (winter)	1.03	0.31	
Annual productivity (ZIP model).			
Model m: known-age birds, n = 253 observations from 121 females.			
Zero-inflation model component (binomial distribution with logit link)			
Constant:			0.66 $\pm$ 0.45
Group type	4.40	0.036	Group: -0.83 $\pm$ 0.40
Habitat	8.60	0.003	Dune thicket: -0.92 $\pm$ 0.32
Female age	3.00	0.083	Age $\geq$ 2 y: -0.75 $\pm$ 0.44
Rainfall (breeding)	2.40	0.12	
Rainfall (winter)	1.60	0.21	
Male age	0.6	0.44	
Count model component (Poisson distribution with log link).			
Constant:			0.62 $\pm$ 0.11
Group type	3.00	0.083	Group: 0.32 $\pm$ 0.18
Habitat	0	1	
Female age	0	1	
Rainfall (breeding)	0.2	0.65	
Rainfall (winter)	0	1	
Male age	0.4	0.53	

\*The first nest in the population each year was assigned starting date = 1, to account for inter-annual variation.

The most parsimonious model for nest survival during the nestling stage included three covariates: an exponential seasonal trend, brood size, and nest age (Table 2), with the following logistic regression equation:

$$\text{Logit}(S) = 3.708 - 0.0002 (T) - 0.363 (\text{brood size})$$

$$-0.038 (\text{nest age})$$

$$(0.249) \quad (0.00005) \quad (0.195) \quad (0.022)$$

This model estimated that daily nest mortality during the nestling period increased from 3.7  $\pm$  0.5% to 19.6  $\pm$  4.9% through the season, increased from 4.6  $\pm$  0.5% to 7.5  $\pm$

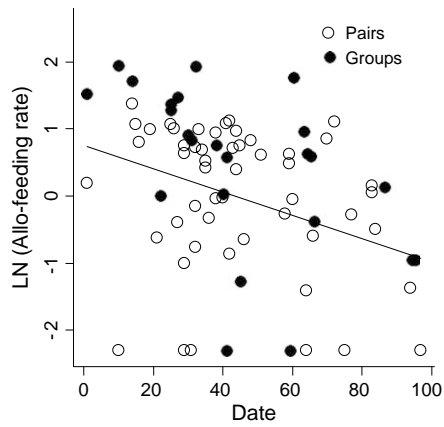


Figure 1. Temporal change through the breeding season in observed allo-feeding rate (feeds per hour of incubation, ln-transformed) to females at the nest during early incubation for pairs breeding with (closed circles), or without (open circles) one or more helpers. The line represents the prediction of a linear mixed effects model (see Table 1a).

2.1% as nestlings aged, and was higher for broods of three nestlings ( $6.4 \pm 0.7\%$ ), than broods of 1–2 nestlings ( $4.7 \pm 0.7\%$ ). Five other models received reasonable levels of support ( $\Delta AIC_c < 2$ ). The model that included group size was the second-best model ( $\Delta AIC_c = 0.73$ ), and this model estimated daily nest mortality to be lower at nests of cooperative groups ( $4.7 \pm 1.0\%$ ), than at nests of pairs breeding alone ( $5.9 \pm 0.6\%$ ). Combining these estimates with the survival estimates during the egg stage, the probability of a nest surviving the 16-d egg stage and the 15-d nestling period was  $(1 - 0.064)^{16} \times (1 - 0.047)^{15} = 0.169$  for cooperative groups and  $(1 - 0.085)^{16} \times (1 - 0.059)^{15} = 0.097$  for pairs breeding alone.

The causes of nest mortality ( $n = 662$  mortality events over seven years) included predation (96.1%), abandonment for unknown reasons (2.6%), abandonment due to adult mortality (0.9%), weather-induced mortality (0.3%), and unknown causes (0.1%). Video evidence and field observations identified the principal nest predators as a

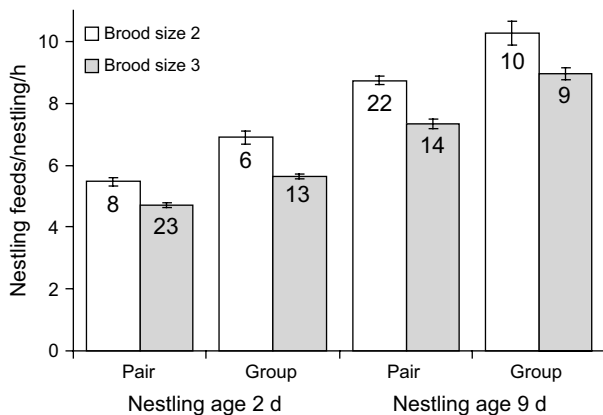


Figure 2. Nestling feeding rates (feeds/nestling/h) are greater at nests of co-operative groups than at nests of pairs, and greater at nests with a brood size of two than three. Figures show predicted means ( $\pm 1$  SE) from a linear mixed effects model (see Table 1c). Sample sizes are number of nests.

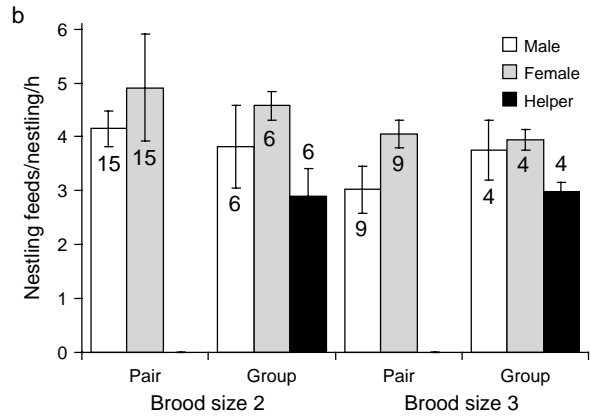
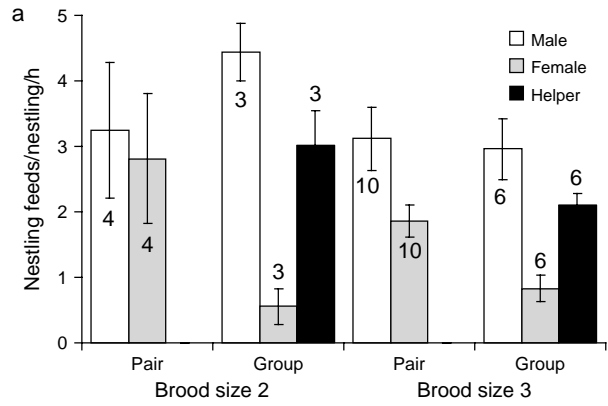


Figure 3. Observed nestling feeding rates (feeds/nestling/h  $\pm 1$  SE) per individual adult (male, female, helper) to broods of two or three nestlings, at (a) 2 d after hatching, and (b) 9 d after hatching, for pairs breeding with (group) or without a helper (pair). Sample sizes are numbers of nests.

variety of snakes (rhombic egg-eater *Dasypeltis scabra*, boomslang *Dispholidus typus*, mole snake *Pseudaspis cana*, and Cape cobra *Naja nivea*), one mammal (Cape grey mongoose *Galerella pulverulenta*) and two birds (pied crow *Corvus albus*, and common fiscal *Lanius collaris*).

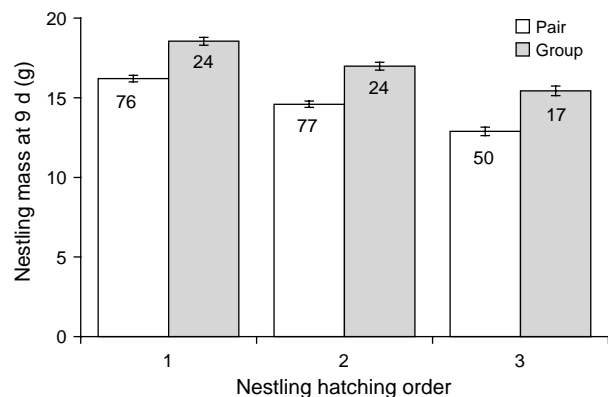


Figure 4. Nestling mass at nine days of age in relation to hatching order and group type (pair breeding alone versus with one or more helpers in a co-operative group). Data show predicted means ( $\pm 1$  SE) from a linear mixed effects model (see Table 1h). Sample sizes are numbers of individuals.

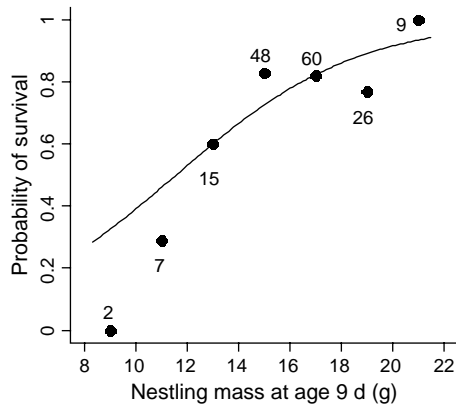


Figure 5. Probability of fledgling survival from fledging to three weeks post-fledging in relation to nestling body mass at 9 d after hatching. The line is the back-transformed prediction of a generalized linear mixed effects model (see Table 1j). The dots indicate the observed proportions surviving, binned into 2-g mass intervals. Sample size is number of individuals.

### Helper effects on female investment and annual productivity

Date of initiation of the first nest for the breeding season was influenced strongly by female age, being later for 1st-year females than females  $\geq 2$  y old, but not by group size (Table 1k). Clutch size ranged between one and four eggs, and differed between group types (Table 1l); females breeding with one or more helpers laid larger clutches than those breeding without a helper. Repeating this analysis for a reduced dataset for known-age females (1st-y vs.

$\geq 2$ nd-y old) only, clutch size was still influenced by group size ( $\chi^2 = 9.63$ ,  $P = 0.002$ ), but not female age ( $\chi^2 = 1.63$ ,  $P = 0.20$ ). Restricting the analysis to a much-reduced dataset that included only those females for which we had clutch-size data for the female breeding on the same territory both with and without a helper in different years ( $n = 204$  clutches from 32 females), clutch size was still greater when the female bred in a group ( $\chi^2 = 7.00$ ,  $P = 0.008$ ; effect size  $\pm$  SE =  $0.13 \pm 0.05$ ).

Annual productivity (fledged young/female/year) ranged from 0 to 6, but most individuals did not fledge young, so the frequency distribution of annual productivity was strongly zero-inflated. Exploratory data analysis found that annual productivity did not differ between males or females aged 2 y and  $\geq 3$  y, so we considered only two age classes for both sexes: 1 y and  $\geq 2$  y. Habitat type and group size were strong predictors, and female age a marginal predictor of whether a female fledged any young or not (Table 1m, Fig. 6). However, the count model, restricted to females that did fledge at least one offspring, found no effect of habitat or female age, but a marginal effect of group size on the total number of young fledged in the season (Table 1m). The combined predictions of the ZIP model estimate that average annual productivity ( $\pm$  1SE) was: 130% greater for females breeding with one or more helpers ( $1.47 \pm 0.04$  fledged young) than females breeding without a helper ( $0.64 \pm 0.01$  fledged young); 71% greater for females breeding in dune thicket habitat ( $1.07 \pm 0.04$  fledged young) than in sand-plain fynbos habitat ( $0.63 \pm 0.02$  fledged young); and 86% greater for females  $\geq 2$  y old ( $0.85 \pm 0.03$  fledged young) than 1st-year females ( $0.46 \pm 0.03$  fledged young).

Table 2. Summary of model selection results for the nest survival of Karoo scrub-robins during each of the egg and nestling stages. Factors in the models included year (2004-2006), habitat (dune thicket, sandplain fynbos), linear (LT), quadratic (QT) or exponential (ET) time trends for the effect of both season and nest age, group size (pair, cooperative group), brood size (1-2 or 3, for nestling stage only), and a model with constant daily nest survival (.) K = number of parameters.

Model	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	Weight	K	Deviance
<b>Egg stage (laying and incubation):</b>					
S <sub>season</sub> ET + nest age LT + habitat + y + group size	1598.2	0.00	0.492	7	1584.1
S <sub>season</sub> ET + nest age LT + habitat + y	1599.7	1.51	0.232	6	1587.6
S <sub>season</sub> LT + nest age LT + habitat + y	1600.2	2.05	0.177	6	1588.2
S <sub>season</sub> LT + QT + nest age LT + habitat + y	1601.6	3.43	0.089	7	1587.6
S <sub>season</sub> ET + nest age ET + habitat + y	1608.1	9.96	0.003	6	1596.1
S <sub>season</sub> ET + habitat + y	1609.0	10.84	0.002	5	1599.0
S <sub>season</sub> ET + nest age LT + habitat	1609.5	11.36	0.002	4	1601.5
S <sub>nest age</sub> LT + habitat + y	1616.8	18.67	0.000	5	1606.8
S <sub>season</sub> ET + nest age LT + y	1628.1	29.89	0.000	5	1618.0
S <sub>(.)</sub>	1667.9	69.76	0.000	1	1665.9
<b>Nestling stage:</b>					
S <sub>season</sub> ET + brood size + nest age LT	734.6	0.00	0.236	4	726.6
S <sub>season</sub> ET + brood size + nest age LT + group size	735.4	0.73	0.163	5	725.3
S <sub>season</sub> ET + brood size	735.4	0.81	0.158	3	729.4
S <sub>season</sub> ET + nest age LT	736.1	1.49	0.112	3	730.1
S <sub>season</sub> ET + brood size + nest age ET	736.2	1.60	0.106	4	728.2
S <sub>season</sub> ET + brood size + nest age LT + habitat	736.5	1.90	0.091	5	726.5
S <sub>season</sub> ET + brood size + nest age LT + habitat + y	740.4	5.77	0.013	7	726.3
S <sub>season</sub> LT + QT + brood size + nest age LT + habitat + y	741.9	7.27	0.006	8	725.8
S <sub>season</sub> LT + brood size + nest age LT + habitat + y	742.9	8.25	0.004	7	728.8
S <sub>brood size</sub> + nest age LT	751.2	16.58	0.000	3	745.3
S <sub>(.)</sub>	753.2	18.59	0.000	1	751.2

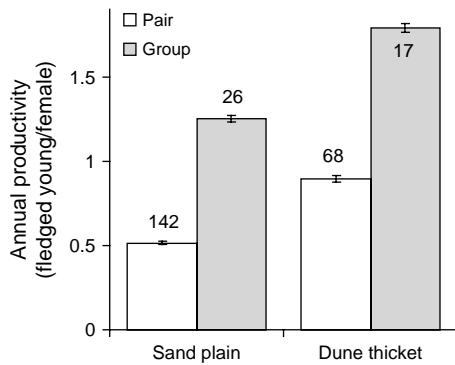


Figure 6. Annual productivity (fledged young/female) of females breeding with (group) or without (pair) one or more helpers in each of sand-plain fynbos and dune thicket habitat types. Figures show the predictions ( $\pm 1$  SE) of a ZIP model with habitat, group type and female age as predictors in the zero-inflation model, and group type as a predictor in the count model. Sample size is number of female/year observations (see Table 1m).

## Discussion

The presence of, in most cases a single helper correlated positively with the annual production of young by Karoo scrub-robin breeding pairs. This positive correlation may be a direct consequence of helper effects, or it may be attributed to greater individual quality of breeders or territories associated with cooperative groups (Legge 2000, Eguchi et al. 2002, Cockburn et al. 2008), given that breeders on such territories have typically been successful in raising young in a prior season if they have retained offspring acting as helpers (Dickinson and Hatchwell 2004). By directly measuring helper contributions to the care of the breeding female and offspring, our study provides strong evidence of direct helper effects on multiple components of breeding performance, particularly the provisioning of dependent young. Some of these effects were confirmed in our comparisons of the performance of pairs in sequential years with and without helpers, but we cannot discount a possible partial contribution of breeder and territory quality in the observed differences between pairs breeding with and without helpers.

### Helper contributions to allo-feeding

An increase in parental visits to the nest often increases the risk of the nest being located by predators (Martin et al. 2000). Despite this risk in a predator-rich environment, male Karoo scrub-robins visited the nest at a relatively low rate to allo-feed the incubating female. Although helpers allo-fed at a lower rate than the breeding male, breeding males with helpers did not allo-feed at a lower rate than breeding males without helpers, meaning that helper allo-feeding was additive to breeder allo-feeding. Thus, the overall allo-feeding rate tended to be higher to females with helpers than females without helpers (Fig. 1), but the effect was only significant in the paired comparisons. Female nest attentiveness increased with allo-feeding rate (Table 1b), similar to analogous studies of allo-feeding (Lyon and Montgomerie 1985, Lifjeld and Slagsvold 1986). Potential

fitness benefits of increased allo-feeding are that increased nest attentiveness may shorten the incubation period (Martin et al. 2007) and reduce the risk of nest predation (Fontaine and Martin 2006). However, the small effect size of allo-feeding on nest attentiveness in the Karoo scrub-robin (Table 1b) suggests that such benefits are likely to be of marginal importance, particularly in the context of helper-mediated benefits.

### Helper contributions to nestling care and correlates with offspring fitness

Helpers provisioned nestlings at almost the same rate as the breeding male at both nestling ages (Fig. 3). Consequently, provisioning rates were higher at group nests than pair nests, a result that was not influenced by breeder age (Table 1c, Fig. 2). Helper provisioning is common among cooperative breeders (Cockburn 1998), but species differ in the way breeders respond, either using the help to produce extra or higher-quality offspring, or reducing their own parental expenditure. In a comparative analysis of 27 cooperative species, Hatchwell (1999) found support for the idea that care is additive when nestling starvation is frequent, but parents exhibit compensatory reductions in care when starvation in the absence of helpers is rare. We found evidence of compensatory reductions by females, but not males, and only when the nestlings were small, and therefore requiring less food (Fig. 3). Females with one or more helpers reduced their provisioning rates to 2-d-old nestlings, with no increase in nestling brooding time. Nestling starvation was relatively common in the absence of helpers and occurred at only one nest with helpers, so our results support the predictions of Hatchwell (1999).

The substantial increase in average provisioning rate for groups compared with pairs had strong effects on nestling mass, condition, and post-fledging survival. First, the incidence of nestling starvation was lower within cooperative groups than pairs (Table 1g), an effect that has been observed in other cooperative breeders (Hatchwell 1999, Woxvold and Magrath 2005). Second, nestlings of cooperative groups had a greater body mass at nine days of age (Table 1h, Fig. 4). Third, nestlings that were heavier at nine days had higher survival during the first three weeks post-fledging (Table 1j, Fig. 5). Early rearing conditions can have important fitness consequences, for both survival and fecundity in a wide variety of animals (Mousseau and Fox 1998, Lindström 1999, Metcalfe and Monaghan 2001, Cam et al. 2003). Among cooperatively-breeding species, helper-mediated improvements in offspring rearing conditions, particularly mass at fledging or independence can improve survival to breeding age (Russell et al. 2002, Hatchwell et al. 2004, Hodge 2005, Ridley 2007), and increase the reproductive potential of offspring (Solomon 1994, Hodge 2005, Ridley and Raihani 2007, Russell et al. 2007). At present, we lack sufficient data to test for helper effects on offspring fitness beyond survival to independence.

### Helper correlates with nest survival

Karoo scrub-robin females select the nest site and build the nest, with limited assistance from the male. Breeder age or

experience has been shown to correlate positively with the selection of safer nest sites in several species (Marzluff 1988, Komdeur 1996, Hatchwell et al. 1999). Yet, we found no support for an effect of female age on nest survival during the most vulnerable egg stage. Daily nest mortality during the egg stage, mostly from predation, was substantially lower among pairs breeding with one or more helpers than among pairs breeding alone (Table 2). Consequently, nests of groups had a 37.5% greater probability of surviving to hatch than nests of pairs breeding alone. Helpers have been shown to reduce nest predation in a number of cooperatively breeding species, including Florida scrub-jay *Aphelocoma coerulescens* (Woolfenden and Fitzpatrick 1990), bicolor wren *Campylorhynchus griseus* (Austad and Rabenold 1985), and white-winged chough *Corcorax melanorhamphos* (Boland 1998). Improved nest defence may be achieved by helper effects on increased vigilance (McGowan and Woolfenden 1989), enhanced group distraction or mobbing behaviours (Boland 1998), as well as female behaviours such as increased nest attentiveness (Fontaine and Martin 2006). In the Karoo scrub-robin, male breeders and helpers act as sentinels at the nest and engage in vocal mobbing of potential nest predators, and females increase nest attentiveness in groups, but the effectiveness of these behaviours, and the helper contribution thereto, remain untested.

The trend of decreasing nest mortality rate as nests age through the incubation period fits well with the pattern expected if predators locate less well-concealed nests earlier, and the remaining pool of nests become progressively more difficult for predators to locate (Martin et al. 2000). This effect is expected to continue through the nestling period, but be counter-acted by a trend of increasing nest predation as either (a) the provisioning rate, and therefore the number of parental visits to the nest increase with nestling age (Martin et al. 2000, Muchai and Plessis 2005), and/or (b) begging intensity increases with nestling age (Kilner and Johnstone 1997), given that begging intensity can increase nest predation risk (Haskell 1994, Leech and Leonard 1997, Briskie et al. 1999). We indeed found that daily nest mortality increased with nestling age, and was 27% lower among broods of 1–2 nestlings than broods of three nestlings. However, group size effects on nestling predation risk are more difficult to interpret. On the one hand, nestling predation is expected to be greater at nests of cooperative groups, because of the helper-mediated increase in nest visitation rate. On the other hand, the greater food delivery rates are expected to reduce the intensity of nestling begging, leading to a reduction in nestling predation risk at nests of cooperative groups. We found that nest mortality during the nestling period, mostly from predation, was marginally lower at nests of cooperative groups (Table 2). This suggests that any increase in nest predation risk from the increased nest visitation rate may be offset by (a) a reduction in nestling begging intensity associated with the greater food delivery rates, and/or (b) helper-mediated improvements in nest defence during the nestling stage. Thus, groups can provide benefits through increased provisioning and still reduce possible costs (i.e., increased predation risk) at the same time, yielding a double-benefit.

## Helper effects on female investment and annual productivity

When helpers improve conditions for the breeding female and/or the conditions for raising young, and the availability of helpers is predictable, theory predicts that females will increase clutch size (Charnov and Krebs 1974, Winkler 1987). Yet, such a response has rarely been demonstrated (Woxvold and Magrath 2005), and in some species, females even reduce investment in egg size in response to helper benefits (Russell et al. 2007). We found that Karoo scrub-robin females laid significantly larger clutches when breeding in a cooperative group (Table 1). This result is unlikely to be confounded by differences in territory quality and/or breeder age or quality between pairs and cooperative groups, as the effect was still apparent when the analysis was restricted to only females that nested with and without helpers in different years. Yet, the average increase in clutch size of just 6% (0.16 more eggs) is relatively small when compared to the magnitude of the helper benefits. By comparison, female apostlebirds *Struthidea cinerea*, which lay clutches of 2–5 eggs, increase clutch size by an average of 0.67 eggs for each additional group member in the group-size range of 2–5 members (Woxvold and Magrath 2005), and dunnocks *Prunella modularis* increase average clutch size from 3.79 to 4.19 (11%) when breeding polyandrously with two males, in response to the additional care provided by the subordinate second male that increases fledging success by 28% (Davies and Hatchwell 1992).

Annual productivity correlated strongly with the presence of helpers, being 130% greater for females breeding with one or more helpers than females breeding without a helper. Despite a greater incidence of nestling starvation for pairs, annual productivity among birds that fledged at least one young was influenced only marginally by group size. Instead, the strong effect of group size on overall annual productivity was associated largely with cooperative groups having a higher probability of fledging any young, which is in turn related to the strong effect of group size on nest survival from predation. This result is unlikely to be confounded by differences in territory and/or breeder quality between pairs and cooperative groups, for two reasons. First, our analyses control for an effect of female age on annual productivity. Second, despite a strong effect of habitat on annual productivity (productivity higher in dune thicket because of lower nest predation), independent of the effect of group size (Fig. 6), cooperative groups did not occupy a greater proportion of territories in dune thicket habitat relative to sand-plain fynbos (14% and 15% respectively).

Helper improvements of breeder performance, particularly the number of young fledged, are typically associated most strongly with elevated feeding rates to dependent young and reduced starvation (Davies and Hatchwell 1992, Hatchwell 1999, Dickinson and Hatchwell 2004). Although Karoo scrub-robin helpers have a significant direct effect in elevating nestling feeding rates and reducing nestling starvation, this mechanism of increasing the number of young fledged was minor compared with a much stronger group-size effect on nest survival during the egg stage. Unfortunately, we are not yet able to confirm the mechanism whereby helpers improve nest survival from predation during

the egg stage. Nonetheless, the helper-mediated improvement in nestling provisioning led to increased nestling body mass. Nestling mass correlated positively with survival in the first three weeks after fledging, and could potentially have an important effect on long-term fitness (Ridley and Raihani 2007). Our results highlight the value of considering multiple mechanisms whereby helpers may contribute to the breeding performance of the breeding pair; a focus on any single mechanism may overlook important alternative routes to the evolution of cooperative breeding.

*Acknowledgements* – We thank the many assistants that helped locate and monitor nests or review video tapes, particularly D. Nkosi, D. Gaglio, P. Becker, J. Taubman, P.-Y. Perroi, J. Shew, S. Auer, A. Chalfoun, K. Decker, and R. Bassar. G. Greef and H. Westman facilitated our work at ESKOM's Koeberg Nature Reserve. G. Fick and the late F. Potgieter kindly provided weather data. Andrew Cockburn, Amanda Ridley and two anonymous reviewers provided useful comments on earlier drafts. Capture, banding and sampling activities were licensed by Cape Nature and SAFRING, the South African banding scheme, and approved by the Animal Ethics Committee, University of Cape Town.

## References

- Anava, A., Kam, M., Shkolnik, A. and Degen, A. A. 2001. Effect of group size on field metabolic rate of Arabian babblers provisioning nestlings. – *Condor* 103: 376–380.
- Austad, S. N. and Rabenold, K. N. 1985. Reproductive enhancement by helpers and an experimental inquiry into its mechanism in the bicolor wren. – *Behav. Ecol. Sociobiol.* 17: 19–27.
- Boland, C. R. J. 1998. Helpers improve nest defence in cooperatively breeding white-winged couds. – *Emu* 98: 320–324.
- Briskie, J. V., Martin, P. R. and Martin, T. E. 1999. Nest predation and the evolution of nestling begging calls. – *Proc. R. Soc. B* 266: 2153–2159.
- Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. – Springer, New York.
- Cam, E., Monnat, J. Y. and Hines, J. E. 2003. Long-term fitness consequences of early conditions in the kittiwake. – *J. Anim. Ecol.* 72: 411–424.
- Charnov, E. L. and Krebs, J. R. 1974. On clutch-size and fitness. – *Ibis* 116: 217–219.
- Clutton-Brock, T. 2002. Breeding together: kin selection and mutualism in cooperative vertebrates. – *Science* 296: 69–72.
- Clutton-Brock, T. H., Gaynor, D., Kansky, R., Maccoll, A. D., McIlrath, G., Chadwick, P., Brotherton, P. N., O'riain, J. M., Manser, M. and Skinner, J. D. 1998. Costs of cooperative behaviour in suricates (*Suricata suricatta*). – *Proc. R. Soc. B* 265: 185–190.
- Cockburn, A. 1998. Evolution of helping behavior in cooperatively breeding birds. – *Ann. Rev. Ecol. Syst.* 29: 141–177.
- Cockburn, A., Sims, R. A., Osmond, H. L., Green, D. J., Double, M. C. and Mulder, R. A. 2008. Can we measure the benefits of help in cooperatively breeding birds: the case of the superb fairy-wren, *Malurus cyaneus*? – *J. Anim. Ecol.* 77: 430–438.
- Crawley, M. J. 2002. Statistical computing: an introduction to data analysis using S-Plus. – Wiley, Chichester.
- Davies, N. B. and Hatchwell, B. J. 1992. The value of male parental care and its influence on reproductive allocation by male and female dunnocks. – *J. Anim. Ecol.* 61: 259–272.
- Dickinson, J. L. and Hatchwell, B. J. 2004. Fitness consequences of helping. – In: Koenig, W. D. and Dickinson, J. L. (eds). *Ecology and evolution of cooperative breeding in birds*. Cambridge Univ. Press, pp. 48–66.
- Dinsmore, S. J., White, G. C. and Knopf, F. L. 2002. Advanced techniques for modeling avian nest survival. – *Ecology* 83: 3476–3488.
- Eguchi, K., Yamagishi, S., Asai, S., Nagata, H. and Hino, T. 2002. Helping does not enhance reproductive success of cooperatively breeding rufous vanga in Madagascar. – *J. Anim. Ecol.* 71: 123–130.
- Emlen, S. T. 1991. Evolution of cooperative breeding in birds and mammals. – In: Krebs, J. R. and Davies, N. B. (eds). *Behavioural ecology: an evolutionary approach*. Blackwell, Oxford, pp. 301–337.
- Fontaine, J. J. and Martin, T. E. 2006. Parent birds assess nest predation risk and adjust their reproductive strategies. – *Ecol. Lett.* 9: 428–434.
- Hamilton, W. D. 1964. The genetical evolution of social behavior. Parts 1 and 2. – *J. Theor. Biol.* 7: 1–52.
- Haskell, D. 1994. Experimental evidence that nestling begging behaviour incurs a cost due to nest predation. – *Proc. R. Soc. B* 257: 161–164.
- Hatchwell, B. J. 1999. Investment strategies of breeders in avian cooperative breeding systems. – *Am. Nat.* 154: 205–219.
- Hatchwell, B. J. and Komdeur, J. 2000. Ecological constraints, life history traits and the evolution of cooperative breeding. – *Anim. Behav.* 59: 1079–1086.
- Hatchwell, B. J., Russell, A. F., Fowlie, M. K. and Ross, D. J. 1999. Reproductive success and nest-site selection in a cooperative breeder: effect of experience and a direct benefit of helping. – *Auk* 116: 355–363.
- Hatchwell, B. J., Russell, A. F., Maccoll, A. D. C., Ross, D. J., Fowlie, M. K. and McGowan, A. 2004. Helpers increase long-term but not short-term productivity in cooperatively breeding long-tailed tits. – *Behav. Ecol.* 15: 1–10.
- Heinsohn, R. and Legge, S. 1999. The cost of helping. – *Trends Ecol. Evol.* 14: 53–57.
- Heinsohn, R. G. 2004. Parental care, load-lightening and costs. – In: Koenig, W. D. and Dickinson, J. L. (eds). *Ecology and evolution of cooperative breeding in birds*. Cambridge Univ. Press, pp. 67–80.
- Hodge, S. J. 2005. Helpers benefit offspring in both the short and long-term in the cooperatively breeding banded mongoose. – *Proc. R. Soc. B* 272: 2479–2484.
- Ihaka, R. and Gentleman, R. 1996. R: a language for data analysis and graphics. – *J. Comput. Graph. Stat.* 5: 299–314.
- Kilner, R. and Johnstone, R. A. 1997. Begging the question: are offspring solicitation behaviours signals of need? – *Trends Ecol. Evol.* 12: 11–15.
- Komdeur, J. 1994. Experimental evidence for helping and hindering by previous offspring in the cooperative-breeding Seychelles warbler, *Acrocephalus sechellensis*. – *Behav. Ecol. Sociobiol.* 34: 175–186.
- Komdeur, J. 1996. Influence of age on reproductive performance in the Seychelles warbler. – *Behav. Ecol.* 7: 417–425.
- Komdeur, J. 2006. Variation in individual investment strategies among social animals. – *Ethology* 112: 729–747.
- Langen, T. A. and Vehrencamp, S. L. 1999. How white-throated magpie-jay helpers contribute during breeding. – *Auk* 116: 131–140.
- Leech, S. M. and Leonard, M. L. 1997. Begging and the risk of predation in nestling birds. – *Behav. Ecol.* 8: 644–646.
- Legge, S. 2000. The effect of helpers on reproductive success in the laughing kookaburra. – *J. Anim. Ecol.* 69: 714–724.
- Lifjeld, J. T. and Slagsvold, T. 1986. The function of courtship feeding during incubation in the pied flycatcher, *Ficedula hypoleuca*. – *Anim. Behav.* 34: 1441–1453.

- Lindström, J. 1999. Early development and fitness in birds and mammals. – *Trends Ecol. Evol.* 14: 343–348.
- Lloyd, P. 1999. Rainfall as a breeding stimulus and clutch size determinant in South African arid-zone birds. – *Ibis* 141: 637–643.
- Low, A. B. and Rebelo, A. G. 1996. Vegetation of South Africa, Lesotho and Swaziland. – Dept of Environm. Affairs and Tourism, Pretoria.
- Lyon, B. E. and Montgomerie, R. D. 1985. Incubation feeding in snow buntings: female manipulation or indirect male parental care? – *Behav. Ecol. Sociobiol.* 17: 279–284.
- Maklakov, A. A. 2002. Snake-directed mobbing in a cooperative breeder: anti-predator behaviour or self-advertisement for the formation of dispersal coalitions? – *Behav. Ecol. Sociobiol.* 52: 372–378.
- Martin, T. E., Auer, S. K., Bassar, R. D., Niklison, A. M. and Lloyd, P. 2007. Geographic variation in avian incubation periods and parental influences on embryonic temperature. – *Evolution* 61: 2558–2569.
- Martin, T. E., Scott, J. and Menge, C. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. – *Proc. R. Soc. B* 267: 2287.
- Marzluff, J. M. 1988. Do pinyon jays alter nest placement based on prior experience? – *Anim. Behav.* 36: 1–10.
- McGowan, K. J. and Woolfenden, G. E. 1989. A sentinel system in the Florida scrub jay. – *Anim. Behav.* 37: 1000–1006.
- Metcalf, N. B. and Monaghan, P. 2001. Compensation for a bad start: grow now, pay later? – *Trends Ecol. Evol.* 16: 254–260.
- Mousseau, T. A. and Fox, C. W. 1998. Maternal effects as adaptations. – Oxford Univ. Press.
- Muchai, M. and Plessis, M. A. 2005. Nest predation of grassland bird species increases with parental activity at the nest. – *J. Avian Biol.* 36: 110–116.
- Nalwanga, D., Lloyd, P., Du Plessis, M. A. and Martin, T. E. 2004. Nest-site partitioning in a strandveld shrubland bird community. – *Ostrich* 75: 250–258.
- Oatley, T. B. 2005. Karoo scrub-robin, *Cercotrichas coryphaeus*. – In: Hockey, P. A. R., Dean, W. R. J. and Ryan, P. G. (eds). Roberts birds of southern Africa, 7th edition. The Trustees of the John Voelcker Bird Book Fund, Cape Town, pp. 942–943.
- Poiani, A. 1992. Feeding of the female breeder by male helpers in the bell miner, *Manorina melanophrys*. – *Emu* 92: 233–237.
- Quinn, G. P. and Keough, M. J. 2002. Experimental design and data analysis for biologists. – Cambridge Univ. Press.
- Radford, A. N. 2004. Incubation feeding by helpers influences female nest attendance in the green woodhoopoe, *Phoeniculus purpureus*. – *Behav. Ecol. Sociobiol.* 55: 583–588.
- Richardson, D. S., Burke, T. and Komdeur, J. 2002. Direct benefits and the evolution of female-biased cooperative breeding in Seychelles warblers. – *Evolution* 56: 2313–2321.
- Ridley, A. R. 2007. Factors affecting offspring survival and development in a cooperative bird: social, maternal and environmental effects. – *J. Anim. Ecol.* 76: 750–760.
- Ridley, A. R. and Raihani, N. J. 2007. Variable postfledging care in a cooperative bird: causes and consequences. – *Behav. Ecol.* 18: 994–1000.
- Russell, A. F., Clutton-Brock, T. H., Brotherton, P. N. M., Sharpe, L. L., McIlrath, G. M., Dalerum, F. D., Cameron, E. Z. and Barnard, J. A. 2002. Factors affecting pup growth and survival in co-operatively breeding meerkats, *Suricata suricatta*. – *J. Anim. Ecol.* 71: 700–709.
- Russell, A. F., Langmore, N. E., Cockburn, A., Astheimer, L. B. and Kilner, R. M. 2007. Reduced egg investment can conceal helper effects in cooperatively breeding birds. – *Science* 317: 941–944.
- Russell, A. F., Young, A. J., Spong, G., Jordan, N. R. and Clutton-Brock, T. H. 2007. Helpers increase the reproductive potential of offspring in cooperative meerkats. – *Proc. R. Soc. B* 274: 513.
- Solomon, N. G. 1994. Effect of the pre-weaning environment on subsequent reproduction in prairie voles, *Microtus ochrogaster*. – *Anim. Behav.* 48: 331–341.
- Spottiswoode, C. N. 2007. Phenotypic sorting in morphology and reproductive investment among sociable weaver colonies. – *Oecologia* 154: 589–600.
- Walters, J. R. 1990. The red-cockaded woodpecker: a primitive cooperative breeder. – In: Stacey, P. B. and Koenig, W. D. (eds). Cooperative breeding in birds: long term studies of ecology and behaviour. Cambridge Univ. Press, pp. 67–102.
- Welsh, A. H., Cunningham, R. B., Donnelly, C. F. and Lindenmayer, D. B. 1996. Modelling the abundance of rare species: statistical models for counts with extra zeros. – *Ecol. Model.* 88: 297–308.
- White, G. C. and Burnham, K. P. 1999. Program MARK: survival estimation from populations of marked animals. – *Bird Study* 46: 120–139.
- Winkler, D. W. 1987. A general model for parental care. – *Am. Nat.* 130: 526.
- Woolfenden, G. E. and Fitzpatrick, J. W. 1990. Florida scrub-jays: a synopsis after 18 years study. – In: Stacey, P. B. and Koenig, W. D. (eds). Cooperative breeding in birds: long-term studies of ecology and behaviour. Cambridge Univ. Press, pp. 239–266.
- Woxvold, I. A. and Magrath, M. J. L. 2005. Helping enhances multiple components of reproductive success in the cooperatively breeding apostlebird. – *J. Anim. Ecol.* 74: 1039–1050.
- Zeileis, A., Kleiber, C. and Jackman, S. 2007. Regression models for count data. – Rep. 53. Dept. of Stat. and Math., Wirtschaftsuniversität, Wien. [Available at: <http://statmath.wu-wien.ac.at/>]