Breeders that receive help age more slowly in a cooperatively breeding bird

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Helping by group members is predicted to lead to delayed senescence by affecting the trade-off between current reproduction and future survival for dominant breeders. Here we investigate this prediction in the Seychelles warbler, *Acrocephalus sechellensis*, in which mainly female subordinate helpers (both co-breeders and non-breeding helpers) often help dominants raise offspring. We find that the late-life decline in survival usually observed in this species is greatly reduced in female dominants when a helper is present. Female dominants with a female helper show reduced telomere attrition, a measure that reflects biological ageing in this and other species. Finally, the probability of having female, but not male, helpers increases with dominant female age. Our results suggest that delayed senescence is a key benefit of cooperative breeding for elderly dominants and support the idea that sociality and delayed senescence are positively self-reinforcing. Such an effect may help explain why social species often have longer lifespans.
Variation in ageing patterns observed across taxa is enormous, but the causes of this variation are still poorly understood. Intriguingly, even within the same species there is often extensive individual variation in the onset and rate of actuarial senescence—the progressive age-dependent decline in survival. Elucidating the causes of among-individual variation in senescence is crucial to our understanding of the mechanisms and trade-offs that drive ageing within and across species. Patterns of sociality contribute significantly to explaining variation in ageing rates across species. However, while studies have investigated relationships between intraspecific competition and senescence, studies investigating the relationship between sociality and senescence at the intraspecific level are rare and the direction of causality of this relationship remains to be resolved.

In cooperative breeding systems, parental care is generally shared between socially dominant individuals and (often related) subordinate helpers. The alloparental care provided by helpers often allows the dominants to reduce their current reproductive investment, which may then reduce the negative impacts of reproductive effort on the condition of dominants (e.g. through reducing oxidative stress and increase the survival of helped dominants). The benefits of having helpers are predicted to be greater for young dominants, because young dominants may have little breeding experience, and for elderly dominants, because elderly individuals may suffer greater costs of reproduction due to senescent declines in physiological condition. Hence, for elderly dominants a key benefit of receiving help might be that it delays the onset, and reduces the rate, of actuarial senescence. However, studies testing whether helping alleviates actuarial senescence in dominants are lacking (but see ref.20). If the benefits of receiving help increase with a dominant’s age, there should be a strong incentive for elderly dominants to recruit and retain helpers. Therefore, we predict that the likelihood of having helpers increases with age in dominants.

In this study, we use 15 years of data on the facultative cooperatively breeding Seychelles warbler *Acrocephalus sechellensis* to study associations between actuarial senescence and cooperative breeding. The Seychelles warbler population on Cousin Island provides a useful model system in which to study associations between actuarial senescence and telomere attrition. In addition, we test whether the likelihood of having female helpers increases with age in dominants. We find that dominant females benefit from having female helpers in terms of delayed senescence and reduced telomere attrition. In addition, we find that older female, but not male, dominants are more likely to have female helpers. Our results suggest that delayed senescence is a key benefit of cooperative breeding for elderly female dominants, and support the idea that sociality and delayed senescence are positively self-reinforcing. Such an effect may help explain why social species often have longer lifespans than non-social species.

### Results

**Incubation attendance.** Female dominants with a female helper had 21% lower incubation attendance (Supplementary Fig. 1; Supplementary Table 1; mean ± SE = 39.9% ± 1.8% of time incubating, n = 69) than dominant females without a female helper (mean ± SE = 50.4% ± 0.8%, n = 277) and the total incubation attendance at a nest was 45% higher for nests with female helpers (Supplementary Table 1; mean ± SE = 73.2% ± 2.0%, n = 69). Incubation attendance was not associated with age of the dominant female (Supplementary Table 1).

**Helping and actuarial senescence.** Survival was strongly age-dependent and declined progressively among elderly dominants.

### Table 1 Age-dependent survival of dominants in relation to helper presence

| (a) Dominant female | (b) Dominant male |
|---------------------|-------------------|
| **Variable**        | **Estimate**      | **SE** | **z** | **P**   | **Estimate** | **SE** | **z** | **P**   |
| Intercept           | 1.98              | 0.14   | 13.84 | <0.001 | 1.73        | 0.17   | 10.20 | <0.001 |
| Age                 | −0.58             | 0.25   | −2.28 | 0.023  | 0.01        | 0.18   | 0.08  | 0.936  |
| Age^2               | −0.67             | 0.23   | −2.93 | 0.003  | −0.60       | 0.22   | −2.80 | 0.005  |
| Territorial quality | 0.41              | 0.17   | 2.44  | 0.015  | 0.05        | 0.16   | 0.33  | 0.742  |
| Helper (Y/N)        | −0.16             | 0.24   | −0.65 | 0.513  | 0.41        | 0.22   | 1.90  | 0.057  |
| Number of subordinates | 0.22          | 0.19   | 1.18  | 0.239  | −0.30       | 0.16   | −1.95 | 0.051  |
| Age × helper        | 1.25              | 0.39   | 3.18  | 0.001  | 0.64        | 0.35   | 1.82  | 0.069  |
| Age × number of subordinates | −0.12     | 0.36   | −0.33 | 0.740  | −0.11       | 0.28   | −0.41 | 0.685  |

Random

| **Variable** | **Variance** | **1571 Observations** | **Variance** | **1581 Observations** |
|--------------|--------------|------------------------|--------------|-----------------------|
| Individual ID| 0.27         | 463 Individuals        | <0.01        | 491 Individuals        |
| Year         | 0.11         | 15 years               | 0.29         | 15 years               |

Final models contained all main effects and significant interaction terms.
of both sexes (Table 1; Fig. 1). When averaged across all ages, annual survival probabilities of female dominants without helpers (84%) and with helpers (86%) were similar (two proportion z-test: $\chi^2 = 0.29$, $P = 0.590$). However, the impact of helpers of either sex on dominant female survival depended on the dominant female’s age. Survival of female dominants that were not assisted by helpers declined strongly with age, but the survival of dominants that received help showed little age-dependence and the late-life decline was much less pronounced (Table 1; Fig. 1). Indeed, survival of female dominants $<7$ years old (i.e. before the onset of reproductive senescence in this species) was similar for individuals with (84%) or without (87%) a helper of either sex (two proportion z-test: $\chi^2 = 0.87$, $P = 0.352$), but among elderly dominants (>6 years) survival was higher for dominants with helpers (89%) than for dominants without (78%; two proportion $z$-test: $\chi^2 = 6.40$, $P = 0.011$), which is due to a decline in survival of elderly dominants without helpers (Fig. 1). The effect of helpers on survival was independent of the number of subordinates (helpers and non-helpers) that were present in the territory, or its interaction with age (Table 1). This indicates that helping by subordinates, rather than (factors associated with) the presence of subordinates, predicted the age-related survival effect in dominants. A model that included two separate binary variables for female and male helper presence instead of presence of a helper of either sex was less well supported ($\Delta$AICc = 2.8). When averaged across all ages, the annual survival probabilities of male dominants without helpers (82%) and with helpers (84%) were similar (two proportion z-test: $\chi^2 = 0.71$, $P = 0.400$). Survival of male dominants $<7$ years old was similar for individuals with (83%) or without (83%) a helper of either sex (two proportion z-test: $\chi^2 = 0.02$, $P = 0.879$). Among elderly dominants (>6 years) survival tended to be higher for male dominants with helpers (86%) than for male dominants without (79%), although this difference was not significant (two proportion z-test: $\chi^2 = 1.44$, $P = 0.230$).

Telomere attrition rate. The within-individual rate of attrition of telomeres (ARTL) differed between dominant females with and without a female helper (Table 2; Fig. 2), or a helper of either sex (Supplementary Table 3). The number of subordinates that was present in a territory also predicted ARTL in dominant females, but this effect was in the opposite direction to that observed for helper presence (Table 2). We then tested whether ARTL was below zero in unassisted dominant females and above zero in dominant females with a female helper. ARTL declined in unassisted dominant females (Fig. 2; one-sided $t$-test: $t_{137} = -2.27$, $P = 0.015$), but the apparent increase in ARTL in dominant females with a helper was not significant (Fig. 2; one-sided $t$-test: $t_{64} = 1.27$, $P = 0.125$). For dominant males, ARTL was not associated with female helper presence (Table 2; Fig. 2).

Age-dependent helper prevalence and subordinate reproduction. Overall, older ($\geq2$ years old) subordinates were more likely to help (mean $\pm$ SE = $0.56 \pm 0.03$, $n = 292$) than younger ($\leq1$ year old) subordinates (mean $\pm$ SE = $0.23 \pm 0.02$, $n = 647$), and female subordinates (mean $\pm$ SE = $0.42 \pm 0.02$, $n = 571$) more than male subordinates (mean $\pm$ SE = $0.20 \pm 0.02$, $n = 368$; Table 3). The likelihood that a subordinate helped was associated with the age of the dominant female, but the direction of this association was dependent on the subordinate’s sex: positive for female subordinates and negative for male subordinates (Table 3; Fig. 3). Indeed, among female dominants with a helper, the likelihood
that a helper was female increased with the female dominant’s age (Table 4). As a result, elderly dominants almost exclusively had female, but not male, helpers (Fig. 4). Neither the likelihood that a male or female subordinate helped, nor the sex ratio among helpers, were related to the dominant male’s age (Tables 3, 4; Figs. 3, 4).

The likelihood that a subordinate female reproduced was higher for older (≥2 years old) subordinates (0.30 ± 0.03, mean ± SE, n = 227), while younger (≤1 year old) subordinates almost never reproduced (0.02 ± 0.01, mean ± SE, n = 344) (Supplementary Table 4). Subordinate reproduction was not related to the age of the dominant female or male, territory quality and the number of subordinates that was present in the territory (Supplementary Table 4).

**Discussion**

Sociality might play a key role in explaining some of the considerable inter-specific and intraspecific variation in senescence observed in nature, but it is currently unclear whether social phenomena like alloparental care can truly affect senescence patterns, or whether senescence can explain variation in social behaviour. In this study, we found that while the survival of

| Variable                        | Estimate | SE  | t    | P     | Estimate | SE  | t    | P     |
|---------------------------------|----------|-----|------|-------|----------|-----|------|-------|
| Intercept                       | −0.20    | 0.05| −4.30| <0.001| −0.07    | 0.07| −0.95| 0.351 |
| Initial RTL                     | −0.72    | 0.07| −10.23| <0.001| −0.56    | 0.08| −6.74| <0.001|
| Age                             | 0.15     | 0.07| 2.08  | 0.044 | −0.08    | 0.09| −0.86| 0.397 |
| Territory quality               | 0.00     | 0.07| −0.04 | 0.971 | 0.12     | 0.08| 1.46 | 0.150 |
| Offspring produced (Y/N)        | 0.03     | 0.07| 0.38  | 0.709 | 0.08     | 0.08| 0.96 | 0.341 |
| Female helper (Y/N)             | 0.45     | 0.12| 3.73  | <0.001| 0.03     | 0.10| 0.25 | 0.802 |
| Number of subordinates          | −0.31    | 0.09| −3.44 | 0.001| −0.01    | 0.09| −0.12| 0.905 |

**Fig. 2** Annual change in relative telomere length (delta RTL) in dominants in relation to female helper presence. **a** Dominant females, **b** dominant males. The dashed line indicates no telomere shortening or lengthening. Filled circles are means and s.e.m. of raw data, open circles are raw data points. Source data are provided as a Source Data file.
unassisted elderly dominants of both sexes declined progressively with age, the age-specific decline in survival of female dominants was greatly reduced if they were assisted by helpers. We also found that helper presence was associated with reduced telomere shortening (a marker of biological ageing in this and many other species) in dominant females, but not in dominant males. In addition, we found that elderly female, but not male, dominants were more likely to have female helpers and less likely to have male helpers. In other words, our results suggest that helpers may contribute to delay senescence in female dominants and that, at the same time, dominant females acquire more female helpers as they get older.

In cooperatively breeding species, dominants often show higher survival when assisted by helpers, but an absence of survival differences between individuals with and without helpers is also frequently observed in cooperatively breeding birds. The finding that in the Seychelles warbler only elderly individuals, that normally have lower survival because of senescence, benefit from receiving help, could be caused by a ceiling effect: the very high annual survival in young and mid-aged individuals means there is little potential for improvement in survival, but there is much more scope for this in elderly individuals with lower survival probabilities. Another explanation may be that the costs of reproduction, or maintaining a territory, only become apparent in individuals suffering senescence, not in younger individuals that are in better physiological condition.

Survival benefits for dominants can arise because helpers allow dominants to reduce their costs of reproduction, thereby allowing them to invest more resources in somatic maintenance. For example, helpers may reduce the costs of incubation and investment in eggs for the dominant female. In dominant female Seychelles warblers, incubation costs are probably lower for those that have a helper as assisted females reduce their incubation attendance by 21% (this study), while hatching success increases. The fact that we only detected reduced telomere shortening in female dominants with female helpers, but not in

**Table 3** The likelihood that a subordinate helped in relation to the dominant’s age and the subordinate’s sex

| Variable                  | Estimate | SE  | z    | P       | Estimate | SE  | z    | P       |
|---------------------------|----------|-----|------|---------|----------|-----|------|---------|
| Dominant female           |          |     |      |         |          |     |      |         |
| Intercept                 | −1.09    | 0.21| −5.14| <0.001  | −1.12    | 0.21| −5.31| <0.001  |
| Dominant age              | 0.43     | 0.22| 1.98 | 0.048   | 0.04     | 0.19| 0.23 | 0.61    |
| Territory quality         | 0.10     | 0.23| 0.42 | 0.674   | 0.14     | 0.23| 0.61 | 0.543   |
| Subordinate sex (male)    | −1.05    | 0.21| −5.10| <0.001  | −0.95    | 0.20| −4.80| <0.001  |
| Subordinate age (older)   | 1.73     | 0.24| 7.26 | <0.001  | 1.85     | 0.24| 7.62 | <0.001  |
| Number of subordinates    | −0.27    | 0.20| −1.38| 0.167   | −0.29    | 0.19| −1.50| 0.134   |
| Dominant age * Subordinate sex | −1.00   | 0.41| −2.43| 0.015   | 0.07     | 0.37| 0.18 | 0.858   |

![Fig. 3](image-url)
male dominants, is perhaps explained by the fact that only females incur significant costs of incubation in this species, and these costs are alleviated by female helpers.

The telomere results contrast with our analysis of survival, where we found that the presence of female helpers appears to have similar effects on age-specific survival of both dominant females and males, although this was only significant for dominant females. This suggests that benefits other than reducing the costs of incubation play a role in survival. Intriguingly, we also observed that telomere lengths tended to increase in female dominants that were assisted by female helpers (although this increase was not significant), but declined in unassisted female dominants. Although measurement error may explain some observations of telomere length increasing over time within individuals, there is increasing evidence that actual telomere length increases do occur, in which telomerase expression may play a key role. Of particular relevance, there is clear evidence that telomere lengthening occurs in the Seychelles warbler, where mortality has been linked to (shorter) telomere length.

Our analyses suggest that the presence of helpers, rather than of subordinate group members per se (which is often challenging to separate in cooperatively breeding species), explains the higher late-life survival of dominants with helpers. A limitation of our study, and of most other studies on cooperatively breeding species, is that we cannot easily disentangle the impact of help from the quality or condition of the dominants. For example, better quality individuals with longer lifespans and higher reproductive output might be more likely to have helpers because they have successfully reproduced in previous years. However, the impact of helpers on survival persisted when the number of subordinates was also included in the models, which suggests that our results are not simply explained by differences in individual quality or territory quality. Moreover, the greater telomere shortening (a longitudinal measure across two points within each female) observed in female dominants that were not helped, compared to the lack of shortening in helped females, suggests that helpers prevent a deterioration of the dominant female’s condition, rather than that dominants with a helper were initially in better condition (of better quality). Future studies should attempt experimental manipulations of the amount of help that dominants receive to confirm the causality of the associations found in our study. Experimental manipulations will also help to test the possibility that subordinates are more likely to help when they assess the dominants as being in better physiological condition or more productive.

The survival benefits of receiving help may reduce the fitness costs of senescence in elderly individuals. Elderly dominant female Seychelles warblers show a drop in reproductive output during the last year of life and the magnitude of this drop increases with age. If having helpers allows dominants to postpone their death, this may compensate for the decline in reproductive output, and enhance the dominant’s late-life reproductive performance. If help is beneficial for elderly dominants, then dominants might offer subordinates incentives to stay and help (e.g. food, protection or opportunities to reproduce), and try to retain subordinates that they would normally have evicted from their territory. Subordinates may benefit from increased survival of the dominants as this enhances the indirect fitness benefits received by related subordinates and survival of the subordinates. It also provides female subordinates with an opportunity to gain direct benefits in the form of co-breeding. Here we do not tease apart whether the effects outlined above arise from co-breeding or allopatrial helping as

| Variable                      | Estimate | SE  | z     | P      | Estimate | SE  | z     | P      |
|-------------------------------|----------|-----|-------|--------|----------|-----|-------|--------|
| Intercept                     | −0.82    | 0.25| −3.25 | 0.001  | −0.62    | 0.22| −2.77 | 0.006  |
| Dominant age                  | −1.07    | 0.42| −2.54 | 0.011  | 0.27     | 0.33| 0.82  | 0.411  |
| Territory quality             | 0.16     | 0.36| 0.44  | 0.662  | 0.24     | 0.35| 0.68  | 0.494  |
| Subordinate age (older)       | −1.47    | 0.36| −4.04 | <0.001 | −1.73    | 0.36| −4.79 | <0.001 |
| Number of subordinates        | −0.07    | 0.36| −0.20 | 0.841  | −0.08    | 0.35| −0.23 | 0.820  |

Table 4 The likelihood that a helper is a male in relation to the age of the dominants

Fig. 4 The likelihood that a helper is a male in relation to the age of the dominants. The dashed lines are the model predicted regression slope ± SE for female dominants and the solid lines are those for dominant males. Circles with error bars are means and binomial 95% confidence intervals for 3-year age intervals based on raw data. Numbers are sample sizes. Source data are provided as a Source Data file.
separating these two types of helpers is difficult in this system, given that some non-breeders may be individuals that have attempted to breed, but failed to do so successfully. Co-breeding also provides an additional benefit for helpers as they can share reproduction and parental care with the dominants (and thus have ‘helpers’ themselves). In addition, previous studies found that having a (co-breeding) helper is beneficial for the dominant’s reproductive success35,49. Therefore, it seems likely that both helpers and dominants benefit from each other, perhaps especially when elderly dominants are suffering senescence.

The logic outlined above leads to the intriguing possibility that elderly individuals might be able to use cooperative breeding as a strategy to increase their lifespan and to maximize lifetime reproductive success. We found some evidence that this might be the case in the Seychelles warbler. Although we do not know the actual mechanism, the likelihood that subordinates helped increased with the age of the dominant female. This increase in helper prevalence was explained by an age-dependent increase in female (not male) helper prevalence, resulting in increasingly female-biased helper sex ratios in territories with elderly dominants (from ca 40% in younger dominants, but nearly 100% in elderly dominants). We can only speculate why we only found this relationship for dominant females, but a potential explanation may be that dominant females benefit most from female helpers because they invest more in reproduction. In turn, female subordinates might have more incentive to stay and help by an offer of a share in reproduction40. Although the likelihood that a female subordinate reproduced appeared to be unrelated to the age of the dominant female or male, future studies should test whether co-breeding frequencies increase—and eviction rates, or levels of aggression towards subordinates, decrease—among elderly dominants in this species. A thorough examination of the direct and indirect benefits for dominant and subordinate group members is required to test whether there may be positive reinforcement between dominants living longer because of the help of subordinates, and subordinates being more likely to stay and help when receiving more benefits when assisting elderly dominants.

In the longer term, helping-enabled improvements in the late-life survival of dominants may drive the evolution of longer lifespan in cooperative breeders, but this prediction remains to be tested. Some comparative studies found no association between longevity and cooperative breeding across bird species47,48 (but see ref. 49). A possible explanation for this is that the impact of receiving help on senescence might differ strongly between species. This could occur if the strength and direction of this relationship depends on the species’ ecology or life-history strategy. Another explanation that remains to be tested is that helping delays actuarial senescence and leads to longer lifespans in the receivers of help, but that the mean lifespan across the population remains similar because helpers show accelerated senescence and shorter lifespans. Furthermore, because the force of natural selection is proportional to the number of individuals alive in a given age class49, the small number of elderly dominants that benefit from help (Fig. 1) means that selection on delayed senescence may be relatively weak compared to factors that improve fitness during early life. However, a positive effect of helpers on the dominant’s fitness in late life should nonetheless select for delayed senescence and longer lifespan in dominants, and thus increased cooperative breeding.

Our results suggest that for elderly dominants, higher late-life survival may be a key benefit of cooperative breeding. More studies investigating how helping affects senescence at the individual level are needed to test how the association between cooperative breeding and senescence differs between the individual and species level. We encourage future studies to investigate how cooperation may delay senescence, how the prevalence of cooperation may change with age, and whether cooperation and delayed senescence may be self-reinforcing31,51–53, thus potentially driving longer lifespans in social species.

Methods

The Seychelles warbler model system. The Seychelles warbler population on the isolated island of Cousin (29°24’20″ S, 55°50’40″ E) contains ca 320 adult individuals, nearly all of which are colour-banded (using a combination of three colour rings and a British Trust for Ornithology metal ring44). The warbler’s life history is characterized by high annual adult survival (84%), mostly single-egg clutches, and extended periods (up to three months) of post-fledging care4,52. Individuals that have acquired a dominant breeding position generally defend the same territory, with the same partner, until their death5. The correlation between the age of the dominant male and female in a territory is, while significant, actually relatively weak (Pearson product-moment correlation: r = 0.16, 1631, 6.53, P < 0.001, Supplementary Fig. 3). This is because the age at which an individual obtains a dominant position varies considerably, pairs of birds do not become dominant at the same age, and the age at which dominant individuals die (one of the pair is always male). Previous studies suggested that male and female dominants have similar breeding tenure, annual survival probabilities and rates of actuarial senescence4,25. The vast 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)57. Seychelles warblers can breed successfully in socially monogamous pairs (where only one of the breeders takes part in cooperative breeding), but, because of a lack of suitable breeding opportunities, young individuals often delay independent breeding and become subordinates within a territory, where they then may help with providing alloparental care (incubation (female subordinates only); provisioning (male and female subordinates)), or not54. Subordinates are often retained offspring from previous breeding attempts33, although a very small number of subordinates disperse to a new subordinate position in a different territory57. Territory inheritance in the Seychelles warbler is rare (only 3.7% of dominant breeding positions are obtained via offspring inheriting this status on their natal territory53, so it is unlikely that inheritance is the main benefit accrued by subordinates. Subordinates benefit from helping as they obtain breeding experience, indirect (kin-selected) fitness benefits through helping related offspring46. Further, older (≥2 year old) female subordinates often (ca 40% in any year) gain direct fitness benefits through co-breeding (laying an egg in the same nest as the dominant female)31,35. Co-breeding subordinates always provide alloparental care and do not discriminate between their own offspring and the dominant female’s offspring (i.e. they help all offspring in the nest)66,60. Further, previous studies found no evidence for reproductive conflict caused by co-breeding females35,40,41,62, except in extreme cases52. Therefore, we considered all subordinates that helped with incubation or provisioning as helpers, irrespective of whether they co-bred or not. Male subordinates acquire fewer benefits than females because they do not appear to benefit through gaining breeding experience31 and very rarely gain direct paternity, which may explain why most helpers (88%; 37% (n = 310) in this study) are female53. Apart from providing the opportunity to obtain indirect fitness benefits, the prolonged presence of the parents may be beneficial for subordinates because it facilitates the eventual acquisition of a dominant position elsewhere. This is because breeders are more likely to allow related subordinates to remain in the territory until they are able to disperse to a dominant position elsewhere, but will erect unrelated subordinates irrespective of such opportunities, resulting in higher mortality31,63.

Data collection. For our analyses, we used data collected between 1995–2016, when the population was most intensively studied. We excluded the years 2000–2002 because fieldwork was limited in this period, with incomplete data on helping behaviour. In addition, we excluded 2004 because 58 individuals (both dominants and subordinates) were translocated to another island just before the main breeding season as part of a conservation programme34, and 2005 because no territory quality data were collected in that year. During the main breeding season, each nest that was monitored before its age was monitored (i.e. we monitored the identity of the number of group members and to assess breeding activity at least once every two weeks by following the resident dominant female for at least 15 min53. As the resighting probability for dominants during the main breeding season is virtually one54, and migration is virtually non-existent51, it is safe to assume that dominants not seen in the entire breeding season have died52. Once nests were given as helper (not helping subordinate) in a given season, we conducted nest watches of at least 60 min during both the incubation and nesting provisioning stages and recorded the start and end times of all provisioning events and incubation bouts and the identity of the individuals providing nest care34. For nests that failed early in the breeding stage (i.e. before an incubation and/or provisioning nest watch could be performed), subordinates were conservatively classified as non-helping subordinates. As in the majority of the territory-years where helpers were present (in 17% (271 out of 1571) of territory-years there was at least one helper present in the territory) there was only one helper of either sex (86% one helper, 14% two helpers, <1% three helpers; n = 271), we treated helper presence as a
binary variable (YN) in our analyses. Helper effects in cooperatively breeding species might result from factors associated with having subordinates (which are often retained offspring and thus indicate successful reproduction in previous years), such as differences in individual or territory quality, rather than from helping per se (see refs. 34,46). Separating the impact of helping from individual or territory quality is extremely difficult, as experimentally manipulating the effect of help is generally not feasible or fraught with methodological issues48. Because in the Seychelles warbler not all subordinates help in any given year we can test statistically whether helper effects are better explained by having subordinates (i.e. living in a larger group), rather than by helping per se14.

Seychelles warblers are almost entirely insectivorous, so we used an index of insect availability in each territory in each main breeding season as a proxy for territory quality (following refs. 54,47). To calculate this, we used the formula $A = \sum (C_x \times I_x)$, where $A$ is the size of the territory in ha, $C_x$ is the amount of foliage cover in tree species $x$, and $I_x$ is the mean monthly insect density for tree species $x$ per unit leaf area in dm$^2$. Territory size was determined from territory maps constructed from detailed observational data of foraging and territorial disputes. Foliage cover was determined by counting the number of insects on the undersides of 50 leaves for each of the 10 dominant tree species present at 14 different locations spread across the island. Insect counts taken at each location were used as an estimate for all territories near that location.

**Statistical analyses.** All models were performed separately for female and male dominants. Continuous predictor variables were centred and divided by two standard deviations for easier interpretation and comparison of standardized regression coefficients49. Non-significant (P > 0.05) interactions were removed, sequentially in order of least significance, from the models and final models contained all main effects and any significant interaction terms. We used R (version 3.2.5) for all analyses.

**Incubation attendance.** To investigate how dominant females respond to additional incubation performed by female helpers, we quantified incubation attendance for dominant females with and without female helpers. Specifically, we compared the percentage of time that the dominant female spent incubating against the percentage of time that female helpers spent incubating. This resulted in 346 nest observations of 192 dominant females in 12 territories. When multiple observations were made of the same nest (i.e. the same female helper) were similar and are reported in Supplementary Table 3. As helper presence may be greater in individuals with higher telomere maintenance, we included as predictors the number of subordinates in the territory. We predicted that female helpers contribute more than male helpers do (see results), so we focussed on comparing RTL in dominants with a female helper to dominants without. The results of a model that included the presence of helpers (irrespective of the sex of the helper) were similar and are reported in Supplementary Table 3. As helper presence may be greater in individuals with higher telomere maintenance, we included as random effects the number of subordinates in the territory and the host individual’s identity, as well as any interaction terms. We tested whether dominants that received help show reduced telomere shortening using LMMs with a Gaussian error structure and an identity link function. Each year during the main breeding season, ca 25% of the adult population is caught using mist nets and blood samples are collected by local field assistants15. For the procedures described in detail elsewhere29–31, we used qPCR to measure relative telomere length (RTL; the concentration of telomeric DNA relative to the concentration of the single-copy gene GAPDH) in blood samples collected from the same individual in two consecutive years. As avian erythrocytes are nucleated, this measure is effectively the RTL of the erythrocytes that comprise the majority of blood cells. We then calculated $\Delta$RTL as the difference between RTL in year $t$ and RTL in year $t+1$ (i.e. one year later) within each individual and related $\Delta$RTL to helper presence, with negative values indicating telomere shortening and positive values lengthening52. As there were only two $\Delta$RTL measures available for female dominants with a male helper, we compared RTL between the first and last observation (i.e. at the start and at the end of the breeding season) for female dominants with and without helpers using LMMs. For the models of telomere length, we included log10 of dominant age, log10 territory quality, helper presence (YN) and the number of subordinates as predictors and included individual identity, year and birth year as random effects.

To test if dominants with helpers had better initial condition than individuals without helpers we compared RTL and the July (i.e. at the start of the breeding season) body mass of dominants with and without helpers using LMMs. For the models of body mass, we included helper presence, age, age$^2$, time of day (as a measure of reproductive investment) and the number of subordinates (irrespective of their helping status) as predictors and included individual identity, year and birth year as random effects.

**Helping and actuarial senescence.** To investigate the impact of helping on age-dependent survival of dominants, we performed Generalized Linear Mixed Models (GLMMs) with a binomial error structure and a linear predictor in R. In this model, age is the dependent variable and the fixed effects were log10 territory quality, the linear and quadratic effects of age (hereafter: age and age$^2$) of the dominant, helper presence (YN), the number of subordinates, and the two-way interactions between helper presence and the dominant’s age and between the number of subordinates and the dominant’s age. Female identity and year were included as random effects. Subsequently, we repeated this analysis with the total incubation attendance by all incubating females (instead of the dominant female’s incubation attendance) as the dependent variable to test the prediction that incubation by helpers leads to an increase in overall incubation attendance.

**Helping and actuarial senescence.** To investigate the impact of helping on age-dependent survival of dominants, we performed Generalized Linear Mixed Models (GLMMs) with a binomial error structure and a linear predictor in R. In this model, age is the dependent variable and the fixed effects were log10 territory quality, the linear and quadratic effects of age (hereafter: age and age$^2$) of the dominant, helper presence (YN), the number of subordinates, and the two-way interactions between helper presence and the dominant’s age and between the number of subordinates and the dominant’s age. Female identity and year were included as random effects. Subsequently, we repeated this analysis with the total incubation attendance by all incubating females (instead of the dominant female’s incubation attendance) as the dependent variable to test the prediction that incubation by helpers leads to an increase in overall incubation attendance.
with helpers and tested whether the sex ratio among helpers changed with the age of the dominants. The sex of the subordinate was the dependent variable, age of the dominant, age of the subordinate, log10 territory quality, and the number of subordinates in the territory were included as fixed effects and dominant identity, family group, and year were included as random effects.

To test how the likelihood that subordinate females reproduced (co-breeding) was related to the age of the dominants, we constructed GLMMs with a binomial error structure and a logit link function. We used genetic parentage analyses based on 30 microsatellites using Masterbayes 2.52 to assign captured and genotyped offspring to subordinate females. It should be noted that this is an underestimate of the total number of offspring that is produced as some offspring die before they can be captured and because we excluded offspring for which the genetic parents could not be assigned with at least 80% confidence.

Whether a subordinate female reproduced or not (Y/N) was the dependent variable and the age of the dominant, age of the subordinate (≤1 year old vs. ≥2 years old), sex of the subordinate, log10 territory quality and the number of subordinates in the territory were included as predictors. Dominant identity, family group and year were included as random effects.

Ethics statement

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

Reporting summary

Further information on experimental design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The data that support the findings of this study are available in figshare with the identifier https://doi.org/10.6084/m9.figshare.7751099.

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Author contributions

M.H., D.S.R., J.K. and S.A.K. designed the study. All authors performed research, including specifically: fieldwork – D.S.R., M.H., S.A.K., and K.B.; molecular work – K.B., L.S. and D.S.R. M.H. wrote the first draft of the manuscript. All authors provided input into concepts and ideas and critically revised the manuscript. M.H. analyzed the data with feedback from D.S.R. and S.A.K. D.S.R., J.K., T.B. and H.L.D. coordinated the long-term study.

Additional information

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