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 managed and 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.

Abstract

1. Divorce – terminating 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 environmental fluctuations affect partnership stability has important implications, including for conservation. Yet, the relationship between the environment and divorce remains largely unstudied.
2. We examined the influence of temporal environmental variability on the prevalence of within- and between-season divorce and the possible underlying mechanisms in a socially monogamous passerine.
3. Analyzing 16 years of data from a longitudinal dataset, we investigated the relationship between rainfall and divorce in the Seychelles warbler (*Acrocephalus sechellensis*). First, we performed climate window analyses to identify the temporal windows of rainfall that best predict reproductive success and divorce. Then, we tested the effects of these temporal windows of rainfall on reproductive success and divorce and the influence of reproductive success on divorce while controlling for covariates.
4. Annual divorce rates varied from 1–16%. The probability of divorce was significantly associated with the quadratic effect of 7 months of total rainfall before and during the breeding season, with divorce increasing in years with low and high rainfall. This quadratic relationship was driven by a heavy rainfall event in 1997, as excluding 1997 from our analyses left a significant negative linear relationship between rainfall and divorce. Although the same temporal window of rainfall predicting divorce 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 other possible drivers. Although the 1997 super El Niño event shows how heavy rainfall may affect socially monogamous partnerships, more data is required to estimate the robustness of this effect. 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. Suboptimal partnerships may be corrected through divorce, whereby a pair bond is terminated while both partners are alive (Choudhury, 1995), which can either increase, decrease, or have no effect on future reproductive success for one or both partners (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 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, one or both 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, previous reproductive success and divorce are often correlated, with reproductive failure being a strong predictor of partnership termination (Culina *et al.,* 2015). Notably, the effect of reproduction on divorce can vary depending on the stage of the breeding cycle, with failures at earlier breeding stages often being stronger predictors of divorce (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 (Ventura *et al.,* 2021). Extreme weather can also increase physiological stress (Kitaysky *et al.,* 2010), an important factor influencing mate selection (Husak & Moore, 2008). Given the rapid timing of climate change, marked by more frequent extreme weather events, such as droughts and floods, and increased global temperatures (NOAA, 2022), which may limit possibilities for adaptation (Spooner *et al.,* 2018), understanding how climate patterns 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). 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 black-browed albatrosses (*Thalassarche melanophris*).

With climate change resulting in more frequent heavy rain and drought events (Marvel *et al.,* 2019), we aimed 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. Extreme rainfall negatively impacts the warblers' reproductive output (Komdeur, 1996a; Borger *et al.,* 2023). As reproductive failures drive divorce in various bird species (Culina *et al.,* 2015), including the Seychelles warbler (Speelman *et al.,* in press), we investigated 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.

We predicted that extreme rainfall increases the prevalence of divorce (P1). As Seychelles warblers are insectivorous, low rainfall decreases food availability by impacting their prey's reproductive cycle (Komdeur, 1996a, Price, 1997). Conversely, high rainfall can affect the ability of birds to maintain optimal body temperatures and cause direct habitat and nest destruction (Kennedy, 1970; Wilson *et al.,* 2004). Consequently, we predicted 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 predicted that divorce would be more prevalent following breeding seasons with poorer breeding conditions, with rainfall having a quadratic effect on divorce. Our findings may provide insights into how harsh environmental conditions affect reproduction and divorce in socially monogamous birds, which, in turn, can inform conservation efforts across multiple species in times of climate change, such as by informing population modeling.

2 Materials and Methods

2.1 Study system

Since 1985, mark-capture-recapture data have been collected on the Seychelles warblers 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 territorial, foraging most of their lives exclusively on their respective territories (Komdeur, 1991; Richardson *et al.*, 2007). Cooperative breeding can occur: around half of the territories including 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 can be maladaptive to breeders in lower-quality territories (Komdeur, 1998).

The main Seychelles warbler breeding season spans from June to October, and the minor breeding season from December to March (Komdeur & Daan, 2005). Our analyses focused on main breeding seasons as data on breeding statuses are limited for minor breeding seasons and, although 30% of pairs breed (90% in main), breeding season type (main/minor) does not affect divorce in our study population (Speelman *et al.*, in press). Most (87%) clutches contain a single egg but can consist of up to three (Richardson *et al.*, 2001). Co-breeding subordinates often lay the additional eggs (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 until 2015. 1999 to 2001 were excluded due to limited fieldwork impacting the quality of partnership data required to classify divorces. During 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). We identified the number of helpers, which influences reproductive success (Hammers *et al.*, 2021), from nest watches of at least 60 minutes during the incubation and provisioning stages (van Boheemen *et al.*, 2019). In case of a failed breeding attempt before incubation or provisioning, subordinates were defined as non-helpers. The ages of unringed birds, usually caught before one year of age, were estimated using lay, hatch, or fledge dates and/or eye color (Komdeur, 1991). DNA was extracted from 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 offspring (see supplementary section 'Pairwise relatedness'). Territory quality was measured using an index of insect availability, territory size, and foliage cover (see supplementary 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 greatly during the study period (monthly range: 0.8–716 mm; annual: 1349–3410 mm).

2.3 Divorce classification

Partnerships were classified as divorced when there was a change in the identity of dominant breeders across breeding seasons while both previously pair-bonded individuals were still alive. As breeding statuses were defined at the end of breeding seasons, divorce can occur within or between seasons. Temporary divorces, where pairs separate but reform after a breeding season, are rare (22 recorded cases: Speelman *et al.*, in press). 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 partner deaths or translocations undertaken for conservation (Richardson *et al.*, 2006; Wright *et al.*, 2014). Our dataset included 416 males and 392 females in 1321 partnerships, 84 (6.4%) of which divorced.

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 and the term 'significant' refers to statistical significance.

2.4.1 Climate window analysis

Following Bailey & van de Pol (2016) (see supplementary 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 analyzed 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 (post-fledgling care period) - classified as a continuous response variable (from now on named: 'genetic fledglings').

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, we included the number of genetic fledglings in our analyses to exclude offspring assigned to co-breeding females.

Lastly, we tested which months of rainfall predicted territory quality (territory-level measure) and insect abundance (population-level measure; the mean number of insects found per unit leaf area across all monthly surveys). By investigating whether the temporal windows of rainfall best-predicting divorce, reproductive success, and territory quality overlapped, we aimed to examine the links between rainfall, divorce, and possible drivers 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 and rainfall^2. The measurement of rainfall included in the model was the total rainfall from the months that 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), the number of helpers, partnership length (in years), pairwise relatedness, male age (in years), male age^2, female age, female age^2, and population density (Komdeur, 1994; 1996a; 1996b; Richardson *et al.,* 2003; van Boheemen *et al.*, 2019; Hammers *et al.,* 2019). All fixed effects were continuous variables. 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 produced (Y/N) - on divorce by including them in four separate models. We also tested our assumption that EPP did not affect divorce by including male and female EPP (Y/N) – when the dominant male or female was assigned parentage of offspring and the opposite-sex parent assigned was not their social partner – in our model. Lastly, we included co-breeder presence (Y/N) in our model to separate helper and co-breeder effects on divorce.

2.4.3 Partnership-level probability of reproductive success

To explore the potential links between rainfall, reproductive success, and divorce, we examined whether rainfall during the months that best predicted 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.

In all models, we tested whether partnership quality buffered the effects of rainfall by including interactions between partnership length and rainfall (all models) and reproductive success and rainfall (divorce models). We also included an interaction between rainfall and population density to test whether the increased availability of potential mates, resulting from extreme rainfall-driven mortality, influenced divorce. Starting from a full model, we removed non-significant quadratic terms and interactions in order of least significance to interpret first-order effects. All models included the random effects: male ID, female ID, territory ID, and field period ID to control for birds sequentially performing worse or better than others and variable quality across territories and field periods (years).

3 Results

3.1 Effect of rainfall on divorce

The mean Seychelles warbler annual divorce rate was 6.6 ± 1.1% and showed considerable inter-annual variability (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; Table S1).

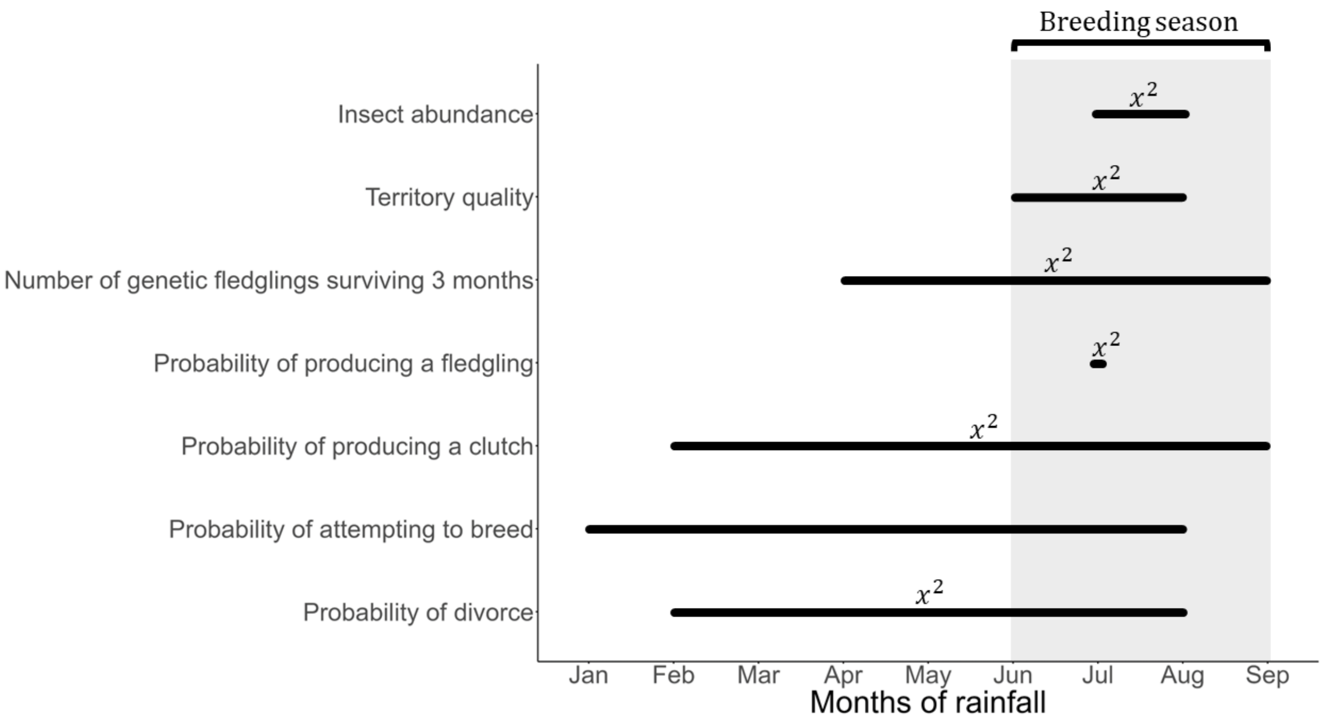

Figure 1. Temporal windows of rainfall that best predict seven response variables in the Seychelles warbler on Cousin Island (n = 1321 partnerships/15 years for insect abundance and territory quality) as predicted by climate window analyses. Relationships between rainfall and the response variables were quadratic if indicated by x^2 and linear if not. The shaded area represents the main breeding season.

At the population level, total rainfall from February to August had a significant quadratic effect on the annual divorce rate, which increased in years with low and high rainfall (GLM, estimate = 0.335 ± 0.091, p-value = 0.003; 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 2a). Notably, the quadratic relationship between rainfall and the probability of divorce was driven by extremely heavy rainfall in 1997, as excluding 1997 from the analysis revealed a significant negative linear relationship between rainfall and divorce (Tables S2 & S3; Figure 2b).

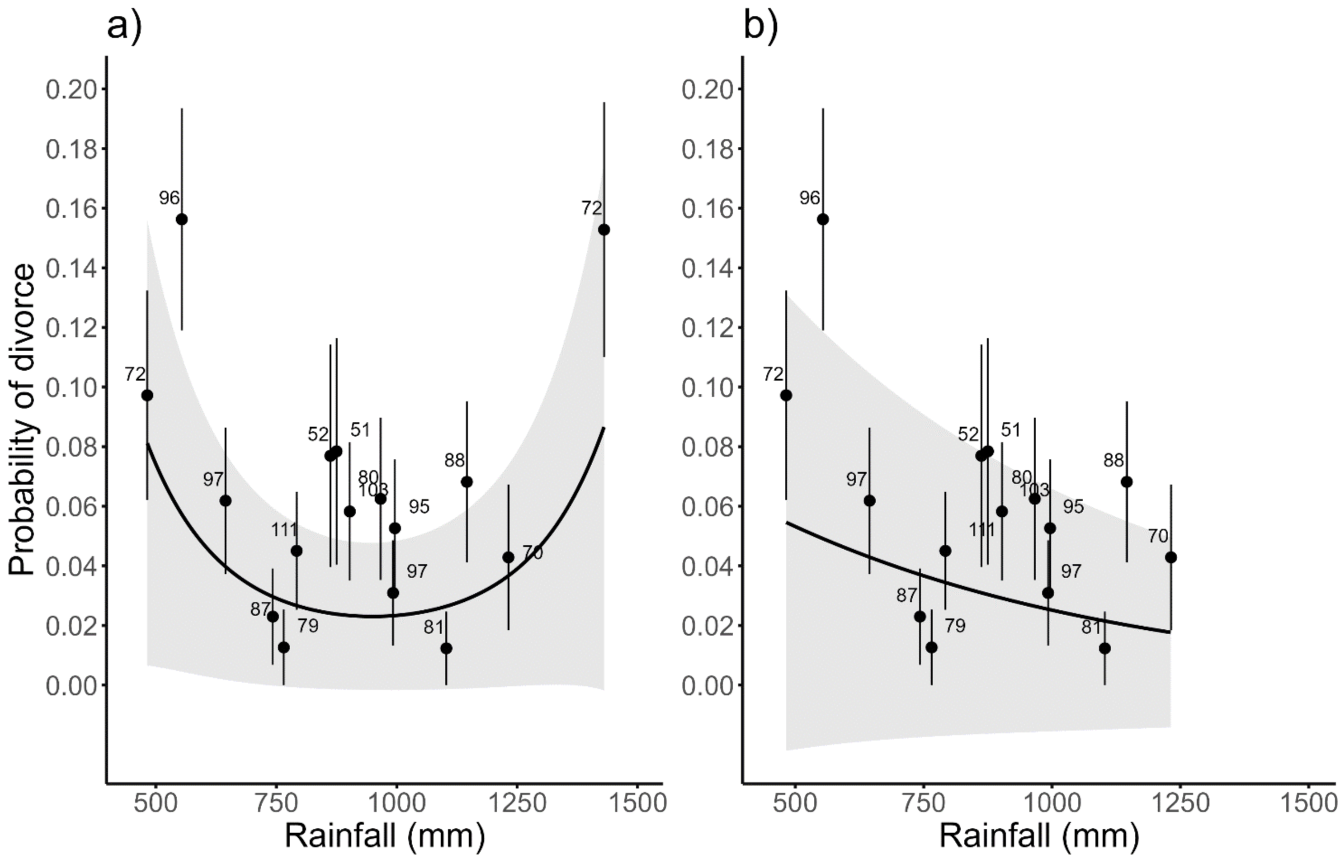

Figure 2. The effect of total rainfall from February to August on the probability of divorce in the Seychelles warbler on Cousin Island as predicted by binomial generalized linear mixed models. a) includes the 1997 heavy rainfall event (n = 1321 partnerships) and b) excludes 1997 (n = 1252 partnerships). 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.

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, female age, and population density. *n* = 1321 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	-3.730	0.555	-4.817 to -2.642	**<0.001**
Rainfall	-0.152	0.113	-0.373 to 0.069	0.177
Rainfall^2	0.336	0.090	0.160 to 0.512	**<0.001**
Partnership length	-0.455	0.231	-0.909 to -0.002	**0.049**
Number of offspring	-0.114	0.145	-0.399 to 0.171	0.431
Pairwise relatedness	0.162	0.141	-0.115 to 0.438	0.252
Number of helpers	-0.228	0.165	-0.552 to 0.095	0.166
Male age	0.076	0.170	-0.257 to 0.410	0.655
Female age	0.204	0.156	-0.102 to 0.511	0.192
Population density	0.018	0.133	-0.242 to 0.278	0.895
Random effects	**Variance**	**Levels**		
Male ID	0.466	416		
Female ID	0.600	392		
Field period ID	0.000	16		
Territory ID	0.282	158		

3.2 Effects of reproductive success and other partnership qualities on divorce

Although we found a trend for reproductively successful partnerships to have lower divorce rates (Figure S2; Tables S4-S7), we found no significant correlations between the probability of divorce and measures of reproductive success (Figure S3; Tables S4-S7). 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 excluding 1997 from the analyses (Table S2 & S3). 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 S8), with heavy rainfall increasing the probability of divorce in shorter but not longer-lasting partnerships (Figure S4). However, this interaction was strongly influenced by outliers and subsequently removed from the final model (see supplementary section 'Interaction between rainfall and partnership length'). EPP and co-breeder presence were not associated with divorce (Table S10).

3.3 Effect of rainfall on reproductive success

3.3.1 Breeding attempted

During the study period, 91% 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; Table S1). The probability of attempting to breed was also significantly positively correlated with the months of rainfall best-predicting divorce (February to August; Table S14; Figure 3a).

3.3.2 Clutch produced

Overall, 83% 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; Table S1), 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 S14; Figure 3b). The quadratic effect of rainfall was marginal (Table S15).

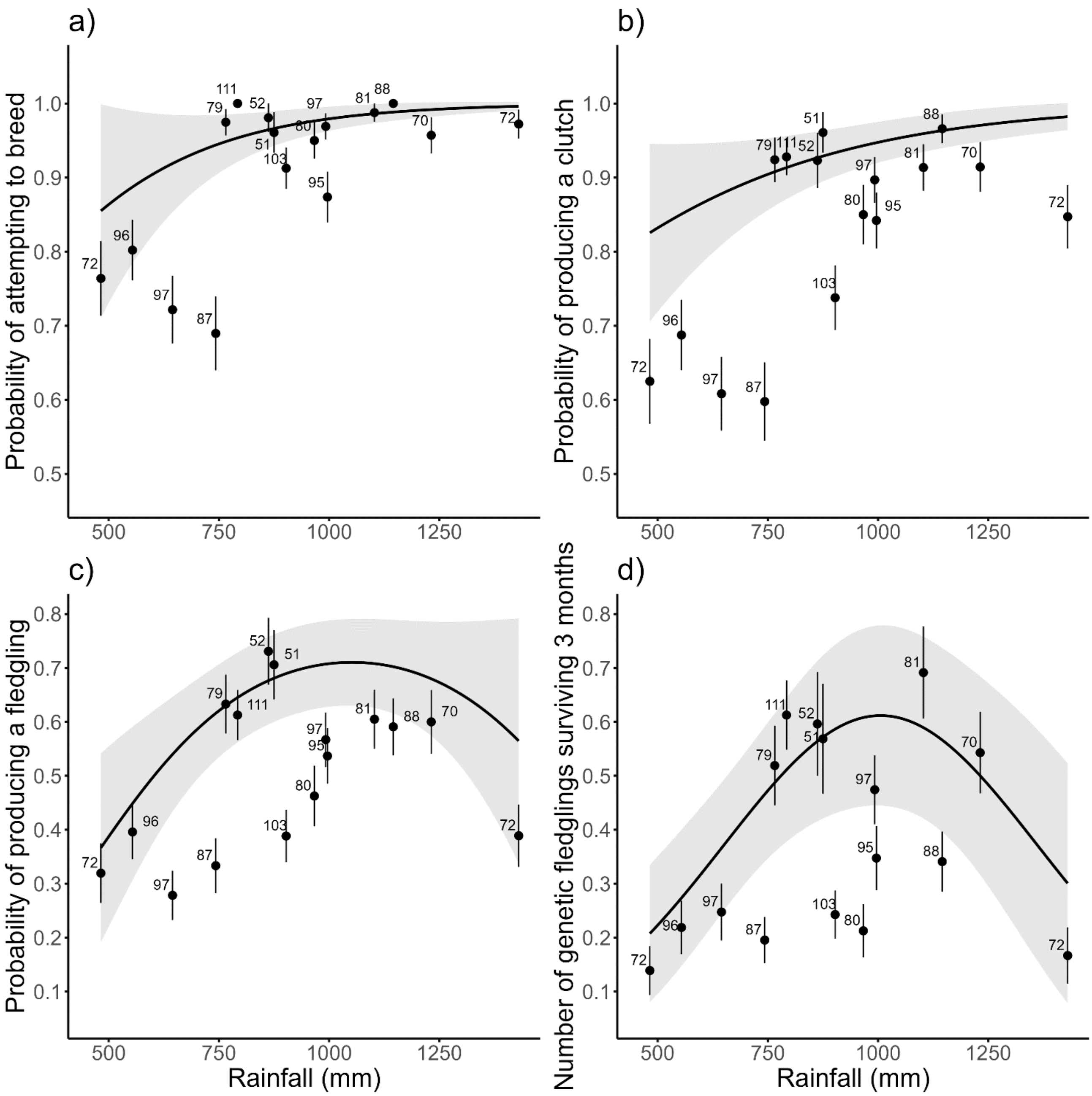

Figure 3. The effect of total rainfall from February to August on the probability of Seychelles warbler partnerships (*n* = 1321): a) attempting to breed; b) producing a clutch; c) producing a fledgling; d) the number of genetic fledglings surviving until three months old, as predicted by binomial (a, 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.

3.3.3 Fledgling produced

Overall, 50% of partnerships 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; Table S1), 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 S14). Again, intermediate levels of rainfall were associated with greater fledgling success (Figure 3c).

3.3.4 Genetic fledglings

32% of partnerships produced a genetic fledgling (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; Table S1). Here, low and high amounts of rain decreased genetic offspring survival post-fledgling care. Also, the number of genetic fledglings surviving was correlated with the quadratic effect of the total rainfall from February to August (Table S14). Again, greater genetic fledgling survival was associated with intermediate levels of rainfall (Figure 3d).

3.4 Effect of rainfall on food availability

A quadratic effect of total rainfall from June to August best predicted territory quality (Figure 1; Table S1). 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 S5a). An increase in insect abundance was best predicted by the increase in total rainfall from July to August (Figure 1; Figure S5b; Table S1).

4 Discussion

4.1 Association between rainfall and divorce

As predicted (P1), rainfall had a quadratic effect on divorce in the Seychelles warbler, where low and high amounts of rain significantly increased the population-level annual divorce rates and partnership-level divorce probabilities. Extremely heavy rainfall in 1997 (a super 'El Niño' event) drove the association between high rainfall and divorce; excluding 1997 from the analyses left a negative relationship between rainfall and divorce. However, we consider 1997 to be 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). Future investigations incorporating more extreme rainfall years would allow us to estimate the robustness of the quadratic effect. The main Seychelles warbler breeding season spans from June to October, and total rainfall from February to August best predicted divorce. Thus, if divorce is a decision informed by the costs and benefits of staying with a partner, it is likely reinforced by various drivers linked to rainfall between February and August.

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 (6.4%) 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 significantly associated with rainfall. As rainfall is associated with food abundance (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 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 reproductive stages. Total rainfall from January to August and February to September best predicted the probability of attempting to breed and producing a clutch, respectively. These reproductive measures were also significantly positively correlated with the temporal window of rainfall best-predicting divorce. These large temporal windows support studies showing rain impacts birds' reproductive success by affecting the health of birds outside of the breeding season (Studds & Marra, 2007). Rainfall can impact individual condition and reproductive success by influencing food abundance (often insects), which explains why rainfall cues breeding for 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 support 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 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 produced was best predicted by rainfall from April to September. Here, rainfall can directly affect fledgling survival or do so indirectly by impacting parental care during the months of post-fledgling care. 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; Wilson *et al.,* 2004). As nestlings often lack 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 required parental investments increase 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 lower reproductive success. Low reproductive success impacting divorce is in line with findings of previous studies (Culina *et al.*, 2015; Mercier *et al.*, 2021; Ventura *et al.*, 2021; Pelletier & Guillemette, 2022), including in our study population (Speelman *et al.,* in press). However, when accounting for rainfall effects in our models, 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). 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, signifying that stress could be the link between rainfall and divorce. Studies analyzing relationships between stress markers, such as glucocorticoids (Sapolsky *et al.*, 2000), rainfall (or other environmental effects), and divorce, are required to investigate this theory.

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 divorce consequences is required to determine whether rainfall-driven divorce 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, rainfall-driven divorce can be maladaptive, making climate change a concern to the future of this species. In the Seychelles warbler, no short or long-term reproductive costs of divorce have been detected (Speelman *et al.*, in press). However, as this study did not test for divorce consequences in the context of environmental effects, studies disentangling divorce fitness consequences in poor and high-quality years are required.

4.4 Non-environmental associations with divorce

Older partnerships were less likely to divorce, fitting the prediction that divorce benefits are highest before individuals have gained the benefits associated with mate familiarity (Choudhury, 1995). While behavioral incompatibilities between individuals can also manifest early in partnerships and influence divorce by impacting reproductive success (Wilson *et al.*, 2022), we found no effect of partnership length on reproductive success. Consistent with studies showing that Seychelles warblers do not seem to avoid inbreeding (Eikenaar *et al.*, 2008), we also found no effect of pairwise relatedness on divorce, indicating that inbreeding avoidance or other genetic incompatibilities are unlikely drivers of divorce in our population (Hidalgo Aranzamendi *et al.*, 2016). Notably, the effect of partnership length on divorce was non-significant when excluding 1997 from the analysis. 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). The mean partnership length in 1997 was considerably shorter than in other years. 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 partnership-level data – required to classify divorces - being collected in those years. Thus, biases in the data may drive the effect of partnership length on divorce.

5 Conclusion

We provide 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 rainfall. We provide correlational evidence that this could result from rain impacting reproductive success, possibly by affecting food availability and parental trade-offs between investing in current versus future reproductive success. We also discuss alternative explanations involving the role of physiological stress, an important avenue for further research in this and 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 rainfall-driven divorce in the Seychelles warbler is adaptive, maladaptive, or neutral. 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 laid, and warblers can then 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. Breeding statuses, which define our characterization of divorce, are finalized at the end of the breeding season, and our study is interested in investigating what happened in between the moment we know a partnership was last together and no longer together. As a result, we tested for all possible temporal windows (all combinations of months) from 12 months leading up to the end of the main breeding season (28th of September). Thus, from one end of the main breeding season to the end of the next.

Importantly, *climwin* is designed to avoid issues regarding multiple comparisons through a randomization scheme that ensures temporal windows are not found due to chance. Thus, 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 ($p\Delta\text{AICc} < 0.001$).

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 $\Delta\text{AIC} > 7$ (Burnham *et al.,* 2011).

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Results

Table S1. Temporal windows of rainfall that best predict seven response variables in the Seychelles warbler on Cousin Island (*n* = 1321 partnerships/15 years for insect abundance and territory quality) as predicted by climate window analyses. The 28th of September (the end of the breeding season) was set as the reference date for climate window analyses and window open/close refers to the number of months relative to this date (2 = July, 1 = August, etc…). Also presented are the function type (quadratic/linear) that best fits the model and the ΔAICc (the difference between the AICc of the model and the null model) of the model that best predicted the response variable.

Response variable	Climate variable	Function type	ΔAICc	Window Open	Window Close
Insect abundance	Rainfall	Quadratic	-394.80	2	1
Territory quality			-332.95	3	1
Number of genetic fledglings surviving 3 months			-62.94	5	0
Probability of producing a fledgling			-39.97	2	2
Probability of producing a clutch			-81.78	7	0
Probability of attempting to breed		Linear	-104.89	8	1
Probability of divorce		Quadratic	-16.89	7	1

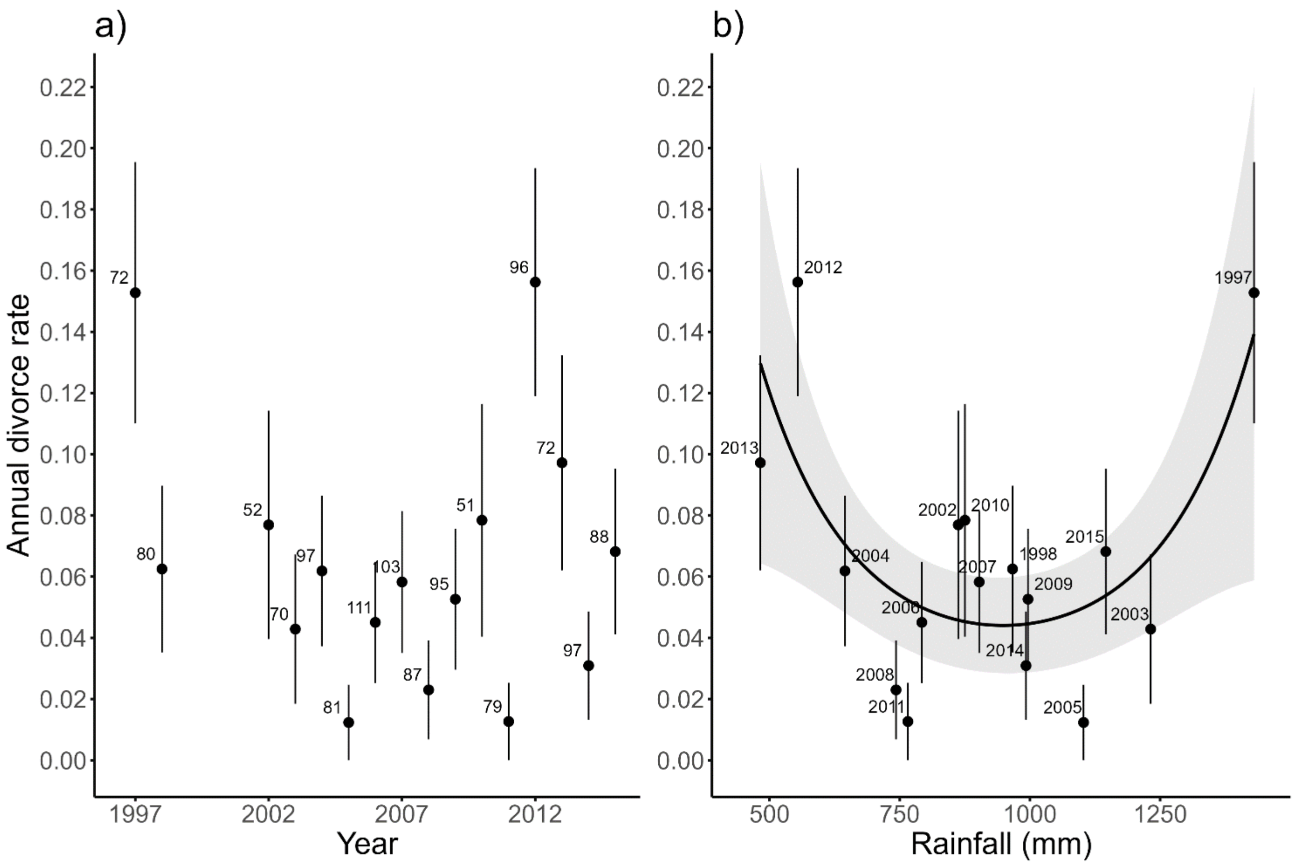

Figure S1. a) Variability in the annual divorce rate of the Seychelles warbler on Cousin Island (n = 1321 partnerships) from 1997 to 2015. The years 1999, 2000, and 2001 were not included due to limited fieldwork during those years. b) The effect of rainfall on the annual divorce rate as predicted by 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 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, female age, and population density. A total of *n* = 1252 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	-4.008	0.696	-5.373 to -2.644	**<0.001**
Rainfall	-0.242	0.175	-0.585 to 0.101	0.167
Rainfall^2	0.273	0.170	-0.059 to 0.606	0.107
Partnership length	-0.324	0.252	-0.818 to 0.170	0.199
Number of offspring	-0.102	0.155	-0.406 to 0.203	0.513
Pairwise relatedness	0.141	0.161	-0.174 to 0.456	0.381
Number of helpers	-0.316	0.194	-0.696 to 0.064	0.103
Male age	-0.014	0.198	-0.401 to 0.374	0.945
Female age	0.186	0.181	-0.168 to 0.540	0.304
Population density	0.037	0.142	-0.241 to 0.316	0.794
Random effects	**Variance**	**Levels**		
Male ID	1.030	392		
Female ID	1.168	372		
Field period ID	0.000	15		
Territory ID	0.182	156		

Table S3. 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, female age, and population density. A total of *n* = 1252 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	-3.485	0.818	-5.087 to -1.882	**<0.001**
Rainfall	-0.367	0.175	-0.709 to -0.025	**0.036**
Partnership length	-0.400	0.247	-0.884 to 0.083	0.105
Number of offspring	-0.098	0.152	-0.396 to 0.201	0.521
Pairwise relatedness	0.114	0.148	-0.177 to 0.404	0.443
Number of helpers	-0.291	0.190	-0.664 to 0.083	0.127
Male age	-0.002	0.181	-0.358 to 0.353	0.989
Female age	0.185	0.170	-0.148 to 0.518	0.277
Population density	0.098	0.144	-0.184 to 0.380	0.497
Random effects	**Variance**	**Levels**		
Male ID	0.370	392		
Female ID	0.550	372		
Field period ID	0.052	15		
Territory ID	0.310	156		

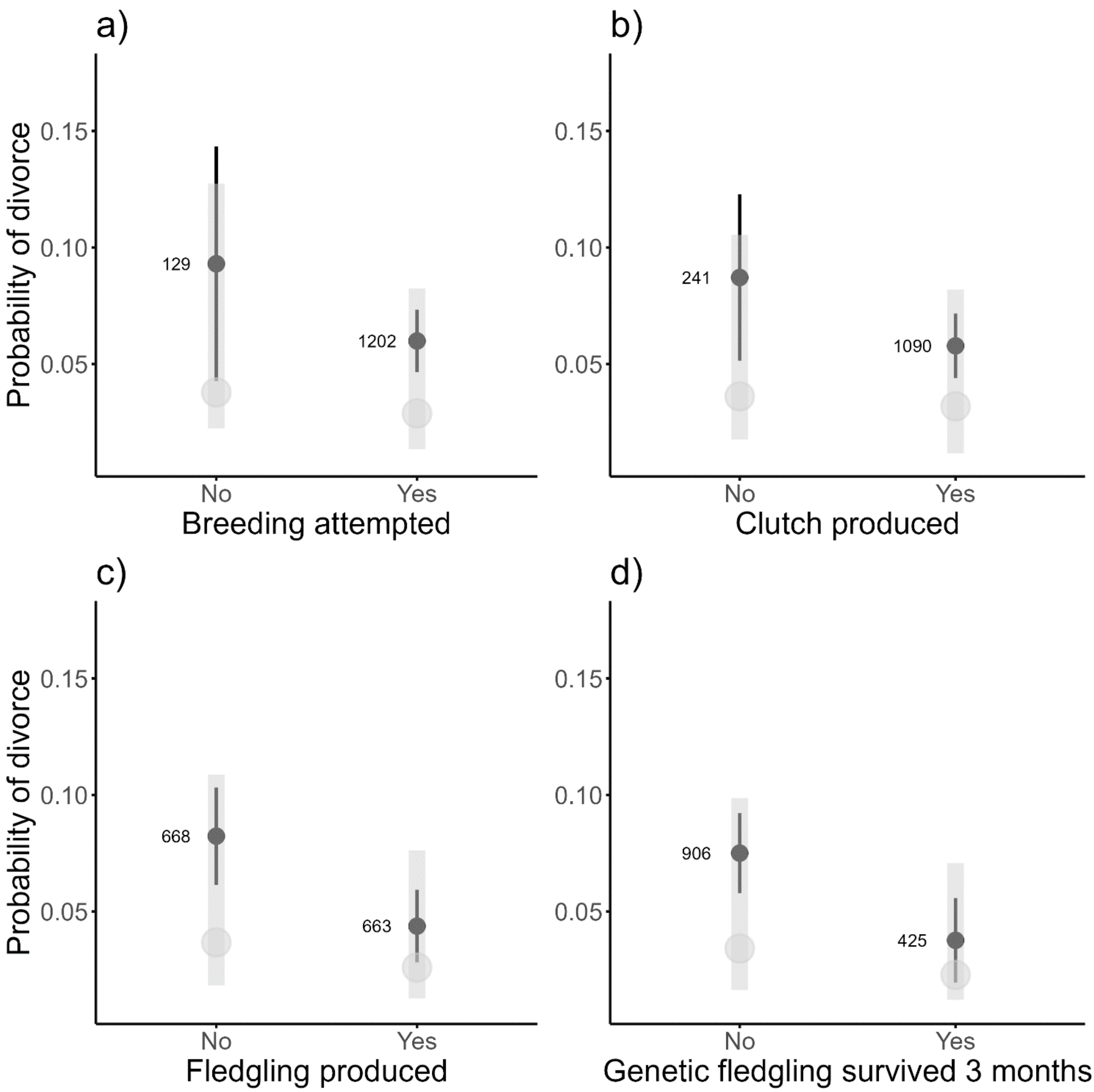

Figure S2. The probability of divorce for Seychelles warbler partnerships (*n* = 1321) that did or did not: a) attempt to breed; b) produce a clutch; c) produce a fledgling; d) produce a fledgling genetically related to the dominant female that survived till at the least three months old. The grey dots 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.

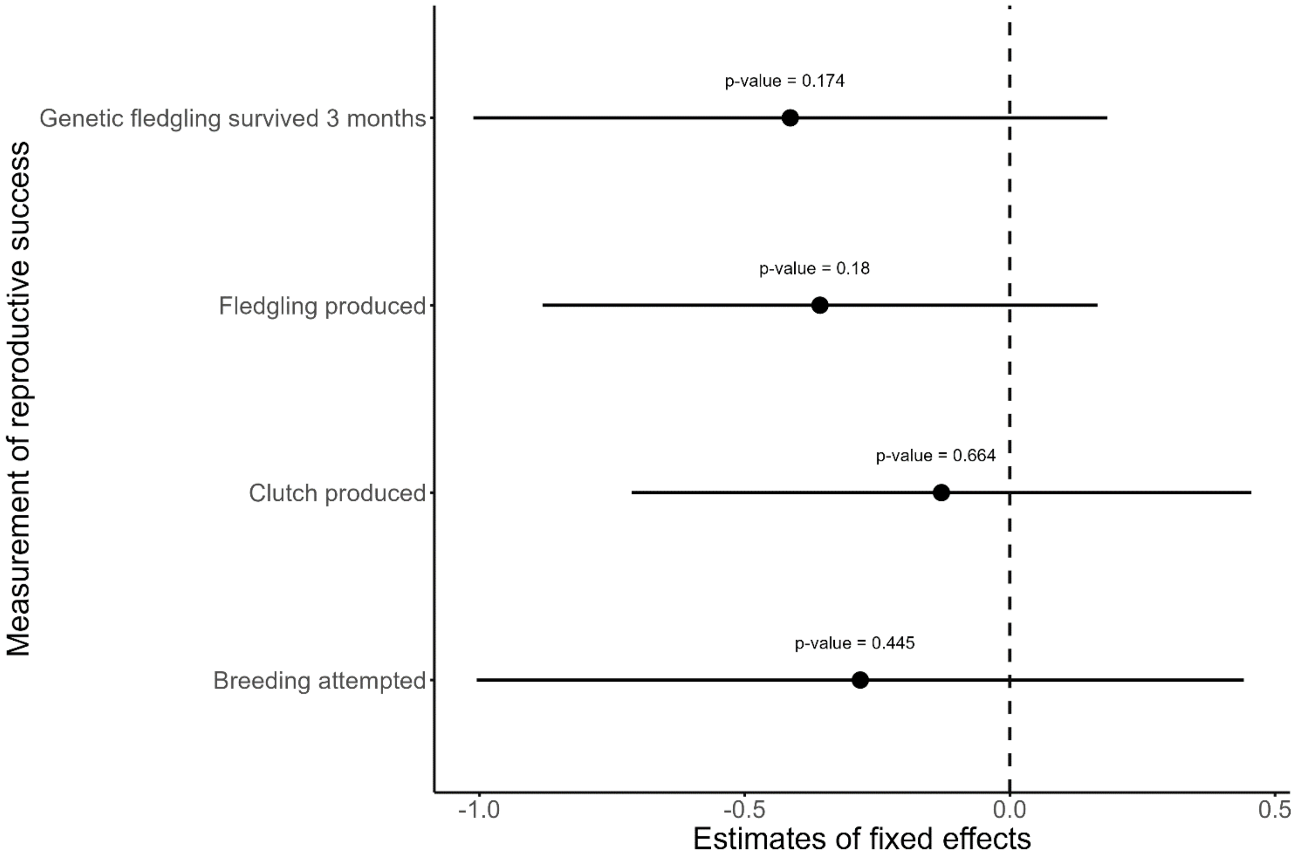

Figure S3. The coefficient estimates (dots) and 95% confidence intervals (bars) of four measures of reproductive success on the probability of divorce in the Seychelles warbler (n = 1325 partnerships) as predicted by binomial generalized linear mixed model. Each reproductive measure was independently included in the model. *p*-values are indicated on the figure.

The following tables (Tables S4 to S7) 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 S4. 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, female age, and population density. n = 1321 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	-3.236	0.469	-4.154 to -2.317	**<0.001**
Rainfall	-0.131	0.115	-0.357 to 0.095	0.257
Rainfall^2	0.325	0.088	0.153 to 0.498	**<0.001**
Partnership length	-0.508	0.217	-0.933 to -0.084	**0.019**
Breeding attempted	-0.282	0.369	-1.006 to 0.442	0.445
Pairwise relatedness	0.150	0.128	-0.100 to 0.401	0.240
Number of helpers	-0.199	0.157	-0.507 to 0.109	0.205
Male age	0.076	0.158	-0.234 to 0.385	0.631
Female age	0.206	0.144	-0.076 to 0.488	0.152
Population density	0.027	0.137	-0.241 to 0.294	0.846
Random effects	**Variance**	**Levels**		
Male ID	<0.001	416		
Female ID	0.272	392		
Field period ID	0.022	16		
Territory ID	0.353	158		

Table S5. 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, female age, and population density. *n* = 1321 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	-3.284	0.351	-3.972 to -2.596	**<0.001**
Rainfall	-0.140	0.114	-0.363 to 0.083	0.217
Rainfall^2	0.322	0.087	0.152 to 0.492	**<0.001**
Partnership length	-0.524	0.208	-0.932 to -0.115	**0.012**
Clutch produced	-0.129	0.298	-0.713 to 0.454	0.664
Pairwise relatedness	0.145	0.124	-0.097 to 0.388	0.240
Number of helpers	-0.199	0.156	-0.505 to 0.107	0.203
Male age	0.080	0.154	-0.222 to 0.381	0.605
Female age	0.203	0.139	-0.068 to 0.475	0.143
Population density	0.026	0.136	-0.241 to 0.293	0.848
Random effects	**Variance**	**Levels**		
Male ID	<0.001	416		
Female ID	<0.001	392		
Field period ID	0.026	16		
Territory ID	0.365	158		

Table S6. 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, female age, and population density. n = 1321 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	-3.267	0.363	-3.978 to -2.556	**<0.001**
Rainfall	-0.129	0.113	-0.351 to 0.092	0.252
Rainfall^2	0.311	0.089	0.138 to 0.485	**<0.001**
Partnership length	-0.490	0.215	-0.911 to -0.069	**0.023**
Fledgling produced	-0.358	0.267	-0.882 to 0.165	0.180
Pairwise relatedness	0.141	0.127	-0.108 to 0.390	0.267
Number of helpers	-0.152	0.161	-0.468 to 0.164	0.345
Male age	0.074	0.157	-0.234 to 0.381	0.638
Female age	0.198	0.142	-0.080 to 0.475	0.163
Population density	0.023	0.137	-0.245 to 0.290	0.869

Random effects	**Variance**	**Levels**
Male ID	0.000	416
Female ID	0.187	392
Field period ID	0.026	16
Territory ID	0.334	158

Table S7. 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, female age, and population density. n = 1321 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	-3.343	0.341	-4.012 to -2.674	**<0.001**
Rainfall	-0.136	0.110	-0.351 to 0.079	0.214
Rainfall^2	0.312	0.087	0.142 to 0.481	**<0.001**
Partnership length	-0.486	0.216	-0.908 to -0.063	**0.024**
Genetic fledgling produced	-0.414	0.305	-1.011 to 0.182	0.174
Pairwise relatedness	0.136	0.128	-0.114 to 0.387	0.286
Number of helpers	-0.196	0.156	-0.502 to 0.109	0.208
Male age	0.075	0.158	-0.234 to 0.384	0.634
Female age	0.190	0.143	-0.090 to 0.471	0.184
Population density	0.019	0.134	-0.244 to 0.281	0.890

Random effects	**Variance**	**Levels**
Male ID	<0.001	416
Female ID	0.253	392
Field period ID	0.015	16
Territory ID	0.349	158

Interaction between rainfall and partnership length

We found a significant interaction between partnership length and rainfall (Table S8), where the model predicted that heavy rainfall increased the probability of divorce in shorter-lasting but not longer-lasting partnerships (Figure S4). However, as the sample sizes of longer-lasting partnerships were small (Table S9), 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 S11; Table S12). 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 S13). As a result, the interaction was not included in the final model.

Table S8. 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, female age, and population density. *n* = 1321 partnerships were analyzed using a binomial GLMM. Significant *p*-values are in bold.

Independent variables	**Estimate**	**Standard error**	**95% Confidence interval**	***p*-value**
Intercept	-3.848	0.541	-4.909 to -2.787	**<0.001**
Rainfall	-0.347	0.165	-0.671 to -0.023	**0.036**
Rainfall^2	0.236	0.118	0.004 to 0.467	**0.046**
Partnership length	-0.624	0.301	-1.215 to -0.034	**0.038**
Number of offspring	-0.088	0.148	-0.377 to 0.202	0.553
Pairwise relatedness	0.162	0.140	-0.112 to 0.436	0.247
Number of helpers	-0.196	0.164	-0.519 to 0.126	0.232
Male age	-0.073	0.201	-0.466 to 0.321	0.717
Male age^2	0.191	0.113	-0.030 to 0.412	0.090
Female age	0.274	0.185	-0.087 to 0.636	0.137
Female age^2	-0.122	0.119	-0.356 to 0.112	0.306
Population density	0.039	0.134	-0.224 to 0.301	0.774
Rainfall * Partnership length	-0.486	0.217	-0.912 to -0.060	**0.025**
Rainfall^2 * Partnership length	-0.063	0.148	-0.354 to 0.227	0.670
Random effects	**Variance**	**Levels**		
Male ID	0.432	416		
Female ID	0.576	392		
Field period ID	<0.001	16		
Territory ID	0.309	158		

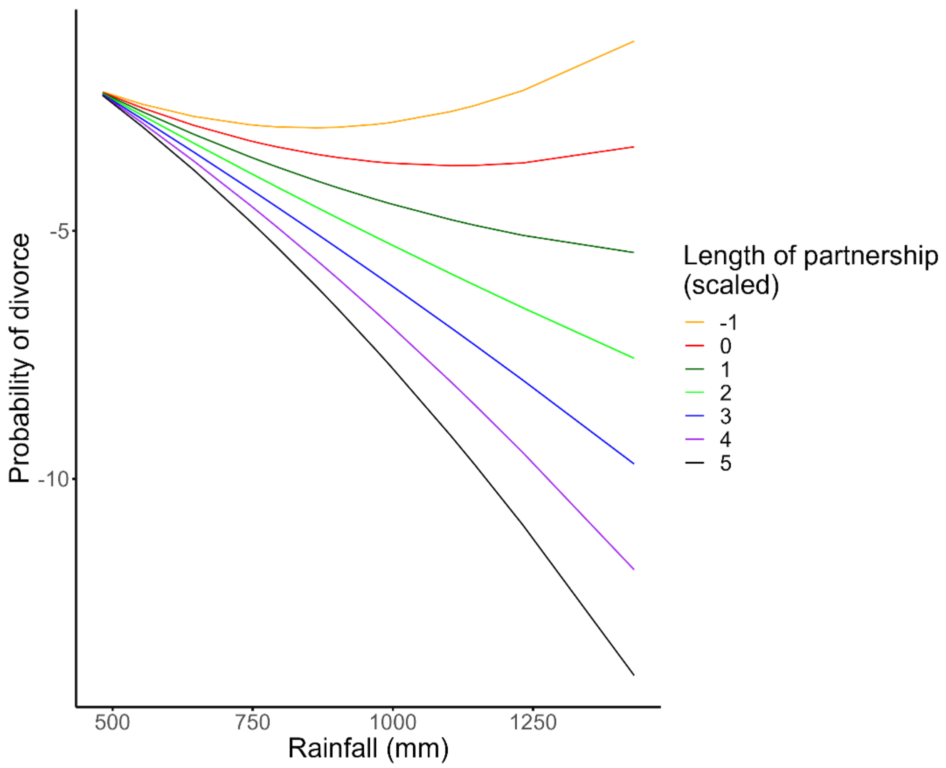

Figure S4. The effect of total rainfall from February to August on the probability of divorce for Seychelles warbler partnerships (n = 1321) that have been together for different lengths of time on Cousin Island as predicted by a binomial generalized linear mixed model.

Table S9. 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	534
0	496
1	183
2	73
3	30
4	10
5	5

Table S10. Associations between the probability of divorce in the Seychelles warbler on Cousin Island with rainfall, the length of the partnership, the relatedness of the breeding pair, the number of helpers, male age, female age, population density, male extra-pair-paternity (EPP; infidelity), female EPP, and co-breeder presence (Y/N). n = 1321 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	-3.352	0.359	-4.056 to -2.649	**<0.001**
Rainfall	-0.157	0.113	-0.377 to 0.064	0.164
Rainfall^2	0.324	0.088	0.152 to 0.496	**<0.001**
Partnership length	-0.490	0.216	-0.913 to -0.067	**0.023**
Number of offspring	0.031	0.217	-0.394 to 0.456	0.886
Pairwise relatedness	0.136	0.127	-0.112 to 0.385	0.283
Number of helpers	-0.211	0.159	-0.522 to 0.101	0.185
Male age	0.069	0.159	-0.243 to 0.380	0.665
Female age	0.192	0.142	-0.087 to 0.472	0.177
Population density	0.018	0.136	-0.248 to 0.285	0.893
Male EPP	-0.016	0.171	-0.350 to 0.319	0.927
Female EPP	-0.324	0.286	-0.884 to 0.237	0.258
Co-breeder presence	0.412	0.333	-0.240 to 1.065	0.215
Random effects	**Variance**	**Levels**		
Male ID	<0.001	416		
Female ID	0.169	392		
Field period ID	0.021	16		
Territory ID	0.364	158		

Table S11. Associations between the probability of divorce in the Seychelles warbler on Cousin Island with the total rainfall from February to August, partnership length, the number of offspring, pairwise relatedness, the number of helpers, male age, female age, and population density. $n = 1296$ 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 analysis.

Independent variables	**Estimate**	**Standard error**	**95% Confidence interval**	***p*-value**
Intercept	-3.464	0.379	-4.206 to -2.721	**<0.001**
Rainfall	-0.299	0.160	-0.613 to 0.014	0.061
Rainfall^2	0.247	0.121	0.010 to 0.484	**0.041**
Partnership length	-0.849	0.336	-1.506 to -0.191	**0.011**
Number of offspring	-0.079	0.144	-0.361 to 0.204	0.585
Pairwise relatedness	0.148	0.129	-0.105 to 0.401	0.252
Number of helpers	-0.200	0.165	-0.523 to 0.123	0.225
Male age	-0.011	0.192	-0.387 to 0.365	0.955
Male age^2	0.134	0.116	-0.093 to 0.361	0.246
Female age	0.327	0.179	-0.024 to 0.677	0.068
Female age^2	-0.297	0.151	-0.593 to 0.000	0.050
Population density	0.077	0.136	-0.189 to 0.344	0.569
Rainfall * Partnership length	-0.360	0.214	-0.779 to 0.059	0.093
Rainfall^2 * Partnership length	-0.028	0.159	-0.340 to 0.284	0.860

Random effects	**Variance**	**Levels**
Male ID	0.000	416
Female ID	0.302	392
Field period ID	0.013	16
Territory ID	0.291	158

Table S12. Associations between the probability of divorce in the Seychelles warbler on Cousin Island with the total rainfall from February to August, partnership length, the number of offspring, pairwise relatedness, the number of helpers, male age, female age, and population density. $n = 1245$ 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	-3.477	0.389	-4.240 to -2.714	**<0.001**
Rainfall	-0.280	0.161	-0.595 to 0.034	0.081
Rainfall^2	0.240	0.123	-0.001 to 0.482	0.051
Partnership length	-0.790	0.353	-1.482 to -0.099	**0.025**
Number of offspring	-0.110	0.147	-0.398 to 0.178	0.453
Pairwise relatedness	0.128	0.130	-0.127 to 0.383	0.324
Number of helpers	-0.194	0.165	-0.518 to 0.130	0.241
Male age	-0.029	0.194	-0.409 to 0.351	0.880
Male age^2	0.152	0.119	-0.082 to 0.386	0.204
Female age	0.323	0.178	-0.026 to 0.673	0.070
Female age^2	-0.268	0.153	-0.569 to 0.033	0.081
Population density	0.082	0.131	-0.176 to 0.339	0.535
Rainfall * Partnership length	-0.337	0.230	-0.789 to 0.114	0.143
Rainfall^2 * Partnership length	-0.035	0.173	-0.374 to 0.303	0.838
Random effects	**Variance**	**Levels**		
Male ID	0.000	416		
Female ID	0.325	392		
Field period ID	0.000	16		
Territory ID	0.284	158		

Table S13. 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, female age, and population density. *n* = 1321 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	-3.248	0.664	-4.549 to -1.946	**<0.001**
Rainfall	0.013	0.159	-0.298 to 0.324	0.936
Rainfall^2	0.240	0.118	0.009 to 0.471	**0.042**
Breeding experience	-0.988	0.429	-1.829 to -0.146	**0.021**
Number of offspring	-0.077	0.148	-0.367 to 0.213	0.604
Pairwise relatedness	0.160	0.140	-0.114 to 0.435	0.252
Number of helpers	-0.201	0.163	-0.520 to 0.119	0.218
Male age	-0.127	0.191	-0.501 to 0.247	0.507
Male age^2	0.164	0.115	-0.061 to 0.389	0.154
Female age	0.226	0.177	-0.120 to 0.572	0.200
Female age^2	-0.138	0.121	-0.374 to 0.099	0.254
Population density	0.036	0.134	-0.227 to 0.298	0.790
Rainfall * Breeding experience	-0.334	0.233	-0.790 to 0.123	0.152
Rainfall^2 * Breeding experience	0.215	0.171	-0.120 to 0.550	0.208
Random effects	**Variance**	**Levels**		
Male ID	0.434	416		
Female ID	0.575	392		
Field period ID	0.000	16		
Territory ID	0.317	158		

Table S14. 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 = 1321 partnerships were analyzed using binomial (models 1 to 3) and poisson (model 4) generalized linear mixed models. Significant terms are in bold.

Independent variables	Model 1	Model 2	Model 3	Model 4
	Estimate (95% Confidence interval)			
Intercept	**3.44*** (2.72 to 4.16)**	**2.63*** (2.11 to 3.14)**	**0.79*** (0.41 to 1.17)**	**-0.54*** (-0.80 to -0.27)**
Rainfall	**0.948** (0.37 to 1.53)**	**0.61** (0.23 to 1.00)**	**0.33** (0.06 to 0.59)**	**0.20* (0.01 to 0.41)**
Rainfall^2	-	-	**-0.23* (-0.44 to -0.05)**	**-0.22** (-0.38 to -0.06)**
Partnership length	-0.16 (-0.50 to 0.19)	0.09 (-0.17 to 0.35)	0.14 (-0.07 to 0.35)	0.04 (-0.11 to 0.18)
Pairwise relatedness	0.00 (-0.24 to 0.24)	-0.03 (-0.21 to 0.14)	**-0.14* (-0.28 to 0.00)**	-0.08 (-0.17 to 0.01)
Number of helpers	-	**1.49*** (0.86 to 2.13)**	**0.76*** (0.58 to 0.94)**	**0.09* (0.02 to 0.17)**
Male age	**0.47* (0.11 to 0.83)**	0.10 (-0.12 to 0.33)	**0.22* (0.01 to 0.43)**	**0.21** (0.06 to 0.35)**
Male age^2	**-0.23* (-0.41 to -0.05)**	-	**-0.19** (-0.31 to -0.08)**	**-0.16*** (-0.25 to -0.07)**
Female age	0.26 (-0.03 to 0.55)	**0.37** (0.14 to 0.61)**	0.16 (-0.04 to 0.36)	0.03 (-0.12 to 0.17)
Female age^2	-	**-0.30*** (-0.44 to -0.17)**	**-0.28*** (-0.39 to -0.16)**	**-0.21*** (-0.32 to -0.12)**

Random effects (Levels)	**Variance**	**Variance**	**Variance**	**Variance**
Male ID (416)	0.00	0.00	0.02	0.00
Female ID (392)	0.34	0.00	0.22	0.00
Field period ID (16)	1.03	0.51	0.21	0.12
Territory ID (158)	0.43	0.35	0.07	0.00

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

Table S15. 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 = 1321 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	2.899	0.294	2.322 to 3.476	**<0.001**
Rainfall	0.682	0.182	0.325 to 1.038	**<0.001**
Rainfall^2	-0.264	0.136	-0.530 to 0.002	0.051
Partnership length	0.084	0.134	-0.178 to 0.347	0.528
Pairwise relatedness	-0.034	0.088	-0.206 to 0.138	0.702
Number of helpers	1.499	0.322	0.868 to 2.131	**<0.001**
Male age	0.100	0.114	-0.123 to 0.324	0.378
Female age	0.373	0.121	0.135 to 0.611	0.002
Female age^2	-0.303	0.069	-0.438 to -0.167	**<0.001**
Random effects	**Variance**	**Levels**		
Male ID	<0.001	416		
Female ID	0.000	392		
Field Period ID	0.403	16		
Territory ID	0.355	158		

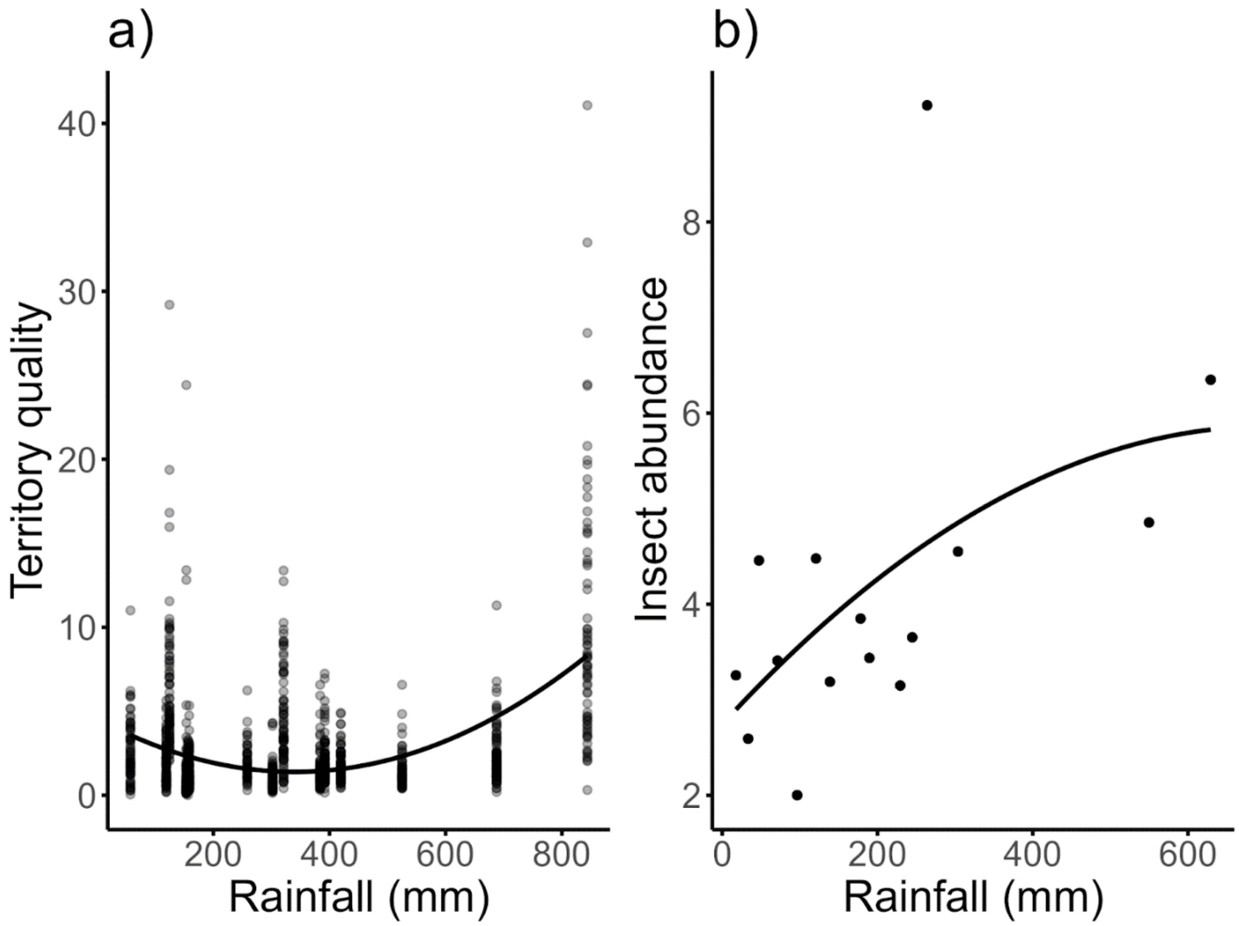

Figure S5. The effect of rainfall on: a) territory quality (scaled 1:10,000); b) insect abundance (the mean number of insects found per unit leaf area across all monthly surveys) on Cousin Island (*n* = 15 years), as predicted (solid line) by a *ClimWin* generated linear model. Territory quality was 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).