Rainfall is associated with divorce in the socially monogamous Seychelles warbler

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Conflict of interest

All authors have no competing interests.

Author's contributions

FJDS and HLD conceived the study question. AAB, FJDS, and HLD designed the hypotheses and methodology. AAB and FJDS performed the data selection. TB, JK, DSR, and HLD maintain the long-term dataset. DSR manages and, with the help of FJDS, undertook fieldwork over the period involved. AAB analyzed the data and wrote the manuscript with input from FJDS, HLD, DSR, and JK. All authors gave final approval for publication.

Statement on inclusion

The aid and input of local stakeholders from Nature Seychelles, who manage Cousin Island, in the conservation of, and research into, the Seychelles warbler is an important part of our work. As a result of this close interaction, underpinned by a memorandum of understanding, DSR is affiliated with Nature Seychelles, and we reciprocate by providing scientific support, intellectual input, and funding for facilities. Nature Seychelles is also included as an author affiliation in all Seychelles warbler publications.

Data availability

Data will be available on the University of Groningen dataverse upon acceptance.

Abstract

1. Divorce – the termination of a pair bond while both members are alive – is a mating strategy observed in many socially monogamous species, often linked to poor reproductive success. As environmental factors directly affect individual condition and reproductive performance, they can indirectly influence divorce. Given current climate change, understanding how partnership stability is affected by environmental fluctuations has important implications, including for conservation. Yet, the relationship between the ecological environment and divorce remains largely unstudied.
2. We examined the influence of temporal environmental variability on the prevalence of divorce and the possible underlying mechanisms in a socially monogamous passerine.
3. Using a 16–year longitudinal dataset, we investigated the relationship between rainfall and divorce in the Seychelles warbler (*Acrocephalus sechellensis*). First, we performed climate window analyses to test if specific temporal windows of rainfall predicted reproductive success and divorce. Then, we analyzed the effects of those temporal windows of rainfall on reproductive success and divorce and the influence of reproductive success on divorce.
4. Annual divorce rates varied from 1–16%. The probability of divorce showed a significant quadratic relationship with rainfall, increasing in years with low and high rainfall. Although the same temporal window of rainfall predicting divorce also significantly influenced reproductive success, we found no significant correlation between reproductive success and divorce.
5. Our findings suggest that rainfall impacts divorce. Given that this effect is likely not directly mediated by reproductive success, we discuss the possible role of physiological stress. By adding to the growing body of literature showing that environmental conditions influence the stability of socially monogamous partnerships, we provide novel insights that may also be important for conservation efforts in times of climate change.

Keywords: Climate window analysis, Divorce, Environmental conditions, Habitat-mediated hypothesis, Passerine, Rainfall, Seychelles warbler, Social monogamy.

1 Introduction

Social monogamy, the mating system where individuals have one social breeding partner at a time, occurs in over 90% of birds (Lack, 1968). In these systems, maintaining a pair bond across multiple breeding seasons can improve reproductive success by reducing the costs associated with mate searching and enhancing mate familiarity (Choudhury & Black, 1994; Sánchez-Macouzet *et al.,* 2014; Culina *et al.,* 2020). However, intra-sexual competition often constrains mate selection, resulting in suboptimal partnerships. Such suboptimal partnerships may be corrected through divorce, whereby a pair bond is terminated while both partners are alive (Choudhury, 1995), potentially improving reproductive success (Culina *et al.,* 2015).

Divorce occurs in 92% of socially monogamous bird species (Jeschke & Kokko, 2008). With significant inter- and intra-species variation in divorce rates (Black, 1996), several hypotheses have been proposed to explain what causes divorce (Choudhury, 1995). For instance, divorce may be a process to correct for genetic or behavioral incompatibilities within partnerships (Wilson *et al.,* 2022) or enable individuals to choose a better-quality partner, such as one with a higher dominance status or one that occupies a better territory than their previous partner (Dhondt & Adriaensen, 1994; Otter & Ratcliffe, 1996; Blondel *et al.,* 2000). Here, pair-bonded individuals instigate divorce. Divorce can also be accidental, occurring due to temporal mismatches during migration (Gilsenan *et al.,* 2017) or forced by the introduction of a third party (Jeschke *et al.,* 2007). Related to several of these hypotheses, studies have found a correlation between previous reproductive success and divorce, with reproductive failure being a strong predictor of partnership termination (Culina *et al.,* 2015; Mercier *et al.,* 2021).

Notably, the effect of reproduction on divorce can vary depending on the stage of the breeding cycle (Culina *et al.,* 2015).

As climate patterns create suboptimal environmental conditions that affect individual condition and reproductive performance, they can influence divorce. The 'habitat-mediated' hypothesis suggests divorce is more prevalent in unstable and lower-quality environments (Blondel *et al.,* 2000). This is because environmental factors can impact the decision-making process underpinning divorce by misinforming individuals about their partnership's quality. For example, when partnerships perform poorly due to harsh environmental conditions, individuals within those partnerships may still attribute their poor performance to their chosen partner and not to the given circumstances. Extreme weather can also increase physiological stress (Kitaysky *et al.,* 2010), an important factor influencing mate selection (Husak & Moore, 2008). The rapid timing of climate change, marked by more frequent extreme weather events, such as droughts and floods, and increased global temperatures (NOAA, 2022), may limit possibilities for adaptation, resulting in possible extinctions (Spooner *et al.,* 2018). Therefore, understanding how changing climates may affect the stability of socially monogamous partnerships is critical.

The relationship between the ecological environment and divorce remains largely unstudied, with only a handful of publications (Blondel *et al.,* 2000; Heg *et al.,* 2003; Botero & Rubenstein, 2012; Ventura *et al.,* 2021; Lerch *et al.,* 2022). These existing studies are primarily cross-sectional, comparing the prevalence of divorce between species or populations of the same species. To our knowledge, Ventura *et al.* (2021) is the only longitudinal study to have analyzed the effects of climate-driven environmental conditions on divorce within the same population, discovering that, due to sea-surface temperatures influencing food abundance and thus reproductive success, warmer sea-surface temperatures increased the probability of divorce in a population of black-browed albatrosses (*Thalassarche melanophris*).

With climate change resulting in more frequent heavy rain and drought events (Marvel *et al.,* 2019), we aim to investigate the relationship between rainfall and divorce by analyzing long-term longitudinal data from the socially monogamous Seychelles warbler (*Acrocephalus sechellensis*), a passerine endemic to the Seychelles archipelago. Rainfall influences the reproductive output of these warblers (Komdeur, 1996a; Borger *et al.,* 2023). As reproductive failures drive divorce in various bird species (Culina *et al.,* 2015), we investigate whether 1) the temporal variability of rainfall affects the prevalence of divorce in the Seychelles warbler, 2) measures of reproductive success at four different stages of reproduction within the breeding season affect divorce, and 3) rainfall influences these four reproductive measures. While exploring these questions, we control for the social environment and genetic relatedness within the breeding pair.

We predict that extreme amounts of rainfall increase the prevalence of divorce (P1). As Seychelles warblers are insectivorous, low rainfall decreases food availability by impacting the reproductive cycle of their prey (Komdeur, 1996a, Price, 1997). On the other hand, high rainfall can affect the ability of birds to maintain optimal body temperatures and also cause direct habitat and nest destruction (Kennedy, 1970; Wilson *et al.,* 2004). Consequently, we predict that low and high amounts of rainfall decrease reproductive success (P2). Specifically, due to decreased food availability, low rainfall impacts the ability of insectivorous birds to initiate breeding and produce a clutch (França *et al.,* 2020). Then, due to decreased food availability and increased metabolic demands in heavy rainfall conditions, low and high rainfall impact nestling and fledgling survival (Monadjem & Bamford, 2009; Heenen & Seymour, 2012). The decreased reproductive success influenced by rainfall is predicted to increase the probability of divorce as reproductive success is used as a marker of a partnership's quality (P3). Overall, in line with the habitat-mediated hypothesis, we predict divorce to be more prevalent in lower-quality years, with rainfall having a quadratic effect on divorce, both at the population and partnership level. Our findings will hopefully provide insights into how harsh environmental conditions affect the breeding behavior of socially monogamous birds, which, in turn, can inform conservation efforts across multiple species in times of climate change.

2 Materials and Methods

2.1 Study system

Since 1985, extensive mark-capture-recapture data have been collected on the Seychelles warbler population on Cousin Island (4°19′53.5″ S 55°39′43.2″ E). From 1997, >96% of the population has been caught and given unique identifiers using colored bands and BTO-numbered metal rings (Richardson *et al.*, 2001). High annual resighting probabilities (98%) and no (<0.1%) inter-island dispersal enable accurate individual-level longitudinal measures of life-history traits (Komdeur *et al.*, 2004; Brouwer *et al.*, 2006).

The insectivorous Seychelles warbler forms long-term pair bonds and has a mean post-fledgling lifespan of 5.5 years and a maximum observed lifespan of 19 years (Hammers & Brouwer, 2017; Raj Pant *et al.*, 2020). Each of the ca. 110 territories on Cousin contains one dominant breeding pair. Dominant breeders are very territorial, foraging most of their lives exclusively on their respective territories (Komdeur, 1991; Richardson *et al.*, 2007). Cooperative breeding sometimes occurs; around half of the territories include 1–5 sexually mature subordinates, some of which (20% of males and 42% of females) act as helpers, providing alloparental care to the dominant breeders' offspring (Richardson *et al.*, 2003; Hammers *et al.*, 2019). Due to resource competition, helpers are more present in higher-quality territories, and their presence can be maladaptive to breeders in lower-quality territories (Komdeur, 1998).

There are two Seychelles warbler breeding seasons. The main breeding season spans from June to October, and the minor breeding season from December to March (Komdeur, 1996a). Our analyses focused on main breeding seasons as, during minor breeding seasons, only 30% of pairs breed (compared to 90% in main breeding seasons), and data on breeding statuses are limited. Most (87%) clutches contain a single egg but can consist of up to three (Richardson *et al.*, 2001; Komdeur & Daan, 2005). Additional eggs are often laid by co-breeding subordinates (Richardson *et al.*, 2003; Komdeur *et al.*, 2004). Insect abundance in a given month is predicted by rainfall two months prior (Komdeur, 1996a), likely cueing the onset of breeding to optimize food availability for nestlings. Although socially monogamous, there is a high rate of extra-pair paternity (EPP), with 44% of offspring sired by males other than the social partner (Richardson *et al.*, 2001; Hadfield *et al.*, 2006). Lastly, parents often provide up to 3 months of post-fledgling care to their offspring (Komdeur, 1991).

2.2 Data collection

We analyzed data from 1997 to 2015 as social pairs have been monitored intensively since 1997, and rainfall measurements were only available up to 2015. The years 1999 to 2001 were excluded due to limited fieldwork impacting the quality of the data required to classify divorces. During the main breeding seasons, all territories were monitored to determine the residency of ringed birds. Observations of foraging, singing, and non-aggressive and aggressive social interactions were used to assign territory boundaries and group membership (Bebbington *et al.*, 2017). The pair-bonded male and female in a territory, determined based on their courtship and nesting behaviors, were defined as the dominant birds (Richardson *et al.*, 2002). Breeding activity was monitored by following the dominant female for at least 15 mins every 1–2 weeks (Richardson *et al.*, 2007). During the incubation and provisioning stages, to determine the identities of subordinates that helped, nest watches of at least 60 minutes were conducted (van Boheemen *et al.*, 2019). In case of a failed breeding attempt before incubation or provisioning, subordinates were defined as non-helpers. DNA was extracted from all caught individuals using brachial venipuncture blood samples (Richardson *et al.,* 2001). Up to 30 microsatellite markers were genotyped to determine the relatedness between the dominant breeding pair and the parentage of the offspring (Raj Pant *et al.*, 2020; Sparks *et al.,* 2022; see supplementary material section 'Pairwise relatedness'). Territory quality was measured using an index of insect availability, territory size, and foliage cover (Komdeur, 1992; van de Crommenacker *et al.,* 2011; see supplementary materials section 'Territory quality').

2.2.1 Rainfall measurements

As rainfall data were not available from Cousin, we obtained mean monthly rainfall measurements from a weather station on Praslin (4°18' 60.0" S 55°43'59.9" E), a neighboring island ca. 1.5 km northeast of Cousin (Seychelles Meteorological Authority, 2016). Mean monthly and annual rainfall varied significantly during the study period (monthly range: 0.8–716 mm; annual: 1349–3410 mm).

2.3 Divorce classification

We classified partnerships as divorced when members of a dominant breeding pair did not form a dominant breeding pair the following main breeding season while both individuals were still alive. As we were solely interested in comparing the years when partnerships did or did not divorce, we excluded the years when partnerships terminated due to widowing (partner death) or translocations undertaken to neighboring islands as part of conservation programs (Richardson *et al.,* 2006; Wright *et al.,* 2014). The resulting dataset included 416 males and 392 females in 1325 partnerships, 87 (6.6%) of which ended in divorce.

2.4 Statistical analyses

All statistical analyses were performed in R 4.2.2 (R Core Team, 2022). Figures were created using *ggplot2* 3.4.1 (Wickham, 2016) and generalized linear mixed models (GLMMs) were run in *lme4* 1.1-31 (Bates *et al.,* 2015). The over or underdispersion of models and residual spatio-temporal autocorrelations were checked (none were found) using *DHARMa* 0.4.6 (Hartig, 2022). Collinearity was determined using *car* 3.1-1 (Fox & Weisberg, 2019), and all variance inflation factors (VIF) were <3.0. Model predictions for visualization were produced using *AICcmodavg* 2.3-1 (Mazerolle, 2020) and *ggeffects* 1.1-5 (Lüdecke, 2018). To facilitate model convergence, all explanatory variables were mean-centered and divided by 1 standard deviation using the scale function in R. Unless stated otherwise, all estimates are given ± SE.

2.4.1 Climate window analysis

Following Bailey & van de Pol (2016) (see supplementary materials section 'Climate window analysis'), we used *climwin* 1.2.3 to determine which temporal windows of rainfall best predicted divorce, reproductive success, and food availability. Previously, total rainfall from June to August was used to study the life-history effects of rain in the Seychelles warbler (Borger *et al.,* 2023). However, we performed an analysis of all possible temporal windows within 12 months before the end of the breeding season (28th of September), as we assumed that divorce is not an instantaneous decision but rather one that follows a long-term decision-making process influenced by multiple factors.

Firstly, we tested which temporal window of rainfall best predicted the probability of divorce (Y/N). Then, we tested which temporal windows of rainfall predicted measurements of reproductive success at four stages of reproduction: 1) The probability of attempting to breed - when a dominant breeding pair initiated nest building (Y/N); 2) The probability of producing a clutch - when the nest of a dominant breeding pair contained an egg (Y/N); 3) The probability of producing a fledgling - when an offspring fledged from the nest of a dominant breeding pair (Y/N); 4) The number of fledglings genetically related to the dominant female that survived until at least three months old (end of the post-fledgling care period) - classified as a continuous response variable.

As all measurements of reproductive success could include offspring resulting from EPP, we assumed that male social partners were unaware of cuckolding and cared for offspring sired by other males as if they were their own. Although a minority (11% of offspring; Sparks *et al.*, 2022), reproductive success measurements 1–3 could also include co-breeders' offspring. Therefore, other than to investigate the post-fledgling care period, we included the number of genetic fledglings to compare measurements of reproductive success including either just genetic, or all, offspring.

Lastly, we tested which temporal windows of rainfall best predicted territory quality and insect abundance (the mean number of insects found per unit leaf area across all monthly surveys) to compare territory-wide and population-wide measurements of food availability. By comparing the temporal windows of rainfall predicting divorce against possible influencers of divorce, we aimed to examine potential patterns explaining the causality of divorce.

2.4.2 Population-level divorce rate

We used a quasi-binomial generalized linear model (GLM) with a logit link function to model the annual population divorce rate as a function of rainfall. As we predicted that both low and high rainfall would affect partnership stability, the model included rainfall and rainfall^2. The measurement of rainfall included in the model was the total rainfall from the months that best predicted divorce determined via the climate window analysis.

2.4.3 Partnership-level probability of divorce

Using a binomial GLMM with a logit link function, we modeled the probability of divorce as a function of rainfall, rainfall^2, the number of offspring (genetic fledglings that survived till at least three months old), the number of helpers, partnership length (in years), pairwise relatedness, male age (in years), male age^2, female age, and female age^2 (Komdeur, 1994; 1996a; 1996b; Richardson *et al.*, 2003; van Boheemen *et al.*, 2019; Hammers *et al.*, 2019). All fixed effects were continuous variables. The identity (ID) of the dominant male and female, and territory and field period, were included as random effects to control for individuals that sequentially performed worse or better than others and the variability of quality across territories and field periods. Next, we compared the effects of reproduction at four different stages - breeding attempted (Y/N), clutch produced (Y/N), fledgling produced (Y/N), and genetic fledglings (Y/N) - on divorce by including them one at a time in the model.

2.4.3 Partnership-level probability of reproductive success

To explore the potential causal links between rainfall, reproductive success, and divorce, we examined whether rainfall during the months that best predict divorce also influenced reproductive success. We used binomial GLMMs with logit link functions to model the probability of attempting to breed, producing a clutch, and producing a fledgling as functions of rainfall, rainfall^2, the number of helpers, partnership length, pairwise relatedness, male age, male age^2, female age, and female age^2. Next, we used a Poisson GLMM with a log link function to model the effect of the same fixed effects on the number of genetic fledglings that survived until three months old. All models included the random effects: male ID, female ID, territory, and field period ID.

In all models, we tested whether mate familiarity buffered the effects of rainfall by including an interaction between partnership length and rainfall. Starting from a full model, non-significant quadratic terms and interactions were removed (in order of least significance) to interpret first-order effects.

3 Results

3.1 Effect of rainfall on divorce

The mean annual divorce rate of Seychelles warbler partnerships during the study period was 6.6 ± 1.1% and showed considerable inter-annual variability, ranging from 1.2–15.6% (Figure S1a). Climate window analyses revealed that the quadratic effect of total rainfall from February to August best predicted the probability of divorce (Figure 1). At the population level, total rainfall from February to August had a significant quadratic effect on the annual divorce rate (GLM, estimate = 0.335 ± 0.091, *p*-value = 0.003), which increased in years with low and high rainfall (Figure S1b). Rainfall effects explained 46.7% of the annual divorce rate's variance (r^2 = 0.467). At the partnership level, the quadratic effect of total rainfall from February to August significantly affected the probability of divorce (Table 1; Figure 2). Notably, the quadratic relationship between rainfall and the probability of divorce was driven by extremely heavy rainfall in 1997, as removing 1997 from the analysis revealed a significant negative linear relationship between rainfall and divorce (Tables S1 & S2; Figure S2).

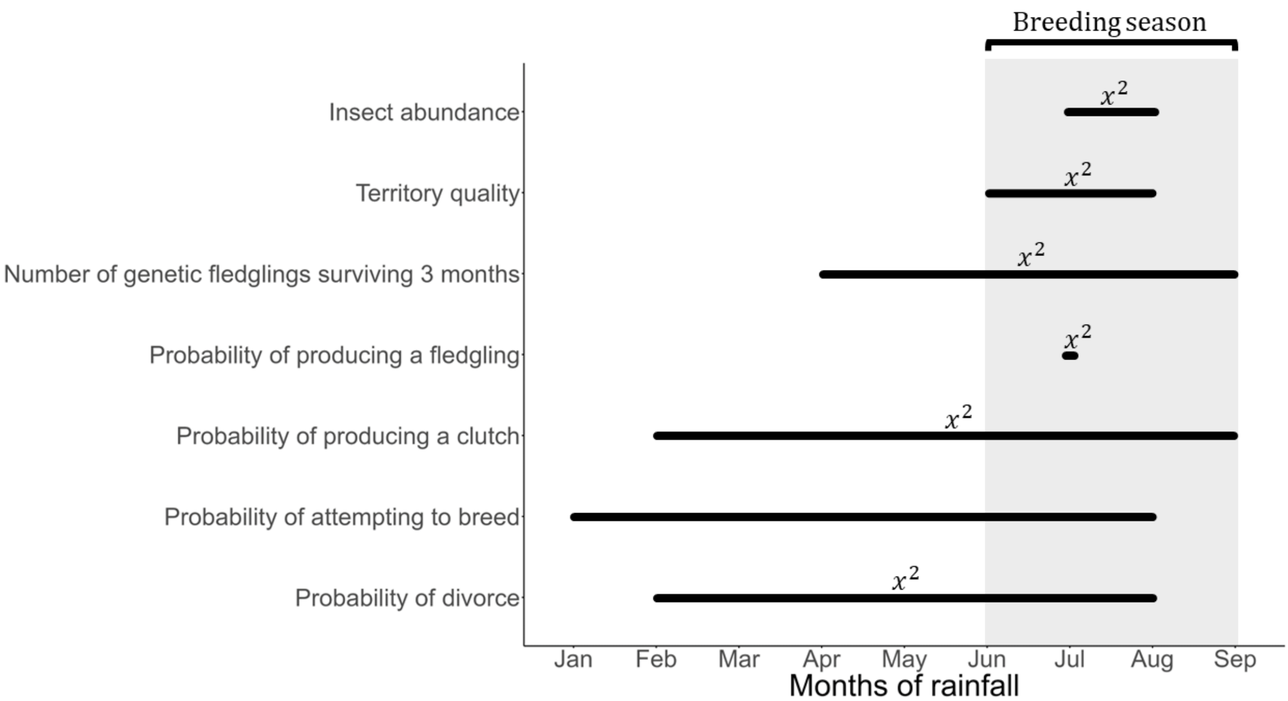

Figure 1. Temporal windows of rainfall that best predict seven response variables in the Seychelles warbler on Cousin Island (*n* = 1325 partnerships/15 years for insect abundance and territory quality). Relationships between rainfall and the response variables were quadratic if indicated by x^2 and linear if not. The shaded area represents the main breeding season and the reference date for the response variables was set as the 28th of September.

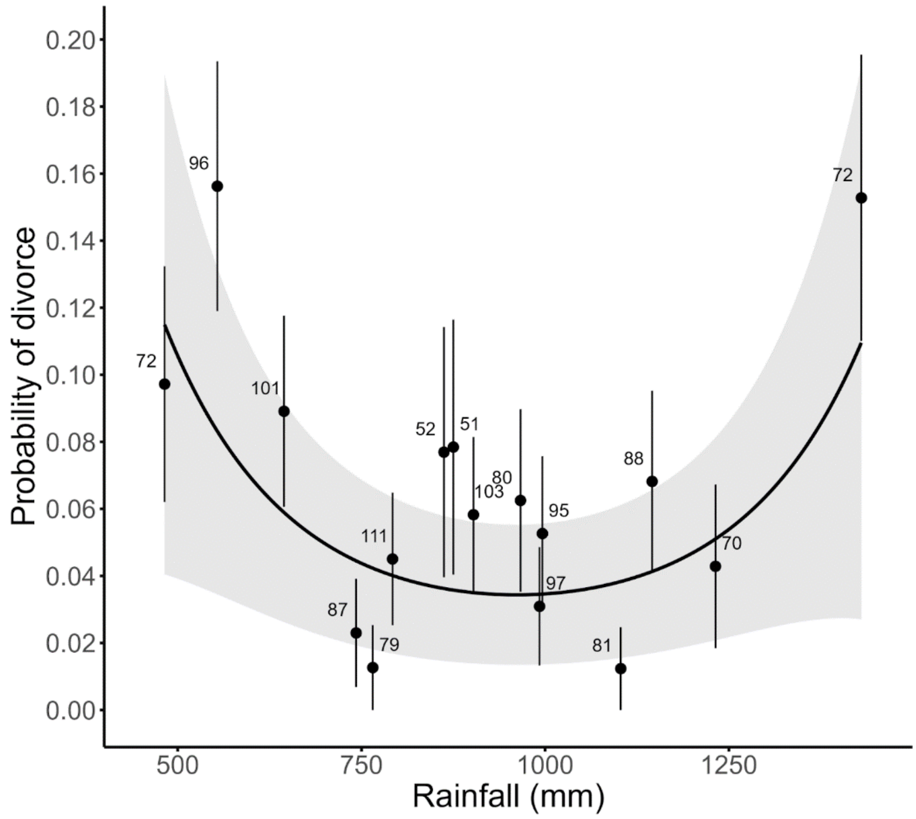

Figure 2. The effect of rainfall on the probability of divorce in the Seychelles warbler on Cousin Island (*n* = 1325 partnerships) as predicted by a binomial generalized linear mixed model. The solid line represents the predicted probability of divorce and the shading indicates the 95% confidence intervals. Dots represent the mean observed divorce rate ± SE, and labels indicate the total number of partnerships observed in a given year.

3.2 Effects of reproductive success and other partnership qualities on divorce

Although there was a trend for reproductively successful partnerships to have lower divorce rates (Figure S3), we found no significant correlations between the probability of divorce and measures of reproductive success (Figures S3 & S4; Tables S3-S6). However, the probability of divorce was significantly negatively correlated with partnership length (Table 1), with shorter partnerships having the highest probability of divorce. Notably, the correlation between rainfall and partnership length was non-significant after removing 1997 from the analyses (Table S1 & S2). The mean partnership length in 1997 (0.8 ± 0.1) was considerably shorter than that of the full study period (2.2 ± 0.07). We also found a significant interaction between partnership length and rainfall (Table S7), with heavy rainfall increasing the probability of divorce in shorter but not longer-lasting partnerships (Figure S8). However, this interaction was strongly influenced by outliers and subsequently removed from the final model (see supplementary material section ‘Interaction between rainfall and partnership length’).

Table 1. Associations between the probability of divorce in the Seychelles warbler on Cousin Island with rainfall, the length of the partnership, the number of offspring, the relatedness of the breeding pair, the number of helpers, male age, and female age. n = 1325 partnerships were analyzed using a binomial generalized linear mixed model. Significant *p*-values are in bold.

Independent variables	**Estimate**	**Standard error**	**95% Confidence interval**	***p*-value**
Intercept	-3.312	0.318	-3.936 to -2.688	**<0.001**
Rainfall	-0.174	0.114	-0.397 to 0.049	0.126
Rainfall^2	0.314	0.087	0.143 to 0.485	**<0.001**
Partnership length	-0.456	0.203	-0.855 to -0.057	**0.025**
Number of offspring	-0.139	0.139	-0.411 to 0.134	0.318
Pairwise relatedness	0.122	0.121	-0.115 to 0.360	0.313
Number of helpers	-0.162	0.147	-0.449 to 0.125	0.269
Male age	0.080	0.150	-0.214 to 0.375	0.592
Female age	0.164	0.138	-0.106 to 0.434	0.234

Random effects	**Variance**	**Levels**
Male ID	0.000	416
Female ID	0.103	392
Field period ID	0.038	17*
Territory ID	0.228	158

*****In 2004, the major breeding season was split up into two field periods, resulting in 17 field periods over 16 years.

3.3 Effect of rainfall on reproductive success

We performed climate window analyses to first identify which months of rainfall best predicted reproductive success. Then, we analyzed the association between reproductive success and the months of rainfall that best predicted divorce (February to August).

3.3.1 Breeding attempted

During the study period, 90% of partnerships attempted to breed. The probability of attempting to breed was best predicted by the linear increase in total rainfall from January to August (Figure 1). The probability of attempting to breed was also significantly positively correlated with the total rainfall from February to August (Table S12; Figure 4a).

3.3.2 Clutch produced

Overall, 82% of partnerships produced a clutch. The probability of producing a clutch was best predicted by the quadratic effect of rainfall from February to September (Figure 1), decreasing in years with low and high rainfall. Although the climate window analysis predicted a quadratic relationship, we found a significant positive linear correlation between total rainfall from February to August and the probability of producing a clutch (Table S12; Figure 4b). The quadratic effect of rainfall was marginal (Table S13).

3.3.3 Fledgling produced

Overall, 50% of partnerships during the study produced a fledgling. The probability of producing a fledgling was best predicted by the quadratic effect of rainfall in July, the peak of egg-laying (Figure 1), where both low and high amounts of rain decreased fledgling success. We also found that total rainfall from February to August had a significant quadratic effect on the probability of producing a fledgling (Table S12). Again, intermediate levels of rainfall were associated with the highest probabilities of fledgling success (Figure 4c).

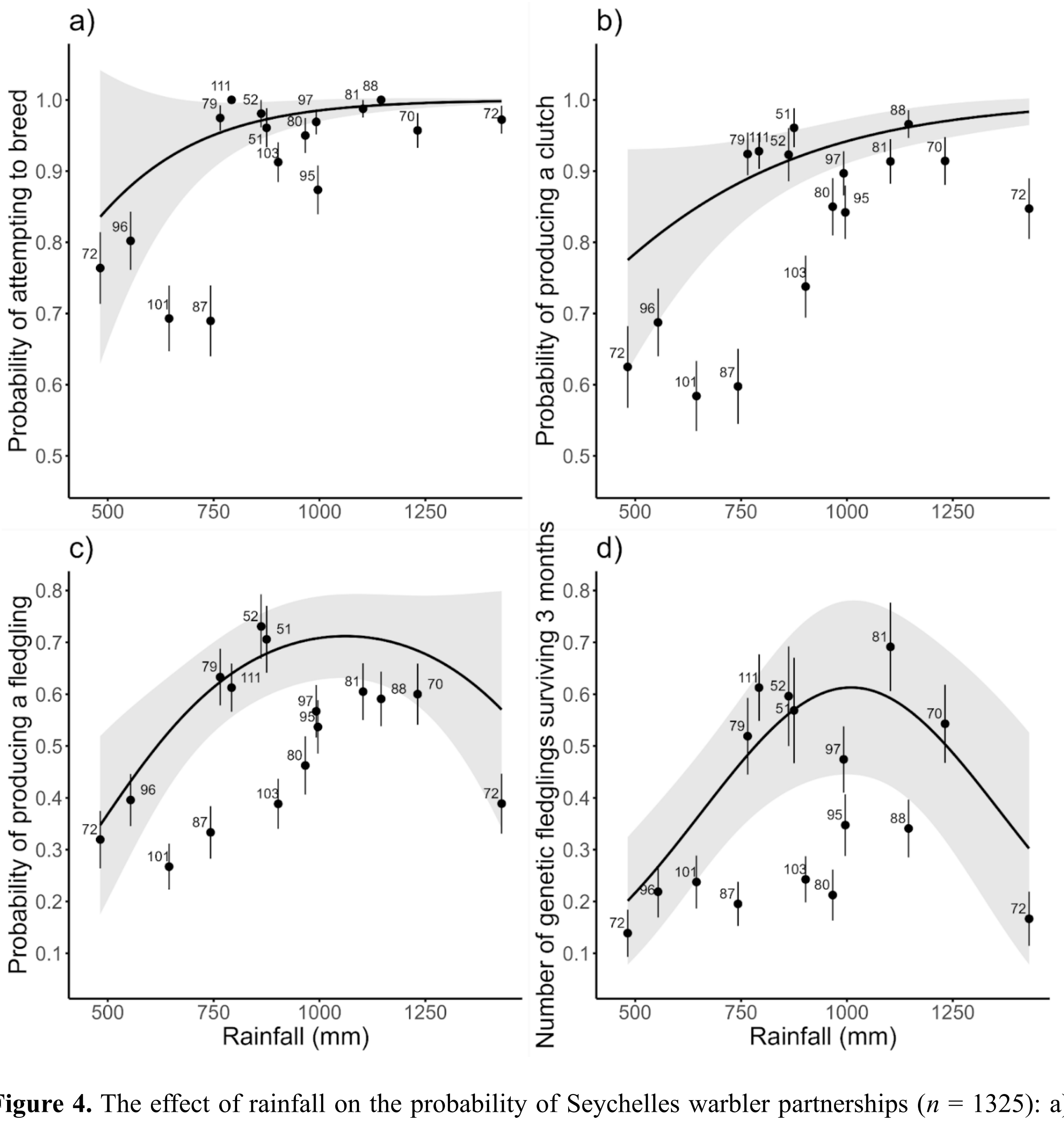

Figure 4. The effect of rainfall on the probability of Seychelles warbler partnerships (n = 1325): a) attempting to breed; b) producing a clutch; c) producing a fledgling; d) the number of genetic fledglings surviving until three months old, as predicted by binomial (a, b, c) and Poisson (d) generalized linear mixed models. The solid line represents the predicted probability of divorce, and the shading indicates the 95% confidence intervals. Dots represent the mean observed divorce rate ± SE, and labels indicate the total number of partnerships observed in a given year.

3.3.4 Genetic fledglings

During the study period, 32% of partnerships produced a genetic fledgling that survived to the end of the post-fledgling care period (mean number of genetic fledglings surviving = 0.40 ± 0.02). The number of genetic fledglings surviving was best predicted by the quadratic effect of rainfall from April to October (Figure 1). Here, low and high amounts of rain decreased genetic offspring survival post-fledgling care. Comparatively, the number of genetic fledglings surviving was correlated with the quadratic effect of the total rainfall from February to August (Table S12). Again, the highest numbers of genetic fledglings surviving were associated with intermediate levels of rainfall (Figure 4d).

3.4 Effect of rainfall on food availability

A quadratic effect of total rainfall from June to August best predicted territory quality (Figure 1). Although quadratic, this relationship was skewed to high rainfall correlating strongly with high territory quality, while low and intermediate rainfall were associated with lower territory quality (Figure S6a). An increase in insect abundance was best predicted by the increase in total rainfall from July to August (Figure 1; Figure S6b).

4 Discussion

4.1 Association between rainfall and divorce

As predicted (P1), the temporal variability of rainfall had a quadratic effect on the prevalence of divorce in the Seychelles warbler, with low and high amounts of rain significantly increasing the population-level annual divorce rates and partnership-level probabilities of divorce. The extremely heavy rainfall in 1997 (leading to a state of emergency being declared nationwide) drove the association between high rainfall and a high prevalence of divorce, as excluding 1997 from the analyses left a negative relationship between rainfall and divorce. However, we consider 1997 to be very biologically valid, as it shows the effects of the heavy rainfall events predicted to become more prevalent because of future climate change (Pezza & Simmonds, 2008; Changnon, 2009; NOAA, 2022). The main Seychelles warbler breeding season spans from June to October, and total rainfall from February to August best predicted the probability of divorce. Thus, if divorce is a decision informed by the costs and benefits of staying with a specific partner, it is not instantaneous but likely reinforced by various drivers over a long time.

Compared to the high divorce rates of some migratory birds, including the congeneric great reed warbler (*Acrocephalus arundinaceus*) (85%: Bench & Hasselquist, 1991), the Seychelles warbler had a relatively low mean annual divorce rate (6.6%). The Seychelles warbler's divorce rate is similar to other birds with high site fidelity (3.7% in black-browed albatrosses: Ventura *et al.*, 2021), fitting with the prediction that birds with stable nesting sites are less likely to divorce (Choudhury, 1995). Nevertheless, inter-annual divorce rates varied considerably, and were strongly associated with rainfall. As rainfall is associated with food abundance on Cousin Island (further discussed below), our study is one of few to provide empirical evidence supporting the habitat-mediated hypothesis of divorce (Ventura *et al.*, 2021).

4.2 Association between rainfall and reproductive success

As predicted (P2), rainfall significantly influenced all measures of reproductive success. Borger *et al.* (2023) discovered that total rainfall from June to August had a quadratic effect on the number of genetic Seychelles warbler fledglings produced. We investigated this further by examining rain effects on all stages of reproduction. Total rainfall from January to August and February to September best predicted the probability of attempting to breed and of producing a clutch, respectively. Both these reproductive measures were also significantly positively correlated with the temporal window of rainfall best predicting divorce. These large temporal windows are in line with studies discovering that rain affects the health of birds outside of the breeding season, impacting their reproductive success (Studds & Marra, 2007). Rainfall often impacts reproductive success by influencing insect abundance, which cues breeding in many birds (Lloyd, 1999; Cavalcanti *et al.*, 2016; França *et al.*, 2020).

On Cousin, the increase in total rainfall from June to August and July to August was associated with increased territory quality and population-wide insect abundance, respectively. As most insects lay their eggs in water, drought significantly limits their development (Price, 1997; Chen *et al.*, 2019), decreasing food availability for the warblers. As mean food availability at the end of the breeding season was best predicted by rainfall around the middle of the breeding season, our results are similar to the two-month temporal window previously found by Komdeur (1996a). Thus, the Seychelles warbler likely uses rainfall to cue breeding to ensure adequate food availability for offspring. Consequently, by limiting the ability to invest in offspring, low rainfall decreases the probability of attempting to breed and of producing a clutch.

The probability of producing a fledgling was predicted by rainfall in July, the month of peak egg-laying, which is consistent with studies that found that the probability of fledging in birds correlated with rainfall during the hatchling period (Monadjem & Bamford, 2009; Schöll & Hille, 2020). Next, the number of genetic fledglings surviving until at least the age of three months old was best predicted by rainfall from April to September. This temporal window is explained by the fact that Seychelles warblers provide up to three months of post-fledgling care (Komdeur, 1991). Total rainfall from February to August had a significant quadratic effect on both measures of fledgling success, where low and high amounts of rain decreased the probability of fledgling survival. Alongside the aforementioned effects of low rainfall on food availability, heavy rainfall, and the often accompanying strong winds, can be detrimental as they can destroy nests and make maintaining optimal body temperatures difficult for birds (Kennedy, 1970; Jones & Barnett, 1971; Wilson *et al.*, 2004). As most nestlings do not have fully developed feathers, hindering their ability to maintain body temperature, it can be detrimental to their survival if they get wet (Mertens, 1977; Newton, 1998). Similarly, heavy rainfall can increase the parental investment required to maintain optimal nest temperatures (Heenan & Seymour, 2012). If parents have to invest more during harsh weather conditions and their foraging ability is limited, they may face a trade-off between provisioning and their health (Radford *et al.*, 2001), impacting the survival of their offspring (Öberg *et al.*, 2015).

4.3 Association between reproductive success and divorce

The temporal window of rainfall that predicted divorce overlapped with the temporal windows of rainfall predicting measures of reproductive success. All measurements of reproductive success were also significantly correlated with total rainfall from the months that best predicted divorce, and there was a trend for higher mean divorce rates in partnerships with low reproductive success. These results reveal a plausible pathway whereby rainfall influences reproductive success by impacting food availability, metabolic processes, and parental tradeoffs. Individuals may then interpret low reproductive success as a marker of poor partnership quality, resulting in divorce. These results are consistent with findings that reproductive failures drive divorce in birds (Culina *et al.*, 2015; Mercier *et al.*, 2021; Ventura *et al.*, 2021; Pelletier & Guillemette, 2022). However, the direct effects of reproductive success on the probability of divorce were non-significant. Thus, reproductive success may not influence divorce in the Seychelles warbler as predicted (P3), and rainfall may influence divorce through alternative pathways.

Physiological stress may influence divorce in the Seychelles warbler. Harsh environmental conditions and food scarcity can increase the concentration of stress hormones in birds (Kitaysky *et al.*, 2010), which are positively associated with an individual's level of dissatisfaction with their social partner (Griffith *et al.*, 2011). Although the role of stress in divorce is currently unknown for the Seychelles warbler, research shows that lower territory quality correlates with higher levels of oxidative stress because of increased foraging effort, especially during the early stages of reproduction (Komdeur 1991; 1996b; van de Crommenacker *et al.*, 2011; Yap *et al.*, 2017). Thus, rainfall and its effects on food availability and parental investments could increase physiological stress in the Seychelles warbler. Individuals may associate their heightened physiological stress with their choice of partner, causing individuals in resource-poor seasons to terminate partnerships regardless of reproductive output. We predicted extreme rainfall to misinform individuals about their partnership's quality by impacting reproduction, but stress could be the link between rainfall and divorce. Studies analyzing relationships between markers of stress, such as glucocorticoids (Sapolsky *et al.*, 2000), rainfall (or other environmental effects), and divorce, are required to investigate this hypothesis.

Divorce can be an adaptive strategy that improves reproductive success (Culina *et al.*, 2015). In times of climate change, behavioral plasticity may help animals minimize the negative consequences of coping with rapid environmental changes (Beever *et al.*, 2017). Our study introduces the possible consequences of climate change on partnership stability. However, further research into the consequences of divorce is required to determine whether divorce driven by rainfall is adaptive and can help the species overcome climatic challenges. An understanding of whether rainfall influences divorce in good- or bad-quality partnerships is currently lacking. If rainfall affects divorce by misinforming individuals about their partnership's quality, either through impacting stress or reproductive performance, divorce can occur in partnerships that may perform adequately in good conditions. Here, divorce driven by rainfall is maladaptive, making climate change a great concern to the future of this species. Further studies on the fitness consequences of divorce are required, but current research suggests that extreme rainfall is associated with poor reproductive success, divorce, and possibly survival in the Seychelles warbler (Borger *et al.* 2023).

4.4 Non-environmental associations with divorce

Shorter partnerships had a higher probability of divorce than older partnerships, fitting the prediction that the benefits of divorce are highest before individuals have had time to gain the benefits associated with mate familiarity (Choudhury, 1995). Behavioral incompatibilities between individuals can also manifest early in partnerships and influence divorce by impacting reproductive success (Wilson *et al.*, 2022). However, we did not find an effect of partnership length on reproductive success. Consistent with studies that show that Seychelles warblers do not seem to avoid inbreeding (Eikenaar *et al.*, 2008), we also found no effect of pairwise relatedness on divorce. This result indicates that inbreeding avoidance or other genetic incompatibilities are unlikely to be drivers of divorce in the Seychelles warbler (Hidalgo Aranzamendi *et al.*, 2016). Notably, the effect of partnership length on divorce was no longer significant when excluding 1997 from the analysis. The year 1997 is when population monitoring intensified, and much more of the Seychelles warbler population became identity-tagged (>96% of the population; Richardson *et al.*, 2001). Compared to other years, the mean partnership length in 1997 was considerably shorter. This may be because the limited nature of the data previous to this year meant that partnership lengths were underestimated that year, and consequently, removing it led to the loss of the significant interaction. Other earlier years (1999 to 2001) were already excluded from the analyses due to reduced data on reproductive success being collected in those years. Thus, biases in the data may drive the effect of partnership length on divorce.

5 Conclusion

Our study provides empirical evidence for an association between rainfall and divorce in a socially monogamous population, thereby contributing to a growing body of literature showing that harsh climates affect partnership stability. The prevalence of divorce in the Seychelles warbler was highest in years with low and high amounts of rainfall. We provide correlational evidence that this could result from rain impacting reproductive success, possibly by affecting food availability and parental tradeoffs. We also discuss alternative explanations involving the role of physiological stress, an important avenue for further research in this and many other species. Studies show that temperature influences divorce in birds, and now we find that rainfall does too. The climate can directly affect survival and indirectly influence population stability by restricting reproductive output. We do not yet understand whether divorce in the Seychelles warbler is adaptive or maladaptive. Therefore, studying the consequences of divorce in this species may highlight to what extent plasticity in breeding behavior can enable socially monogamous species to adapt to a rapidly changing world.

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Supplementary materials for the manuscript titled "Rainfall is associated with divorce in the socially monogamous Seychelles warbler".

Materials & Methods

Pairwise relatedness

Seychelles warbler DNA was extracted from brachial venipuncture blood samples using a Qiagen DNeasy Blood and Tissue Kit (2013 onwards) or modified ammonium acetate protocol (before 2013). DNA samples were used to determine sex using 1 to 3 markers and genotyping using a panel of 30 microsatellite markers (Richardson *et al.,* 2004; Raj Pant *et al.,* 2020; Sparks *et al.,* 2022). Parentage was assigned using MasterBayes 2.52 (Hadfield *et al.,* 2006), which was used to build a genetic pedigree (Sparks *et al.,* 2022). We calculated pairwise relatedness between partners using the Queller and Goodnight estimation using the R-package *related* 0.8 (Queller & Goodnight, 1989; Pew *et al.,* 2015). This estimation of pairwise relatedness also reflects pedigree relatedness in the Seychelles warbler (Brouwer *et al.,* 2007), and heterozygosity across the microsatellite panel reflects genome-wide heterozygosity (van de Crommenacker *et al.*, 2011).

Territory quality

Territory quality in the main breeding seasons was measured using an index of insect availability, territory size, and foliage cover (Komdeur, 1992; van de Crommenacker *et al.,* 2011). This was done using the equation $A \times \sum(Cx \times lx)$, where A is territory size in ha, Cx is the percentage of foliage cover for tree species x, and lx is the per unit leaf area mean monthly insect density for tree species x in dm^2. Insect abundance was estimated by counting the number of insects on the underside of 50 leaves for ten dominant tree species, once a month at 14 different island locations. Estimates of insect counts for all territories were estimated based on their proximity to one of these locations. Foliage cover was estimated by scoring the presence or absence of ten dominant tree species at various heights during the middle of the breeding season (typically July). This was done at 20 different points in all territories and each tree species' total number of presence scores was its estimated foliage cover. In 2002, no territory quality data was collected resulting in 15 years of food abundance data.

Climate window analysis

We used *climwin* 1.2.3 (Bailey & van de Pol, 2016) to determine which temporal windows of rainfall best predicted divorce, measurements of reproductive success, and measurements of territory quality.

The *slidingwin* function determined the months of rainfall best predicting the variation in response variables using a sliding window technique. July is the peak of breeding, which is when the most eggs are being laid, and warblers can provide up to three months of post-fledgling care. As a result, we used the end of the main breeding season (28th of September) as the *slidingwin* reference date and tested for temporal windows up to 12 months leading up to this date. After finding a temporal window, we tested whether the result was found due to chance (which was never the case) using the function *randwin*. We performed the *randwin* randomization procedure 1000 times and confirmed that observing such a negative value for the ΔAICc of the best model was statistically significant (*p*ΔAICc < 0.001).

For all response variables, both the linear and quadratic functions of rainfall were tested. AIC values of the models created were used to determine whether the linear or quadratic relationship best fit the data. A better fit for the more complicated model (quadratic) was defined as a ΔAIC > 7 (Burnham *et al.,* 2011).

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Results

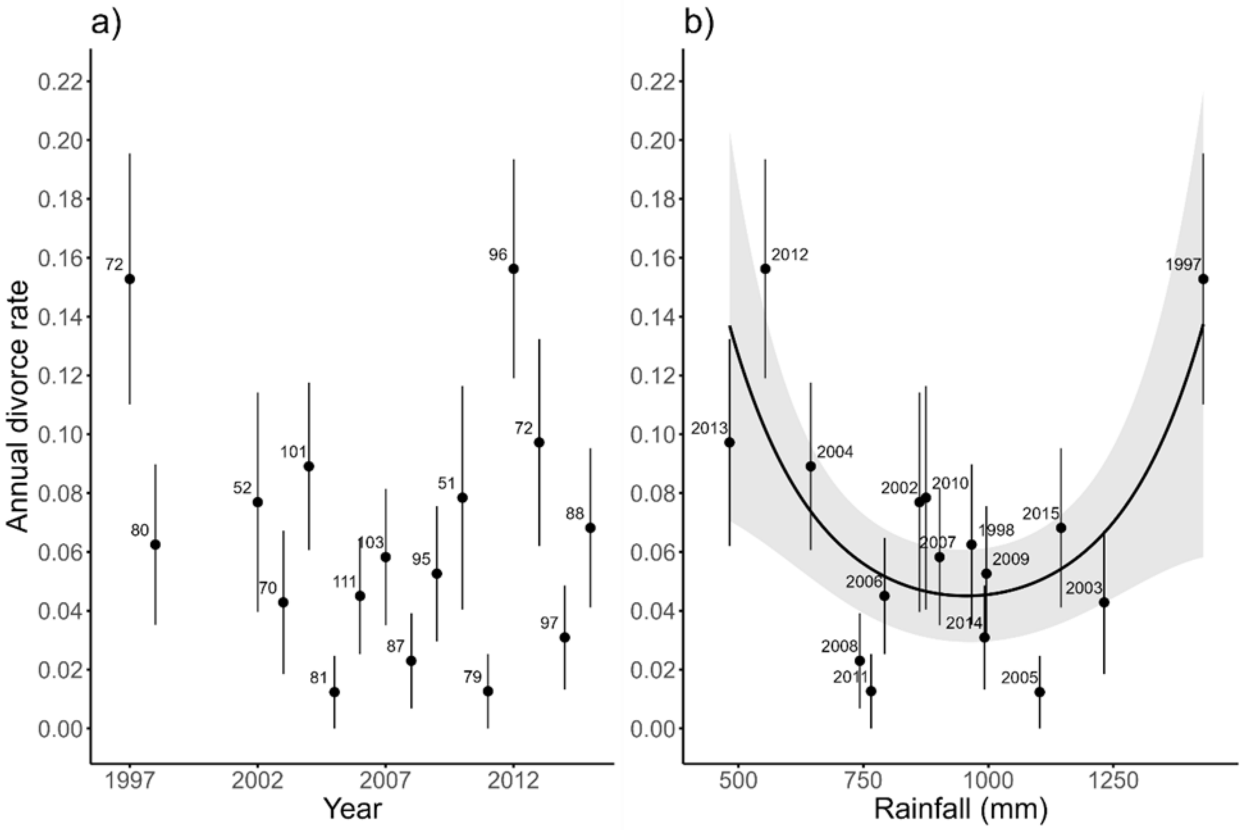

Figure S1. a) Variability in the annual divorce rate of the Seychelles warbler on Cousin Island (*n* = 1325 partnerships) from 1997 to 2015. The years 1999, 2000, and 2001 were not included due to limited fieldwork during those years. b) The effect of rainfall on the annual divorce rate as predicted by a quasi-binomial generalized linear model. The solid line represents the predicted divorce rate, and the grey shading indicates the 95% confidence intervals. Dots represent the mean observed annual divorce rate ± SE, and labels indicate the total number of partnerships in a given year (a) or the sample year (b).

Table S1. Associations between the probability of divorce in the Seychelles warbler on Cousin Island with the total rainfall from February to August, the length of the partnership, the number of offspring, the relatedness of the breeding pair, the number of helpers, male age, and female age. A total of n = 1256 partnerships were analyzed using a binomial generalized linear mixed model. Significant *p*-values are in bold. Data from 1997 were removed from this analysis and the non-significant quadratic term of rainfall is included.

Independent variables	Estimate	Standard error	95% Confidence interval	*p*-value
Intercept	-3.326	0.348	-4.007 to -2.645	**<0.001**
Rainfall	-0.270	0.180	-0.623 to 0.082	0.133
Rainfall^2	0.223	0.167	-0.105 to 0.551	0.183
Partnership length	-0.352	0.211	-0.766 to 0.061	0.095
Number of offspring	-0.123	0.144	-0.405 to 0.160	0.394
Pairwise relatedness	0.091	0.130	-0.163 to 0.345	0.484
Number of helpers	-0.236	0.168	-0.566 to 0.094	0.161
Male age	-0.003	0.165	-0.326 to 0.319	0.984
Female age	0.129	0.149	-0.163 to 0.421	0.386
Random effects	**Variance**	**Levels**		
Male ID	<0.001	392		
Female ID	0.232	372		
Field period ID	0.061	16		
Territory ID	0.255	156		

Table S2. Associations between the probability of divorce in the Seychelles warbler on Cousin Island with the total rainfall from February to August, the length of the partnership, the number of offspring, the relatedness of the breeding pair, the number of helpers, male age, and female age. A total of n = 1256 partnerships were analyzed using a binomial generalized linear mixed model. Significant *p*-values are in bold. Data from 1997 were removed from this analysis and the non-significant quadratic term of rainfall is excluded.

Independent variables	**Estimate**	**Standard error**	**95% Confidence interval**	***p*-value**
Intercept	-3.131	0.297	-3.714 to -2.548	**<0.001**
Rainfall	-0.397	0.176	-0.743 to -0.051	**0.024**
Partnership length	-0.376	0.209	-0.785 to 0.034	0.072
Number of offspring	-0.126	0.144	-0.409 to 0.156	0.382
Pairwise relatedness	0.088	0.128	-0.163 to 0.339	0.494
Number of helpers	-0.228	0.167	-0.555 to 0.100	0.174
Male age	0.001	0.163	-0.319 to 0.321	0.996
Female age	0.136	0.147	-0.152 to 0.424	0.354
Random effects	**Variance**	**Levels**		
Male ID	0.000	392		
Female ID	0.150	372		
Field period ID	0.119	16		
Territory ID	0.231	156		

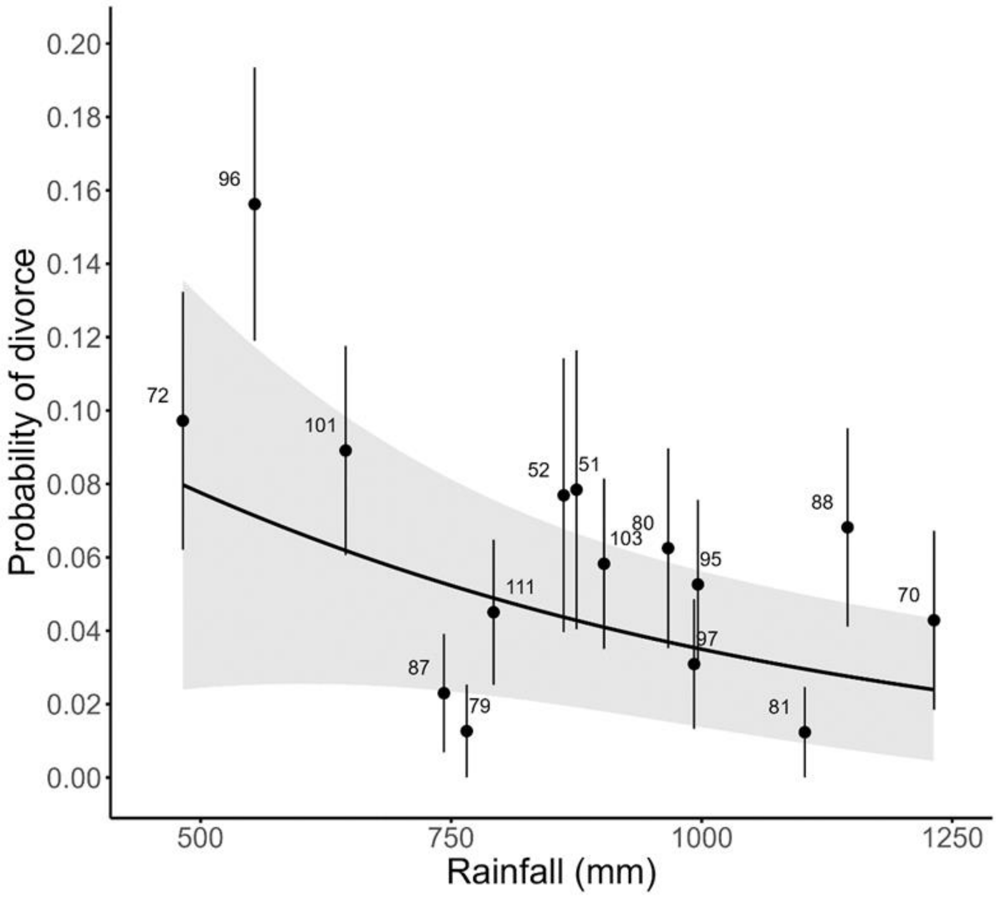

Figure S2. The effect of total rainfall from February to August on the probability of divorce in the Seychelles warbler on Cousin Island (n = 1325 partnerships) as predicted by a binomial generalized linear mixed model (Table S2) where data from 1997 was removed from the analysis. The solid line represents the predicted probability of divorce, and the grey shading indicates the 95% confidence intervals. Dots represent the mean observed divorce rate ± SE, and labels indicate the total number of partnerships in a given year.

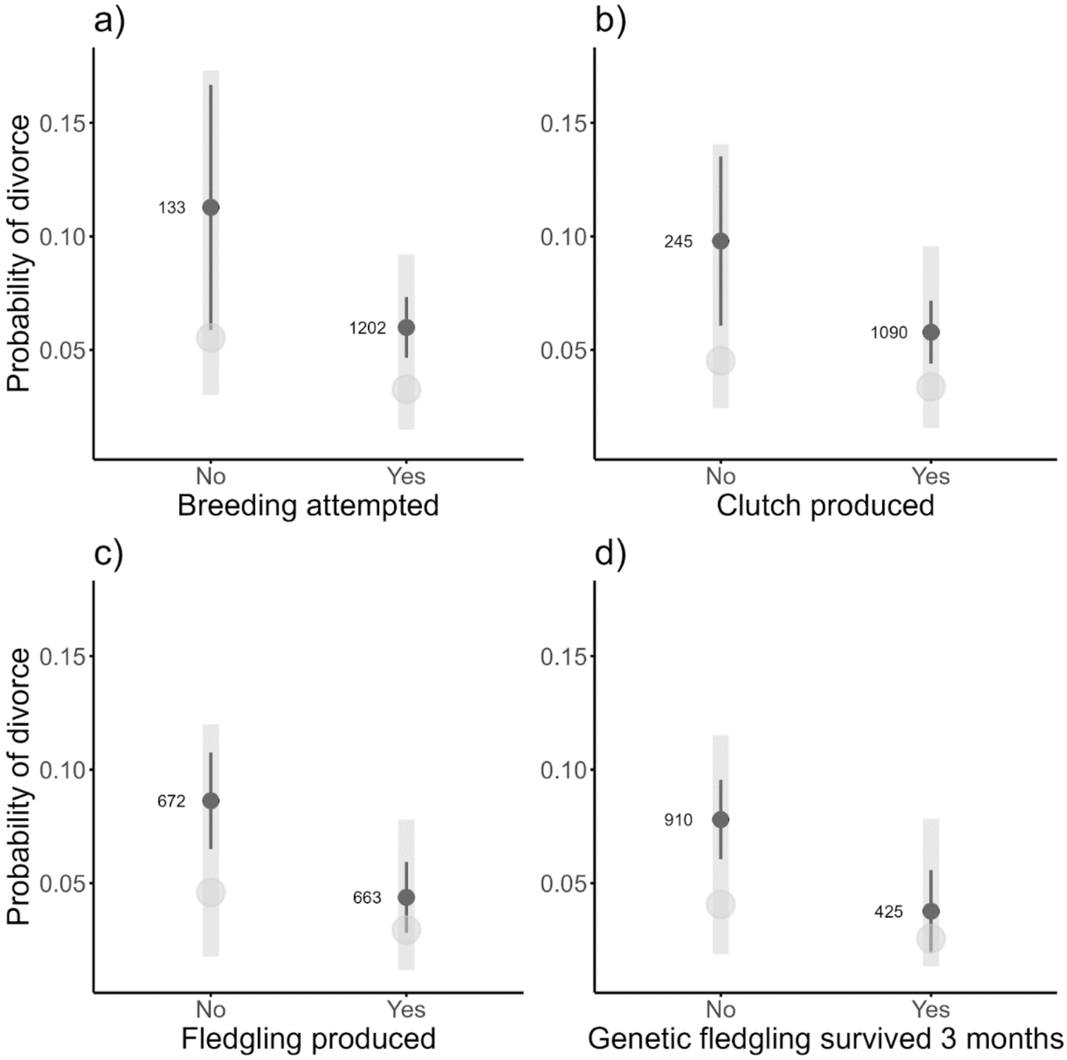

Figure S3. The probability of divorce for Seychelles warbler partnerships (*n* = 1325) that did or did not: a) attempt to breed; b) produce a clutch; c) produce a fledgling; d) produce a fledgling genetically related to the dominant female that survived till at the least three months old. The grey dots and shaded area represent the probability of divorce ± 95% confidence intervals as predicted by binomial generalized linear mixed model. The black dots indicate the mean observed divorce rate ± 95% confidence intervals, and labels indicate the number of partnerships.

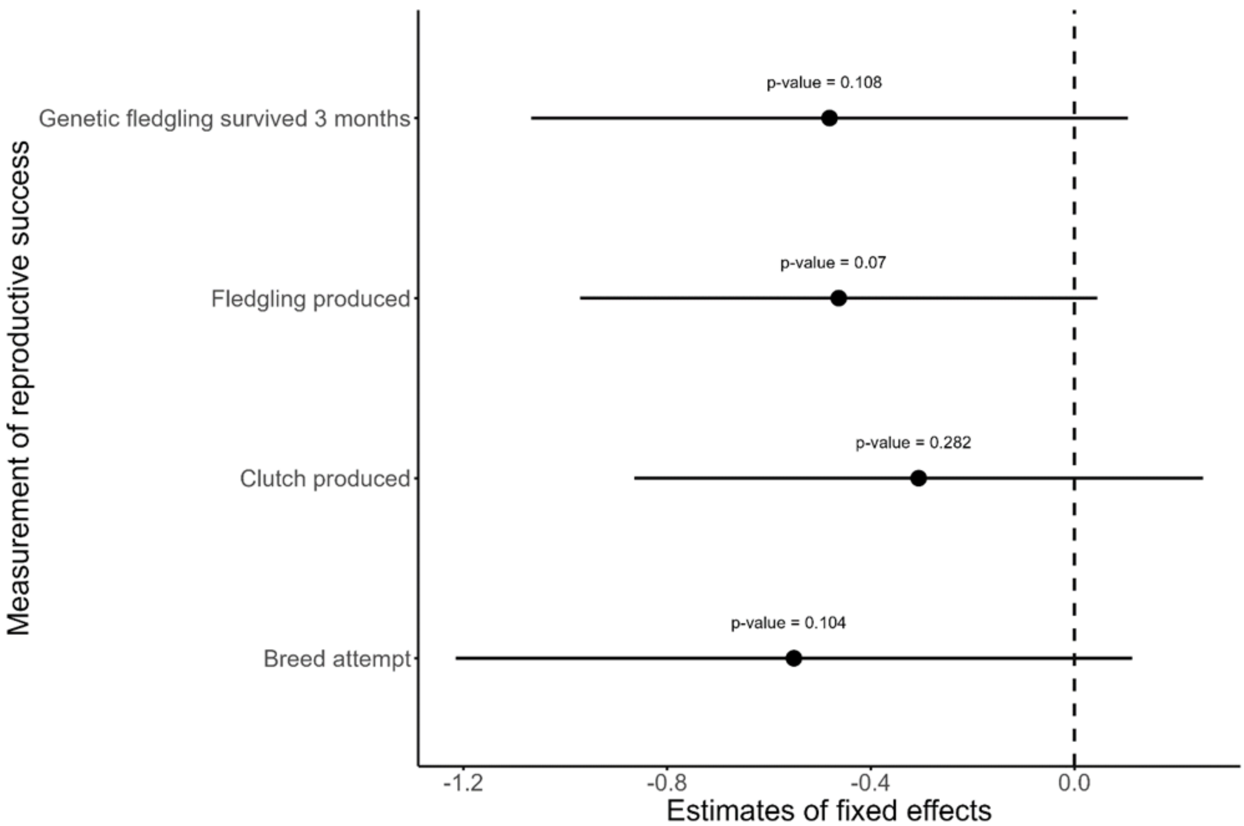

Figure S4. The coefficient estimates (dots) and 95% confidence intervals (bars) of four measures of reproductive success on the probability of divorce in the Seychelles warbler (n = 1325 partnerships) as predicted by binomial generalized linear mixed model. Each reproductive measure was independently included in the model. *p*-values are indicated on the figure.

The following tables (Tables S3 to S6) compare the effects of reproduction at four different stages - breeding attempted (Y/N), clutch produced (Y/N), fledgling produced (Y/N), and genetic fledglings (Y/N) - on divorce by including them one at a time in the partnership-level probability of divorce model. The reproductive measures are italicized in the table legends and table contents for ease of comparison between the four different model summary tables.

Table S3. Associations between the probability of divorce in the Seychelles warbler on Cousin Island with rainfall, the length of the partnership, *breeding attempted*, the relatedness of the breeding pair, the number of helpers, male age, and female age. n = 1325 partnerships were analyzed using a binomial generalized linear mixed model. Significant p-values are in bold.

Independent variables	**Estimate**	**Standard error**	**95% Confidence interval**	***p*-value**
Intercept	-2.838	0.421	-3.662 to -2.013	**<0.001**
Rainfall	-0.141	0.121	-0.379 to 0.096	0.244
Rainfall^2	0.317	0.090	0.141 to 0.492	**<0.001**
Partnership length	-0.474	0.204	-0.872 to -0.075	**0.020**
Breeding attempted	-0.551	0.339	-1.216 to 0.114	0.104
Pairwise relatedness	0.131	0.122	-0.108 to 0.370	0.281
Number of helpers	-0.142	0.147	-0.431 to 0.147	0.335
Male age	0.083	0.150	-0.211 to 0.377	0.581
Female age	0.182	0.138	-0.089 to 0.453	0.189
Random effects	**Variance**	**Levels**		
Male ID	0.000	416		
Female ID	0.142	392		
Field period ID	0.050	17		
Territory ID	0.219	158		

Table S4. Associations between the probability of divorce in the Seychelles warbler on Cousin Island with rainfall, the length of the partnership, *clutch produced*, the relatedness of the breeding pair, the number of helpers, male age, and female age. n = 1325 partnerships were analyzed using a binomial generalized linear mixed model. Significant p-values are in bold.

Independent variables	**Estimate**	**Standard error**	**95% Confidence interval**	***p*-value**
Intercept	-3.049	0.408	-3.848 to -2.249	**<0.001**
Rainfall	-0.157	0.119	-0.391 to 0.077	0.188
Rainfall^2	0.317	0.089	0.142 to 0.491	**<0.001**
Partnership length	-0.469	0.203	-0.866 to -0.071	**0.021**
Clutch produced	-0.306	0.285	-0.864 to 0.252	0.282
Pairwise relatedness	0.130	0.121	-0.106 to 0.367	0.28
Number of helpers	-0.142	0.148	-0.433 to 0.149	0.338
Male age	0.080	0.149	-0.213 to 0.373	0.591
Female age	0.178	0.136	-0.089 to 0.446	0.191

Random effects	**Variance**	**Levels**
Male ID	0.000	416
Female ID	0.074	392
Field period ID	0.048	17
Territory ID	0.214	158

Table S5. Associations between the probability of divorce in the Seychelles warbler on Cousin Island with rainfall, the length of the partnership, *fledgling produced*, the relatedness of the breeding pair, the number of helpers, male age, and female age. *n* = 1325 partnerships were analyzed using a binomial generalized linear mixed model. Significant *p*-values are in bold.

Independent variables	**Estimate**	**Standard error**	**95% Confidence interval**	***p*-value**
Intercept	-3.034	0.259	-3.543 to -2.526	**<0.001**
Rainfall	-0.159	0.118	-0.389 to 0.072	0.177
Rainfall^2	0.303	0.089	0.129 to 0.477	**0.001**
Partnership length	-0.452	0.198	-0.840 to -0.064	**0.022**
Fledgling produced	-0.463	0.259	-0.971 to 0.045	0.074
Pairwise relatedness	0.119	0.120	-0.116 to 0.354	0.32
Number of helpers	-0.092	0.150	-0.387 to 0.203	0.539
Male age	0.081	0.148	-0.210 to 0.371	0.586
Female age	0.168	0.135	-0.096 to 0.432	0.212

Random effects	**Variance**	**Levels**
Male ID	0.000	416
Female ID	0.000	392
Field period ID	0.052	17
Territory ID	0.205	158

Table S6. Associations between the probability of divorce in the Seychelles warbler on Cousin Island with rainfall, the length of the partnership, *genetic fledgling produced*, the relatedness of the breeding pair, the number of helpers, male age, and female age. n = 1325 partnerships were analyzed using a binomial generalized linear mixed model. Significant p-values are in bold.

Independent variables	**Estimate**	**Standard error**	**95% Confidence interval**	***p*-value**
Intercept	-3.162	0.327	-3.804 to -2.520	**<0.001**
Rainfall	-0.166	0.113	-0.388 to 0.055	0.142
Rainfall^2	0.305	0.087	0.135 to 0.475	**<0.001**
Partnership length	-0.448	0.203	-0.846 to -0.05	**0.027**
Genetic fledgling produced	-0.481	0.299	-1.067 to 0.106	0.108
Pairwise relatedness	0.113	0.122	-0.125 to 0.352	0.351
Number of helpers	-0.153	0.146	-0.440 to 0.134	0.298
Male age	0.082	0.150	-0.212 to 0.376	0.586
Female age	0.160	0.137	-0.110 to 0.429	0.245

Random effects	**Variance**	**Levels**
Male ID	0.000	416
Female ID	0.110	392
Field period ID	0.036	17
Territory ID	0.224	158

Interaction between rainfall and partnership length

We found a significant interaction between partnership length and rainfall (Table S7), where the model predicted that heavy rainfall increased the probability of divorce in shorter-lasting but not longer-lasting partnerships (Figure S5). However, as the sample sizes of longer-lasting partnerships were small (Table S8), this relationship was strongly influenced by outliers. Outliers were defined as categories with less than 50 partnerships (low estimate) or less than 100 partnerships (high estimate). In both cases, removing outliers from the analysis removed the significant interaction (Table S9; Table S10). Also, running the model with breeding experience, defined as if a partnership has been together for at least one breeding season (Y/N), instead of partnership length removed the significant interaction (Table S11). As a result, the interaction was not included in the final model.

Table S7. Associations between the probability of divorce in the Seychelles warbler on Cousin Island with the total rainfall from February to August, length of partnership, the number of offspring, the relatedness of the breeding pair, the number of helpers, male age, and female age. $n = 1325$ partnerships were analyzed using a binomial GLMM. Significant *p*-values are in bold.

Independent variables	**Estimate**	**Standard error**	**95% Confidence interval**	***p*-value**
Intercept	-3.511	0.358	-4.213 to -2.808	**<0.001**
Rainfall	-0.379	0.165	-0.702 to -0.057	**0.021**
Rainfall^2	0.208	0.118	-0.023 to 0.438	0.077
Partnership length	-0.598	0.273	-1.134 to -0.063	**0.028**
Number of offspring	-0.109	0.142	-0.387 to 0.169	0.441
Pairwise relatedness	0.127	0.123	-0.115 to 0.369	0.303
Number of helpers	-0.142	0.149	-0.435 to 0.151	0.342
Male age	-0.064	0.182	-0.421 to 0.293	0.727
Male age^2	0.174	0.103	-0.028 to 0.376	0.092
Female age	0.206	0.168	-0.124 to 0.535	0.221
Female age^2	-0.076	0.104	-0.280 to 0.129	0.469
Rainfall * Partnership length	-0.484	0.207	-0.889 to -0.079	**0.019**
Rainfall^2 * Partnership length	-0.085	0.141	-0.361 to 0.191	0.545

Random effects	**Variance**	**Levels**
Male ID	0.000	416
Female ID	0.212	392
Field period ID	0.027	17
Territory ID	0.250	158

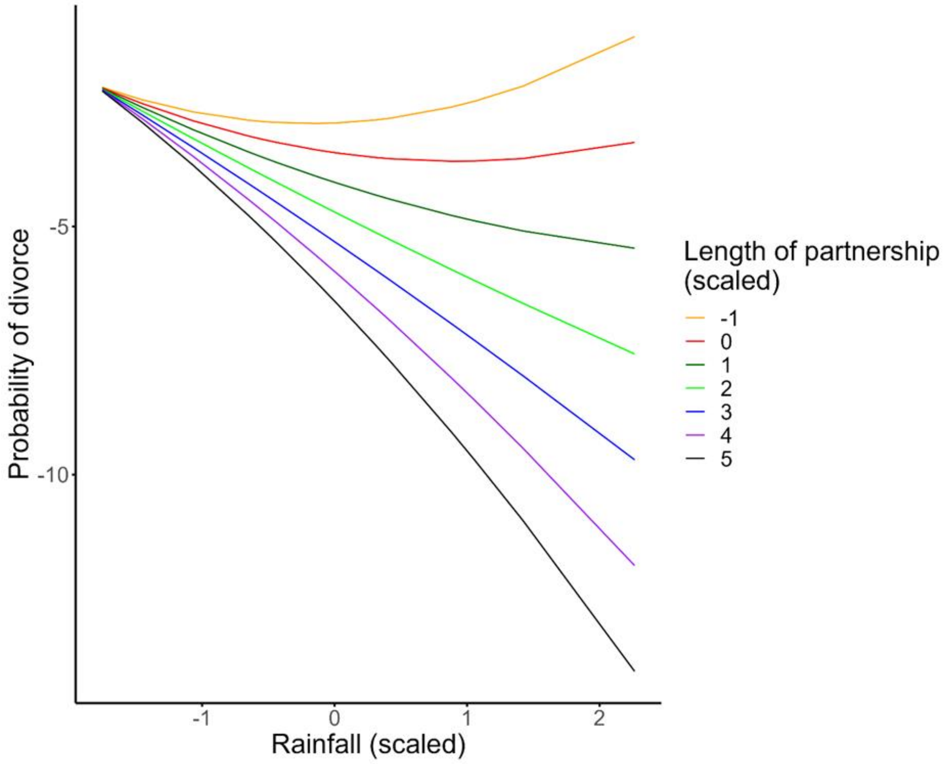

Figure S5. The effect of total rainfall from February to August on the probability of divorce for Seychelles warbler partnerships (n = 1325) that have been together for different lengths of time on Cousin Island as predicted by a binomial generalized linear mixed model.

Table S8. The number of available samples of Seychelles warbler partnerships that have been together for different lengths of time on Cousin Island.

Partnership length (scaled)	Number of partnerships
-1	535
0	497
1	183
2	74
3	31
4	10
5	5

Table S9. Associations between the probability of divorce in the Seychelles warbler on Cousin Island with the total rainfall from February to August, length of partnership, the number of offspring, the relatedness of the breeding pair, the number of helpers, male age, and female age. $n = 1301$ partnerships were analyzed using a binomial generalized linear mixed model. Significant *p*-values are in bold. Partnerships with a partnership length greater than 3 (scaled value) were removed from this analyses.

Independent variables	Estimate	Standard error	95% Confidence interval	*p*-value
Intercept	-3.366	0.365	-4.081 to -2.650	**<0.001**
Rainfall	-0.346	0.164	-0.668 to -0.024	**0.035**
Rainfall^2	0.224	0.121	-0.013 to 0.462	0.064
Partnership length	-0.733	0.313	-1.346 to -0.119	**0.019**
Number of offspring	-0.107	0.142	-0.384 to 0.171	0.452
Pairwise relatedness	0.129	0.123	-0.112 to 0.370	0.294
Number of helpers	-0.157	0.154	-0.459 to 0.146	0.311
Male age	-0.019	0.184	-0.379 to 0.341	0.918
Male age^2	0.137	0.110	-0.079 to 0.353	0.213
Female age	0.253	0.171	-0.082 to 0.588	0.139
Female age^2	-0.204	0.134	-0.466 to 0.058	0.127
Rainfall * Partnership length	-0.395	0.211	-0.808 to 0.017	0.060
Rainfall^2 * Partnership length	-0.064	0.154	-0.365 to 0.237	0.676

Random effects	Variance	Levels
Male ID	0.000	416
Female ID	0.192	392
Field period ID	0.034	17
Territory ID	0.166	158

Table S10. Associations between the probability of divorce in the Seychelles warbler on Cousin Island with the total rainfall from February to August, length of partnership, the number of offspring, the relatedness of the breeding pair, the number of helpers, male age, and female age. $n = 1248$ partnerships were analyzed using a binomial generalized linear mixed model. Significant *p*-values are in bold. Partnerships with a partnership length greater than 2 (scaled value) were removed from this analyses.

Independent variables	**Estimate**	**Standard error**	**95% Confidence interval**	***p*-value**
Intercept	-3.377	0.389	-4.14 to -2.615	**<0.001**
Rainfall	-0.293	0.160	-0.606 to 0.020	0.067
Rainfall^2	0.242	0.122	0.003 to 0.482	**0.047**
Partnership length	-0.811	0.348	-1.494 to -0.128	**0.020**
Number of offspring	-0.136	0.145	-0.420 to 0.148	0.349
Pairwise relatedness	0.093	0.125	-0.152 to 0.339	0.455
Number of helpers	-0.141	0.154	-0.443 to 0.161	0.359
Male age	-0.015	0.186	-0.379 to 0.349	0.937
Male age^2	0.150	0.115	-0.075 to 0.375	0.192
Female age	0.266	0.171	-0.069 to 0.602	0.119
Female age^2	-0.234	0.147	-0.523 to 0.055	0.112
Rainfall * Partnership length	-0.312	0.227	-0.756 to 0.132	0.169
Rainfall^2 * Partnership length	-0.037	0.171	-0.372 to 0.297	0.827

Random effects	**Variance**	**Levels**
Male ID	0.000	416
Female ID	0.154	392
Field period ID	0.005	17
Territory ID	0.195	158

Table S11. Associations between the probability of divorce in the Seychelles warbler on Cousin Island with the total rainfall from February to August, breeding experience, the number of offspring, the relatedness of the breeding pair, the number of helpers, male age, and female age. n = 1325 partnerships were analyzed using a binomial generalized linear mixed model. Significant p-values are in bold.

Independent variables	**Estimate**	**Standard error**	**95% Confidence interval**	***p*-value**
Intercept	-2.879	0.442	-3.745 to -2.013	**<0.001**
Rainfall	-0.033	0.154	-0.335 to 0.268	0.829
Rainfall^2	0.231	0.112	0.011 to 0.451	**0.040**
Breeding experience	-1.019	0.400	-1.803 to -0.235	**0.011**
Number of offspring	-0.095	0.142	-0.373 to 0.183	0.505
Pairwise relatedness	0.124	0.123	-0.117 to 0.365	0.312
Number of helpers	-0.143	0.148	-0.433 to 0.147	0.335
Male age	-0.104	0.173	-0.442 to 0.235	0.548
Male age^2	0.140	0.104	-0.064 to 0.344	0.178
Female age	0.166	0.160	-0.149 to 0.480	0.301
Female age^2	-0.094	0.107	-0.304 to 0.115	0.377
Rainfall * Breeding experience	-0.295	0.211	-0.709 to 0.119	0.163
Rainfall^2 * Breeding experience	0.201	0.159	-0.111 to 0.514	0.206
Random effects	**Variance**	**Levels**		
Male ID	0.000	416		
Female ID	0.186	392		
Field period ID	0.035	17		
Territory ID	0.250	158		

Table S12. Associations between the probability of attempting to breed (model 1), producing a clutch (model 2), producing a fledgling (model 3), and the number of genetic fledglings surviving till at least three months old (model 4) in the Seychelles warbler on Cousin Island with rainfall, partnership length, pairwise relatedness, the number of helpers, male age, and female age. n = 1325 partnerships were analyzed using binomial (models 1 to 3) and poisson (model 4) generalized linear mixed models. Significant terms are in bold.

	Model 1	**Model 2**	**Model 3**	**Model 4**
Independent variables	**Estimate (95% Confidence interval)**			
Intercept	**3.68*** (2.75 to 4.61)**	**2.48*** (1.95 to 3.0)**	**0.78*** (0.40 to 1.16)**	**-0.54*** (-0.81 to -0.26)**
Rainfall	**1.17** (0.41 to 1.93)**	**0.71** (0.28 to 1.14)**	**0.36** (0.09 to 0.62)**	**0.22* (0.01 to 0.42)**
Rainfall^2	-	-	**-0.26* (-0.45 to -0.06)**	**-0.22** (-0.38 to -0.06)**
Partnership length	-0.14 (-0.48 to 0.19)	0.07 (-0.19 to 0.33)	0.13 (-0.08 to 0.34)	0.04 (-0.11 to 0.18)
Pairwise relatedness	0.01 (-0.22 to 0.25)	-0.04 (-0.21 to 0.14)	**-0.14* (-0.27 to 0.0)**	-0.08 (-0.17 to 0.01)
Number of helpers	**1.58** (0.61 to 2.54)**	**1.32*** (0.8 to 1.84)**	**0.75*** (0.57 to 0.93)**	**0.09* (0.02 to 0.17)**
Male age	**0.43* (0.08 to 0.78)**	0.11 (-0.11 to 0.33)	**0.23* (0.02 to 0.44)**	**0.21** (0.06 to 0.35)**
Male age^2	**-0.22* (-0.40 to -0.04)**	-	**-0.19** (-0.31 to -0.08)**	**-0.16*** (-0.25 to -0.07)**
Female age	0.17 (-0.12 to 0.46)	**0.39** (0.15 to 0.62)**	0.17 (-0.03 to 0.36)	0.03 (-0.12 to 0.17)
Female age^2	-	**-0.31*** (-0.44 to -0.18)**	**-0.28*** (-0.40 to -0.17)**	**-0.21*** (-0.32 to -0.12)**
Random effects (Levels)	**Variance**	**Variance**	**Variance**	**Variance**
Male ID (416)	0.00	0.00	0.01	0.00
Female ID (293)	0.17	0.00	0.26	0.00
Field period ID (17)	2.01	0.67	0.21	0.12
Territory ID (158)	0.38	0.32	0.04	0.00

*: p-value < 0.05; **: p-value = 0.001: ***: p-value < 0.001

Table S13. Associations between the probability of producing a clutch in the Seychelles warbler on Cousin Island with total rainfall from February to August, length of partnership, the relatedness of the breeding pair, the number of helpers, male age, and female age. n = 1325 partnerships were analyzed using a binomial generalized linear mixed model. Significant p-values are in bold. The non-significant quadratic term of rainfall is included.

Independent variables	**Estimate**	**Standard error**	**95% Confidence interval**	***p*-value**
Intercept	2.783	0.300	2.195 to 3.372	**<0.001**
Rainfall	0.771	0.202	0.376 to 1.166	**<0.001**
Rainfall^2	-0.285	0.150	-0.579 to 0.008	0.057
Partnership length	0.068	0.132	-0.192 to 0.327	0.608
Pairwise relatedness	-0.035	0.087	-0.205 to 0.136	0.689
Number of helpers	1.325	0.266	0.802 to 1.847	**<0.001**
Male age	0.104	0.113	-0.117 to 0.325	0.357
Female age	0.386	0.121	0.149 to 0.623	**0.001**
Female age^2	-0.309	0.068	-0.443 to -0.175	**<0.001**
Random effects	**Variance**	**Levels**		
Male ID	0.000	416		
Female ID	0.000	392		
Field Period ID	0.514	17		
Territory ID	0.331	158		

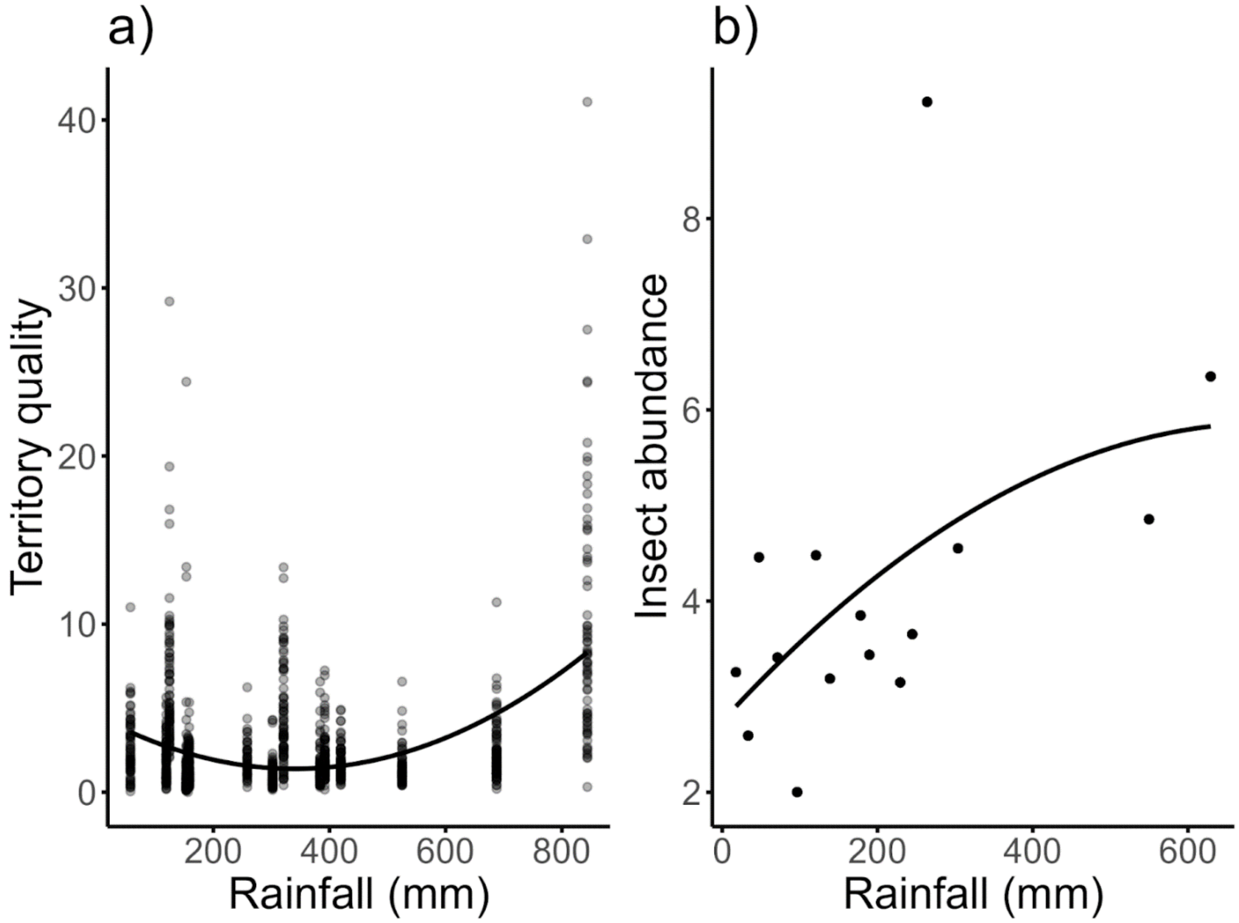

Figure S6. The effect of rainfall on: a) territory quality (scaled 1:10,000); b) insect abundance (the mean number of insects found per unit leaf area across all monthly surveys) on Cousin Island (n = 15 years), as predicted (solid line) by a *ClimWin* generated linear model. Territory quality was best predicted by rainfall from June to August, and insect abundance was best predicted by rainfall from July to August. Data are indicated as points where the shade of the points represents the sample size (darker represents more samples).