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ORIGINAL PAPER

SPECIAL ISSUE. Impact of global change on social interactions: Ecological and fitness implications

Testing the environmental buffering hypothesis of cooperative breeding in the Seychelles warbler

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Abstract

Species are facing environmental challenges caused by rapidly changing environments. Globally, extreme weather events, like droughts or extreme rainfall, are increasing in frequency. Natural selection usually acts slowly, while adaptations through phenotypic plasticity are limited. Therefore, organisms may utilise other mechanisms to cope with such rapid change. Cooperative breeding is hypothesised to be one such mechanism, as helpers could increase survival probabilities of offspring, especially in harsh years. Rainfall is a cue for onset of breeding in many tropical species, to ensure young are born when food abundance is highest. Using 21 years of data, we investigate the effect of rainfall on social behaviour and life history in the insectivorous Seychelles warbler (*Acrocephalus sechellensis*), a facultative cooperative breeder. We found that low rainfall is associated with reduced reproductive output and possibly with decreased survival. However, there were no statistical differences in response between groups with helpers, groups with only non-helping subordinates, and breeding pairs without subordinates. With low rainfall, more sons (the sex less likely to help) were produced, and those subordinate males already present were less likely to help. Thus, in contrast to expectations, cooperative breeding does not seem to buffer against harsh environments in Seychelles warblers, indicating that group living may be costly and thus not a mechanism for coping with changing environments. Our study showed that the interaction between the environment and life histories, including social behaviour, is complex, but that this interaction is important to consider when studying the impact of changing environments on species survival.

Keywords Environmental change · Cooperation · Seychelles warbler · Life history · Offspring sex ratio bias

Introduction

In this era of climate change, individuals and populations need to cope with challenging environmental conditions (Chevin et al. 2010; Sih et al. 2011; Ummenhofer and Meehl 2017). Climate change not only causes the temperature to rise globally (NOAA 2021) but also increases the frequency of extreme weather, like droughts or floods (NOAA 2021). Changing environments can be challenging habitats as individuals and populations may have little time to adapt, which may lead to reduced reproduction and survival (Allen et al. 2015; Rey et al. 2017; Spooner et al. 2018), and ultimately extinction. Evolutionary adaptation occurs slowly, especially in long-lived species, as it involves changes in allele frequencies across generations, and might therefore not be fast enough for adaptation to environmental change (Merilä 2012). Individuals may also adapt during their own lifetime through phenotypic plasticity, potentially enabling them to cope with changing environments. However, phenotypic plasticity is limited by the variation in phenotypes that genotypes can produce, and may not be enough to enable populations to cope with extreme change (Visser et al. 2004).

The effect of climate change on individuals and populations, and the way they cope with this change has mainly been studied in temperate zones (Orgeret et al. 2022), where

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temperature increases occur faster than in the tropical zone (NOAA 2021). Even though the effect of rising temperatures is relatively smaller in tropical zones, an increasing number of extreme weather events do occur. For example, El Niño events happen more frequently now than in past decades (McPhaden et al. 2021). As species richness and abundance is highest in the tropics (Stevens 1989), it is also important to consider the effects of climate change in this part of the world.

When individuals are maladapted to new and changing environmental conditions, as evidenced by lower survival and reproductive success, this may result in a reduction in abundance and eventually lead to populations going extinct (Butchart et al. 2010; Barnosky et al. 2011). However, organisms might show complex changes in their behaviour in response to environmental change. These changes may be positive, enabling individuals to mitigate the impact of environmental change on fitness. Alternatively, they may be negative, for example when behaviour that used to be beneficial is now maladaptive (e.g. reproducing too late in a season, because a cue for onset of reproduction is no longer aligned optimally with food abundance; Both et al. 2006).

One hypothesised way through which organisms may buffer the negative effects induced by environmental change is by forming groups, becoming social, and cooperatively breeding (Rubenstein and Lovette 2007; Cockburn and Russell 2011; Jetz and Rubenstein 2011; Rubenstein 2011; Griesser et al. 2017; Komdeur and Ma 2021). Most cooperative breeding species live in unpredictable and variable environments (Jetz and Rubenstein 2011; Komdeur and Ma 2021), or in harsh environments (Lukas and Clutton-Brock 2017). Becoming social can decrease predation risk (e.g. safety in numbers; Lehtonen and Jaatinen 2016) or increase food availability per individual, when food is difficult to find and distributed in patches, or when larger territories can be defended in groups (Fitzpatrick and Bowman 2016). When the environment becomes too harsh for breeding pairs to raise offspring alone (e.g. high predation risk or extreme weather), cooperative breeding may be beneficial as the breeding pair may be able to successfully raise offspring if assisted by helpers (MacColl and Hatchwell 2002; Canário et al. 2004; Covas et al. 2008). Breeders themselves may also survive better when helped (Russell et al. 2007; Kingma et al. 2010; Hammers et al. 2019), because they have to invest less in offspring (Russell et al. 2007; Wiley and Ridley 2016; van Boheemen et al. 2019). Thus, group living could increase the fitness of breeders both via increased fecundity and viability. However, a growing body of studies has found no evidence for a buffering effect of cooperative breeding (or sociality) on survival and reproduction in species living in harsh or unpredictable environments (Gonzalez et al. 2013; Van de Ven et al. 2019; Bourne et al. 2020a, b, c; Guindre-Parker and Rubenstein 2020; Bourne et al. 2021; D'Amelio et al. 2022). Understanding why cooperation seems to have a buffering effect in some species, while in others it does not, is important to our understanding of the vulnerability of species to environmental change. Therefore, studying this question across multiple species in different environments, phylogenetic lineages, and with different life history traits is important to unravel when and why cooperation can be helpful in environmental buffering, or not.

Changing environments could also impact populations if the life histories of different groups within the population are differently affected. For example, in species with sexual size dimorphism where the larger sex needs more resources for survival, the larger sex may have lower survival than the smaller sex when food becomes scarce (Toïgo and Gaillard 2003), which could result in an adult sex ratio skew (Wong-Muñoz et al. 2011). This could, in turn, lead to a more skewed offspring sex ratio, as the rarer sex now has a fitness advantage and therefore parents may be selected to overproduce this sex (Fisher 1930). As another example, subordinates might be more disadvantaged in harsh situations than dominants, as dominants generally have preferential access to resources. Subordinates might therefore choose to leave the group (Vehrencamp 1983; Kingma et al. 2014). Alternatively, helping subordinates might choose to help less, to better preserve themselves (van de Crommenacker et al. 2011; Covas et al. 2022), as helping is often costly (Heinsohn and Legge 1999; Kingma et al. 2014). Conversely, under stressful conditions, dominants might share relatively more resources with subordinates as a strategy to assure subordinates remain in the group. Understanding these complex interactions between changing environmental conditions and possible shifts in behaviour is important, as it helps us understand how species may cope with rapid environmental change, and how we could better conserve them. This study aims to explore these interactions between the environment and life histories, including social behaviour and sex allocation. To do so, we study the Seychelles warbler (*Acrocephalus sechellensis*), a facultative cooperative breeder, where subordinates sometimes help raise offspring of a dominant breeding pair. Using differences in rainfall levels among years as proxy of environmental harshness, we aim to explore if and how rainfall influences the (social) behaviour of Seychelles warblers.

Low rainfall is expected to have negative effects on Seychelles warblers, as they are insectivorous and most of their prey need water to reproduce. On the other hand, extreme rainfall is also expected to have negative effects, as it becomes more difficult to maintain body temperature (and possibly other basal body functions), and because extreme rainfall can destroy the habitat of Seychelles warblers. Therefore, we expect rainfall to have a quadratic effect both on survival and reproduction, with the highest levels of these occurring at intermediate rainfall levels. If there is an environmental buffering effect of cooperative breeding, we expect that the negative effects of rainfall during dry and extreme wet years will be mitigated in groups with helpers, but not in breeding pairs.

We also test whether changes in rainfall are associated with changes in the offspring sex ratio. If cooperative breeding is a coping mechanism for harsh environments, we expect warblers to produce more daughters (the sex more likely to help) when it is dry (and food availability is low), when more help is necessary to raise offspring. Alternatively, if cooperative breeding is not a mechanism to cope with harsh environments, we expect warblers to produce more daughters in periods of favourable environments, as more offspring could be sustained in a wet environment and therefore helping could be beneficial to raise more offspring than would be possible for a breeding pair. If cooperation is a buffer against unpredictable environments, we expect no correlation between offspring sex ratio and rainfall. However, in that case, we expect that the offspring sex ratio is associated with social information (e.g. are helpers currently present or not) to assure availability of helpers also in the future. Lastly, we test if the helping behaviour of subordinates (whether they helped or not) was associated with rainfall. In Seychelles warblers, subordinates do not always become helpers. Instead, they can reside on the territory without directly helping at the nest, though possibly they help indirectly, for example by protecting the territory. If cooperation is a buffer against harsh or unpredictable environments, we expect the number of helping subordinates to increase during extreme weather — i.e. very dry and very wet years. Alternatively, if cooperation is not a buffer against harsh or unpredictable environments, we expect the number of helping subordinates to be highest during favourable conditions, as in harsh periods, subordinates might not want to help, but instead preserve their own resources (van de Crommenacker et al. 2011).

Methods

Study population

The population of Seychelles warblers on Cousin Island (4°19′53.5″ S 55°39′43.2″ E) has been studied intensively since 1985. From 1997 onwards, > 95% of individuals in the population have been caught, colour-banded, and given a metal ring with a unique BTO number (Hammers et al. 2019). Since 1992, blood samples (~50 μl) have been collected by brachial venipuncture from all caught birds, diluted in 800 ml of 100% ethanol, and stored at room temperature. DNA extraction from blood samples followed Richardson et al. (2001) and sex was confirmed following Griffiths et al. (1998) and Sparks et al. (2021).

Seychelles warblers are insectivorous, gleaning insects from the underside of leaves (Komdeur 1996). They are territorial and form long-term pair bonds. About half of the ca 115 territories on Cousin contain 1–5 sexually mature subordinates in addition to the dominant breeding pair. Some (20% of males and 42% of females) of these subordinates act as helpers and provide alloparental care, assist in incubation (females only) and the provisioning of offspring (Richardson et al. 2003b; Hammers et al. 2019). Helpers are mostly present on high quality territories, and can be maladaptive in low quality territories (Komdeur 1998). Seychelles warblers usually produce a clutch size of 1 (ca 80% of the time, Richardson et al. 2001). They have previously been found to produce skewed offspring sex ratios, such that daughters (the sex more likely to help) are produced when having an (additional) helper in subsequent seasons results in higher future fitness of the breeding pair (Komdeur et al. 1997). Seychelles warblers have their major breeding season in June–October (Komdeur and Daan 2005). Rainfall is used as a cue to initiate nesting to ensure nestling feeding aligns with the peak in insect prey abundance (Komdeur 1996). If there is a mismatch between food abundance and breeding activity, warblers are not successful in their breeding attempt (Komdeur 1996). This can have a major impact on their fitness as they generally produce one offspring per year and live on average 5.5 years (Raj Pant et al. 2020).

To determine the status of all birds and to census adult population size, observations in the territory and at the nest were performed. The dominant male and female were defined as the pair-bonded male and female in a territory (Richardson et al. 2003b). Each territory was monitored for breeding activity and the presence of ringed individuals. High annual resighting probabilities (98%, Brouwer et al. 2006) and extremely rare inter-island dispersal (Komdeur et al. 2004) allow for accurate measures of annual survival and fecundity. Breeding data were collected between June and October each year from 1995 to 2015 for this study. In our dataset, the number of territories ranged from 96 to 123, and the number of adult birds in the population ranged from 252 to 342 individuals.

Rainfall measurements

Previously, Komdeur (1996) showed that rainfall peaks on Cousin strongly correlated with subsequent insect peak abundance 2 months later. In the present dataset, monthly precipitation was measured on the neighbouring island Praslin (~1.5 km distance from Cousin) by the Seychelles Meteorological Authority Praslin from 1995 to 2015 (Seychelles Meteorological Authority 2016). As rainfall measurements on Praslin were precise and there is no reason to assume a bias in any specific direction between rainfall on Cousin and Praslin, we used rainfall on Praslin as a measure of rainfall on Cousin.

Since we only obtained monthly total rainfall, we used the total rainfall of June, July, and August as a measure of the timing of peak rainfall. The dry season always starts somewhere in this period (Komdeur and Daan 2005; this dataset), and thus, any changes in life history strategies based on the amount of rain are most likely made in this period (e.g. when it keeps raining, the birds might start reproducing later and

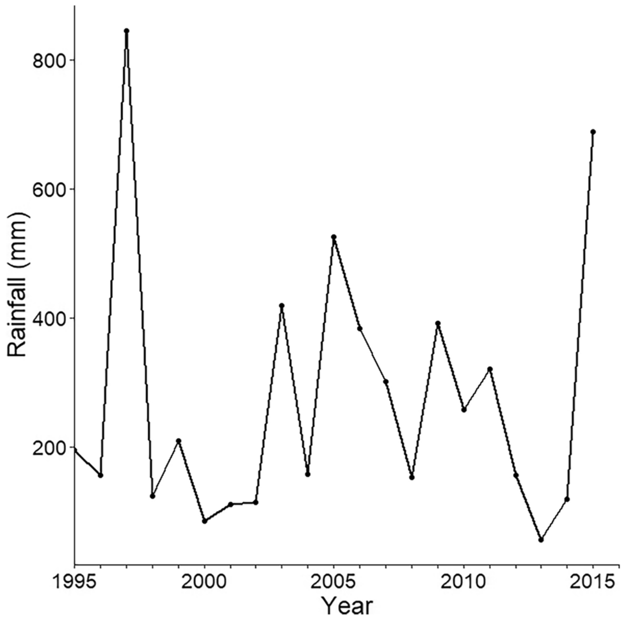

Fig. 1 Total rainfall (mm) at Praslin airport (1.5 km from Cousin Island) in June, July, and August during the period 1995–2015

therefore possibly have a lower reproductive output as fewer broods can be raised). Rainfall therefore partially reflected insect abundance, but could also reflect other effects on Seychelles warblers, like the costs of maintaining body temperature or moving (which could be higher in extreme rain). Rainfall fluctuated strongly over the years (mean = 275 ± 45 (SE) mm, range = 57–844 mm, see Fig. 1). As a second measure of insect abundance, we tried to include mean insect abundance during the breeding season (from Spurgin et al. 2018) in our models. However, as this caused statistical problems (e.g. over parameterisation), we excluded mean insect abundance during the breeding season from our models. However, see Appendix A in the supplementary materials where we show the models with this factor included, yet its inclusion results in little change overall to the results.

Statistical analyses

All analyses were performed in R, version 4.2.1, with packages lme4 (version 1.1.30, Bates et al. 2015) and glmmTMB (version 1.1.4, Brooks et al. 2017) when convergence problems arose with lme4. To check for over- or underdispersion, DHARMa was used (version 0.4.5, Hartig 2022). When a model was over- or underdispersed, the assumed underlying distributions were changed to quasi-Poisson or quasi-binomial distributions. To check for collinearity, the package performance was used (version 0.9.2, Lüdecke et al. 2021), see Appendix C in the supplementary materials for all VIF values. Data visualisation was done with ggplot (version 3.3.6, Wickham 2016) and cowplot (version 1.1.1, Wilke 2019).

Extreme values in rainfall were not removed from the models, as we were interested in the behavioural responses of warblers to such extremes. We expected negative effects of both little rainfall and a lot of rainfall on behavioural responses. In dry periods, insect abundance is lower, as most of these insects lay their eggs in water. In extremely high rainfall years, trees and leaves can get seriously damaged, and it might therefore be harder to find food for Seychelles warblers. Also, during heavy rainfall, the costs of maintenance will change for individuals, as more energy needs to be invested in a stable body temperature. Therefore, both rainfall and rainfall^2 were added to our models. Models with and without rainfall^2 were compared with ANOVAs and only when rainfall^2 significantly improved the models ($p < 0.05$), it was included in our results.

In multiple models (see descriptions below), "group composition" (a factor describing if a territory contained a breeding pair, a group with only non-helping subordinates, or a group with at least one helping subordinate) was used. In these cases, the model was ran twice, with a different group composition as the reference value, so that all comparisons between the group compositions were made, see Supplementary Appendix B for this model output.

Survival

Our goal was to test if rainfall affected the survival of adult warblers. We expected rainfall measured during the breeding season to have direct effects on survival during the breeding season. However, survival during a breeding season cannot be accurately measured directly, as not all individuals were observed with equal intensities (due to differences in visibility as a consequence of vegetation type and density in different territories). In order to estimate if survival during a breeding season was correlated with rainfall, we correlated the adult population size (based on observations) with rainfall both measured in the same period. To do so, a generalised linear model with Poisson distribution was used. However, this method only yields a rough estimate of the association between rainfall and survival, as the method is also influenced by the visibility of birds (which is higher when it is sunny because they are more active then) and by the possibility to observe them (when it is extremely wet, it is more difficult for observers to see anything).

As our yearly survival measure is much more accurate than our within season survival estimate, we also investigated whether rainfall affected individual survival to the next year (from now on termed "annual survival"). Annual survival was based on observations, where individuals are presumed dead when they are not seen at all for two consecutive field seasons, which is a reliable method as resighting probabilities are extremely high (98%, Brouwer et al. 2006). For this, a generalised linear mixed model with binomial error structure was used. As random effects, Bird ID and year were included. Sex, status (breeder or subordinate), adult population size, age, group size, and group composition (the composition of the breeding group an individual is part of: breeding groups with at least one helper, breeding groups with only non-helping subordinates, or breeding pairs) were added as fixed effects. An interaction between rainfall and group composition was added to test whether groups with helpers responded differently to different environments than breeding pairs and groups with only non-helping subordinates, and thus to analyse whether cooperative breeding could buffer changing or harsh environments. The adult population size was added to the model as population density has a negative effect on survival (Brouwer et al. 2006).

Reproduction

Our second goal was not only to understand if reproduction was associated with rainfall but also to get a better understanding of differing life history strategies due to changes in climatic conditions. To do so, we analysed whether the offspring sex ratio was correlated with rainfall. Offspring sex could only be determined after catching (as a DNA sample was necessary to determine molecular sex), which usually happens anywhere between the nestling stage and when fledglings become independent around 3 months of age. Thus, any changes observed in offspring sex ratio could have been influenced not only by changes in sex allocation strategy but also by differences in sex-specific mortality up until catching. To explore any possible effects of rainfall on offspring sex, where each young represents one data point, a generalised linear mixed model with binomial error distribution was used. In this model, rainfall and natal breeding group composition were included, as well as an interaction term between them to test whether groups with helpers have a different strategy under different climatic conditions than breeding pairs, and/or breeding groups with only non-helping subordinates. In this model, territory ID and year were included as random effects.

To explore whether rainfall was associated with offspring production, a correlation between rainfall and number of offspring produced per breeding group was performed. Population size was added as a fixed effect to the model to correct for any possible density dependent effects. Group size was added as a fixed effect as more individuals could help to increase the survival of young until catching (as only caught offspring were included in the model). Group composition was also included in the model, since positive group effects were mostly to be expected when helpers were present. Again, an interaction between rainfall and group composition was added to the model to test whether cooperative breeding could buffer negative effects of harsh environments. A generalised linear mixed model with Poisson distribution was used, as number of offspring is count data.

Subordinate behaviour

To further investigate whether cooperative breeding may buffer reproductive output in harsh or unpredictable environments, we also analysed the effect of rainfall on the proportion of subordinates acting as helpers. To do so, we tested if the proportion of subordinates that helped (on the entire island, separately for male and female subordinates) correlated with rainfall, using a binomial and quasi-binomial distribution.

Sampling bias

In general, there should not be a strong sampling bias in our dataset. As discussed above, patterns of association between adult population size and rainfall could be caused by an observation bias, but this bias would be most pronounced in periods with extreme rainfall. As there are few data points in this area anyway (there are only a few years with extreme rainfall), the results in these ranges should always be considered with care. Any bias due to observing frequency would lead to fewer observations (of birds or of activities like feeding) with increasing rain, so would cause a negative slope in our adult population size model. Any positive slopes found could therefore only be conservative estimates if there was a bias. As the annual resighting probability is very high (98%, Brouwer et al. 2006) for Seychelles warblers on Cousin, we know that our estimated year of death is accurate and not dependent on where the birds reside or on rainfall in specific months. Also as discussed above, the offspring sex ratio data is measured once the offspring are caught. Therefore, it is unclear if possible patterns are caused by sex-specific offspring mortality prior to catching, or if these really reflect differential sex allocation strategies. This will further be explored in our discussion, but we think that both possibilities are relevant. The number of offspring produced could also be biased, as only offspring that were caught were included in our analysis. However, because offspring that survive are most important for future fitness, we do not think this bias would cause a different interpretation of our results. Lastly, the correlation between the proportion of subordinates that help and rainfall is again based on observations and thus has the same potential sampling problems as adult population size. Therefore, if a negative correlation is found, it should be considered with care, but any positive correlation could be considered a conservative estimate.

Results

Adult population size and survival

The adult population size ranged from 252 to 342 individuals in a year (mean = 293 ± 5.5 SE) and was significantly associated with rainfall, with a quadratic effect (rain^2 estimate = $1.2*10^{-6} \pm 4.0*10^{-7}$ (SE), $p = 0.0066$; rain estimate = 0.0011 ± 0.00034, $p = 0.0041$, $n = 21$ years; Fig. 2a). With increasing rainfall, adult population size increased and reached its peak at intermediate rainfall values and declined afterwards. Thus, dry or extreme wet years may result in lower adult survival during the breeding season. Inter-annual survival of individuals was correlated with sex, social status, age, and group composition (Table 1, Fig. 2). Individuals from groups with helpers had a higher survival compared to groups without helpers (but not to breeding pairs); however, there was no significant interaction between group composition and rainfall. There was a very marginal effect of sex on adult survival; males had slightly lower survival than females (mean survival females = 79%, $n = 4339$; mean survival males = 76%, $n = 4225$; see Table 1). However, subordinates had significantly lower survival than dominants (mean survival dominants = 78%, $n = 6539$; mean survival subordinates = 72%, $n = 2025$), see Table 1 and Fig. 2. Mean survival to the next year for breeding females was 79% ($n = 3162$), for breeding males 77% ($n = 3377$), for subordinate females 74% ($n = 1177$), and for subordinate males 71% ($n = 848$). Rainfall did not significantly affect annual survival (Table 1, Fig. 2).

Influence of rainfall on offspring sex ratio and number of offspring

Offspring sex was significantly associated with rainfall. In dry years, more sons were produced, while in wetter years, more daughters were produced (Table 2, Fig. 3a). There was a significant interaction between rainfall and group composition (Table 2, Fig. 3a). In dry years, all groups produced mostly sons. Yet in wet years, groups with helpers still produced mostly sons, while pairs and groups with only non-helping subordinates produced mostly daughters. The number of offspring produced in a breeding season was also correlated with rainfall and group composition (Table 3, Fig. 3b). With increasing rain, more offspring were produced, until a maximum after which the number of offspring decreased again. Groups with helpers produced more offspring than the other groups, but there was no significant interaction between rainfall and group composition (Table 3, Fig. 3b), as would have been expected if cooperative breeding would buffer the effects of harsh environments.

Influence of rainfall on subordinate helping behaviour

The proportion of female subordinates that helped did not correlate with rainfall (rain estimate = 0.0013 ± 0.00081 (SE), $p = 0.12$, $n = 21$ year, with in total 766 subordinate females; Fig. 4). The proportion of male subordinates that helped did significantly correlate with rainfall (rain^2 estimate = $-5.0*10^{-6} \pm 2.4*10^{-6}$, $p = 0.041$; rain estimate = 0.0052 ± 0.0021, $p = 0.012$, $n = 21$ years, with in total 512 subordinate males). In this dataset, the mean proportion of female subordinates that helped was 39% ($n = 21$ years, 766 subordinate females in total), while the mean proportion of male subordinates that helped was 19% ($n = 21$ years, 512 subordinate males in total). For females, the squared-term of rainfall did not improve the model, and therefore, the linear (non-significant) estimate is shown in Fig. 4a.

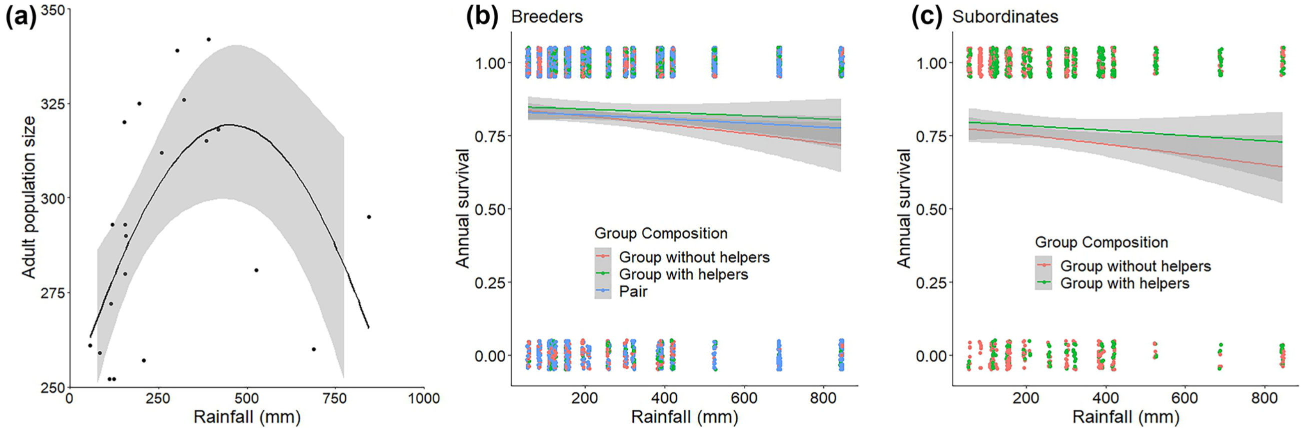

Fig. 2 **a** Associations between the adult population size of the Seychelles warbler on Cousin Island and rainfall (rain^2 estimate = $12*10^{-6} \pm 4.0*10^{-7}$ (SE), $p = 0.0066$; rain estimate = 0.0011 ± 0.00034, $p = 0.0041$, $n = 21$ years, from 1995 to 2015). Associations between survival to the next year of **b** dominant breeders and **c** subordinate individuals (total $n = 6054$ individuals, dominant breeders $n = 4784$, subordinate individuals $n = 1270$, from 2995 to 2015). For statistics of **b** and **c**, see Table 1. Grey shading indicates confidence intervals. For **a**, a generalised linear model with a quasi-Poisson distribution was used, and for **b** and **c**, a generalised linear model with binomial error distribution was used

Table 1 Association between survival to the next year and total rainfall, sex, status, adult population size, age, group composition, and size of the group an individual belongs to, in the Seychelles warbler

Independent variables	Estimate	Standard error	95% Confidence interval	p-value
Intercept	*2.05*	*0.28*	*1.50* to *2.61*	*<0.001*
Rainfall	−0.16	0.090	−0.33 to 0.017	0.076
Sex (0=female, 1=male)	*−0.19*	*0.096*	*−0.38* to *−0.0020*	*0.048*
Status (0=breeder, 1=subordinate)	*−0.51*	*0.12*	*−0.74* to *−0.28*	*<0.001*
Population size	−0.066	0.075	−0.21 to 0.082	0.38
Age	*−0.15*	*0.027*	*−0.20* to *−0.095*	*<0.01*
Group size	−0.010	0.075	−0.16 to 0.14	0.89
Group composition (compared to groups with non-helping subordinates)				
Groups with helpers	*0.25*	*0.11*	*0.033* to *0.46*	*0.024*
Breeding pairs	0.021	0.13	−0.24 to 0.28	0.87
Rainfall * Group composition				
Rainfall * Groups with helpers	0.065	0.11	−0.14 to 0.27	0.54
Rainfall * Breeding pairs	0.075	0.082	−0.086 to 0.24	0.36
Random effects				
	Variance		***n***	
Bird ID	1.16		1450	
Year	0.079		21	

Data from 1995 to 2015 were used with $n=6054$ individuals. An individual's status could either be a breeder or a subordinate. Group composition was divided into groups with at least one helping subordinate, groups with only non-helping subordinates, and breeding pairs. A generalised linear model was used with a binomial error distribution. Significant effects are indicated in italics

Discussion

In our study, rainfall correlates with variation in the life history of Seychelles warblers in several ways. Low to medium rainfall is associated with adult population size increases, but with extremely high rainfall, the adult population size decreases. This suggests that adult survival during the breeding season is highest when there is intermediate rainfall. Rainfall during the breeding season was not associated with survival to the next year. However, annual survival was correlated with sex, status, age, and group composition. Males had slightly lower survival than females, breeders had higher survival than subordinates, survival decreased with increasing age, and groups with helpers had higher survival than groups with only non-helping subordinates (but not than breeding pairs). The number of offspring produced was correlated with rainfall (also the quadratic term) and with group composition, so that most offspring were produced during intermediate

Table 2 Associations between offspring sex (1=male and 0=female) and rainfall and group composition in the Seychelles warbler

Independent variables	Estimate	Standard error	95% Confidence interval	p-value
Intercept	−0.020	0.13	−0.27 to 0.23	0.88
Rainfall	*−0.40*	*0.15*	*−0.70* to *−0.10*	*0.009*
Group composition (compared to groups with subordinates)				
Groups with helpers	0.10	0.18	−0.24 to 0.45	0.56
Breeding pairs	0.055	0.16	−0.26 to 0.37	0.73
Rainfall * Group composition				
*Rainfall * Groups with helpers*	*0.38*	*0.19*	*0.0059* to *0.76*	*0.046*
Rainfall * Breeding pairs	0.27	0.18	−0.081 to 0.62	0.13
Random effects				
	Variance		***n***	
Territory ID	2.45e-8		114	
Year	2.07e-9		21	

A territory contained either a breeding pair, a group (a breeding pair and only non-helping subordinate individuals), or a group with helpers (where at least one subordinate actively helps in raising offspring). Data from 1995 to 2015 was used, with $n=959$ offspring. A generalised linear mixed model was used with binomial error distribution. Significant effects are indicated in italics

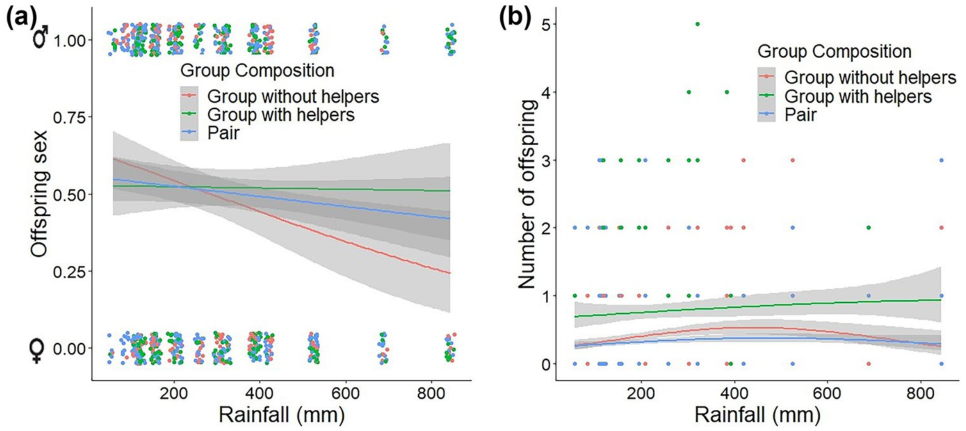

Fig. 3 **a** Association between offspring sex (1 = son, 0 = daughter) and rainfall (*n* = 959 offspring, from 1995 to 2015). **b** Association between number of offspring produced during the main breeding season and rainfall (*n* = 2363 breeding groups). Grey shading indicates 95% confidence intervals. See Tables 2 and 3 for statistics

rainfall. Groups with helpers produced most offspring; however, there was no significant interaction term between rainfall and group composition. The higher reproductive output of groups with helpers could be explained by positive effects of helping on survival of offspring from dominant breeders, but could also be affected by co-breeding of some helping subordinate females (Richardson et al. 2002). Offspring sex was also linearly correlated with rainfall. With increasing rainfall, more daughters were produced. Group composition did not affect offspring sex. However, there was an interaction between rainfall and group composition; groups with helpers produced relatively more sons in wetter conditions compared to groups with only non-helping subordinates and breeding pairs, who mostly produced daughters in wet conditions. Lastly, the proportion of male subordinates that showed helping behaviour varied with rainfall; they helped most at intermediate rainfall. There was no correlation between rainfall and the proportion of female subordinates that helped.

Does cooperation buffer harsh and unpredictable environments

In comparative studies, Rubenstein and Lovette (2007), Jetz and Rubenstein (2011), Sheehan et al. (2015), and Cornwallis et al. (2017) all showed that cooperative breeding mainly occurs in unpredictable environments. Consequently, it was hypothesised

Table 3 Associations between the number of offspring produced and rainfall and group composition in the Seychelles warbler

Independent variables	Estimate	Standard error	95% Confidence interval	*p*-value
Intercept	0.51	0.95	− 1.35 to 2.36	0.59
Rainfall	*0.47*	*0.16*	*0.17 to 0.78*	*0.0025*
Rainfall^2	*− 0.26*	*0.090*	*− 0.44 to − 0.086*	*0.0037*
Population size	− 0.0057	0.0030	− 0.012 to 0.16	0.057
Group size	0.014	0.075	− 0.13 to 0.16	0.85
Group composition (compared to groups with subordinates)				
Groups with helpers	*0.46*	*0.11*	*0.24 to 0.68*	*< 0.001*
Breeding pairs	− 0.22	0.14	− 0.49 to 0.046	0.10
Rainfall * Group composition				
Rainfall * Groups with helpers	− 0.22	0.15	− 0.51 to 0.07	0.14
Rainfall * Breeding pairs	− 0.10	0.13	− 0.35 to 0.15	0.43
Rainfall^2 * Groups with helpers	0.16	0.082	− 0.0038 to 0.32	0.056
Rainfall^2 * Breeding pairs	0.076	0.075	− 0.071 to 0.22	0.31
Random effects				
	Variance		***n***	
Territory ID	0.72		182	
Year	0.073		21	

A territory contained either a breeding pair, a group (a breeding pair and subordinate individuals), or a group with helpers (where at least one subordinate actively helps in raising offspring). Data from 1995 to 2015 was used, with *n* = 2363 breeding groups. A generalised linear mixed model was used with Poisson distribution. Significant effects are indicated in italics

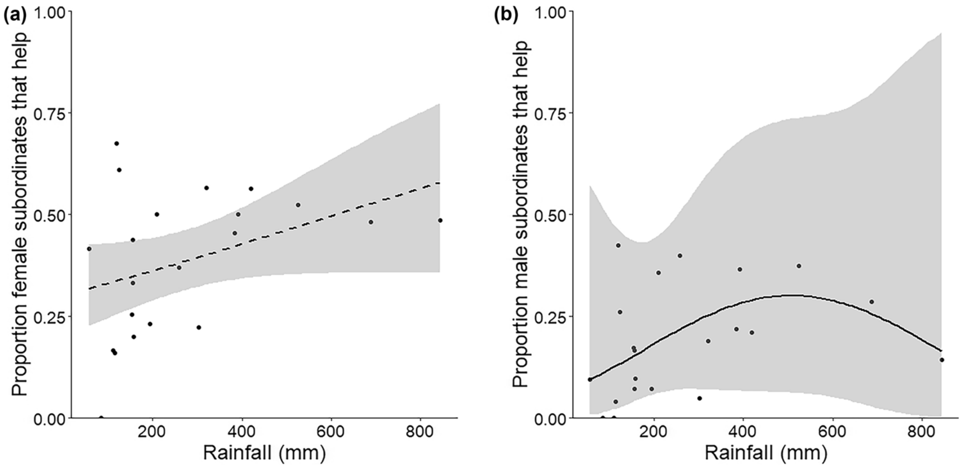

Fig. 4 Association between the proportion of subordinate Seychelles warblers acting as helpers and rainfall for **a** females (rain estimate$=0.0013\pm0.00081$ (SE), $p=0.12$, $n=21$ year, with 766 subordinate females) and **b** males (rain^2 estimate$=-5.0*10^{-6}\pm2.4*10^{-6}$, $p=0.041$; rain estimate$=0.0052\pm0.0021$, $p=0.012$, $n=21$ years, with 512 subordinate males). Grey shading indicates 95% confidence intervals. For **a**, a quasi-binomial distribution and for **b**, a binomial distribution was used

that cooperative breeding could be a mechanism to cope with unstable environments, i.e. helpers help offspring to survive under bad conditions thus decreasing variability in reproductive output (Cockburn and Russell 2011; Jetz and Rubenstein 2011; Griesser et al. 2017). In contrast, non-cooperative individuals would produce less offspring under harsh conditions and therefore show more variance in reproduction over time and space. Similarly, it has been hypothesised that cooperation could buffer the effects of harsh (but not necessarily unpredictable) environments (Canário et al. 2004; Covas et al. 2008; Shen et al. 2012; Wiley and Ridley 2016; Cornwallis et al. 2017; Lukas and Clutton-Brock 2017). Neither of these hypotheses are supported by our results, as there was no interacting effect of rainfall and group composition on survival and reproduction. In other words, individuals might show different behaviours during harsher or easier periods, but there are no differences in this change in behaviour between groups with and without helpers, thus helpers do not truly buffer the negative effects of harsh periods. Yet, cooperative breeding could provide benefits if the environment keeps fluctuating (and does not have many harsh years in a row). In these cases, cooperative breeding may not truly buffer negative effects within a harsh year, but in later favourable years, individuals can compensate by cooperation, as it leads to higher reproductive output in these favourable years (Bourne et al. 2020a). It is possible this is also the case for Seychelles warblers, as forgoing reproduction in a harsh year could increase survival of not only breeders (Hammers et al. 2013, showed a trade-off between reproduction and survival in Seychelles warbler) but possibly also of (kin) subordinates. Furthermore, in the Seychelles warbler, subordinates abstain from helping when in low condition and their condition improved during the breeding season when not helping (Van de Crommenacker et al. 2011). Thus, abstaining from breeding for a season could increase the condition of both breeders and subordinates, so that they are in good condition for the next breeding season. Next to that, if subordinates did help in harsh environments, the reproductive success of these breeding groups stayed higher than that of pairs and groups without helpers (though lower than the reproductive success of groups with helpers in good years; Fig. 3, but see also Busana et al. 2022). Thus, there is potential for partial buffering, if subordinates decide to help. Understanding what factors drive the choice of subordinates to help or not is therefore important to understand the evolution of cooperative breeding and the ability of populations to cope with harsh and unpredictable environments. However, it is important to take into account population size as well in this question. If many breeders die during a harsh year, helpers might get more fitness benefits by taking over these breeding positions in the next year instead of staying a helper.

Understanding why some studies find a buffering effect of cooperative breeding (MacColl and Hatchwell 2002; Canário et al. 2004; Rubenstein and Lovette 2007; Covas et al. 2008; Jetz and Rubenstein 2011; Rubenstein 2011; Shen et al. 2012; Sheehan et al. 2015; Langmore et al. 2016; Wiley and Ridley 2016; Cornwallis et al. 2017; Griesser et al. 2017; Lukas and Clutton-Brock 2017; Kennedy et al. 2018), while others do not (Gonzalez et al. 2013; Van de Ven et al. 2019; Bourne et al. 2020b, c; Guindre-Parker and Rubenstein 2020; D'Amelio et al. 2022), is vital for understanding the potential role of sociality in decreasing the vulnerability of species to environmental change. One reason might be that species vary in their social and spatial organisation. For example, positive buffering effects of cooperative breeding have been found in various species that breed in colonies (e.g. azure-winged magpies *Cyanopica cyanus*, Canário et al. 2004; sociable weavers

Philetairus socius, Covas et al. 2008; *Polistes wasps*, Sheehan et al. 2015), while no effects were found in multiple territorial breeding species (e.g. Seychelles warblers, this study; southern pied babbler *Turdoides bicolor*, Bourne et al. 2020b, c). These species could have different trade-offs between resource acquisition and reproductive benefits through helping. For example, helpers could decrease food availability for offspring in territories in harsh environments, as the limited resource needs to be divided up between more individuals. However, in species that are not territorial, like colonial breeding species, helpers could increase food availability for offspring in harsh environments, as more adults can forage and can reach more places to forage, while taking care of the offspring. In hornbills (*Bucerotidae*), it was found that cooperative breeding was positively associated with climatic stability (Gonzalez et al. 2013), thus showing an opposite correlation as was found in the other comparative studies. Hornbills are mostly frugivorous, and their food resources are thus less dependent on environmental fluctuations, meaning that hornbills again may have different trade-offs linked to resource acquisition and sociality. In species with relatively stable food resources, cooperation could have evolved to decrease inter- and intraspecific competition or predation risks instead of coping with harsh or fluctuating environments. Lin et al. (2019) pointed out that whether cooperative breeding affects range size (and thus food availability) could also completely change the expectations on whether or not species should be cooperative in harsh and unpredictable environments or, conversely, in stable and favourable conditions. Additionally, Shen et al. (2017) pointed out that the type of environmental variation (spatial or temporal) could also lead to vastly different conclusions on whether cooperation could buffer negative environmental effects. Next to that, it is important to take into account sample size. While some studies used data from only a couple of years, others use long-term datasets. This could influence the environmental variation captured by the study and therefore could vastly impact the conclusions that are drawn. For example, Covas et al. (2008) found a buffering effect using 2 years of data, while D'Amelio et al. (2022) found no effect using 7 years of data, despite both studies being performed on the exact same population of sociable weavers. In other words, long-term datasets are key for understanding if sociality could buffer negative effects from harsh or unpredictable environments.

Another reason for differences between species and taxa in the relationship between sociality and environmental factors could be their evolutionary mechanism behind cooperation. In some species, like long-tailed tits (*Aegithalos caudatus*) (MacColl and Hatchwell 2002) and azure-winged magpies (Canário et al. 2004), species can change their helping behaviour within a breeding season and can start helping after their own reproductive attempt has failed. In these cases, increases in helping behaviour occur automatically in hard years, as more breeding attempts fail, which in turn results in a buffering of the survival of the remaining nests and offspring (that had already survived until help was provided). Hence, it is important to consider the type of cooperation when studying the effect of sociality on adapting to new environments.

Lastly, one important point regarding the different outcomes of these studies was made by Cockburn (2020), who argues that possibly the comparative methods that found correlations between the stability or harshness of the environment and the number of social species were not sufficient to understand the underlying evolution of cooperation. He argues that many attempts to understand the evolution of cooperation have been done using phylogenetic comparative methods, but that they often do not include all possible hypotheses and can therefore not discriminate which are most likely to explain the majority of variance. Thus, within-species studies using empirical data are vital to understand if cooperation could buffer unfavourable environments, as well as understanding the differences between the species focused on in those studies, which could potentially cause opposing results. Cockburn (2020) also suggested that the relationship between cooperative breeding and temporal variability may in fact be an artefact of geographical and habitat biases in sampling effort, for example showing high sampling effort in Australia, but low sampling in tropical habitats. To understand if this is truly the case, our study on a tropical passerine could be important in disentangling these effects, but more studies across tropical habitats are necessary.

Offspring sex ratios in changing environments

Interestingly, groups with helpers produced more sons independent of rainfall, while breeding pairs, and groups without helpers, produced mostly sons in dry years and mostly daughters in wet years. Potentially, this could be adaptive. Survival of offspring can only be increased to a certain extent, thus there is a limit on the benefits of having more helpers for parents, while on the contrary, more helpers deplete more resources. Thus, in groups with helpers, additional helpers might be disadvantageous. Conversely, in groups without helpers, obtaining helpers might be beneficial in years that food is plentiful, while it might be disadvantageous in years with low food abundance. Yet, producing the optimal offspring sex ratio could be more complicated than expected for parents, especially in changing environments. Daughters have a higher probability of becoming helpers in Seychelles warblers (Komdeur et al. 1997; Richardson et al. 2002; Hammers et al. 2019; Fig. 4) and help substantially more than sons (Richardson et al. 2003a). From the perspective of the dominants then, daughters could be more beneficial under extreme circumstances than sons. However, the decision to help (instead of being a non-helping subordinate) seems to be made by the subordinate and not by the dominant (van de Crommenacker et al. 2011). Thus, accurately predicting the helping behaviour of daughters is complex. As the adult population is usually female-biased in the Seychelles warbler population on Cousin (Speelman et al. Under review), males should have higher direct fitness (following directly from Fisher's reproductive value theory; Fisher (1930)), thus producing sons could be beneficial as well. Moreover, the social environment (e.g. whether helpers are present or not) seems to be important as well in determining the optimal sex allocation strategy (Komdeur et al. 1997; Fig. 3; Table 2) and seems to interactively influence the offspring sex ratio together with environmental factors. In addition, the environment on Cousin seems unpredictable, and there is a lag between offspring production and potential help from this offspring, thus predicting which offspring might yield the highest fitness benefits is difficult. Accordingly, the trade-off between producing sons and daughters is complex, and needs to be better understood in combination with environmental and social factors to determine if sex allocation is adaptive and in which cases it would be more beneficial to produce one sex instead of the other.

Moreover, offspring sex ratio in Seychelles warblers was measured rather late during offspring development, as nests are often unreachable. Thus, disentangling the effects of potential sex allocation strategies and sex-specific mortality (adaptive or non-adaptive) in early development is not possible. Therefore, understanding if patterns in offspring sex ratio are adaptive or not is complex.

Generality of results

Sampling bias does not seem to have a large effect on our results. As discussed in the "Methods" any potential sampling bias would have caused our results to be opposite of what they are currently. Only the results during extreme rainfall could be caused by sampling bias, so these results should be handled with care. Yet, we think that the patterns found between low to intermediate rain were not affected by sampling bias.

Future research

To further understand the effects of the environment in general, and rainfall specifically, on social behaviour and other life history traits, it is important to better understand which time period of weather affects these traits, and what aspects of the weather individuals use as cue (e.g. peak rainfall, total rainfall, and average rainfall). While Komdeur (1996) provides valuable information towards understanding this question, it should be studied in more detail. On another note, understanding how general environmental change (e.g. changes in rainfall or temperature) impacts local environments (e.g. the microhabitat within a territory) and the differences between local environments is also important to understand the vulnerability of species to this general change, and possible changes in life history strategies of individuals. For example, Groenewoud (2016) showed there was considerable spatio-temporal variation in insect abundance on Cousin Island. Understanding whether and how these differences in insect abundance between territories are affected by environmental change and how this in turn affects life history traits of animal species may be beneficial to conserve these species.

Conclusion

This study shows that variation in rainfall is linked to life history, including cooperative behaviour, and thus that environmental change will have complex effects on populations of this species. Yet, we also show with this long-term study that it is unlikely that cooperative breeding is capable of buffering against harsh or unpredictable environments in Seychelles warblers. Thus, these results add to a growing body of studies finding no evidence for this hypothesis. Although our study is exploratory and correlational, we hope it stimulates future research to gain a better understanding of the complex interactions between changing environments and the life history of species. This is vital if we are to conserve these species in times of climate change. We think that a focus on cooperation specifically deserves attention in this context, as it could be a beneficial trait for species facing change, but also could be deleterious.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10211-022-00408-y.

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Data availability Data is available following the link: https://doi.org/10.34894/AKUSMG.

Declarations

Ethical note Fieldwork was conducted with the permission of the Seychelles Bureau of Standards and the Seychelles Ministry of Environment, Energy and Climate Change. Research adhered with all local and university ethical guidelines and regulations. Nature Seychelles provided permission to work on Cousin Island. All authors agree on publication of the manuscript.

Conflict of interest The authors declare no competing interests.

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