The impact of helping on helper life-history and fitness in a cooperatively breeding bird

Running title: Fitness consequences of helping

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Author contributions

Project was conceived by EC and HLD, with input from AMS. Data collection was done by all authors. Statistical analyses were designed and run by EC with input from HLD, AMS and DSR. EC wrote the draft, with input from all authors throughout. All authors agreed to submission.

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ABSTRACT

Cooperative breeding occurs when helpers provide alloparental care to the offspring of a breeding pair. One hypothesis of why helping occurs is that helpers gain valuable experience (skills) that may increase their own future reproductive success. However, research typically focuses on the effect of helping on short-term measures of reproductive success. Fewer studies have considered how helping affects long-term fitness measures. Here, we analyse how helping experience affects key breeding and fitness-related parameters in the Seychelles warbler (*Acrocephalus sechellensis*). Importantly, we control for females that have co-bred, as they have experience with direct reproduction. Helping experience alone had no impact on any of the metrics considered, except that helpers had an older age at first dominance. Females that had co-bred had longer dominant tenures, produced more recruits as dominant breeders and had a higher lifetime reproductive success than females that had never co-bred. Our results suggest that helping experience alone does not increase direct fitness in Seychelles warblers and highlights the importance of separating the effects of helping from co-breeding. Our findings also emphasise the importance of analysing the effect of helping at various life-history stages, as higher short-term fitness may not translate to an overall increase in lifetime fitness.

Key words: helper direct fitness benefits, cobreeding, cooperative breeding, Seychelles warbler, skills hypothesis, lifetime reproductive success

INTRODUCTION

Cooperative breeding is a breeding system wherein more than two individuals help to raise offspring. These helpers often forgo their own reproduction, at least temporarily, to help raise non-descendant offspring (Sherman et al., 1995) which is energetically costly (Heinsohn and Legge, 1999). Why an individual would choose to help despite these apparent reproductive and energetic costs has been a topic of great interest to evolutionary biologists.

The ‘skills hypothesis’ proposes that helpers obtain valuable breeding experience from helping, and that helpers may be more successful and proficient breeders later in life than non-helpers (Selander, 1965). Helpers may therefore gain delayed direct fitness benefits through their helping behaviour by maximising their future reproductive potential. Initial support for the skills hypothesis came from the Seychelles warbler (*Acrocephalus sechellensis*), where females with prior helping experience bred faster, built stronger nests and incubated longer in their first breeding attempt as a dominant breeder (Komdeur, 1996). In long-tailed tits (A*egithalos caudatus)*, helpers that gained a dominant breeding position built more successful nests than individuals that had never helped (Hatchwell et al., 1999), although this had no impact on breeding success in their first or second year (Meade and Hatchwell, 2010). Studies on other taxa such as the acorn woodpecker (*Melanerpes formicivorus*; Koenig and Walters, 2011), red-cockaded woodpecker (*Leuconotopicus borealis*; Khan and Walters, 1997), and white-fronted bee-eater (*Merops bullockoides*; Emlen and Wrege, 1989) found no effect of prior helping experience on short-term breeding success. In the Western bluebird (*Sialia mexicana*), helpers fledged fewer chicks in their first year as dominant breeders compared to non-helpers (Dickinson et al., 1996). Consequently, support for the skills hypothesis in wild populations is mixed.

Whilst a number of studies have considered how helping experience affects short-term breeding success, fewer studies have considered the effect of helping on longer-term fitness metrics, such as lifetime reproductive success (LRS), that ultimately determine the amount of genetic material passed on to the next generation (Link et al., 2002). The limited number of studies considering the longer-term fitness benefits of helping is likely because longitudinal data are required; life-long data from birth to death are needed, which many studies cannot obtain due to system ecology. The few studies that have considered the effect of helping on LRS, such as those on the lance-tailed manakin (*Chiroxiphia lanceolata;* DuVal, 2013), long-tailed tit (Maccoll and Hatchwell, 2004), and female Seychelles warblers (Busana et al., 2022) have shown that helping has no effect on the LRS of helpers compared to non-helpers. Further work is needed to determine whether there are longer-term fitness consequences of having helping experience, and at what life history stages these effects are seen.

Here, we investigate the fitness benefits of being a helper in the cooperatively breeding Seychelles warbler population on Cousin Island, where breeding positions are saturated. Previously, helping experience was found to have positive short-term fitness effects (Komdeur, 1996). When female subordinates were translocated to unoccupied islands, those with helping experience bred faster in their first breeding attempt (Komdeur, 1996), built stronger nests, and spent more time incubating than females without helping experience (Komdeur, 1996). However, 44% of subordinate females co-breed (Richardson et al., 2001, Sparks et al., 2021) which was not accounted for in Komdeur (1996). As such, it cannot be concluded that helping experience *per se* increased future breeding success, as females may have had direct breeding experience. Since 1997, >96% of warblers on Cousin have been ringed (Richardson et al., 2001), with 98% of ringed birds having been blood sampled and genotyped (Sparks et al., 2021), allowing genetic parentage and the rate of co-breeding to be accurately determined (Richardson et al., 2001, Hadfield et al., 2006, Sparks et al., 2021). With genetic parentage established, we can now test whether any initial reproductive benefits of having helping experience translate into longer-term fitness benefits. Busana et al. (2022) found that female helpers were less likely to obtain a dominant breeding position and had similar LRS to non-helpers. However, Busana et al. (2022) did not analyse male helpers, and co-breeders and helpers were not separated. In addition, whilst Busana et al. (2022) considered the effect of helping on female LRS, they did not consider the number of offspring produced after acquiring dominance, so did not address the skills hypothesis.

Seychelles warblers rarely disperse between islands (<0.1% of all birds studied; Komdeur et al., 2004) and the yearly resighting probability on Cousin is high (0.92 ± 0.02 for <2-year-olds and 0.98 ± 0.01 for older birds; Brouwer et al., 2010). If a warbler is not seen for two consecutive field seasons, we can therefore confidently assume that they are dead (Brouwer et al., 2006), thus lifetime fitness can be calculated accurately, which is rare in natural populations. Consequently, it is possible to analyse the effect of helping on helper fitness at various life-history stages, allowing us to test for effects during both early and late-life whilst controlling for additional, potentially confounding variables. If helping improves the short-term breeding success of helpers, helping may be an important investment in long-term fitness (Selander, 1965, Komdeur, 1996), especially in long-lived species such as the Seychelles warbler (maximum lifespan: 19 years; Hammers and Brouwer, 2017).

Using a 21-year genetic pedigree spanning a maximum of 12 generations, we investigate short and long-term fitness consequences of helping experience in both sexes, controlling for the effect of previous co-breeding experience. Specifically, we test the predictions that helpers, compared to non-helpers, have an: increased likelihood of obtaining a dominant breeding position (i.e., prestige hypothesis), older age at acquiring dominance and shorter breeding tenure (as they spend time helping), produce more adult offspring as dominant breeders (i.e., skills hypothesis), and have a similar overall LRS (as helping and non-helping are both stable strategies).

METHODS

Study system and data collection

There are *ca*. 320 adults in the closed population of Seychelles warblers on Cousin Island (0.29 km^2; 4°20′S, 55°40′E; Komdeur et al., 2016). The Seychelles warbler project began in 1985, with more intensive monitoring from 1997 onwards (Richardson et al., 2002). The population is studied during the major (June–September) and minor (January–March) breeding seasons (Richardson et al., 2002). The island contains ~115 Seychelles warbler territories (Komdeur, 2003), each of which is occupied by a breed group consisting of a dominant breeding pair and 0-5 helping and non-helping subordinates (Komdeur, 1992, Richardson et al., 2002). Roughly 42% of female and 20% of male subordinates help (Hammers et al., 2019). The dominant breeding pair in each territory are determined by observations of contact calls and mate-guarding (Richardson et al., 2002). Subordinates are defined as additional, sexually mature individuals that reside within the territory. One hour nest watches are performed to see whether subordinates help, either by incubating or provisioning offspring (Komdeur, 1994). Co-breeding females are subordinates that are the genetic mother of an offspring in their territory (Richardson et al., 2001).

Each season, as many individuals as possible are caught in mist-nests or as nestlings in the nest. Unringed birds are ringed with a unique combination of three ultraviolet-resistant colour rings, along with a British Trust for Ornithology metal ring. Blood samples (*ca*. 25µl) are then taken from all birds via brachial venepuncture and stored at room temperature in 100% ethanol for later DNA extraction and analysis. Up to 30 microsatellite loci (Richardson et al., 2000) are used to determine genetic parentage, and molecular sexing is performed using 1–3 loci (Sparks et al., 2021). The R package MASTERBAYES 2.52 (Hadfield et al., 2006) was used to assign parentage to 1809 offspring that hatched between 1991 and the minor season in 2018 (Edwards et al., 2018, Sparks et al., 2021), with fathers and mothers assigned to 87% and 84% of offspring, respectively, at ≥80% accuracy.

Groups typically produce one egg per season (Komdeur, 1996), although ~20% of clutches consist of 2–3 eggs (Richardson et al., 2001). Subordinate females occasionally lay eggs in the dominant female's nest, with ~11% of offspring being the product of co-breeding (Raj Pant et al., 2019, Sparks et al., 2021) by 44% of subordinate females (Richardson et al., 2001, Raj Pant et al., 2019, Sparks et al., 2021). Intra-specific egg dumping does not occur (Richardson et al., 2001). Extrapair paternity is common, with 41% of offspring sired by dominant males from a different territory (Raj Pant et al., 2019). Within-group subordinate males rarely gain paternity, siring just 0.6% of offspring (Sparks et al., 2021).

Seychelles warblers are territorial and insectivorous, so territory quality was estimated based on the amount of arthropod prey available within each territory (Komdeur, 1992, Brouwer et al., 2009). Missing territory quality data (151 territories across 40 seasons) were estimated using the mean territory quality values of the previous and subsequent breeding season of the same season-type within a particular territory (following Brouwer et al., 2006), as there is seasonal variation in territory quality (Komdeur and Daan, 2005).

Estimation of life-history traits and fitness metrics

We investigated the relationship between helping experience and five measures of life-history and fitness: likelihood of becoming a dominant breeder, the age at which they become a dominant breeder, the length of an individual's dominant breeding tenure, the number of offspring produced during their dominant breeding tenure, and their LRS. Likelihood of dominance was a binary metric of whether an individual was ever assigned a dominant breeding status. For age at first dominance, dominance tenure, and number of offspring produced as a dominant breeder, only individuals that had obtained dominance at some point during their lifetime were included. Age at first dominance was the time difference between an individual's estimated hatch date and the midpoint of the first breeding season that they were assigned a dominant breeding status. Length of dominance tenure was calculated as the total length of time that an individual spends in a dominant breeding position. The number of offspring produced throughout an individual's dominant breeding tenure was calculated as the total number of genetic offspring that an individual produced as a dominant breeder, determined using the Seychelles warbler genetic pedigree. Only offspring that survived to adulthood (≥1 year old) were included, as they were capable of propagating the lineage. LRS was calculated in the same way, except instead of the number of offspring (≥1 year old) produced over an individual's breeding tenure, it was the total number of offspring (≥1 year old) produced over an individual's lifetime. LRS therefore included offspring that were produced pre- and post-dominance, either through co-breeding (females) or subordinate extra-pair paternity (males). In addition, LRS provided a measure of fitness for individuals that never acquired dominance and, instead, remained life-long subordinates.

Dataset and statistical analyses

For all analyses, generalised linear mixed-effects models (GLMMs) were performed in *R* 4.2.1. (R Core Team, 2022) using glmmTMB 1.1.4 (Brooks et al., 2017).

The dataset included deceased individuals that had hatched from 1997 to the minor breeding season in 2018. Only individuals that survived to independence (≥3 months) were included in the models to remove potential biases in the dataset; nests located high in the canopy are hard to reach, so individuals raised in these nests are often only ringed and sampled after they have fledged and are independent (~3 months). Individuals that had not been assigned a helper status *prior to dominance* and lived during a field period in which their helper status could not be determined (e.g., if no nest-watch had been performed on a known nest) were excluded from these analyses (males: *n*=175; females: *n*=125), resulting in a dataset of 340 individuals (males: *n*=161; females: *n*=188), of which 34 males and 62 females had previous helping experience. For the likelihood of obtaining dominance and LRS models, if, during any field period within an individual's *lifetime*, a bird with no assigned helper status lived during a field period in which their helper status could not be determined, they were excluded from these analyses (males: *n*=279; females: *n*=231), resulting in a dataset of 545 individuals (males: *n*=251; females: *n*=294), of which 57 males and 120 females had previous experience as a helper.

Models were run separately for each sex. 42% of female and 20% of male subordinates help in the Seychelles warbler (Hammers et al., 2019), and males and females differ in their life-history strategies; they have different dispersal tactics (Komdeur, 1992, Kingma et al., 2016), age-related differences in territory acquisition (Eikenaar et al., 2008), and greater variance in male than female LRS (Sparks et al., 2022) and so analysing them separately allowed for the disentanglement of sex-related benefits. All models included the following fixed effects: whether the individual had experience as a helper (factor: yes/no), maternal age at conception (years) as both linear and squared variables to control for maternal effects that affect reproductive success (Sparks et al., 2022), and territory quality as this can affect individual dispersal (Komdeur, 1992; Komdeur et al., 1995) and reproductive success (Sparks et al., 2022). Territory quality was incorporated in different ways depending on the model and our hypotheses. For the likelihood of dominance models, natal territory quality was included. For the age at first dominance model, territory quality was incorporated as the mean territory quality prior to obtaining dominance. For the dominance tenure and number of offspring produced during dominance models, the mean territory quality during dominance was included. For the LRS models, the mean territory quality over an individual's lifetime was incorporated. For the male likelihood of acquiring dominance model, whether the focal individual received help when they were a nestling (i.e., had a "natal helper") was also included, as males with helpers have a reduced likelihood of acquiring dominance. For the dominance tenure and number of offspring produced during dominance models, the proportion of years as a dominant breeder that an individual had helpers was also included, as the presence of helpers can affect dominant breeder lifespan (Hammers et al., 2019) and reproductive success (Komdeur, 1994, Hammers et al., 2021). In addition, all female models included an additional variable addressing whether they had co-bred as a subordinate either before dominance (for the age at first dominance, length of dominance breeding tenure, and number of offspring produced throughout dominant breeding tenure models) or at any point over their lifetime (for the likelihood of dominance and LRS models). This was not appropriate for the male models as subordinate males rarely gain paternity (0.6%; Sparks et al., 2021). Cohort, genetic mother ID, and social father ID were included as random effects.

All models were checked for over-dispersion and zero-inflation using PERFORMANCE 0.5.1 (Lüdecke et al, 2021), and variance inflation factors (all <3; (Dormann et al., 2013). Model fit was determined by assessing plots of the observed values against the simulated squared residuals using DHARMa 0.3.3.0 (Hartig, 2022), as well as comparing the AIC values of candidate models, with the model of lowest AIC being preferred (Akaike, 1973). We fitted the following error distributions: binomial (likelihood of dominance models), negative binomial (male age at first dominance), quasi-Poisson distribution (female age at first dominance and breeding tenure models), and zero-inflated Poisson (number of offspring produced during tenure and LRS). Non-significant maternal age^2 effects were removed from the models to facilitate the interpretation of first-order age effects (see Table S1 for full models). Significance of random effects were determined using likelihood ratio tests comparing models with and without each random effect. Marginal effects and predicted counts of each variable of interest were calculated using GGEFFECTS 1.1.0 (Lüdecke, 2018). Marginal effects refer to the effect size of a variable of interest, after adjusting for all other model variables.

Ethical note

Fieldwork procedures were approved by the University of East Anglia's Ethical Review Committee and ratified by the University of Leeds.

RESULTS

Dominant breeding position acquisition

Having helping experience had no effect on whether a male or female Seychelles warbler acquired a dominant breeding position (Table 1). However, males that had natal helpers were less likely to become dominant breeders than males that did not have natal helpers (Table 1). In contrast, females hatched on higher quality territories were more likely to become dominant breeders than females hatched on lower quality territories (Table 1), but this was not the case in males.

Age at first dominance

For both male and female Seychelles warblers, having experience as a helper was associated with becoming a dominant breeder at an older age (Table 2; Fig. 1a). Female co-breeders also acquired dominance later than females that did not co-breed (Table 2; Fig. 1b).

Breeding tenure

Having experience as a helper had no significant effect on the tenure of dominant breeding in either sex (Table 3). Dominant females that had helpers for a greater proportion of their breeding tenure had longer breeding tenures than dominant females that had helpers for a lower proportion of their breeding tenure (Table 3). Co-breeding females also had longer breeding tenures than females that not previously co-bred (Table 3).

Number of adult offspring produced as a dominant breeder

We found no association between having experience as a helper and the number of adult offspring (≥1 year old) produced during their dominant breeding tenure in either males or females (Table 4). However, females that had co-bred prior to obtaining dominance produced more adult offspring during their dominant breeding tenure than females that did not co-breed (Table 4; Fig. 2). In addition, dominant females that had helpers over a greater proportion of their dominant tenure produced more adult offspring during this period than dominant females who had helpers for a lower proportion of their dominant tenure (Table 4). Females hatched by younger mothers also produced more adult offspring during their dominance tenure than females hatched by older mothers (Table 4).

Lifetime reproductive success

We found no relationship between having experience as a helper and the LRS of either males or females (Table 5). However, females that had co-bred had a higher LRS than females that had never co-bred (Table 5; Fig. 3). Females hatched by younger mothers also produced more adult offspring that survived to adulthood over their lifetimes than females hatched by older mothers (Table 5).

Table 1. Socio-ecological predictors of whether an individual becomes a dominant breeder in the Seychelles warbler, estimated using sex-specific GLMMs with binomial error distributions. Total number of males: 251 (males with helping experience: 57; males with a natal helper: 55), total number of females: 294 (females with helping experience: 120, females with co-breeding experience: 54). The parameter estimate, standard error (SE), z-value, and p-value are given for each fixed effect, along with the conditional r^2 for each model. Significant results are shown in bold and are underlined. Territory quality = natal territory quality. Reference level for helped ever/ natal helper/ co-bred ever = no.

		Males (*n*=251)					**Females (*n*=294)**				
Fixed effect	**Levels**	**Estimate**	**SE**	**z**	**p**	**r^2**	**Estimate**	**SE**	**z**	**p**	**r^2**
(Intercept)		0.52	0.50	1.04	0.298	0.28	0.10	0.36	0.29	0.771	0.09
Helped ever	Yes	0.35	0.41	0.85	0.395		0.20	0.29	0.68	0.496	
Co-bred ever	Yes	/	/	/	/		-0.14	0.36	-0.38	0.704	
Maternal age		0.43	1.01	0.43	0.670		-0.34	0.67	-0.51	0.611	
Natal helper	Yes	-1.04	0.42	-2.47	**0.014**		/	/	/	/	
Territory quality		0.63	1.68	0.38	0.707		2.80	1.32	2.12	**0.034**	
Random effect		**Levels**	**Variance**	**p**			**Levels**	**Variance**	**p**		
Mother ID		184	0.05	0.955			203	0.00	1.000		
Social father ID		177	0.61	0.483			196	0.02	0.960		
Cohort		22	0.44	**0.048**			22	0.20	0.139		

Table 2. Socio-ecological predictors of the age that Seychelles warblers become dominant breeders, estimated using sex-specific GLMMs with a quasi-Poisson distribution (nbinom2) for males and negative binomial distribution (nbinom1) for females. Total number of males: 161 (males with helping experience: 34); total number of females: 188 (females with helping experience: 62, females that co-bred prior to dominance: 19). The parameter estimate, standard error (SE), z-value, and p-value are given for each fixed effect, along with the conditional r^2 for each model. Significant results are shown in bold and are underlined. Territory quality = mean territory quality prior to dominance. Reference level for helped/co-bred before dom (dominance) = no

		Males (*n*=161)					**Females (*n*=188)**				
Fixed effect	**Levels**	**Estimate**	**SE**	**z**	**p**	**r²**	**Estimate**	**SE**	**z**	**p**	**r²**
(Intercept)		6.06	0.10	59.64	**<0.001**	0.54	6.14	0.08	74.33	**<0.001**	0.70
Helped before dom	Yes	0.74	0.08	9.06	**<0.001**		0.67	0.07	9.35	**<0.001**	
Co-bred before dom	Yes	/	/	/	/		0.51	0.09	5.53	**<0.001**	
Maternal age		0.09	0.20	0.45	0.654		-0.07	0.18	-0.41	0.681	
Territory quality		0.02	0.38	0.06	0.950		0.09	0.30	0.31	0.754	
Random effect		**Levels**	**Variance**	**p**			**Levels**	**Variance**	**p**		
Mother ID		129	0.03	0.111			145	0.07	**0.024**		
Social father ID		128	0.00	1.000			136	0.00	0.882		
Cohort		21	0.02	**0.035**			20	0.00	0.887		

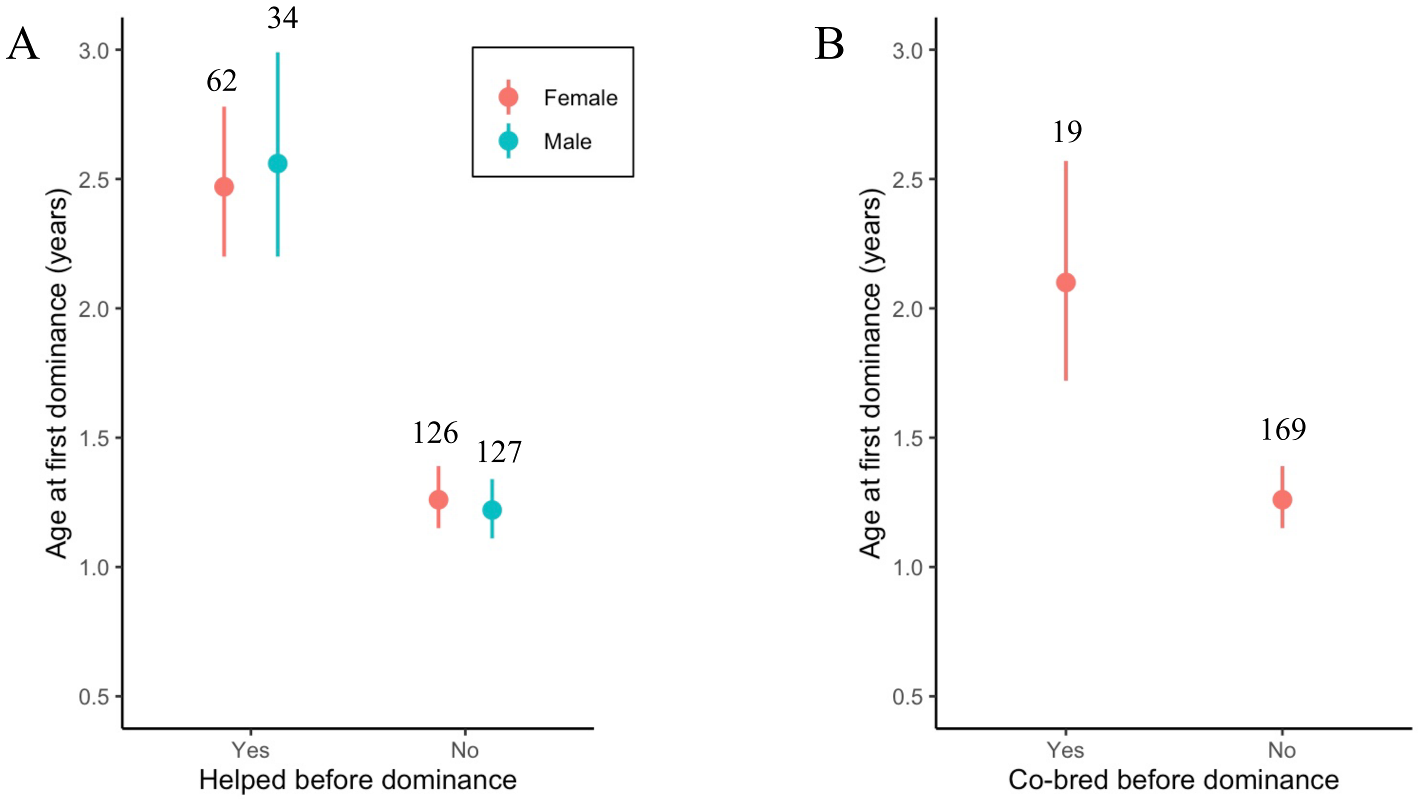


Fig. 1. Marginal effects of having experience as a helper (**A**; males and females) or co-breeding experience (**B**; females only) on the age that an individual first becomes a dominant breeder. The ggpredict function from the GGEFFECTS package (Lüdecke, 2018) in R was used to calculate the marginal effects and create the graphs: the solid points indicate the mean predicted value for each group, with associated 95% confidence intervals, after adjusting for all other model variables (Table 2). Numbers indicate the sample size for each group.

Table 3. Socio-ecological predictors of the length of breeding tenure, estimated using sex-specific GLMMs with a quasi-Poisson distribution (nbinom2) for males and negative binomial distribution (nbinom1) for females. Total number of males: 161 (males with helping experience: 33); total number of females: 187 (females with helping experience: 62, females that co-bred prior to dominance: 19). The parameter estimate, standard error (SE), z-value, and p-value are given for each fixed effect, along with the conditional r^2 for each model. Significant results are shown in bold and are underlined. Territory quality= mean territory quality during dominance. Reference level for helped/co-bred before dom (dominance) = no

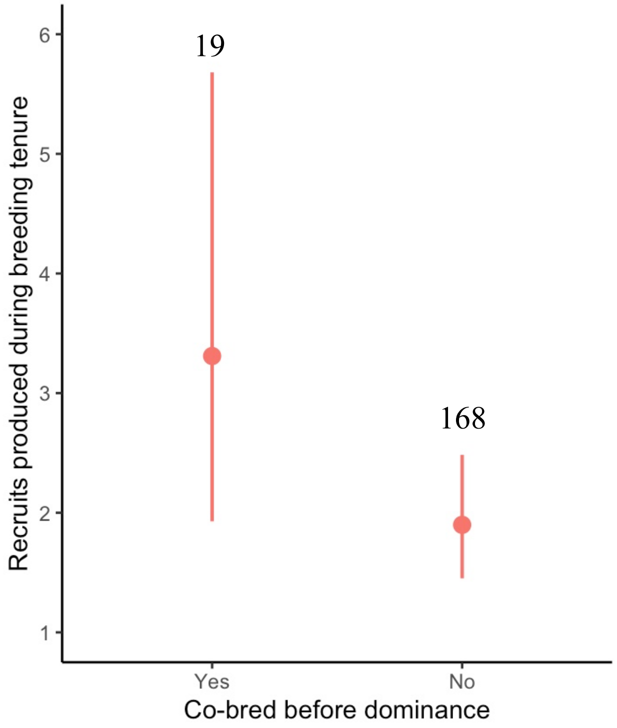
		Males (*n*=161)					**Females (*n*=187)**				
Fixed effect	**Levels**	**Estimate**	**SE**	**z**	**p**	**r^2**	**Estimate**	**SE**	**z**	**p**	**r^2**
(Intercept)		5.90	0.23	25.14	**<0.001**	0.18	6.03	0.16	37.20	**<0.001**	0.09
Helped before dom	Yes	-0.24	0.18	-1.32	0.188		-0.17	0.13	-1.32	0.186	
Co-bred before dom	Yes	/	/	/	/		0.39	0.19	2.05	**0.040**	
Maternal age		0.48	0.41	1.15	0.249		-0.02	0.29	-0.05	0.958	
Territory quality		-0.18	0.75	-0.25	0.806		0.14	0.44	0.33	0.744	
Proportion of tenure with helpers		0.59	0.53	1.12	0.262		1.00	0.29	3.43	**<0.001**	
Random effect		**Levels**	**Levels**	**p**			**Levels**	**Levels**	**p**		
Mother ID		129	0.00	1.000			145	0.00	0.999		
Social father ID		128	0.06	0.631			136	0.00	0.999		
Cohort		21	0.07	0.142			20	0.03	0.147		

Table 4. Socio-ecological predictors of the number of offspring an individual produces after acquiring a dominant breeding position, estimated using sex-specific GLMMs with zero-inflated Poisson distributions. Total number of males: 161 (males with helping experience: 33); total number of females: 187 (females with helping experience: 62; females that co-bred prior to dominance: 19). The parameter estimate, standard error (SE), z-value, and p-value are given for each fixed effect, along with the conditional r^2 for each model. Significant results are shown in bold and are underlined. Territory quality = mean territory quality during dominance. Reference level for helped/co-bred before dom (dominance) = no

		Males (*n*=161)					**Females (*n*=187)**				
Fixed effect	**Levels**	**Estimate**	**SE**	**z**	**p**	**r^2**	**Estimate**	**SE**	**z**	**p**	**r^2**
(Intercept)		0.73	0.38	1.91	0.056	0.60	1.02	0.29	3.56	**<0.001**	0.42
Helped before dom	Yes	-0.28	0.26	-1.09	0.278		-0.33	0.19	-1.70	0.090	
Co-bred before dom	Yes	/	/	/	/		0.56	0.26	2.16	**0.031**	
Maternal age		-0.62	0.56	-1.11	0.266		-1.01	0.46	-2.18	**0.029**	
Territory quality		-0.93	1.01	-0.92	0.356		-0.86	0.85	-1.01	0.314	
Proportion of tenure with helpers		0.68	0.69	0.99	0.320		1.50	0.64	2.36	**0.018**	
Zero-inflated model											
(Intercept)		-1.16	0.34	-3.39	**<0.001**		-1.18	0.31	-3.83	**<0.001**	
Random effect		**Levels**	**Variance**	**p**			**Levels**	**Variance**	**p**		
Mother ID		129	0.00	1.000			145	0.18	0.244		
Social father ID		128	0.29	0.176			136	0.00	1.000		
Cohort		21	0.43	**<0.001**			20	0.02	0.596		

Table 5. Socio-ecological predictors of LRS in the Seychelles warbler, estimated using sex-specific GLMMs with zero-inflated Poisson models. Total number of males: 250 (males with helping experience: 57); total number of females: 294 (females with helping experience: 120; females with co-breeding experience: 54). The parameter estimate, standard error (SE), z-value, and p-value are given for each fixed effect, along with the conditional r^2 for each model. Significant results are shown in bold and are underlined. Territory quality = mean territory quality over lifetime. Reference level for helped/co-bred ever = no.

		Males (*n*=250)					**Females (*n*=294)**				
Fixed effect	**Levels**	**Estimate**	**SE**	**z**	**p**	**r^2**	**Estimate**	**SE**	**z**	**p**	**r^2**
(Intercept)		0.38	0.47	0.81	0.415	0.68	1.02	0.43	2.34	**0.019**	0.54
Helped ever	Yes	-0.17	0.26	-0.64	0.521		-0.16	0.19	-0.81	0.418	
Co-bred ever	Yes	/	/	/	/		0.68	0.24	2.91	**0.004**	
Maternal age		-0.52	0.58	-0.90	0.371		-1.17	0.44	-2.65	**0.008**	
Territory quality		-0.91	1.31	-0.69	0.489		-1.21	1.28	-0.94	0.346	
Zero-inflated model											
(Intercept)		-0.33	0.23	-1.43	0.154		-0.44	0.29	-1.51	0.132	
Random effect		**Levels**	**Variance**	**p**			**Levels**	**Variance**	**p**		
Mother ID		183	0.00	1.000			203	0.26	**0.007**		
Social father ID		176	0.35	0.368			196	0.00	1.000		
Cohort		22	0.83	**<0.001**			22	0.11	0.152		



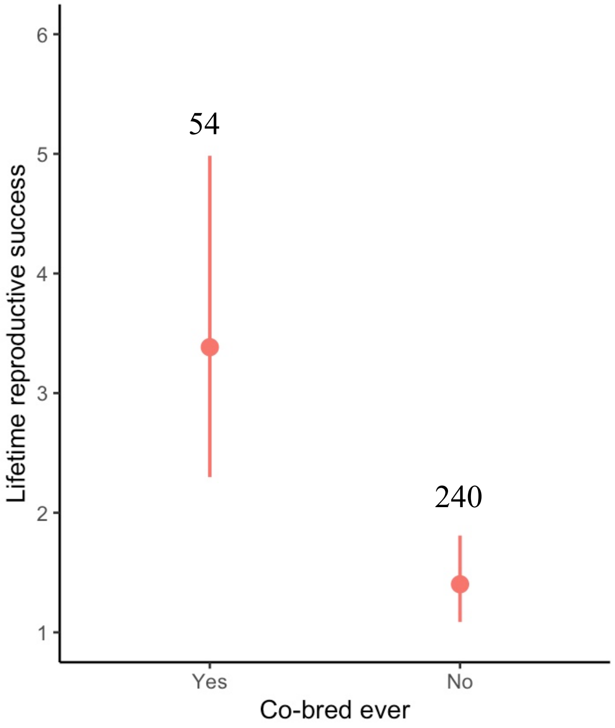


Fig. 2. Marginal effects of having co-bred prior to dominance on the number of offspring a female Seychelles warbler produces after acquiring dominance. The ggpredict function from the GGEFFECTS package (Lüdecke, 2018) in R was used to calculate the marginal effects and create the graphs: the solid points indicate the mean predicted value for each group, with associated 95% confidence intervals, after adjusting for all other model variables (Table 4). Numbers indicate the sample size for each group.

Fig. 3. Marginal effects of having co-bred on the lifetime reproductive success of female Seychelles warblers. The ggpredict function from the GGEFFECTS package (Lüdecke, 2018) in R was used to calculate the marginal effects and create the graphs: the solid points indicate the mean predicted value for each group, with associated 95% confidence intervals, after adjusting for all other model variables (Table 5). Numbers indicate the sample size for each group.

DISCUSSION

Having helping experience had no effect on the likelihood of an individual acquiring dominance, length of breeding tenure, number of offspring produced as a dominant breeder, or LRS in either male or female Seychelles warblers. Individuals that helped, and females that co-bred, had a higher age at first dominance than individuals that did not help and females that did not co-breed, respectively. Additionally, females that co-bred as subordinates had longer dominant breeding tenures, produced more offspring as dominant breeders and had higher LRS than females that did not co-breed.

We found that experience as a helper had no effect on whether an individual acquired a dominant breeding position in either males or females. At first sight, this finding conflicts with a previous study on the Seychelles warbler, which found that female helpers were *less* likely to acquire a dominant breeding position than female non-helpers (Busana et al., 2022). However, Busana et al. (2022) analysed female subordinate non-helpers versus female subordinate helpers, whereas we analysed all subordinate helpers versus any bird with no helping experience, which includes birds that had no subordinate status and went straight to first being a floater or a dominant, as well as a subordinate non-helper.

Our findings indicate that helping experience has no effect on the likelihood of an individual becoming a dominant breeder, which could provide evidence against the ‘social prestige’ hypothesis in the Seychelles warbler (Zahavi, 1995). The social prestige hypothesis posits that helping serves as a way for an individual to advertise their phenotypic quality and caregiving abilities, making them more attractive to potential mates, thus providing future direct fitness benefit (Zahavi, 1995). The social prestige hypothesis has limited evidence in other taxa, with the majority of studies finding that helping has no effect on an individual's likelihood of acquiring dominance or future breeding opportunities (Wright, 2007, McDonald et al., 2008, Nomano et al., 2013). Indeed, it has been argued that social prestige likely requires a level of cognitive processing that most species are unlikely to be capable of (Wright, 2007, McDonald et al., 2008). In addition, studies on other taxa have shown that helping may be associated with an increased likelihood of obtaining dominance (Field et al., 2006, Cockburn et al., 2008), not due to social prestige, but because helping serves as a way for an individual to remain in the 'breeding queue' on their natal territory (Wiley and Rabenold, 1984, Koenig and Dickinson, 2004, Stacey and Koenig, 1990). However, in the Seychelles warbler, the majority of dominant statuses are acquired when a subordinate moves to a vacant breeding position on a non-natal territory (Komdeur and Edelaar, 2001), which may explain why we found no effect of helping on acquisition of a dominant breeding position.

Whilst we found no effect of helping experience on dominant breeding position acquisition, we did find that helpers became dominant breeders later in life than those that did not help. This result is consistent with previous studies on female Seychelles warblers (Busana et al., 2022) and the lance-tailed manakin (Duval et al. 2013). If individuals spend time helping prior to gaining a dominant breeding position, it follows that they become a dominant breeder at an older age compared to individuals that did not help and, instead, acquired dominance at their earliest opportunity.

Even though helpers become dominant breeders at an older age, there was no significant difference in dominant breeding tenure between birds that have helping experience and those that do not. If helpers obtain dominance at an older age yet there is no significant difference in the length of tenure, this could suggest that helpers have longer lifespans than birds without helping experience. Indeed, after running a supplementary analysis on our dataset, we found that dominant females that had previously helped had significantly longer lifespans than dominant females that had never helped (Table S2). This complements the findings of Hammers et al., (2013), where Seychelles warblers that delayed reproduction had delayed late-life survival senescence. Our findings, therefore, provide additional support for the ‘disposable soma’ hypothesis–a trade-off between early-life reproductive investment and late-life declines in reproduction and survival (Kirkwood and Rose, 1991). As female helpers spend time helping, they delay independent reproduction which is linked to increased longevity. The reason this effect was found in females, and not males, could be because female birds bear the cost of egg production (Nilsson and Råberg, 2001, Williams, 2005) and, in the Seychelles warbler, dominant breeding females provide more parental care than dominant breeding males: only females incubate (Komdeur, 1994) and dominant breeding males have lower provisioning rates than dominant breeding females (van Boheemen et al., 2019). These analyses controlled for the effect of female co-breeding, and we found that females that had previously co-bred had longer dominant breeding tenures than females that had not co-bred. One untested explanation for this is that as co-breeding females have demonstrated their proficiency as breeders, they may be less likely to be divorced or demoted to a subordinate position than breeding females that have not co-bred.

Having helping experience did not increase the number of adult offspring produced as a dominant, providing evidence against the skills hypothesis. Female Seychelles warblers with helping experience build stronger nests and make their first breeding attempt quicker than non-helpers after acquiring a dominant breeding position (Komdeur, 1996). It was suggested that these early reproductive benefits could then translate into improvements in long-term reproductive success. Having tested this here, reproductive success as a dominant did not differ with helping experience. However, Komdeur (1996) did not separate helpers and co-breeders, and so the early reproductive benefits that were identified could possibly be attributed to co-breeders that had experience with direct reproduction. Indeed, we found that females with prior co-breeding experience produced more adult offspring that survived to adulthood throughout their dominant breeding tenure than females that had never co-bred. This suggests that experience of direct reproduction improves the future reproductive success of dominant females, as opposed to helping experience. Higher reproductive success could be driven by females with co-breeding experience having longer dominant tenures; however, it is also possible that females with co-breeding experience are more proficient breeders, producing more successful offspring per unit time, although this was not tested here. In other species, individuals with prior breeding experience can be more successful at raising offspring (Limmer and Becker, 2009, Baran and Adkins-Regan, 2014), although this is not the case in all taxa (Cichoñ, 2003, Pärt, 1995). Additionally, the apparent benefits of prior breeding experience could be due to age-related effects i.e., that older individuals are better at foraging or increase their breeding effort with age (see Forslund and Pärt (1995) for review; Cichoñ, 2003). Whilst we did not account for age-related effects, the fact that both helpers and co-breeders commence breeding at an older age, yet only co-breeders benefit from an increase in reproductive success throughout their dominant breeding tenures, suggests that this effect is not due to age-related improvements in reproductive performance, but prior breeding experience specifically.

Alternatively, co-breeding experience may not *cause* an improvement in reproductive success throughout an individual's dominant breeding tenure. Instead, underlying factors that enable a female to co-breed may also enable them to be more successful dominant breeders later in life. For instance, better quality females may be more likely to co-breed alongside a dominant female (van de Crommenacker et al. (2011), and, because of their higher quality, may also be more successful breeders once they acquire dominance. However, whether co-breeders are in better condition than helpers or non-helping subordinates is unknown in the Seychelles warbler.

Helping experience had no effect on male or female LRS (offspring that survived to ≥1 year of age), as predicted, and as previously demonstrated in female Seychelles warblers using offspring that survived to at least 6 months of age (Busana et al., 2022). As there was no difference between the LRS of helpers and non-helpers of either sex, helping and non-helping could be viewed as equally successful life-history strategies in terms of the direct fitness benefits acquired. Additionally, co-breeding increased the LRS of females. Many females never produce offspring (58.6%) and, by definition, co-breeding females produce at least one offspring. It is unsurprising, therefore, that co-breeders had a higher LRS than females that did not co-breed.

Whilst we found no effect of helping on any of the fitness metrics measures, it must be noted that we only considered the effect of helping on the direct fitness of helpers. However, individuals may gain indirect fitness benefits from helping to raise relatives (Hamilton, 1964). If helpers are related to these offspring, this will increase the amount of shared genetic material that is passed on to the next generation (Hamilton, 1964). Whilst the level of relatedness between helpers and non-descendant offspring is relatively low in the Seychelles warbler due to high levels of extra-pair paternity (0.13 ± 0.23 and 0.08 ± 0.25 for male and female subordinates, respectively; Richardson et al., 2002), when direct reproduction is not possible, the indirect fitness benefits obtained through helping may not be insignificant.

CONCLUSION

We demonstrate that helping experience has no effect on the long-term reproductive success of Seychelles warblers. Our results do not align with the skills hypothesis, as helping had no effect on the future breeding success of helpers. Helping~~,~~ consequently, is an equally successful life-history strategy of Seychelles warblers in terms of future direct reproductive benefits compared to individuals with no helping experience. Our findings highlight the importance of separating helpers from co-breeders, as co-breeders produced more adult offspring as dominants and had higher LRS than females that did not co-breed. Whilst previous Seychelles warbler studies have shown helping experience to have short-term reproductive benefits, here, we have shown that this does not result in greater long-term reproductive success. Future studies on cooperative breeders should therefore consider the benefits of helping at various life-history stages, as any effect of helping on short-term breeding success may not translate into longer-term fitness benefits.

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