Helpers compensate for age-related declines in parental care and offspring survival

Short title: Cooperation and parental senescence

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ABSTRACT

Offspring from elderly parents often have a lower survival probability because of parental senescence. In cooperatively breeding species, alloparental care provided by helpers is predicted to mitigate age-dependent declines in parental performance. We tested this prediction in the facultatively cooperative-breeding Seychelles warbler (*Acrocephalus sechellensis*). We find that the provisioning rates of female, but not male, breeders decline sharply with age, and that female breeders reduce their provisioning rates when helpers are present. However, helpers increase the total amount of food provided to the offspring and almost fully compensate for the lower provisioning rates of older female breeders. In territories without helpers, offspring survival declines with age of the female breeder, but not with age of the male breeder, but this decline is counteracted when helpers are present. These results suggest that alloparental care alleviates the costs of senescence for breeders, which may promote cooperative breeding in families with elderly parents.

INTRODUCTION

Senescence – a progressive age-dependent decline in reproductive performance and survival, e.g. as a result of a decline in physiological condition – occurs in a wide variety of organisms (*1*, *2*). An increasing number of studies have investigated how age-dependent declines in reproduction and survival between individuals within a species are shaped by environmental conditions, individual characteristics and trade-offs between early-life reproductive investment and late-life performance(*1, 3, 4*). However, surprisingly little is known about how, and to what extent, the social environment explains inter-individual variation in senescence(*5*-*7*).

In many cooperatively breeding species, care for offspring is shared between the dominant breeding pair and a variable number of sexually mature subordinate helpers that provide alloparental care(*8*). The dominant breeders often reduce the amount of care they provide to their offspring in response to being helped, which may improve their own survival and future reproductive output (*9, 10*). Furthermore, the alloparental care provided by helpers may reduce offspring mortality when the total amount of care delivered to the offspring is increased(*9, 10*), as has been shown in many species, including humans(*11*).

Negative associations between parental age and the survival of offspring are frequently observed in wild animals(e.g. *12, 13*). Such age-dependent declines in offspring survival could arise because elderly parents produce offspring that are of lower intrinsic (e.g. genetic) quality(*14*) or are less able to provide sufficient parental care. While several studies have provided evidence for late-life declines in foraging efficiency (*15-17*), there is a surprising lack of studies that have investigated how the amount of parental care provided to the offspring changes in older individuals. Furthermore, if the ability to provide parental care declines with age, the additional care provided to offspring by helpers might alleviate the negative effects of parental senescence on parental care and offspring survival in cooperatively breeding species. While the few studies that have tested this prediction in mammals found no support for it(*18, 19*), studies on other taxonomic groups with different modes of reproduction (e.g. birds, insects), are lacking and clearly needed to determine whether cooperation can buffer the adverse effects of senescence.

In this study, we investigated the impact of parental age and alloparental care on the rate of food provisioning to offspring and offspring first-year survival. This was done using the long-term individual-level dataset collected on the Cousin Island population of the Seychelles warbler (*Acrocephalus sechellensis*). In this facultatively cooperative-breeding bird species, the pair-bonded dominant breeding pair (dominants) often have one or two subordinates of either sex in their territory. Some of these subordinates help the dominants with various aspects of reproductive duties, including provisioning offspring(*20*). This is an excellent system in which to study the effects of cooperative breeding and senescence on offspring survival because the almost complete absence of emigration means that mortality is not confounded by dispersal and because extrinsic mortality is low due to a lack of predation on adults. This, combined with intensive monitoring resulting in high annual resighting rates, means that individuals can be followed throughout their entire lives(*7*). Furthermore, because only one third of all subordinates help(*21*), it is possible to disentangle the benefits of help from group size(*21, 22*), which is challenging or impossible in many cooperatively breeding species (e.g. subordinates may be the result rather than the cause of high reproductive success(*23*)).

Here, we test whether nestling provisioning rate and offspring survival decline with the ages of male and female dominant breeders and whether helpers mitigate such declines. Our results suggest that alloparental care alleviates the costs of senescence for female breeders and their offspring, which may promote cooperative breeding in elderly breeders.

RESULTS

Provisioning rates

Provisioning rates of dominant females to nestlings were on average 24% higher than those of males (mean ± SE = 9.78 ± 0.34 vs. 7.88 ± 0.30 feeds per hour) during the same observation session (Wilcoxon matched-pairs test: V = 10882, $P < 0.001$, n = 186; Figure 1). Provisioning rates of dominant males and females were weakly, but positively correlated (r = 0.19, $t_{184} = 2.66$, $P = 0.008$).

The provisioning rates of dominant females, with and without helpers, strongly declined with their age (Table 1, Figure 1). Overall, dominant females with a helper had 16% lower provisioning rates (mean ± SE = 8.85 ± 0.44 (n = 81) feeds per hour with help vs. 10.49 ± 0.49 (n = 105) without help; Table 1, Figure 1). Provisioning rates were not associated with the total number of subordinates (i.e. helpers and non-helpers) that was present in the territory (Table 1). The effects of dominant female age and helper presence remained significant when we accounted for selective disappearance effects (Supplementary Table 1). Although the raw data (Figure 1) suggested that the impact of helper presence might be larger for younger dominant females, there was little evidence for this as the interactions between dominant female age and helper presence were not significant (Table 1).

In contrast to dominant females, provisioning rates of dominant males were not significantly associated with their age and helper presence (Table 1, Figure 1). Dominant male provisioning rates were lower when more subordinates were present in the territory (Table 1), but this effect was no longer statistically significant after accounting for dominant male lifespan (Supplementary Table 1).

The total provisioning rate (i.e. by all feeders at the nest combined) was, on average, 26% higher in territories with helpers than in territories without (mean ± SE = 23.95 ± 7.65 (n = 81) vs. 18.96 ± 7.59 (n = 105) feeds per hour; Table 2, Figure 2). As expected based on the analyses of dominant female and male provisioning rates presented above, the total provisioning rate declined with age of the dominant female (Figure 2). The significant interaction between the age of the dominant female and helper presence (Table 2) indicated that for nests with helpers, the decline in total provisioning rate due to female age was less severe compared to the decline for nests without helpers (Figure 2). Repeating these analyses separately for nests with and without helpers showed that the total provisioning rate declined with dominant female age when no helpers aided in provisioning (Figure 2; GLMM: $\beta \pm SE = -0.28 \pm 0.08$, $z = -3.71$, n = 105, $P < 0.001$), but did not significantly decline when helpers were present (Figure 2; GLMM: $\beta \pm SE = -0.07 \pm 0.07$, $z = -0.90$, n = 81, $P = 0.368$). The total provisioning rate was not significantly associated with dominant male age or its interaction with helper presence (Table 2, Figure 2).

Offspring survival

The first-year survival probability of offspring declined strongly with age of the dominant female (Table 3, Figure 3). The marginally non-significant quadratic effect of age for dominant females indicated that the rate of this decline tended to become steeper for older females (Table 3). Offspring survival was not associated with age of the dominant male (Table 3) and the number of subordinates in the territory. Although, overall, we detected no effect of helpers on offspring survival (Table 3), the significant interaction between dominant female age and helper presence indicated that helpers mitigated, or even reversed, the age-dependent decline in offspring survival (Table 3, Figure 3a). This effect remained significant after accounting for the lifespan of the dominants (Supplementary Table 2). Separate analyses for offspring survival with and without helpers show that offspring survival declined with dominant female age when no helpers aided in provisioning (Figure 3; GLMM: β dominant female age ± SE = -0.93 ± 0.30, $z = -3.09$, n = 242, $P = 0.002$). However, this decline was not observed when helpers were present (Figure 3; GLMM: β dominant female age ± SE = 0.61 ± 0.63, $z = 0.97$, n = 55, $P = 0.331$).

DISCUSSION

We found that nestling provisioning rate of dominant female, but not male, Seychelles warblers declined with age. This decline was associated with a lower total provisioning rate to nestlings in territories with older dominant females that did not receive help from subordinates. However, the total provisioning rate to nests from older female dominants was not reduced when a helper was present, which indicates that helpers mitigated the age-dependent decline in provisioning by dominant females. Similarly – and possibly as a consequence of the different amounts of parental care provided to the offspring – the first-year survival of offspring from unassisted pairs declined with the age of the dominant female, but not with age of the dominant male, but the presence of helpers counteracted this decline.

In the Seychelles warbler, dominant females invest more in parental care than dominant males, as only females incubate the egg and females have higher provisioning rates(*20*). The lower parental investment of dominant males may potentially be explained by the high levels of extra-group paternity in this species(*24*). Males with lower confidence in paternity may be predicted to provide parental care at a rate that is well below their maximum sustainable rate(*25, 26*)’ but see(*27*). The sex that invests more in parental care is predicted to show a higher rate of parental care senescence(*28*). The steep age-dependent decline in provisioning in dominant females, compared to no such decline in dominant males, in our study concurs with this prediction. One explanation for this greater decline in dominant females than in males is that females may not be able to maintain their initially higher provisioning rate (Figure 1) when age-related declines in physiological condition occur. In addition, the fact that young dominant females show higher provisioning rates than young dominant males means that there is more scope for age-dependent declines in provisioning rates for dominant females. In contrast, incubation attendance - another energetically demanding aspect of parental care - does not decline in older females in the Seychelles warbler(*21*). An explanation for this may be that there is strong selection against reductions in incubation attendance because lower incubation attendance is associated with a higher risk of egg predation and thus failure of the entire reproductive attempt in this species(*29*).

We expected that offspring survival would be higher in territories with helpers, as was found in earlier studies(*20, 30*). Contrary to this expectation, we found that effects of helper presence on offspring survival were only apparent when older dominant females resided in the territory. This difference between the current study and earlier studies might be explained by increases in habitat quality and productivity over time. During the early stages of the overall Seychelles warbler study, higher-quality territories were more likely to have helpers than lower-quality territories and offspring were also more likely to survive in those higher-quality territories(*31, 32*). However, these effects were not detected in studies that analysed more recent data from the Seychelles warbler(*33, 34*). These studies suggested that these changes are the consequence of habitat restoration on the island that has led to a drastic decrease in among-territory variation in territory quality, an overall increase in territory quality and an island-wide increase in productivity. Further, earlier studies on Seychelles warblers did not eliminate the presence of subordinate co-breeders from the analyses, thus likely inflating the link between group productivity and helper presence.

The finding that helpers compensate for senescent declines in provisioning rate and offspring survival of dominant females extends the results of a previous study on Seychelles warblers(*21*), which showed that having helpers was associated with higher late-life survival and delayed senescence for dominant females. A similar effect has also been described for Alpine marmots (*Marmota marmota*)(*35*). Such late-life fitness benefits of breeding cooperatively lead to the prediction that older dominant females should be more inclined to recruit helpers to improve their survival and reproduction. Indeed, in the Seychelles warbler, subordinates are more likely to help when the dominant female is older, but no such relationship between helping propensity and age was observed for dominant males(*21*). Future studies may test if helpers also alleviate the costs of parental senescence in other cooperatively breeding species and explore the possibility that dominants strategically recruit helpers to mitigate the impact of senescence, which may lead to more cooperative breeding behaviour among elderly individuals.

Our results suggest that cooperative breeding in the Seychelles warbler may yield limited benefits overall in terms of improved offspring survival when viewed across dominants of all ages. However, the improvement in late-life fitness associated with cooperative breeding may lead to selection on helping behaviour and longer lifespan. Our study also illustrates that to reveal and understand the factors that shape variation in senescence rates, as well as the evolutionary forces behind the maintenance of cooperation, it may be important to apply a fine-scale assessment of the context in which these processes occur.

MATERIALS AND METHODS

Study design

The Seychelles warbler population on Cousin Island (29 ha; 4°20’ S, 55°40’ E) has been monitored since 1985. We used data collected between 1994 and 2016, when the population was most intensively studied. Each year, the population contains *ca* 320 colour-ringed adult individuals (> 96% of individuals colour ringed since 1997) of known sex and age in *ca* 115 territories(*24*). The warbler’s life history is characterized by high annual adult survival (84%), mostly single-egg clutches and a long period of offspring dependency for a small passerine (up to three months)(*20, 36*). Individuals that have acquired a dominant breeding position generally defend the same territory, with the same partner, until their death. However, the correlation between the age of the dominant male and female in a territory is weak (this study: $r = 0.17$, $t_{188} = 2.41$, $P = 0.017$), because individual dominants that die are replaced by a younger individual(*21*). Male and female dominants have similar breeding tenure duration, annual survival probabilities and rates of actuarial (survival) senescence(*36, 37*). Although warblers can breed year-round, the majority of breeding activity occurs in June–September (hereafter: main breeding season), when food availability is highest (breeding occurs in 94% of territories in this period(*31*). Female subordinates often (44% of female subordinates) lay an egg in the same nest as the dominant female(*24*). Extra-group paternity is common (ca 40% of offspring are sired by a dominant male from outside the breeding group, while subordinate males very rarely obtain paternity and extra-group maternity (i.e. conspecific brood parasitism) does not occur(*24*).

All territories were checked for the presence of colour-ringed individuals each year during the main breeding season. Any unringed individuals were caught using mist nets and given a combination of three colour rings and a British Trust for Ornithology metal ring. The age of individuals was determined based on the long-term demographic data and eye colour(*31*). As the annual resighting probability is high (0.97 for dominants and 0.83 for juveniles and subordinates(*30*)), and the emigration rate is low (0.10%; *38*), we could confidently assume that individuals that were not observed for two consecutive years had died in the first year that they were not seen. The dominance status of individuals (dominant or subordinate) in each territory was determined from behavioural interactions (affiliative behaviour and mate-guarding) during regular territory visits during the breeding season. We checked each territory for breeding activity at least once every two weeks by following the resident dominant female for at least 15 minutes. Once a nest was found, breeding attempts were monitored every 3-4 days until the nestling(s) fledged or the breeding attempt failed. To establish whether a subordinate provided nest care (helper) or not (non-helping subordinate) we conducted nest watches of at least 60 minutes (max. 90 minutes) during both the incubation and nestling provisioning stages(*21, 39*). We used the nest watches performed during the nestling provisioning stage to assess provisioning rates. Previous work on Seychelles warblers has shown that a single 60-minute nest watch provides a representative measure of provisioning rate at the focal nest throughout the provisioning stage(*39*).We recorded the number of provisioning events (i.e. each food delivery to the nestling) by each provisioning individual in the territory (i.e. the dominant female and male and any subordinates).

Data selection

For our provisioning rate analyses, we used nest watches from the main breeding season where the individuals bringing food to the nest were identified in >90% of provisioning events. We excluded watches where nestlings were still brooded, as brooding and food provisioning are mutually exclusive behaviours. For our analyses of offspring first-year survival, we used data from nestlings and fledglings that hatched during the main breeding season and for which the identity of the genetic parents could be assigned with at least 80% confidence based on 30 microsatellites using Masterbayes 2.52. These offspring were first caught and ringed as a nestling (10 – 17 days old) or as a fledgling (18 days – 3 months old) within their natal territory. Offspring that were ringed outside the main breeding period were excluded because the lower fieldwork intensity in periods outside the main breeding season means that the age and first-year survival cannot be estimated as reliably for these individuals. To avoid sibling competition confounding our results(*39*), we only included nests that contained a single nestling (which in this species is the vast majority of nests(*31*) and, for first-year survival, only nestlings and fledglings that originated from nests with a single nestling. As we were interested in the survival of offspring in relation to the age of the dominants, we excluded nestlings and fledglings that resulted from eggs laid by subordinate females (n = 31).

Statistical analyses

We used generalized linear mixed models (GLMM) with either a Poisson error structure and log link function (individual and total provisioning rate), or with a binomial error structure and logit link function (offspring first-year survival). The GLMMs were fitted with the package *lme4* version 1.1-12 in R version 3.2.5. We checked for collinearity between the fixed effects by calculating Variance Inflation Factors (VIF). As all VIF were < 3, collinearity was not an issue in our analyses. As variables are often on very different scales, and to aid interpretation of the model coefficients (e.g. in the presence of interaction terms), continuous predictor variables were standardized prior to analyses to a mean of zero and a standard deviation of 0.5 using package arm (v.1.9-1). Non-significant (i.e. $P > 0.05$) interactions, were removed from the models. This was done sequentially, in order of least significance and starting with the interactions between main effects and ending with the quadratic effects of age (see below). All other main effects remained in the models, irrespective of their significance. The model-predicted regression slopes in the figures were calculated from parameter estimates from the final models. For these predictions, all continuous covariates, except age (and age^2 if significant) of the focal dominant (male or female), were set to their mean.

Provisioning rates

First, we determined the impact of the dominant’s age and helper presence on the provisioning rates of dominant females and males. In the majority of territories with helpers there is only a single helper of either sex (one helper: 86%; two helpers: 14%; three helpers: <1%(*21*)), therefore we treated helper presence as a binary variable (Y/N). We included as random effects in the models the identity of the focal dominant bird, (i.e. the dominant male or female) to control for repeated observations of the same dominants, and year, to control for unmeasured annual variation. Because provisioning nest watches varied in duration, we included the log of nest watch duration as an offset in the analyses. Age of both dominants (i.e. the focal dominant and its partner), the quadratic effects of age (age^2) and helper presence (Y/N) were included as predictors. Importantly, we also included the interactions between age of the focal dominant (i.e. the dominant male or female) and helper presence to test the prediction that the slope of the relationship between the dominant's age and offspring provisioning rates changes depending on the presence of a helper. We also included the number of subordinates in the territory (i.e. both helping and non-helping subordinates) and its interaction with age of the focal dominant as predictors to disentangle the impact of helping subordinates from subordinate presence *per se*(*21, 22*). Then, for dominants for which the age of death was known (i.e. individuals that died within the study period and also were not translocated to other islands as part of an ongoing conservation program), we also included the age of death of the focal dominant as a predictor in the model. This accounts for the potential selective disappearance of lower-quality individuals with a shorter lifespan(*40*). The results of models that also included the age of death as a predictor did not differ qualitatively from those that did not (Supplementary Table 1), so the results are reported without age of death to maximise statistical power.

Second, we investigated how the total provisioning rate to a nestling by all provisioning group members varied with age of the dominants and helper presence. The predictors in this analysis were the same as in the analysis of the dominant’s provisioning rate, except that the identities of both the male and the female dominant were included as random effects and that interactions between age and helper presence and age and the number of subordinates were included for both the male and the female dominant.

Offspring first-year survival

First-year survival was a binary variable stating whether a nestling/fledgling survived until one year after the season in which it hatched. We investigated whether survival of offspring is related to the age of the dominant female, the dominant male, and helper presence. Year was included as a random effect. We did not include dominant male and female identity as random effects because their inclusion caused convergence issues. Moreover, the estimates of the variance that was explained by these effects were zero. Dominant male and female age and age^2, helper presence, the number of subordinates, the sex of the nestling/fledgling, and the interactions between dominant female and male age and helper presence and the number of subordinates were included as predictors. In addition, we included a binary variable stating whether an individual was first caught as a nestling or as a fledgling, as age at the first catch is positively associated with first-year survival (because fledglings have already survived the nestling stage). Similar as for the analysis of provisioning rates, the result of this model did not differ qualitatively when we reran this model on a subset of the data for which the age of death was known for both dominants to account for selective disappearance effects (Supplementary Table 2).

Ethics statement

The work was conducted with the permission of Nature Seychelles, the Seychelles Bureau of Standards and the Seychelles Ministry of Environment, Energy and Climate Change and complied with all local ethical guidelines and regulations.

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General

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Author contributions

MH designed the study, wrote the manuscript and analyzed the data. All authors performed research, including specifically; fieldwork – MH, DSR, SAK, and LAB; compilation of the dataset – MH, HLD

and LAB. All authors provided input into concepts and ideas, provided feedback on the analyses and critically revised and edited the manuscript. DSR, JK, TB, HLD, MH and SAK acquired funding. DSR, JK, TB and HLD coordinated the long-term study and maintained the database.

Competing interests

The authors declare no competing interests.

Data availability

All data will be deposited in the Figshare depository before publication

FIGURES AND TABLES

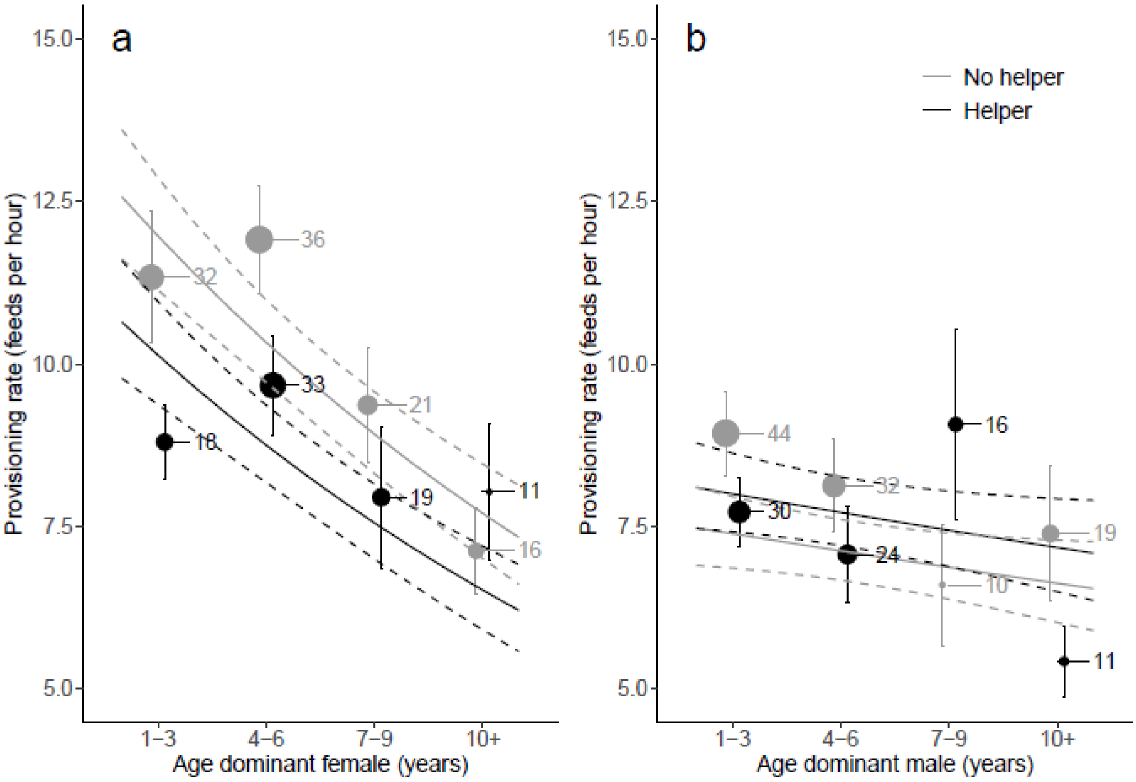

Figure 1. Provisioning rates to offspring in relation to helper presence for (a) dominant female and (b) dominant male Seychelles warblers. Data points are means ± SE of raw data (black = helper present; grey = no helper present) and the size of the points is proportional to the sample size for each age group, which is also given. In the analyses, age was considered as a continuous variable, but for graphical purposes, age is split here into five age groups. Lines are model predicted regression slopes ± s.e.m from the models in Table 1 and not lines of best fit to the raw data.

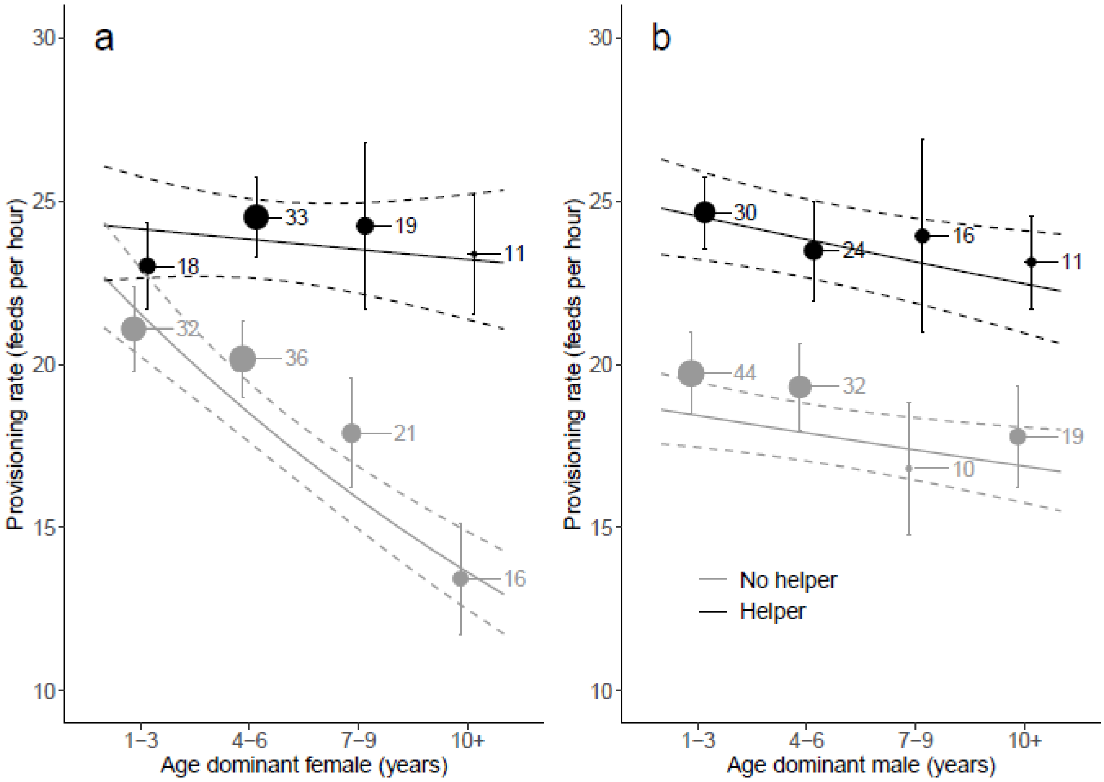

Figure 2. Total provisioning rates to offspring by all feeders in territories with (black) and without helpers (grey) present in relation to the age of (a) dominant female and (b) dominant male Seychelles warblers. Data points are means ± SE of raw data and the size of the points is proportional to the sample size for each age group, which is also given in numbers. In the analyses, age was considered as a continuous variable, but for graphical purposes, age is split here into four age groups. Lines are model predicted regression slopes ± SE and not lines of best fit to the raw data.

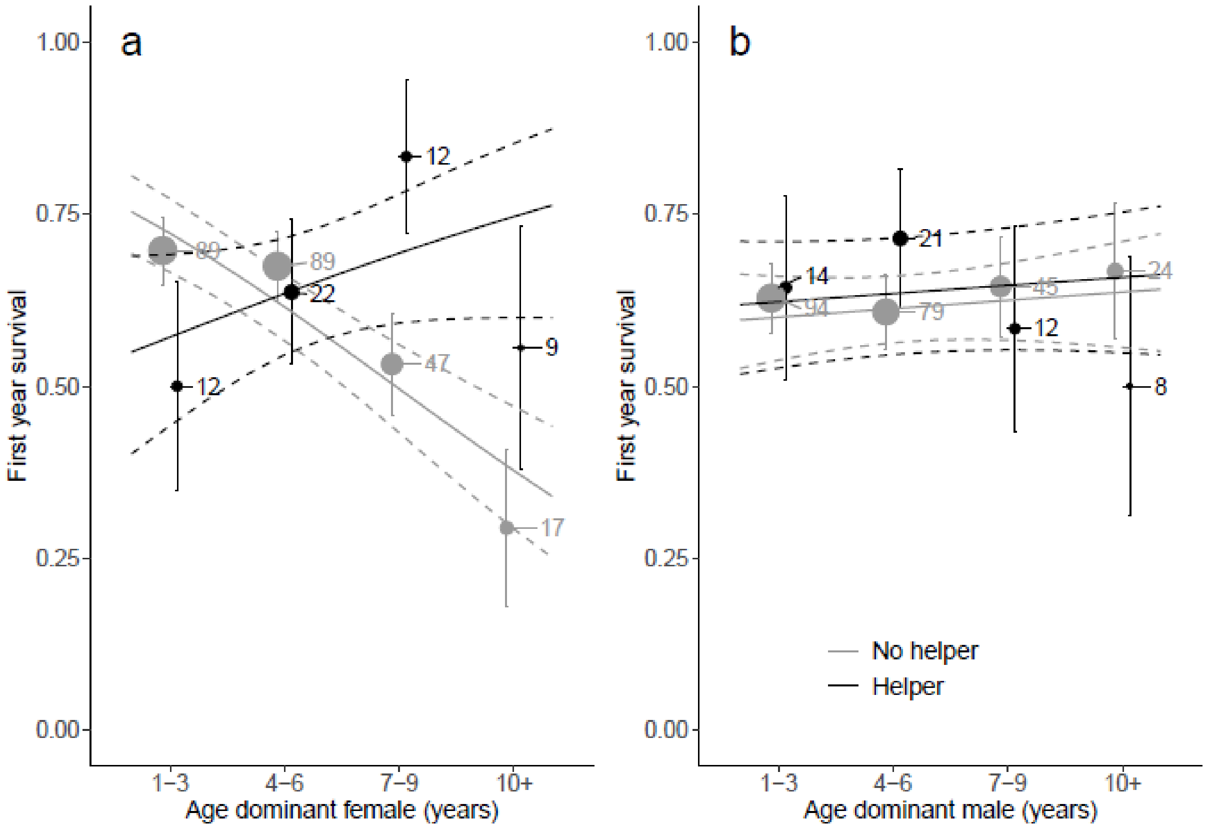

Figure 3. Offspring first-year survival in relation to age and helper presence for (a) dominant female and (b) dominant male Seychelles warblers. Panels show offspring first-year survival. Data points are means ± SE of raw data (black = helper present; grey = no helper present) for each age group and the size of the points is proportional to sample size, which is also given. In the analyses, age was considered as a continuous variable, but for graphical purposes, age is split here into four age groups. Lines are model predicted regression slopes ± SE and not lines of best fit to the raw data.

Table 1: Provisioning rates of dominant female (A) and male (B) Seychelles warblers in relation to age of the dominants and helper presence. Statistically significant variables are in bold and underlined.

A) dominant female					B) dominant male			
	Estimate	SE	*z*	*P*	Estimate	SE	*z*	*P*
Intercept	**2.30**	**0.06**	**37.33**	**<0.001**	**1.96**	**0.07**	**29.96**	**<0.001**
Age dominant female	**-0.30**	**0.08**	**-4.03**	**<0.001**	-0.14	0.08	-1.83	0.068
Age^2 dominant female	-0.18	0.12	-1.57	0.115	-0.03	0.12	-0.21	0.831
Age dominant male	-0.08	0.07	-1.06	0.290	-0.09	0.08	-1.04	0.298
Age^2 dominant male	0.20	0.15	1.35	0.176	-0.08	0.16	-0.51	0.614
Helper (Y/N)	**-0.17**	**0.08**	**-2.11**	**0.035**	0.08	0.09	0.93	0.353
Number of subordinates	0.04	0.08	0.45	0.650	**-0.22**	**0.09**	**-2.39**	**0.017**
Age focal dominant x helper	0.17	0.15	1.13	0.261	-0.05	0.19	-0.27	0.784
Age focal dominant x number of subordinates	0.00	0.20	0.00	1.00	0.06	0.20	0.32	0.751
Random	Variance	N			Variance	N		
Dominant female ID	0.09	132			-	-		
Dominant male ID	-	-			0.10	131		
Year	0.02	18			0.01	18		
		Total N: 186				Total N: 186		

Table 2. The total provisioning rates to the offspring (combining all provisioning individuals) in relation to helper presence and age of dominant female (A) and male (B) Seychelles warblers. Statistically significant variables are in bold and underlined.

	Estimate	SE	*z*	*P*
Intercept	**2.88**	**0.05**	**58.56**	**<0.001**
Age dominant female	**-0.31**	**0.08**	**-4.11**	**<0.001**
Age^2 dominant female	-0.06	0.08	-0.78	0.435
Age dominant male	-0.07	0.06	-1.25	0.211
Age^2 dominant male	0.13	0.11	1.14	0.254
Helper (Y/N)	**0.29**	**0.06**	**4.95**	**<0.001**
Number of subordinates	-0.02	0.06	-0.31	0.754
Age dominant female x helper	**0.29**	**0.10**	**2.80**	**0.005**
Age dominant male x helper	0.02	0.13	0.14	0.889
Age dominant female x number of subordinates	0.10	0.15	0.68	0.496
Age dominant male x number of subordinates	0.11	0.13	0.89	0.372
Random	Variance	N		
Dominant female ID	0.03	132		
Dominant male ID	0.02	131		
Year	0.01	18		
		Total N: 186		

Table 3. Offspring first-year survival in relation to helper presence and age of the dominants. Statistically significant variables are in bold and underlined.

	Estimate	SE	*z*	*P*
Intercept	**-0.80**	**0.38**	**-2.07**	**0.038**
Age dominant female	**-0.90**	**0.30**	**-2.94**	**0.003**
Age^2 dominant female	-0.94	0.48	-1.95	0.052
Age dominant male	0.10	0.28	0.37	0.713
Age^2 dominant male	-0.24	0.47	-0.50	0.614
Caught as fledgling (vs. nestling)	**1.40**	**0.37**	**3.78**	**<0.001**
Offspring sex (male vs. female)	0.43	0.27	1.59	0.112
Helper (Y/N)	0.09	0.39	0.24	0.811
Number of subordinates	-0.24	0.32	-0.75	0.456
Age dominant female x helper	**1.38**	**0.65**	**2.13**	**0.033**
Age dominant male x helper	-0.88	0.70	-1.25	0.213
Age dominant female x number of subordinates	-0.46	0.66	-0.70	0.481
Age dominant male x number of subordinates	0.24	0.60	0.41	0.684
Random	Variance	N		
Year	0.31	21		
		Total N: 297		

SUPPLEMENTARY MATERIALS

Supplementary Table 1: Provisioning rates of dominant female (A) and male (B) Seychelles warblers in relation to their age and helper presence. To account for selective disappearance effects, we included the age of death of the focal dominant. Statistically significant variables are in bold and underlined.

A) dominant female					B) dominant male			
	Estimate	SE	*z*	*P*	Estimate	SE	*z*	*P*
Intercept	**2.29**	**0.07**	**33.76**	**<0.001**	**1.99**	**0.07**	**28.39**	**<0.001**
Age dominant female	**-0.48**	**0.12**	**-4.01**	**<0.001**	-0.14	0.08	-1.60	0.109
Age^2 dominant female	-0.21	0.13	-1.59	0.111	-0.04	0.12	-0.33	0.741
Age dominant male	-0.06	0.09	-0.65	0.517	-0.18	0.12	-1.43	0.153
Age^2 dominant male	0.19	0.16	1.21	0.228	-0.02	0.17	-0.10	0.918
Helper (Y/N)	**-0.23**	**0.09**	**-2.49**	**0.013**	-0.01	0.10	-0.10	0.919
Age of death dominant	**0.24**	**0.12**	**1.97**	**0.049**	0.22	0.12	1.73	0.085
Number of subordinates	0.05	0.09	0.56	0.578	-0.19	0.10	-1.91	0.056
Age focal dominant x helper	0.21	0.18	1.15	0.252	0.13	0.20	0.63	0.527
Age focal dominant x number of subordinates	-0.01	0.22	-0.07	0.947	0.00	0.24	0.02	0.998
Random	Variance	N			Variance	N		
Dominant female ID	0.11	112			-	-		
Dominant male ID	-	-			0.10	108		
Year	0.02	18			0.01	18		
		Total N: 153				Total N: 152		

Supplementary Table 2: Offspring first-year survival in relation to helper presence and age of the dominants. The age of death dominants is included to account for selective disappearance effects. Statistically significant variables are in bold and underlined.

	Estimate	SE	*z*	*P*
Intercept	**-0.69**	**0.41**	**-1.69**	**0.091**
Age dominant female	**-0.93**	**0.39**	**-2.39**	**0.017**
Age^2 dominant female	-1.01	0.53	-1.90	0.058
Age dominant male	-0.35	0.40	-0.88	0.380
Age^2 dominant male	-0.17	0.51	-0.34	0.736
Caught as fledgling (vs. nestling)	**1.16**	**0.39**	**3.00**	**0.003**
Offspring sex (male vs. female)	0.53	0.30	1.78	0.076
Helper (Y/N)	0.33	0.43	0.76	0.445
Number of subordinates	-0.21	0.34	-0.62	0.536
Age of death dominant female	0.02	0.38	0.05	0.960
Age of death dominant male	0.58	0.40	1.44	0.150
Age dominant female x helper	**2.00**	**0.76**	**2.63**	**0.008**
Age dominant male x helper	1.38	0.80	-1.74	0.082
Age dominant female x number of subordinates	-0.36	0.72	-0.51	0.612
Age dominant male x number of subordinates	0.22	0.64	0.34	0.731
Random	Variance	N		
Year	0.38	21		
		Total N: 250		