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Chesterton, E., Sparks, A.M., Burke, T. et al. (2024) The impact of helping experience on helper life-history and fitness in a cooperatively breeding bird. Evolution, 78 (4). pp. 690-700. ISSN: 0014-3820

https://doi.org/10.1093/evolut/qpad199

Evolution, 2024, **78(4)**, 690–700
https://doi.org/10.1093/evolut/qpad199
Advance access publication 8 November 2023
Original Article

OXFORD

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

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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 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 analyze how helping experience affects key breeding and fitness-related parameters in the Seychelles warbler (*Acrocephalus sechellensis*). Importantly, we control for females that have cobred (reproduced as a subordinate by laying an egg within a territory in which they are not a dominant breeder), as they already have experience with direct reproduction. Helping experience had no significant association with any of the metrics considered, except that helpers had an older age at first dominance. Accounting for helping experience, females that had cobred produced more adult offspring (≥1 year) after acquiring dominance and had a higher lifetime reproductive success (LRS) than females that had never cobred. Our results suggest that, in the Seychelles warbler, helping experience alone does not increase the fitness of helpers in any of the metrics considered, and highlights the importance of separating the effects of helping from cobreeding. Our findings also emphasize the importance of analyzing the effect of helping at various life-history stages, as higher short-term fitness may not translate to an overall increase in LRS.

Keywords: helper 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 nondescendant offspring (Sherman et al., 1995) which is energetically costly (Heinsohn & 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 nonhelpers (Selander, 1965). Helpers may therefore gain delayed fitness benefits through their helping behavior by maximizing 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 (*Aegithalos caudatus*), helpers that gained a dominant breeding position built more successful nests than individuals that had never helped (Hatchwell et al., 1999). Studies on other taxa such as the acorn woodpecker (*Melanerpes formicivorus*; Koenig & Walters, 2011), red-cockaded woodpecker (*Leuconotopicus borealis*; Khan & Walters, 1997), and white-fronted bee-eater (*Merops bullockoides*; Emlen & 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 nonhelpers (Dickinson et al., 1996). Consequently, support for the skills hypothesis in wild populations is mixed. If helping experience does, indeed, provide individuals with more skills, an increase in future reproductive success is expected for those dominant breeders who have helping experience relative to those without (Komdeur, 1996).

The "social prestige" hypothesis (Zahavi, 1974, 1977, 1990, 1995) proposes that helpers are signaling their phenotypic quality and caregiving abilities, making them more attractive to potential mates by increasing their social rank. If the social prestige hypothesis holds true, individuals with helping experience may then be more likely to acquire a dominant breeding position relative to individuals without helping experience (Zahavi, 1995). Social prestige was initially reported in Arabian babblers (*Turdoides squamiceps*; Zahavi, 1995), but this was not corroborated by later

Received January 5, 2023; revisions received September 1, 2023; accepted November 8, 2023
Associate Editor: Bram Kuijper; Handling Editor: Tim Connallon

work on the same population (Wright, 2007). Provisioning analyses in other species such as the bell miner (*Manorina melanophrys*; McDonald et al., 2008), chestnut-crowned babbler (*Pomatostomus ruficeps*; Nomano et al., 2013), and acorn woodpecker (Koenig & Walters, 2016) were also not consistent with the social prestige hypothesis. Additionally, false-feeding behavior observed in species such as carrion crows (*Corvus corone corone*; Canestrari et al., 2004) and meerkats (Clutton-Brock et al., 2005) is not consistent with the social prestige hypothesis, rather the behavior is more parsimonious with individuals assessing the needs of their offspring versus their own. Overall, there is no support for the social prestige hypothesis.

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). The limited number of studies in natural populations 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 the open nature of many systems. 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 & Hatchwell, 2004), and female Seychelles warblers (Busana et al., 2022) have shown that helping has no effect on the LRS of helpers compared to nonhelpers. Further work is needed to determine whether there are, indeed, long-term fitness consequences of having helping experience, and, if so, at what life-history stages these effects are seen.

In cooperatively breeding species, individuals may pass on their own genes to the next generation by reproducing themselves, and by helping to raise the offspring of their relatives (Hamilton, 1964). Fitness metrics can therefore be decomposed into indirect fitness (from helping relatives to produce offspring) and direct fitness (where social effects are stripped from an individual's own reproductive success) components, which can be summed to estimate inclusive fitness. Quantifying lifetime inclusive fitness is challenging in natural populations, as, for example, individuals can help or not help, and reproduce with and without helpers over their lifetime (Koenig et al., 2023). A first step to this quantification is estimating the LRS of individuals with different helping histories. Estimating LRS is challenging in itself in natural populations, as individuals have to be followed over their entire lifetime and often parentage must be assigned with molecular methods.

Here, we investigate the fitness benefits, including LRS, 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 cobreed (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 reproductive 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 cobreeding to be accurately determined (Hadfield et al., 2006; Richardson et al., 2001; 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 nonhelpers. However, Busana et al. (2022) did not analyze male helpers, and cobreeders and helpers were not separated. In addition, whilst Busana et al. (2022) considered the effect of helping on female LRS, they did not test for an effect of helping experience on the number of offspring produced after acquiring dominance, so did not address the skills hypothesis which predicts that helping experience increases future reproductive success.

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 LRS can be calculated accurately, which is rare in natural populations. Consequently, it is possible to analyze the effect of helping experience on 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 (Komdeur, 1996; Selander, 1965), 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 cobreeding experience. Specifically, we test the predictions that helpers, compared to nonhelpers have: an increased likelihood of obtaining a dominant breeding position (i.e., prestige hypothesis), an older age at acquiring dominance and shorter breeding tenure (as they spend time helping), more adult offspring after acquiring dominance (i.e., skills hypothesis), and a lower overall LRS (as helping and nonhelping are both evolutionary stable strategies but helpers also gain indirect fitness through kin selection).

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 breeding group consisting of a dominant breeding pair and 0–5 helping and nonhelping subordinates (Komdeur, 1992; Richardson et al., 2002). Roughly 42% of female and 20% of male subordinates help (Hammers et al., 2019). Helpers are often, but not always, the offspring of the dominant pair from a previous breeding attempt (Kingma et al., 2016). 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, subdivided into "helpers" and "non-helpers" depending on whether they have been observed incubating or provisioning offspring during a 1-hr next watch once an active nest has been located (Komdeur, 1994). Helpers and nonhelpers are determined using data obtained across all breeding seasons; if a bird is identified as a helper during any season throughout their lifetime, they are assigned a helper status. Cobreeding 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 color rings, along with a British Trust for Ornithology metal ring. Blood samples (ca. 25 µl) 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 1,809 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 two to three eggs (Richardson et al., 2001). Subordinate females occasionally lay eggs in the dominant female's nest, with ~11% of offspring being the product of cobreeding (Raj Pant et al., 2019; Sparks et al., 2021) by 44% of subordinate females (Raj Pant et al., 2019; Richardson et al., 2001; Sparks et al., 2021). Intra-specific egg dumping, within and between groups, does not occur (Richardson et al., 2001). Extra-pair 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 within the population (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 (Brouwer et al., 2009; Komdeur, 1992). 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 & 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 after acquiring a dominant breeding position, 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 after acquiring a dominant breeding position, 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. Hatch dates are estimated from nest watches based on observed lay dates, hatch dates, or fledge dates (Komdeur, 1991). Alternatively, if this information is unavailable, hatch dates may be estimated using eye color at first catch as Seychelles warblers display different colored eyes up to adulthood, or breeding status (Komdeur, 1991). Length of dominance tenure was calculated as the total length of time that an individual spends in a dominant breeding position. Once dominance has been acquired within a territory, an individual may stay in that breeding position until death. Alternatively, they may be demoted back to a subordinate position or acquire a dominant breeding position on a different territory. The number of offspring produced after acquiring dominance was calculated as the total number of genetic offspring that an individual produced after acquiring their first dominant breeding position, determined using the Seychelles warbler genetic pedigree. Only offspring that survived to adulthood (≥1 year old) were included, as they have been recruited into the adult breeding population and are capable of reproducing and passing on the genetic information that they share with the focal individual. LRS was calculated in the same way, except instead of the number of offspring (≥1 year old) produced after an individual acquired dominance, 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 cobreeding (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, generalized linear mixed-effects models 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). For the age at first dominance, length of breeding tenure, and number of offspring produced after acquiring dominance models, 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 351 individuals (males: $n = 163$; females: $n = 188$), of which 34 males and 62 females had previous helping experience. For the models investigating the likelihood of obtaining dominance and differences in LRS, any individual whose helper status could not be determined in any field periods during their *lifetime* were excluded (males: $n = 279$; females: $n = 231$), resulting in a dataset of 548 individuals (males: $n = 254$; females: $n = 294$), of which

59 males and 120 females had previous experience as a helper. For these two models, the datasets were larger than the others as they included all individuals that had data for the variables of interest, not just those that had acquired dominance.

Models were run separately for each sex. Males and females differ in the amount they help in the Seychelles warbler (Hammers et al., 2019), and in their life-history strategies; they have different dispersal tactics (i.e., females disperse further than males, Kingma et al., 2016; Komdeur, 1992), age-related differences in territory acquisition (Eikenaar et al., 2008), and greater variance in male than female LRS (Sparks et al., 2022) and so analyzing 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 after first acquiring dominance, 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 reared with helpers have a reduced likelihood of acquiring dominance. For the dominance tenure and number of offspring produced after first acquiring dominance models, the proportion of breeding seasons 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

Table 1. Socioecological predictors of whether an individual becomes a dominant breeder in the Seychelles warbler, estimated using sex-specific generalized linear mixed-effects models (GLMMs) with binomial error distributions. Total number of males: 254 (males with helping experience: 59; males with a natal helper: 58), total number of females: 294 (females with helping experience: 120, females with cobreeding experience: 54). The parameter estimate, standard error (SE), *z*-value, and *p*-value are given for each fixed effect, along with the marginal r^2 for each model. Territory quality = natal territory quality. Reference level for helped ever/natal helper/ cobred ever = no.

		Males ($n = 254$)					Females ($n = 294$)				
Fixed effect	Levels	Estimate	SE	*z*	*p*	r^2	Estimate	SE	*z*	*p*	r^2
Intercept		0.64	0.49	1.29	.196	0.04	0.10	0.36	0.29	.771	0.04
Helped ever	Yes	0.31	0.40	0.78	.435		0.20	0.29	0.68	.496	
Cobred ever	Yes	/	/	/	/		−0.14	0.36	−0.38	.704	
Maternal age		0.20	1.00	0.20	.841		−0.34	0.67	−0.51	.611	
Natal helper	Yes	−1.00	0.41	−2.42	.016		/	/	/	/	
Territory quality		0.39	1.68	0.24	.814		2.80	1.32	2.12	.034	
Random effect		**Levels**	**Variance**	***p***			**Levels**	**Variance**	***p***		
Mother ID		186	0.31	0.709			203	0.00	1.000		
Social father ID		179	0.36	0.679			196	0.02	0.960		
Cohort		22	0.38	0.068			22	0.20	0.139		

Table 2. Socioecological predictors of the age that Seychelles warblers become dominant breeders, estimated using sex-specific generalized linear mixed-effects models (GLMMs) with quasi-Poisson distributions (nbinom2). Total number of males: 163 (males with helping experience: 34); total number of females: 188 (females with helping experience: 62, females that cobred prior to dominance: 19). The parameter estimate, standard error (SE), *z*-value, and *p*-value are given for each fixed effect, along with the marginal r^2 for each model. Territory quality = mean territory quality prior to dominance. Reference level for helped/cobred before dom (dominance) = no.

		Males ($n = 163$)					Females ($n = 188$)				
Fixed effect	Levels	Estimate	SE	*z*	*p*	r^2	Estimate	SE	*z*	*p*	r^2
Intercept		6.05	0.10	59.63	<.001	0.44	6.17	0.08	76.43	<.001	0.55
Helped before dom	Yes	0.73	0.08	8.94	<.001		0.67	0.07	9.30	<.001	
Cobred before dom	Yes	/	/	/	/		0.54	0.11	4.86	<.001	
Maternal age		0.14	0.20	0.68	.494		−0.11	0.17	−0.67	.504	
Territory quality		0.02	0.38	0.05	.956		0.05	0.29	0.16	.871	
Random effect		**Levels**	**Variance**	***p***			**Levels**	**Variance**	***p***		
Mother ID		130	0.03	0.112			145	0.03	0.024		
Social father ID		130	0.00	1.000			136	0.00	1.000		
Cohort		21	0.02	0.044			20	0.00	1.000		

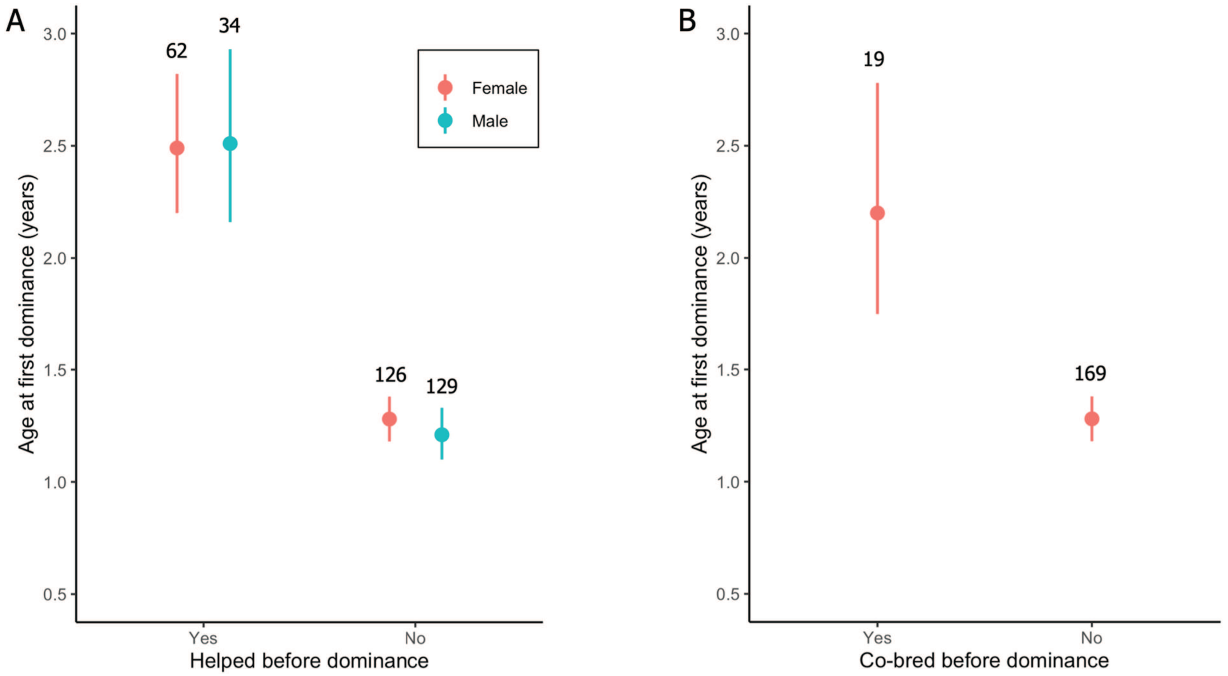

Figure 1. Marginal effects of having experience as a helper (A; males and females) or cobreeding experience (B; females only) on the age that an individual first becomes a dominant breeder. The ggpredict function from the GGEFFECTS package (Lüdecke, 2018) in R was used to calculate the marginal effects 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. Socioecological predictors of the length of breeding tenure, estimated using sex-specific generalized linear mixed-effects models (GLMMs) with negative binomial distributions (nbinom1). Total number of males: 163 (males with helping experience: 34); total number of females: 187 (females with helping experience: 62, females that cobred prior to dominance: 19). The parameter estimate, standard error (SE), *z*-value, and *p*-value are given for each fixed effect, along with the marginal r^2 for each model. Territory quality = mean territory quality during dominance. Reference level for helped/cobred before dom (dominance) = no.

		Males (n = 163)					Females (n = 187)				
Fixed effect	Levels	Estimate	SE	z	p	r^2	Estimate	SE	z	p	r^2
Intercept		6.91	0.23	30.15	<.001	0.03	6.95	0.20	35.03	<.001	0.06
Helped before dom	Yes	−0.28	0.17	−1.65	.099		−0.22	0.15	−1.49	.137	
Cobred before dom	Yes	/	/	/	/		0.36	0.23	1.59	.113	
Maternal age		0.36	0.43	0.85	.398		0.05	0.33	0.14	.887	
Territory quality		0.03	0.63	−0.04	.965		0.30	0.50	0.61	.544	
Proportion of breeding seasons with helpers		0.25	0.38	0.67	.501		1.19	0.36	3.32	<.001	
Random effect		**Levels**	**Variance**	p			**Levels**	**Variance**	p		
Mother ID		130	0.00	1.000			145	0.00	1.000		
Social father ID		130	0.09	0.429			136	0.03	0.784		
Cohort		21	0.08	0.019			20	0.08	0.016		

reproductive success (Hammers et al., 2021; Komdeur, 1994). In addition, all female models included an additional variable addressing whether they had cobred as a subordinate either before dominance (for the age at first dominance, length of dominance breeding tenure, and number of offspring produced after first acquiring dominance 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 overdispersion 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 and testing their normality using DHARMa 0.3.3.0 (Hartig, 2022). For models where multiple distributions passed these checks and QQ plots were similar, the model with the lowest AIC was preferred (Akaike, 1973). We fitted the following error distributions: binomial (link = “logit”; likelihood of dominance models), quasi-Poisson distribution (link = “log”; age at first

Table 4. Socioecological predictors of the number of offspring an individual produces after acquiring a dominant breeding position, estimated using sex-specific generalized linear mixed-effects models (GLMMs) with zero-inflated Poisson distributions. Total number of males: 163 (males with helping experience: 34); total number of females: 187 (females with helping experience: 62; females that cobred prior to dominance: 19). The parameter estimate, standard error (SE), *z*-value, and *p*-value are given for each fixed effect, along with the marginal r^2 for each model. Territory quality = mean territory quality during dominance. Reference level for helped/cobred before dom (dominance) = no.

		Males (n = 163)					Females (n = 187)				
Fixed effect	Levels	Estimate	SE	z	p	r^2	Estimate	SE	z	p	r^2
Intercept		0.82	0.36	2.26	.024	0.05	1.02	0.29	3.56	<.001	0.15
Helped before dom	Yes	−0.28	0.25	−1.11	.266		−0.33	0.19	−1.70	.090	
Cobred before dom	Yes	/	/	/	/		0.56	0.26	2.16	.031	
Maternal age		−0.69	0.55	−1.24	.215		−1.01	0.46	−2.18	.029	
Territory quality		−1.01	0.99	−1.02	.309		−0.86	0.85	−1.01	.314	
Proportion of breeding seasons with helpers		0.69	0.67	1.03	.303		1.50	0.64	2.36	.018	
Zero-inflated model											
Intercept	−1.13	0.34	−3.37	<0.001		−1.18	0.31	−3.83	<0.001		
Random effect		Levels	Variance	p			Levels	Variance	p		
Mother ID		130	0.00	1.000			145	0.18	0.244		
Social father ID		130	0.28	0.176			136	0.00	1.000		
Cohort		21	0.36	<0.001			20	0.02	0.596		

dominance models), negative binomial (link = "log"; breeding tenure models), and zero-inflated Poisson (link = "log"; number of offspring produced after first acquiring dominance and LRS). Statistically nonsignificant maternal age^2 effects were removed from the models to facilitate the interpretation of first-order age effects (see Supplementary Table S1 for full models). Statistical 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 was not statistically associated with whether a male or female Seychelles warbler acquired a dominant breeding position (Table 1). There was also no significant difference in the probability of acquiring a dominant breeding position between females who did and did not cobreed (Table 1).

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; Figure 1A). Female cobreeders also acquired dominance later than females that did not cobreed (Table 2; Figure 1B).

Breeding tenure

Having experience as a helper had no statistically significant association with the tenure of dominant breeding in either sex (Table 3).

Number of adult offspring produced after acquiring dominance

We found no association between having experience as a helper and the number of adult offspring (≥1 year old) produced after first acquiring dominance in either males or females (Table 4). However, females that had cobred prior to obtaining dominance produced more adult offspring after acquiring dominance than females that did not cobreed (Table 4; Figure 2).

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 cobred had a higher LRS than females that had never cobred (Table 5; Figure 3).

Discussion

Having helping experience was not statistically associated with the likelihood of an individual acquiring dominance, length of breeding tenure, number of offspring produced after first acquiring a dominant breeding position, or LRS in either male or female Seychelles warblers. Individuals that helped, and females that cobred, had a higher age at first dominance than individuals that did not help and females that did not cobreed, respectively. Additionally, females that cobred as subordinates had longer dominant breeding tenures, produced more offspring after first acquiring a dominant breeding position and had higher LRS than females that did not cobreed.

We found that experience as a helper was not statistically associated with whether an individual acquired a dominant breeding position in either males or females. Seemingly, 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 nonhelpers (Busana et al., 2022). However, Busana et al. (2022) included only females that had previously been a subordinate in a territory, whereas our study additionally includes females that had no subordinate status and went straight to first being a floater or a dominant. Therefore, it is probable that the difference between studies is driven by females who have had a floater status being less likely to acquire a dominance status.

Our findings suggest that there was no association between helping experience and the likelihood of an individual becoming a dominant breeder, which could provide evidence against the "social prestige" hypothesis in the Seychelles warbler. 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 (McDonald et al., 2008; Nomano et al., 2013; Wright, 2007). Indeed, it has been argued that social prestige likely requires a level of cognitive processing that most species are unlikely to be capable of (McDonald et al., 2008; Wright, 2007). In addition, studies on other taxa have shown that helping may be associated with an increased likelihood of obtaining dominance (Cockburn et al., 2008; Field et al., 2006), 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 (Koenig & Dickinson, 2004; Stacey & Koenig, 1990; Wiley & Rabenold, 1984). However, in the Seychelles warbler, the majority of dominant statuses are acquired when a subordinate moves to a vacant breeding position on a nonnatal territory (Komdeur & Edelaar, 2001), which may explain why we found no association between helping and the acquisition of a dominant breeding position.

Whilst we found no association between 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, 2013). If individuals spend time helping prior to gaining a dominant breeding position, it is perhaps unsurprising 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 statistically 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 statistically significant difference in the length of tenure, this could suggest that helpers have longer lifespans than birds without helping experience. Indeed, after running a post hoc analysis on our dataset, we found that dominant females that had previously helped

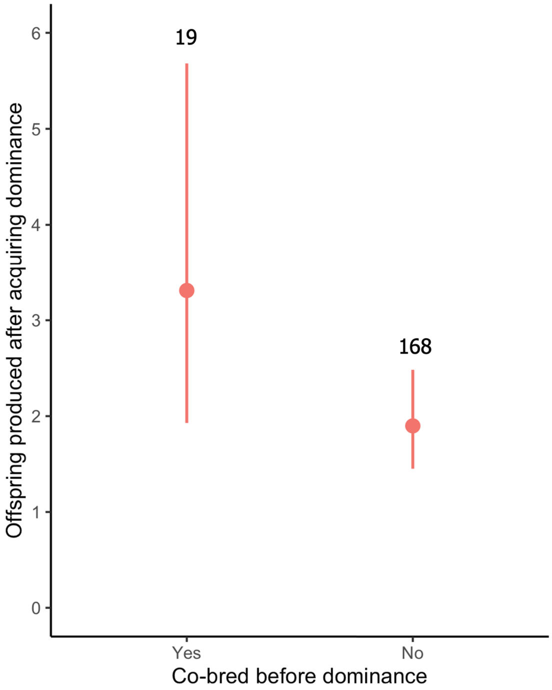

Figure 2. Marginal effects of having cobred prior to dominance on the number of offspring a female Seychelles warbler produces after acquiring dominance. The ggpredict function from the GGEFFECTS package (Lüdecke, 2018) in R was used to calculate the marginal effects and create the graphs: the solid 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.

Table 5. Socioecological predictors of lifetime reproductive success (LRS) in the Seychelles warbler, estimated using sex-specific generalized linear mixed-effects models (GLMMs) with zero-inflated Poisson distributions. Total number of males: 253 (males with helping experience: 59); total number of females: 294 (females with helping experience: 120; females with cobreeding experience: 54). The parameter estimate, standard error (SE), *z*-value, and *p*-value are given for each fixed effect, along with the marginal r^2 for each model. Territory quality = mean territory quality over lifetime. Reference level for helped/cobred ever = no.

		Males ($n = 253$)					Females ($n = 294$)				
Fixed effect	Levels	Estimate	SE	*z*	*p*	r^2	Estimate	SE	*z*	*p*	r^2
Intercept		0.51	0.45	1.15	.251	0.01	1.02	0.43	2.34	.019	0.23
Helped ever	Yes	−0.15	0.26	−0.58	.562		−0.16	0.19	−0.81	.418	
Cobred ever	Yes	/	/	/	/		0.68	0.24	2.91	.004	
Maternal age		−0.68	0.58	−1.16	.247		−1.17	0.44	−2.65	.008	
Territory quality		−1.01	1.31	−0.78	.438		−1.21	1.28	−0.94	.346	
Zero-inflated model											
Intercept	−0.32	0.25	−1.43	0.202		−0.44	0.29	−1.51	0.132		
Random effect		Levels	Variance	*p*			Levels	Variance	*p*		
Mother ID		185	0.29	0.517			203	0.26	0.007		
Social father ID		178	0.06	0.854			196	0.00	1.000		
Cohort		22	0.68	0.517			22	0.11	0.152		

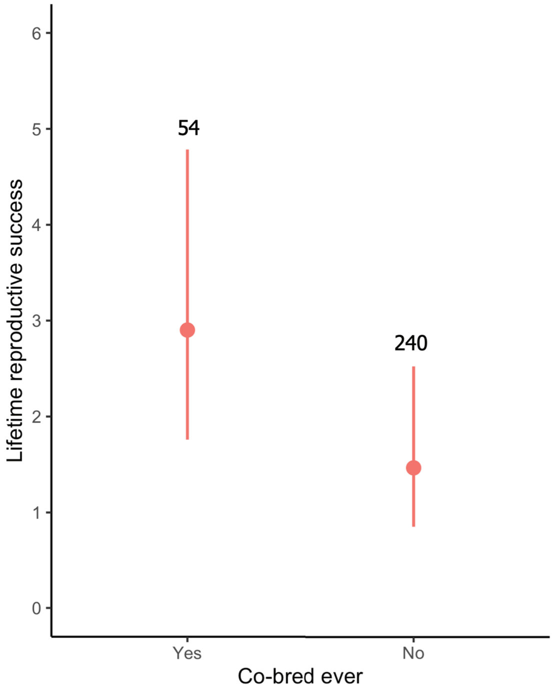

Figure 3. Marginal effects of having cobred on the lifetime reproductive success of female Seychelles warblers. The ggpredict function from the GGEFFECTS package in R (Lüdecke, 2018) was used to calculate the marginal effects and create the graphs: the solid points indicate the mean predicted value for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

had statistically significantly longer lifespans than dominant females that had never helped (Supplementary 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 & Rose, 1991). As female helpers spend time helping, they delay independent reproduction which is linked to increased longevity. The reason this association was found in females, and not males, could be because female birds bear the cost of egg production (Nilsson & 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).

Individuals with helping experience did not produce significantly more adult offspring after acquiring a dominant breeding position, providing no clear support for the skills hypothesis. Female Seychelles warblers with helping experience build stronger nests and make their first breeding attempt quicker than nonhelpers 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. However, we have shown that reproductive success after acquiring a dominant breeding position does not significantly differ with helping experience. As Komdeur (1996) did not separate helpers and cobreeders, the early reproductive benefits that were identified could possibly be attributed to cobreeders that had reproductive experience. Indeed, we found that females with prior cobreeding experience produced more offspring that survived to adulthood after acquiring dominance than females that had never cobred. This suggests that reproductive experience as a cobreeder improves the future reproductive success, as opposed to helping experience itself. One possible explanation for this is that females with cobreeding 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 (Baran & Adkins-Regan, 2014; Limmer & Becker, 2009), 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 that is, that older individuals are better at foraging or increase their breeding effort with age (see Forslund & Pärt, 1995 for review; Cichoñ, 2003). Whilst we did not account for age-related effects, the fact that both helpers and cobreeders commence breeding at an older age, yet only cobreeders benefit from an increase in reproductive success after acquiring dominance, suggests that this association is not due to age-related improvements in reproductive performance, but prior breeding experience specifically.

Alternatively, cobreeding experience may not *cause* an improvement in reproductive success after acquiring dominance. Instead, underlying factors that enable a female to cobreed may also enable them to be more successful breeders later in life (Wilson & Nussey, 2010). Better quality females may be more likely to cobreed alongside a dominant female (van de Crommenacker et al., 2011), and, because of their higher quality, may also be more successful dominant breeders. However, whether cobreeders are in better condition than helpers or nonhelping subordinates is unknown in the Seychelles warbler. In the Seychelles warbler, body condition changes throughout the breeding season (van de Crommenacker et al., 2011) and individuals are often sampled at different timepoints in the breeding season, making it difficult to collect data that are comparable across individuals. In addition, we do not yet have a deep enough understanding of body condition in the Seychelles warbler to be able to select a biologically meaningful timepoint within the breeding season to compare the body condition of cobreeders to helpers and nonhelping subordinates.

Helping experience showed no significant association with 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 evidence of a difference between the LRS of helpers and nonhelpers of either sex, helping and nonhelping could be viewed as equally successful life-history strategies. Additionally, cobreeding increased the LRS of females. Many females never produce offspring (58.6%) and, by definition, cobreeding females produce at least one offspring. It is unsurprising, therefore, that cobreeders had a higher LRS than females that did not cobreed.

Whilst we found no significant associations between helping and any of the fitness measures analyzed, it must be noted that we did not strip social effects from fitness components to quantify direct fitness, nor did we did consider indirect fitness benefits (Hamilton, 1964). Whilst the level of relatedness between helpers and nondescendant 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 subordinates cannot reproduce themselves, the indirect fitness benefits obtained through helping may not be insignificant.

Finally, a study by van Boheemen et al. (2019) analyzed 449 (22%) Seychelles warbler nests between 1996 and 2015, of which 99 were observed more than once during the nestling provisioning stage. Of these 99 nests, 12 (13%) nests had a subordinate that was classified as a natal helper in one visit and a nonhelper in the other. Some helpers may therefore have been misidentified as nonhelpers, which would hinder detection of helper effects.

Conclusion

We did not find any evidence that helping experience was statistically associated with the long-term reproductive success of Seychelles warblers. Our results do not align with the skills hypothesis, as helping was not statistically associated with the future breeding success of helpers. Being a helper or having no helping experience are, consequently, equally successful life-history strategies in terms of an individual's own future reproduction. Our findings highlight the importance of separating helpers from cobreeders, as cobreeders produced more adult offspring after acquiring a dominant breeding position and had higher LRS than females that did not cobreed. 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.

Supplementary material

Supplementary material is available online at *Evolution*.

Data availability

DOI: 10.5061/dryad.ht76hdrnd.

Author contributions

Project was conceived by E.C. and H.L.D., with input from A.M.S. Data collection was done by all authors. Statistical analyses were designed and run by E.C. with input from H.L.D., A.M.S., and D.S.R. E.C. wrote the draft, with input from all authors throughout. All authors agreed to submission.

Funding

E.C. was supported by a Leeds Doctoral Scholarship and a Climate Research Bursary Fund, University of Leeds, and A.M.S. was supported by a Natural Environment Research Council (NERC) grant (NE/P011284/1 to H.L.D. and D.S.R). The long term data gathering that enabled this study was supported by various NERC grants including NE/B504106/1 (T.A.B. and D.S.R.), NE/I021748/1 (H.L.D.), and NE/F02083X/1 and NE/K005502/1 (D.S.R.); as well as a Dutch Research Council (NWO) Rubicon (825.09.013), Lucie Burgers Foundation, and Royal Netherlands Academy of Arts and Sciences (KNAW) Schure Beijerinck Popping grant (SBP2013/04) to H.L.D., NWO visitors grant (040.11.232 to J.K. and H.L.D.) and NWO grants (854.11.003 and 823.01.014 to J.K.).

Conflict of interest: The authors declare no conflict of interest.

Acknowledgments

We thank all of the researchers that collected the long-term data, Ian Stevenson, Owen Howison and Maaike Versteegh for maintaining the database, and Marco van der Velde for microsatellite genotyping. Thanks to Nature Seychelles for providing access to the Cousin Island Nature Reserve, and the Seychelles Department of Environment and Seychelles Bureau of Standards for approving protocol locally and providing research permits.

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