Lack of parental mate-switching effects on offspring fitness components in a long-lived socially monogamous species

Frigg J. D. Speelman[1,2]; Terry Burke[3]; Jan Komdeur[2]; David S. Richardson[4,5]; Hannah. L. Dugdale[2];

AFFILIATIONS

1. Macquarie University, School of Biological Sciences, Sydney, Australia
2. University of Groningen, Groningen Institute of Evolutionary Life Sciences, The Netherlands
3. University of Sheffield, School of Biosciences, Sheffield, UK
4. University of East Anglia, Biological Sciences, Norwich, UK
5. Nature Seychelles, Mahé, Republic of Seychelles

STATEMENT OF AUTHORSHIP

FJDS and HLD conceived the study design and methodology. FJDS performed the analyses, with input from HLD. FJDS wrote the manuscript, with input from HLD, DSR, and JK. DSR organised and (with many others - see acknowledgements) undertook fieldwork. Molecular parentage assignment methods were developed and undertaken by DSR and HLD. HLD, DSR, JK, and TB managed the long-term Seychelles warbler study system and database including gaining the relevant funding. All authors gave final approval for submission.

CORRESPONDING AUTHORS

Frigg J.D. Speelman

Frigg.speelman@hdr.mq.edu.au

+61428518204

Hannah L. Dugdale

h.l.dugdale@rug.nl

+31 50 36 39683

ACKNOWLEDGEMENTS

We thank the Seychelles Bureau of Standards and the Department of Environment for fieldwork permission and sample export-permits. We are also grateful to Nature Seychelles for facilitating fieldwork on Cousin Island. We thank all the fieldworkers and technicians who contributed to the Seychelles warbler project, without them the current long-term dataset would not exist.

FUNDING

FJDS was funded by a PhD scholarship from the University of Groningen and Macquarie University, the Lucie Burgers Foundation, Ecology Fund Grant of the Royal Netherlands Academy of Arts and Sciences 705/202219, and by a Dobberke grant 2349/202113 of the Dr. J.L. Dobberke Foundation. The long-term data gathering that enabled this study was supported by various NERC grants: NE/B504106/1 to TAB and DSR, NE/I021748/1 to HLD, NE/P011284/1 to HLD and DSR, and NE/F02083X/1, NE/K005502/1 and NE/S010939/1 to DSR; as well as a NWO Rubicon 825.09.013 and RUG Rosalind Franklin Fellowship to HLD, NWO visitors grant 040.11.232 to JK and HLD, and NWO TOP grant 854.11.003 and NWO VICI 823.01.014 to JK.

Abstract

In many species, individuals form socially monogamous pair-bonds lasting multiple breeding seasons, or even whole lifetimes. Studies often suggest social monogamy to be adaptive, but this is usually quantified through the survival and annual reproductive success of the partners. However, beyond the number of offspring produced, parental partnerships may also affect their offspring's phenotype, health, and ultimately fitness. Using multigenerational data on the Seychelles warbler (*Acrocephalus sechellensis*), we investigated the impact of parental pair-bond tenure (pair-bond duration) and pair-bond fidelity (pair-bond maintained across breeding seasons) on offspring fitness components. First, we addressed juvenile-stage fitness using indicators reflecting physiological state (haematocrit, telomere length, and body mass). Second, we assessed long-term fitness components using offspring lifespan and lifetime reproductive success (LRS). We found male (but not female) offspring whose parents both died had 73% increased mortality risk compared to male offspring whose parents remained together. We found no evidence of pair-bond tenure- or fidelity-effects on other short-term measures (telomere length, haematocrit, body mass) or LRS. To our knowledge, this is the first study quantifying long-term parental effects of pair-bond tenure and fidelity on offspring fitness components in wild populations. This work provides insights into intergenerational implications of long-term socially monogamous partnerships.

Keywords: reproductive success, lifespan, telomere length, haematocrit, body mass, divorce

1. Introduction

In many species individuals form socially monogamous pair-bonds that are often maintained over multiple breeding seasons or even entire lifetimes (i.e. pair-bond fidelity). Especially in birds, social monogamy is common (~90% of species; 1,2). Sticking with the same partner over multiple breeding attempts can reduce sexual conflict, especially in long-lived species with biparental care where individuals have to cooperate to raise offspring (3,4). Here, over-exertion of one partner in the current reproductive attempt will be detrimental for both partners if this reduces future reproductive investment. This means the evolutionary interests (i.e. in future reproductive success) of both individuals are more aligned within long-term than short-term partnerships. Additionally, pair-bond fidelity can reduce mate searching costs (5,6). Finally, staying together for longer (i.e. increased pair-bond tenure) can improve coordination and familiarity between the pair (7,8). This, in turn, can increase reproductive success, competitiveness and survival of pair-bonded individuals (8). Many studies have found evidence of social monogamy being an adaptive strategy, but this is usually quantified by addressing the effects of social monogamy on the survival of the partners (9,10) and their annual reproductive success (11). However, especially in species with biparental care, partnership quality may ultimately affect the offspring's phenotype and health. If newer partners are not yet well-aligned or coordinated, offspring sired early in partnerships may suffer fitness costs (both in the short- and long-term) as a result of less than optimal parental care (3) and increased parental stress (12). Partnership termination may also have detrimental effects on offspring condition and survival; especially when the partnership is terminated while offspring are still dependent or closely associated with their parents.

Partnership termination effects on offspring fitness can be defined as parental effects, whereby the parent's phenotype causally influences their offspring's phenotype beyond the genes they inherit (13). These are often shaped by natural selection (14) and can both accelerate and decelerate evolutionary responses to selection since traits respond to both current (on the offspring) and previous (on the parents) selective forces (15). In birds, direct parental effects arise through, for example, investment in the egg composition and production, provisioning and other forms of parental care (14). Indirect parental effects can also occur if a parent themselves gains care from their mate (e.g. nuptial feeding) and also through the benefits of mate choice (14,16). Parental effects can have a pronounced influence on offspring in early life when they are still dependent on their parents (17). However, a growing number of studies have identified parental effects on offspring throughout their life, e.g. influencing offspring survival and lifetime reproductive success (18–21).

Since mothers typically invest more in offspring than fathers, maternal effects are frequently the focus of parental effect studies. For socially monogamous species with biparental care, the phenotype of both parents, not just mothers, may have considerable influence on offspring fitness. Although many studies to date have identified that the early-life environment can shape offspring fitness (22), no studies to date have investigated how pair-bond fidelity and pair-bond tenure of the parents in early life affect offspring, with the exception of psychological and sociological studies on humans (23,24).

In this study, we investigate the impact of pair-bond tenure and pair-bond fidelity during offspring dependency on the parents on offspring fitness in the Seychelles warbler (*Acrocephalus sechellensis*) population on Cousin Island. Seychelles warblers are long-lived (up to 21 years) and form socially monogamous partnerships in breeding territories that they defend year-round (25). Partnerships can last from one breeding season up to at least 15 years, and can end through the death of a partner (widowhood), or less commonly divorce and human-induced translocation of one partner as part of a conservation programmes (26,27). Both parents provide parental care through provisioning and nest guarding during a long period (~3 months) of offspring dependence for an altricial bird species (28,29). The study system provides an excellent model system since it is an isolated population with virtually no migration (30) that has been extensively monitored over many generations. Therefore we can accurately identify and track individuals of known age throughout their lives, generating extremely accurate survival estimates that are not confounded by dispersal (31,32). Additionally, we have detailed information on territory residency and social status, thus we can accurately identify partnerships. Individuals are captured and blood sampled throughout their lifetime; so we have access to individual measurements of physiological state. Finally, we have a genetically verified population pedigree (33) which allows us to accurately estimate lifetime reproductive success (LRS).

Multiple parameters have been used to investigate the health and condition of individuals within the Seychelles warbler. Telomeres - repetitive DNA sequences at the end of linear chromosomes - protect against DNA damage and can shorten due to oxidative stress (34). In the Seychelles warbler, telomere length generally declines with age, especially in early life -although telomere lengthening also occurs (35)- predicts future mortality (36) and has been linked to genetic, parental, and environmental conditions (33,35). Importantly, in this species telomere shortening indicates costs associated with inbreeding (37), social conflict (38), reduced parental care (39), food availability (40,41) and malaria (40). Haematocrit, the proportion of blood comprised of erythrocytes, reflects aerobic capacity in vertebrates, which affects individual health and performance (42). In the Seychelles warbler, haematocrit increases with age in early life, and high haematocrit indicates poor condition for juveniles (43). Finally, body mass is often used as an indicator of physiological state in animals, as it is determined by body fat content (i.e. energy reserves) and structural size, and can affect survival (44,45). Juvenile body mass in Seychelles warblers predicts adult condition and performance (46). Juvenile and adult mass decrease in more competitive environments (38,47), and adult mass is positively correlated with food abundance (48).

Here, we investigate the short- and long-term consequences of parental pair-bond tenure and pair-bond fidelity on offspring fitness using a 25-year dataset of Seychelles warblers. First, we addressed juvenile-stage fitness using three indicators that reflect physiological state: (1) telomere length, (2) haematocrit, and (3) body mass. Second, we tested whether pair-bond fidelity was associated with (4) lifespan and (5) LRS. We hypothesize that parents in longer partnerships rear offspring in better physiological state which go on to have higher fitness. In contrast, we expect that pair-bond disruption while the offspring is still dependent on parental care will negatively affect offspring physiological state and fitness. Offspring produced in the breeding season prior to pair-bond termination will likely experience physiological stress, as they are still dependent on parental care, and may be affected by potential stress expressed by the parent(s), as well as the disruption of group stability and potential subsequent social conflict in the breeding territory.

2. Material and methods

(a) Study population

Seychelles warblers are insectivorous passerines (49) endemic to the Seychelles archipelago. The population of ~320 birds in ~115 territories (27,33) on Cousin Island (29 ha, 04°20’S, 55°40’E) has been intensively monitored since 1997 (25,50), with virtually all breeding attempts followed each year during the major breeding season (Jun-Sept) and during most minor breeding seasons (Jan-Mar). Seychelles warblers are territorial and form socially monogamous pairs that defend the same territory year-round (25,51) but can be accompanied by one or more adult subordinates of either sex (51,52). The dominant breeding pair is identified every season using behavioural observations including contact calls, pair interactions, mate guarding, and intensive breeding effort (50). Subordinates are assigned as helpers or non-helpers based on whether they incubate and/or provision offspring in the breeding territory (25,50). Individuals can be reliably assumed dead when they are not observed for two consecutive seasons, as inter-island dispersal is virtually absent (<0.1%, 30) and resighting rates are very high (98%+/-1% SE for adults, 31,32).

(b) Partnerships

Parental pair-bonds can last between one breeding season and a lifetime, with the longest recorded partnership being 15 years (27). Partnerships can end (between or within breeding seasons) in different ways; most commonly through the death of one partner (widowhood) or both. Partnerships can result in divorce, whereby both partners are still alive but at least one partner lost the dominant breeding position in the focal territory. Partnerships were assessed throughout each breeding season and the partnership statuses assigned at the end of each breeding season. A partnership can have six different transitions from the end of one breeding season (major or minor) to the end of the next: (1) pair-bond fidelity (stay together), (2) widowhood by female’s death, (3) widowhood by male’s death, (4) death of both partners, (5) divorce, and (6) translocation. Divorces caused by one breeder ‘stepping down’ to a subordinate position for a single breeding season whilst still present in the territory were removed from our dataset (*N*=22 out of 1362 pair bond observations). Pair-tenure was defined as the duration from the start date of the first season the pair were pair-bonded to each other, until the end of the last breeding season when the focal offspring was reared.

(c) Reproduction

A maximum of one clutch is produced per breeding season and most clutches have a single egg, with only 8% of clutches having 2-3 eggs (27). When nests contain multiple eggs, this usually indicates co-breeding subordinate females within the territory (50,53), which account for 11% of all maternities (54). Extra-pair fertilizations are common in the Seychelles warbler, with ~44% of all offspring being sired by a dominant male other than the socially pair-bonded male (53–55). Offspring remain dependent on parental care for ~3 months, long after fledging after ~18 days, and survival during this period is dependent on the amount of provisioning that is received (28).

(d) Individual sampling

Each breeding season, as many birds as possible are caught using mist nets or captured as nestlings in the nest, after which they are ringed with a unique BTO ring and 3 colour rings, and blood sampled (ca. 50 µl) from the brachial vein. Individuals caught for the first time are aged based on lay, hatch, or fledge date and/or eye colour (49). Their body mass is measured using an electronic scale (±0.1g) and their structural size is assessed (tarsus length) using sliding callipers (±0.1mm), resulting in 623 mass and size measures in 497 offspring. Haematocrit was assessed for 456 individuals (579 samples) by measuring the proportion of erythrocytes relative to the whole-blood volume using sliding callipers (±0.01mm), on a microcapillary tube centrifuged within 3-hr of collection for 8 min at 6,000g (43). A small subset of the blood sample (ca. 10 µl) is stored in absolute ethanol, and used for molecular sexing, parentage assignment, and telomere length measurement. Genetic parents were assigned ($p >= 0.8$) using *MasterBayes* 2.5.2 (33,55). Our data included all 1581 individuals that hatched between 1997 and 2018 and were assigned a pair-bonded mother (excluding subordinate mothers). We used available telomere data for offspring that were sampled between 1997 and 2014. Samples that did not show signs of degradation were used for relative telomere length (RTL) assessment using quantitative polymerase chain reaction (33,35), and samples that did not meet quality criteria were removed (33,37), resulting in 661 RTL samples for 546 offspring. Within-plate repeatability was 0.74 (95%CI=0.74–0.75) for GAPDH and 0.73 (95%CI=0.71-0.74) for telomere Cq values, and between-plate repeatability was 0.68 (95%CI=0.65-0.70) using 422 samples measured at least twice at different time points (35).

(e) Statistical analyses

We performed all statistical analyses in *R* 4.3.0 (56). Models were fitted with *lme4* 1.1.13 (57) or *glmmTMB* 1.1.17 (58). For all models, we first z-transformed (mean centred and divided by 1SD) all continuous predictors and checked for collinearity between fixed effects using variance inflation factor (all <3) using *performance* 0.10.8 (59), checked for under- or overdispersion, and residual spatial or temporal autocorrelation using *DHARMa* 0.4.6 (60), finding none in the final models. While all first-order factors were kept in the model irrespective of their significance, all non-significant interactions were removed from the models sequentially, least significant first, to facilitate interpretation of the first-order effects. As we were interested in the effects of both pair-bond tenure and fidelity, we included both parental pair-bond tenure (in days) and fidelity categories (1; pair-bond fidelity, 2; widowhood by female's death, 3; widowhood by male's death, 4; death of both partners, 5; divorce, and 6; translocation). When there were less than 6 observations of a pair-bond fidelity category for an analysis it was removed from the corresponding model.

We first assessed the effect of parental pair-bond fidelity on condition measures of fledged offspring using linear mixed models (LMMs) with Gaussian error distribution.

(i) Telomere length (RTL) models

The extremely rapid initial RTL decrease in very early-life only stabilises after 40 days in the Seychelles warbler (35), so we excluded offspring younger than 40 days. RTL was square-root transformed and z-transformed to be consistent with previous protocols in this study population (33,35). We fitted all offspring RTL measures and included log-transformed offspring sampling age (35), offspring sex, parental pair-bond tenure, pair-bond fidelity category, paternal and maternal age (33), helper presence in the natal territory (present/absent) and technician identity (two levels, A/B; 21). We included interactions between offspring age and both parental pair-bond tenure and fidelity category, since RTL is age-dependent (35), and we predict the effect of age on RTL to differ depending on the parental pair-bond (e.g. a more negative relationship between offspring age and RTL for offspring whose parents have been together for less time). As random effects, we added offspring, mother and father identity, hatch season, and qPCR plate (21). To assess whether the relationship remained when including very young individuals, we ran a separate model including juveniles younger than 40 days (minimum 19 days).

To assess whether there was an effect of parental pair-fidelity on within-individual longitudinal changes in offspring RTL, we used within-subject centering (61). Here, we included the mean age per offspring across sampling events and the within-individual deviation from the mean age in the LMM of RTL. Effects of selective disappearance of individuals with short telomeres and/or higher telomere shortening rates could be masked by most individuals having only one early-life telomere measurement. Therefore we compared relationships between RTL and age within and among individuals with multiple RTL measurements (*N*=536 measurements of 226 individuals) using the same procedure described above.

(ii) Heamatocrit models

We included fixed effects: offspring sampling age (linear and squared covariates), offspring sex, parental pair-bond tenure, pair-bond fidelity category, paternal and maternal age, and sampling time to account for daily variation in haematocrit (43). We also tested interactions between age (linear and quadratic) and pair-bond tenure and pair-bond fidelity, respectively. As random effects, we included offspring, mother, and father identity, and hatch season.

(iii) Body mass models

We included offspring sampling age, offspring sex, parental pair-bond tenure, pair-bond fidelity category, paternal and maternal age, offspring structural size (tarsus length), and sampling time to account for potential daily variation in provisioning rates affecting body mass. Since sample sizes of pair-bond fidelity categories were sometimes low (variable depending on the condition measure model), we ran all of the offspring condition models with a binary pair-bond termination category (yes/no). As we found no significant interactions between age and pair-bond tenure and pair-bond fidelity in the haematocrit and body mass model, we did not test for within-individual longitudinal changes in offspring haematocrit and body mass using within-subject centering.

(iv) Lifespan and LRS models

We included offspring that survived to at least one year of age (*N*=671) and had both genetic (300 mothers and 278 fathers) and social (294 mothers and 307 fathers) parents assigned. We used sex-specific Generalised Linear Mixed Models (GLMMs) with a negative binomial error (lifespan) and zero-inflated negative binomial (LRS) error distributions. We included sibling presence, helper presence, group size, and maternal age at conception as these early-life social environmental effects affect long-term survival and LRS (21,47,62). Group size was the number of adults within the territory (range: 2-7). We included hatch season since offspring hatched more recently in our data hadn't died yet (63). As random effects, we added offspring, mother and father identity, and hatch season. To calculate the hazards ratio for parental pair-bond tenure and fidelity on lifespan, we ran Cox mixed effects proportional hazards model using *coxme* 2.2.18.1 (64). We used the same random and fixed effects as above but excluded hatch season, since individuals still alive at the latest sampling date (*N*=166) or translocated to another island (*N*=79) were right censored. Year of death was defined as the first year in which the individual was no longer seen. We confirmed that assumptions of proportional hazards were met using Schoenfeld's residuals (65).

3. Results

Of the 1581 offspring hatched between 1997 and 2021, 1325 (84%) had parents that remained pair-bonded to the end of the next season (after offspring became independent). In the remaining cases, the parental pair-bonds ended before the end of the next season as a result of maternal death 111 (7%), paternal death 125 (8%), both parents' death 47 (3%), divorce 35 (2%), and translocation of one parent to another island 19 (1%) times.

(a) Parental pair-bond fidelity and short-term offspring fitness condition measures

In the cross-sectional analysis, there was an age-dependent effect of parental pair-bond tenure on early-life offspring RTL. Offspring whose parents had been together longer had a less negative slope between age and RTL (Table 1, Fig. 1). This result remained consistent when we also included 20 offspring younger than 40 days (Table S1). In the partially longitudinal analysis, there was a between-individual, but not a within-individual, age-dependent effect of parental pair-bond tenure on early-life offspring RTL (Table S2). When we ran the model on a subset of our data including only offspring that had >1 RTL measure (199 samples from 96 offspring; Table S3), we found no between- nor within-individual age interaction effect with parental pair-bond tenure. We found no evidence that parental pair-bond fidelity affected RTL (Table 1), even when in the model with a binary parental pair-bond fidelity (yes/no; Table S4).

We found no significant association between offspring body mass (Table 5), nor haematocrit (Table S6), with parental pair-bond tenure or parental pair-bond fidelity category, nor was there an interaction with age. When using the binary parental pair-bond fidelity category, the results remained consistent for both the offspring body mass (Table S7) and haematocrit (Table S8).

(b) Parental pair-bond fidelity and long-term offspring fitness proxies

Male offspring whose parents both died before the end of the breeding season after they were sired had a 73% increased mortality risk compared to male offspring whose parents stayed alive and remained pair-bonded (Table 2B). This effect was not detected in female offspring (Table 2A). We found no significant association between parental pair-bond fidelity and offspring lifespan (Table S9) nor did we find any relationship between parental pair-bond fidelity and LRS (Table 3) in a reduced dataset, that excluded offspring that were still alive. The parental pair-bond effects (tenure and fidelity) remained consistent for lifespan (Cox mixed effects proportional hazards model, Table S10; GLMM, Table S11) and LRS (Table S12) models when using the binary parental pair-bond fidelity (remain together yes/no) category.

4. Discussion

This study adds to the growing body of literature on short- and long-term parental effects on offspring fitness (17,66), and to our knowledge is the first to test for long-term effects of parental pair-bonds in species other than humans (23,24). We found an age-dependent effect of parental pair-bond tenure on offspring telomere length. Offspring from parents who had been together for longer durations had a less negative change in telomere length over the first year of life compared to offspring from parents who had been together for a shorter time (correcting for maternal and paternal age at offspring hatching), detected in a between-offspring, not a within-offspring effect. Furthermore, male, but not female, offspring had increased mortality risk when both parents died within half a year after hatching compared to those whose parents both remained alive. We found no other effect of parental pair-bond tenure or -fidelity on other short-term proxies (haematocrit, body mass) or long-term fitness components (longevity, LRS) of offspring.

The effect of parental pair-bond tenure on age-dependent telomere length could be driven by pairs that are together for longer being able to produce offspring that experience less stress early in life and thereby face a smaller reduction in telomere length with age. However, we did not detect a within-individual effect but did detect a between-individual age-dependent effect of parental pair-bond tenure on telomere length. Consequently, this effect could be driven by any between-individual difference that leads to a higher likelihood of offspring reared by long-term partners having longer telomeres at one-year of age compared to offspring reared by short-term partners. For example, offspring with relatively longer telomeres, i.e. being of relatively higher quality, may have lower survival when raised by parents breeding together for the first time, if there is a survival cost associated with parents being first-time breeders together. This survival cost could be caused by parental care being less efficient in earlier stages of the partnership, due to limited experience with the current partner. For offspring, the effect of parental pair-bond tenure may be less important for survival than having short telomeres, meaning the survival effect of pair-bond tenure is not detected for these offspring. Another explanation would be that there is a bias in offspring with short telomeres that are caught more easily (e.g. in poorer-quality territories) that is directly related to poorer-quality parents and their partnerships. We have no significant direct (longitudinal) support for telomere shortening being greater in offspring reared by short-term partners. However, the sample size of offspring with repeated measurements of telomere length was limited in our dataset (*N*=199). Running identical models with only individuals that were sampled more than once caused the between-offspring age-effect to also disappear, despite the age of individuals only sampled once being relatively evenly distributed. Altogether, this suggest that there was not enough power to detect early-life age-effects using the dataset including only repeatedly sampled offspring.

We found no evidence of a relationship between parental pair-bond duration or fidelity on the other short-term offspring fitness condition measures. This suggests that haematocrit and body mass may not be sensitive enough to capture the stress juveniles experience due to having parents with little pair-breeding experience or following parental pair-disruption. However, body mass (46) and haematocrit (43) both correlate with other early-life environmental factors, and, subsequently with survival, in the Seychelles warbler. The alternative is that this lack of a detectable effect on body mass and haematocrit suggests that parental pair-breeding experience is not a major component of the socio-environmental stressors experienced by offspring. That said, we do detect an effect of parental breeding experience through telomere dynamics, which may be a more sensitive measure.

Male offspring had a 73% higher risk of mortality when both parents died within 6-months after the natal breeding season when the male hatched than males whose parents stayed alive. Males who lost one parent, or whose parents divorced, did not show such an effect. This suggests males suffer fitness costs from being orphaned within the first half year after the season in which they hatch, likely due to a drastic reduction in parental care, e.g. post-fledging provisioning. Female offspring did not show this increased mortality, suggesting females face fewer fitness costs when losing both parents. Why this is the case is unknown, although - since female offspring are more likely to become natal subordinates and helpers/cobreeders than malesL (25,50) - allowing juvenile females to stay and feed within the territory may be more beneficial for the new dominant breeders. Consequently, male juveniles may be more likely to be evicted by breeders taking over the territory, leading to lower survival. This is consistent with previous findings on Seychelles warblers, showing offspring are more likely to be evicted when parents are not present and that eviction leads to lowered survival rates (52). Additionally, males are larger than females (46), and may be more affected by a reduction or absence of post-fledging provisioning than males due to higher nutritional requirements.

Parental pair-bond duration did not affect offspring fitness components in the Seychelles warbler. When controlling for age, partners who have been together for a long time either do not yield higher-quality offspring, compared to those with newer partners, or any effects on offspring early-life condition (e.g. telomere length) of offspring do not translate into any long-term effect on fitness components in the present study. However, early-life sociological and environmental conditions have been linked to juvenile condition and long-term performance in the Seychelles warbler (21,35,46,62), suggesting parental pair-bond tenure does not directly affect offspring performance long-term. Additionally, disruption of the pair-bond when offspring are still dependent on their parents and/or the parental territory did not negatively affect long-term performance of these offspring in this study. Parental pair-bond tenure may yield other benefits rather than increasing offspring quality, such as higher annual survival of the parents (10,67). In the Seychelles warbler, pair-bond tenure and pair-bond disruption through widowhood and divorce do not affect individual reproductive success, but females that are divorced and lose their breeding position have lowered survival compared to females that stayed in their partnership (27). Altogether, these results suggest pair-bonded Seychelles warblers do not yield significant synergistic reproductive benefits by staying and breeding together in terms of offspring quantity or quality.

Finally, it is possible that parental pair-bond tenure and pair-bond fidelity do affect offspring phenotype and fitness, but only in very early-life during the egg and hatchling stage. In this case, the effect will not be detected by our study since we are often unable to assess eggs or nestlings at very early stages in this system due to the inaccessibility of many nests. It could be that adversity of pair-bond disruption and/or short pair-bond tenure means that parents experiencing these are more likely to lose their offspring very early on (as eggs or hatchlings), or do not attempt to breed in that season. Thus, these parents will not be captured in our study (i.e. selective disappearance). Investment in egg composition is commonly influenced by maternal effects (68,69), often mediated by maternal deposition of hormones in the egg (70) and maybe one route by which pair-bonds may impact egg or nestling quality. Furthermore, chicks are entirely dependent on parental care during the nest stage in altricial birds, which may also be negatively affected by pair-bond factors leading to selective disappearance. Post-natal parental care is argued to be the most important maternal effect during this period (71), so much so that it can mask other maternal effects such as investment in the egg (72). However, divorcing and widowhood in the Seychelles warbler do not affect reproductive output at the egg-laying or fledgling stage (27), thus any strong parental effect on offspring survival prior to the point at which they are included in this study, appears unlikely.

5. Conclusion

This study highlights the surprising lack of intergenerational effects of social breeding partnerships on fitness in the Seychelles warbler. Although social monogamy is a common mating system, especially in avian taxa (1,2), the implications of staying with the same partner for extended periods on offspring fitness are understudied. This study sets the groundwork for quantifying long-term parental effects of mate switching and pair-bond tenure in socially monogamous breeders. We hope this study stimulates future research to test if the lack of influence of parental pair-bonds on offspring fitness components that we found is ubiquitous across taxa. A focus on the potential mechanisms through which long-term partnerships in socially monogamous species may have intergenerational effects may provide important insights. Additionally, experimental studies will allow for elucidating the causal link between parental pair-bond and offspring fitness proxies.

Tables & Figures

Table 1. Linear mixed model results on the effect of parental pair-bond tenure and fidelity relative telomere length in on early-life offspring in the Seychelles warbler (*N*=633). Significant fixed effects are in bold. Each pair-bond fidelity category includes the sample size in brackets. Reference categories are pair-bond fidelity = remain together (*N*=527), sex = female, helper presence = no, technician ID = a.

Fixed effects		Estimate	SE	t	p
Intercept		0.611	0.355	1.720	0.086
Pair-bond fidelity	Divorce (*N*=14)	-0.013	0.259	-0.051	0.959
	Female died (*N*=32)	-0.114	0.175	-0.652	0.515
	Male died (*N*=45)	-0.065	0.152	-0.429	0.668
	Translocation (*N*=23)	-0.250	0.228	-1.097	0.274
Offspring age		-0.261	0.157	-1.657	0.098
Maternal age		0.065	0.042	1.539	0.125
Paternal age		-0.067	0.040	-1.701	0.090
Sex	Male	0.023	0.074	0.310	0.757
Helper presence	Yes	-0.052	0.099	-0.530	0.596
Pair-bond tenure		**-0.829**	**0.326**	**-2.546**	**0.011**
Technician ID	A	0.137	0.140	0.981	0.327
Age * Pair-bond tenure		**0.382**	**0.151**	**2.527**	**0.012**
Random effects		sd	N		
Offspring ID		0.162	522		
Mum ID		<0.001	253		

Dad ID	<0.001	240
Hatch season	0.329	30
Plate ID	0.324	56
Residual	0.875	

Table 2. Cox mixed effects proportional hazards model results including the hazards ratio (HR) on the effect of parental pair-bond tenure and fidelity on offspring lifespan in the Seychelles warbler in (A) females (N=599) and (B) males (N=583). Significant fixed effects are in bold. Each pair-bond fidelity category includes the sample size in brackets. Reference categories are pair-bond fidelity = remain together (N_f=502; N_m=481), helper presence = no, sibling presence = no.

		A. Females				B. Males			
Fixed effects		HR	SE	z	p	HR	SE	z	p
Pair-bond fidelity	Both died (N_f=9; N_m=6)	0.791	0.406	-0.58	0.565	**2.676**	**0.469**	**2.10**	**0.036**
	Divorce (N_f=8; N_m=14)	0.930	0.477	-0.15	0.878	1.050	0.310	0.16	0.880
	Female died (N_f=31; N_m=37)	1.198	0.227	0.79	0.428	1.311	0.187	1.45	0.150
	Male died (N_f=41; N_m=37)	1.012	0.197	0.06	0.953	1.075	0.200	0.36	0.720
	Translocation (N_f=8; N_m=8)	1.202	0.435	0.42	0.672	1.301	0.486	0.54	0.590
Mum age		1.070	0.059	1.16	0.244	1.041	0.052	0.78	0.430
Helper presence	Yes	1.3273	0.137	1.76	0.078	1.135	0.141	0.90	0.370
Sibling presence	Yes	1.177	0.113	1.44	0.149	**1.284**	**0.119**	**2.10**	**0.036**
Group size		1.023	0.062	0.36	0.716	0.963	0.065	-0.57	0.570

Pair-bond tenure	1.071	0.059	1.16	0.244	0.982	0.055	-0.33	0.740
Territory quality	0.904	0.060	-1.69	0.091	**0.884**	**0.059**	**-2.12**	**0.034**
Random effects	sd	N			sd	N		
Social mum ID	0.019	272			0.006	289		
Social dad ID	0.018	284			0.015	296		
Mum ID	0.349	36			0.159	302		
Dad ID	0.015	283			0.020	276		
Hatch season	0.195	263			0.141	37		

Table 3. Zero-inflated generalised linear mixed model results on the effect of parental pair-bond tenure and fidelity on offspring lifetime reproductive success in the Seychelles warbler in (A) females (*N*=500) and (B) males (*N*=457). Significant fixed effects are in bold. Each pair-bond fidelity category includes the sample size in brackets Reference categories are pair-bond fidelity = remain together (N_f=425; N_m=389), helper presence = no, sibling presence = no. NAs indicate absence of a pair-fidelity category due to low sample size (*N*<6).

		A. Females				B. Males			
Fixed effects		Estimate	SE	z	p	Estimate	SE	z	p
Intercept		**1.055**	**0.109**	**9.719**	**<0.001**	**0.568**	**0.200**	**2.836**	**0.005**
Zero-inflated intercept		0.098	0.141	0.692	0.489	-0.568	0.464	-1.225	0.220
Pair-bond fidelity	Both died (N_f=8)	-0.160	0.474	-1.084	0.278	NA	NA	NA	NA
	Divorce (N_m=127)	NA	NA	NA	NA	-1.009	0.642	-1.572	0.116
	Female died (N_f=26; N_m=34)	-0.344	0.318	-1.084	0.278	-0.120	0.347	-0.346	0.729
	Male died (N_f=36; N_m=30)	-0.264	0.234	-1.129	0.259	0.114	0.384	0.296	0.767
	Translocation (N_f=7)	-0.303	0.670	-0.452	0.651	NA	NA	NA	NA
Maternal age		-0.127	0.087	-1.464	0.143	0.085	0.102	0.830	0.406
Helper presence	Yes	-0.372	0.210	-1.769	0.077	0.216	0.280	0.774	0.439
Sibling presence	Yes	-0.012	0.144	-0.085	0.932	-0.265	0.253	-1.048	0.295
Group size		-0.091	0.083	-1.098	0.272	0.041	0.115	0.357	0.721
Pair-bond tenure		0.062	0.080	0.777	0.437	0.116	0.100	1.159	0.247
Territory quality		0.012	0.064	0.195	0.845	0.062	0.107	0.582	0.561

Hatch season	**-0.495**	**0.082**	**-6.018**	**<0.001**	**-0.562**	**0.132**	**-4.249**	**<0.001**
Random effects	sd	N			sd	N		
Social mum ID	0.0001	235			<0.00001	247		
Social dad ID	<0.00001	246			<0.00001	258		
Mum ID	<0.00001	246			<0.00001	254		
Dad ID	<0.00001	230			0.0001	243		
Hatch season	0.0001	36			0.392	36		
Breeding group	0.00002	462			0.00001	423		

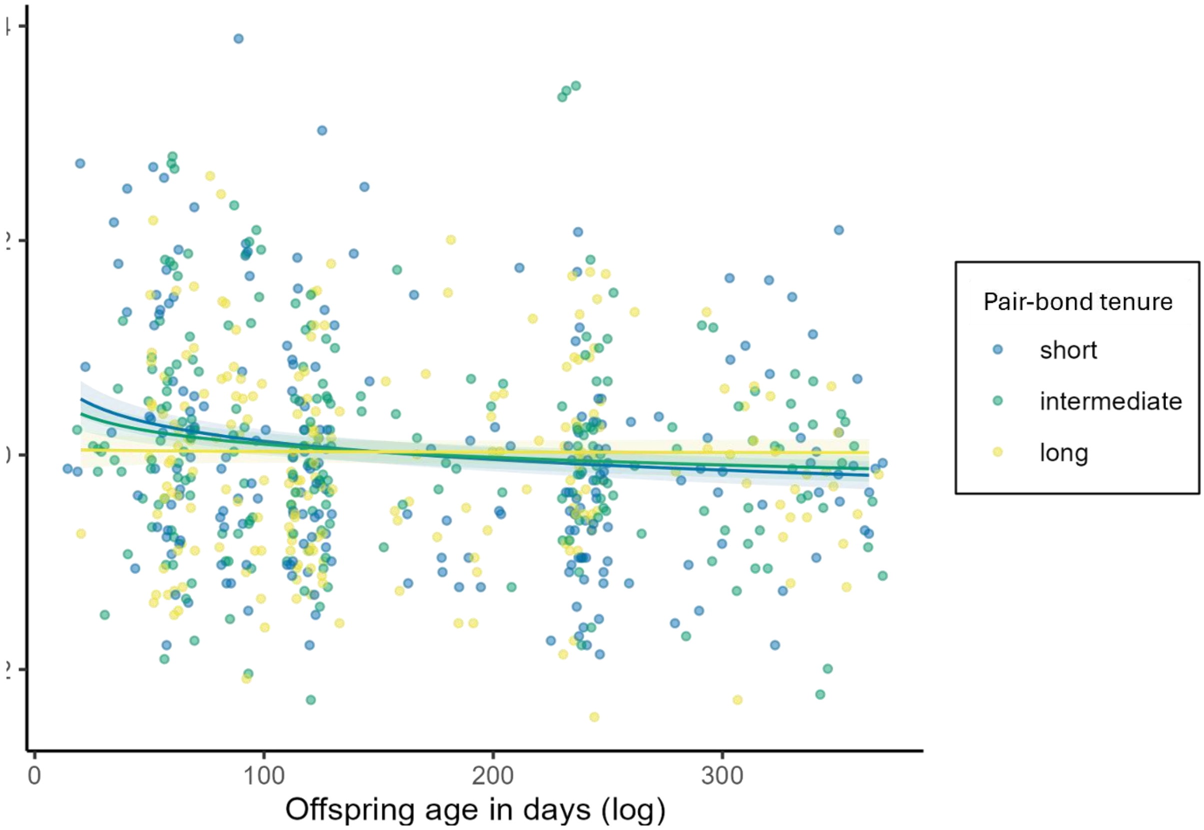

Figure 1. Association between relative telomere length (RTL; Z-transformed) from the Seychelles warbler against age-at-sampling in relation to parental pair-bond tenure (*N*=652), for offspring between 40 days and one year old (*N*=538). For ease of visualization, parental pair-bond tenure is categorized as short (in blue, lowest 33%, 0-1.1 years), intermediate (in green, middle 33%, 1.1-2.7 years) and long (in yellow, highest 33%, 2.7-13.1 years) but is a continuous variable in the analyses. Lines depict the model prediction with the standard error (shaded area). Points depict raw data that are semi-transparent to show overlapping values.

Supplementary material

Table S1. Linear mixed model results on the effect of parental pair-bond tenure and fidelity on relative telomere length in early-life offspring in the Seychelles warbler including offspring less than 40 days old (*N*=652). Significant fixed effects are in bold. Each pair-bond fidelity category includes the sample size in brackets. Reference categories are pair-bond fidelity = remain together (*N*=545), sex = female, technician ID = a, helper presence = no.

Fixed effects	Category	Estimate	SE	t	p
Intercept		0.561	0.317	1.771	0.077
Pair-bond fidelity	Divorce (*N*=14)	-0.010	0.257	-0.040	0.968
	Female died (*N*=33)	-0.139	0.171	-0.812	0.417
	Male died (*N*=46)	-0.097	0.149	-0.653	0.514
	Translocation (*N*=23)	-0.254	0.227	-1.120	0.264
Offspring age		-0.244	0.141	-1.729	0.084
Maternal age		0.066	0.041	1.607	0.109
Paternal age		-0.070	0.039	-1.797	0.073
Sex	Male	0.032	0.073	0.432	0.666
Helper presence	Yes	-0.061	0.096	-0.631	0.528
Pair-bond tenure		**-0.955**	**0.307**	**-3.116**	**0.002**
Technician ID	B	0.120	0.135	0.889	0.374
Offspring age * Pair-bond tenure		**0.439**	**0.143**	**3.075**	**0.002**
Random effects		Std.Dev.	N		
Offspring ID		0.214	538		
Maternal ID		<0.001	257		
Paternal ID		<0.001	244		
Hatch season		0.323	30		
Plate ID		0.324	57		
Residual		0.856			

Table S2. Linear mixed model results on the effect of parental pair-bond tenure and fidelity on between- and within-individual change in offspring relative telomere length in the Seychelles warbler (*N*=633, including *N*=99 offspring with repeat samples of RTL). The model investigates between-offspring age effects (mean age) and within-offspring age effects (deviation from the mean age). Significant fixed effects are in bold. Each pair-bond fidelity category includes the sample size in brackets. Reference categories are pair-bond fidelity = remain together (*N*=527), sex = female, technician ID = a, helper presence = no.

Fixed effects		Estimate	SE	t	p
Intercept		0.684	0.399	1.714	0.087
Pair-bond fidelity	Divorce (*N*=14)	-0.012	0.259	-0.044	0.965
	Female died (*N*=32)	-0.116	0.175	-0.657	0.511
	Male died (*N*=45)	-0.065	0.152	-0.428	0.669
	Translocation (*N*=23)	-0.249	0.227	-1.096	0.274
Between-offspring age		-0.294	0.179	-1.647	0.100
Within-offspring age		-0.107	0.335	-0.318	0.751
Maternal age		0.064	0.042	1.519	0.130
Paternal age		-0.066	0.040	-1.674	0.095
Sex	Male	0.024	0.074	0.327	0.744
Helper presence	Yes	-0.054	0.099	-0.551	0.582
Pair-bond tenure		**-0.859**	**0.365**	**-2.354**	**0.019**
Technician ID	A	0.133	0.140	0.953	0.341
Between-offspring age * Pair-bond tenure		**0.396**	**0.170**	**2.332**	**0.020**
Random effects		sd	N		
Offspring ID		0.141	522		

Mum ID	<0.001	253
Dad ID	<0.001	240
Hatch season	0.329	30
Plate ID	0.320	56
Residual	0.881	

Table S3. Linear mixed model results on the effect of parental pair-bond tenure and fidelity on between- and within-individual change in offspring relative telomere length in the Seychelles warbler for offspring using repeat samples only (*N*=205). The model investigates between-offspring age effects (mean age) and within-offspring age effects (deviation from the mean age). Significant fixed effects are in bold. Each pair-bond fidelity category includes the sample size in brackets. Reference categories are pair-bond fidelity = remain together (*N*=179), sex = female, technician ID = a, helper presence = no.

Fixed effects		Estimate	SE	t	p
Intercept		0.251	1.253	0.200	0.841
Pair-bond fidelity	Male died (*N*=10)	-0.218	0.346	-0.629	0.530
	Translocation (*N*=18)	-0.247	0.282	-0.878	0.381
Between-offspring age		-0.071	0.561	-0.127	0.899
Within-offspring age		-0.108	0.355	-0.304	0.761
Maternal age		0.022	0.083	0.263	0.793
Paternal age		-0.060	0.073	-0.812	0.418
Sex	Male	0.090	0.141	0.638	0.524
Helper presence	Yes	-0.332	0.176	-1.884	0.061
Pair-bond tenure		-0.041	0.084	-0.486	0.627
Technician ID	A	0.053	0.252	0.211	0.833
Random effects		**sd**	**N**		
Offspring ID		<0.001	99		
Mum ID		<0.001	72		
Dad ID		<0.001	79		
Hatch season		0.164	20		
Plate ID		0.360	50		

Residual	0.928

Table S4. Linear mixed model results on the effect of parental pair-bond tenure and fidelity on relative telomere length in early-life offspring in the Seychelles warbler (*N*=652) using a binary variable for pair-bond fidelity (yes/no). Significant fixed effects are in bold. Reference categories are pair-bond fidelity = yes (remain together), sex = female, technician ID = a, helper presence = no.

Fixed effects		Estimate	SE	t	p
Intercept		0.552	0.313	1.761	0.079
Pair-bond fidelity	No	-0.127	0.099	-1.289	0.198
Offspring age		-0.239	0.140	-1.711	0.088
Maternal age		0.068	0.041	1.651	0.099
Paternal age		-0.069	0.039	-1.797	0.073
Sex	Male	0.032	0.073	0.442	0.659
Helper presence	Yes	-0.058	0.095	-0.605	0.545
Pair-bond tenure		**-0.956**	**0.306**	**-3.126**	**0.002**
Helper presence	Yes	-0.058	0.095	-0.605	0.545
Technician ID	A	0.126	0.134	0.943	0.346
Offspring age * Pair-bond tenure		**0.440**	**0.143**	**3.089**	**0.002**
Random effects		sd	N		
Offspring ID		0.198	538		
Mum ID		<0.001	257		
Dad ID		<0.001	244		
Hatch season		0.326	30		
Plate ID		0.323	57		
Residual		0.858			

Table S5. Linear mixed model results on the effect of parental pair-bond tenure and fidelity on body mass in early-life offspring in the Seychelles warbler (*N*=591). Significant fixed effects are in bold. Each pair-bond fidelity category includes the sample size in brackets. Reference categories are pair-bond fidelity = remain together (*N*=524), sex = female.

Fixed effects		Estimate	SE	t	p
Intercept		**14.335**	**0.170**	**84.456**	**<0.001**
Pair-bond fidelity	Both died (*N*=13)	-0.324	0.368	-0.879	0.380
	Divorce (*N*=19)	0.181	0.224	0.809	0.419
	Female died (*N*=24)	-0.348	0.192	-1.808	0.071
	Male died (*N*=30)	0.214	0.167	1.284	0.200
	Translocation (*N*=13)	-0.467	0.282	-1.658	0.098
Offspring age		**0.106**	**0.037**	**2.877**	**0.004**
Maternal age		0.033	0.041	0.801	0.423
Paternal age		-0.038	0.040	-0.966	0.335
Sex	**Male**	**0.906**	**0.114**	**7.979**	**0.000**
Pair-bond tenure		0.001	0.044	0.033	0.974
Tarsus length		**0.260**	**0.056**	**4.654**	**0.000**
Catch time		**0.034**	**0.011**	**2.931**	**0.004**
Random effects		sd	N		
Offspring ID		0.558	468		
Mum ID		0.098	246		
Dad ID		0.000	237		
Hatch season		0.323	29		
Residual		0.856			

Table S6. Linear mixed model results on the effect of parental pair-bond tenure and fidelity on haematocrit in early-life offspring in the Seychelles warbler (*N*=579). Significant fixed effects are in bold. Each pair-bond fidelity category includes the sample size in brackets. Reference categories are pair-bond fidelity = remain together (*N*=487), sex = female.

		Estimate	SE	t	p
Intercept		0.457	0.008	58.639	<0.001
Pair-pond fidelity	Both died (*N*=12)	-0.005	0.018	-0.284	0.777
	Divorce (*N*=18)	0.002	0.011	0.166	0.868
	Female died (*N*=20)	0.010	0.009	1.068	0.286
	Male died (*N*=28)	0.011	0.008	1.359	0.175
	Translocation (*N*=14)	0.008	0.012	0.624	0.533
Age		**0.021**	**0.002**	**11.536**	**<0.001**
Age^2		**-0.008**	**0.002**	**-3.843**	**<0.001**
Maternal age		0.002	0.002	1.006	0.315
Paternal age		0.001	0.002	0.538	0.591
Sex	**Male**	**-0.009**	**0.004**	**-2.618**	**0.009**
Pair-bond tenure		-0.001	0.002	-0.280	0.780
Catch time		**-0.002**	**0.001**	**-2.916**	**0.004**
Random effects		sd	N		
Offspring ID		0.021	430		
Mum ID		0.000	222		
Dad ID		0.007	2		
Hatch season		0.008	28		
Residual		0.030			

Table S7. Linear mixed model results on the effect of parental pair-bond tenure and fidelity on body mass in early-life offspring in the Seychelles warbler (*N*=591) using a binary variable for pair-bond fidelity (yes/no). Significant fixed effects are in bold. Reference categories are pair-bond fidelity = yes (remain together), sex = female.

Fixed effects		Estimate	SE	t	p
Intercept		**14.314**	**0.171**	**83.894**	**<0.001**
Pair-bond fidelity	No	-0.067	0.105	-0.636	0.525
Offspring age		**0.104**	**0.037**	**2.816**	**0.005**
Maternal age		0.030	0.042	0.712	0.477
Paternal age		-0.033	0.040	-0.823	0.411
Sex	**Male**	**0.919**	**0.114**	**8.087**	**<0.001**
Pair-bond tenure		0.008	0.044	0.179	0.858
Tarsus length		**0.253**	**0.056**	**4.531**	**<0.001**
Catch time		**0.035**	**0.011**	**3.062**	**0.002**
Random effects		sd	N		
Offspring ID		0.56688	468		
Mum ID		0.08806	246		
Dad ID		0.05682	237		
Hatch season		0.30099	29		
Residual		0.59568			

Table S8. Linear mixed model results on the effect of parental pair-bond tenure and fidelity on haematocrit in early-life offspring in the Seychelles warbler (*N*=550) using a binary variable for pair-bond fidelity (yes/no). Significant fixed effects are in bold. Reference categories are pair-bond fidelity = yes (remain together), sex = female.

Fixed effects		Estimate	SE	t	p
Intercept		**0.457**	**0.008**	**58.854**	**<0.001**
Pair-bond fidelity	No	0.007	0.005	1.522	0.129
Age		**0.021**	**0.002**	**11.573**	**<0.001**
Age^2		**-0.008**	**0.002**	**-3.862**	**<0.001**
Mum age		0.002	0.002	0.998	0.319
Dad age		0.001	0.002	0.612	0.541
Sex	**Male**	**-0.009**	**0.004**	**-2.577**	**0.010**
Pair-bond tenure		0.000	0.002	-0.239	0.811
Catch time		**-0.002**	**0.001**	**-2.961**	**0.003**
Random effects		sd	N		
Offspring ID		0.021	430		
Mum ID		0.000	222		
Dad ID		0.007	209		
Hatch season		0.008	28		
Residual		0.030			

Table S9. Generalised linear mixed model results on the effect of parental pair-bond tenure and fidelity on offspring lifespan in the Seychelles warbler in (A) females (*N*=502) and (B) males (*N*=475). Significant fixed effects are in bold. Each pair-bond fidelity category includes the sample size in brackets. Reference categories are pair-bond fidelity = remain together (N_f=425; N_m=389), helper presence = no, sibling presence = no. NAs indicate absence of a pair-bond fidelity category due to low sample size (*N*<6).

		A. Females				B. Males			
Fixed effects		Estimate	SE	z	p	Estimate	SE	z	p
Intercept		**0.882**	**0.134**	**6.561**	**<0.001**	0.320	0.642	0.499	0.618
Pair-bond fidelity	Both died (N_f=8)	0.244	0.492	0.496	0.620	NA	NA	NA	NA
	Divorce (N_m=12)	NA	NA	NA	NA	0.535	0.736	0.726	0.468
	Female died (N_f=26; N_m=34)	-0.306	0.300	-1.019	0.308	0.432	0.677	0.638	0.524
	Male died (N_f=36; N_m=30)	0.027	0.243	0.112	0.911	0.540	0.677	0.797	0.425
	Translocation (N_f=7)	0.051	0.537	-0.095	0.925	NA	NA	NA	NA
Maternal age		-0.023	0.073	-0.314	0.754	-0.002	0.066	-0.026	0.979
Helper presence	Yes	-0.291	0.173	-1.683	0.092	-0.033	0.176	-0.191	0.849
Sibling presence	Yes	0.027	0.140	0.194	0.846	-0.241	0.143	-1.691	0.091
Group size		-0.071	0.073	-0.968	0.331	-0.017	0.071	-0.231	0.817
Pair-bond tenure		0.018	0.072	0.257	0.797	0.030	0.065	0.453	0.979
Territory quality		0.078	0.066	1.185	0.236	0.023	0.060	0.402	0.688
Hatch season		**-0.343**	**0.068**	**-5.023**	**<0.001**	**-0.278**	**0.067**	**-4.151**	**<0.001**

Random effects	sd	N	sd	N
Social mum ID	0.00003	235	0.00002	256
Social dad ID	0.00002	247	0.00002	266
Mum ID	0.00002	246	0.00004	265
Dad ID	0.00003	231	0.00003	249
Hatch season	0.00004	36	0.138	36
Breeding group	0.00001	464	0.00003	440

Table S10. Cox mixed effects proportional hazards model results including the hazards ratio (HR) on the effect of parental pair-bond tenure and fidelity on offspring annual survival in the Seychelles warbler in (A) females (*N*=599) and (B) males (*N*=582) using a binary variable for pair-bond fidelity (yes/no). Significant fixed effects are in bold. Reference categories are pair-bond fidelity = yes (remain together), helper presence = no, sibling presence = no.

		A. Females				B. Males			
Fixed effects		HR	SE	z	p	HR	SE	z	p
Pair-bond fidelity	No	1.044	0.135	0.32	0.750	1.216	0.127	1.54	0.120
Mum age		1.071	0.057	1.21	0.230	0.976	0.055	-0.44	0.660
Helper presence	Yes	1.275	0.134	1.81	0.071	1.133	0.140	0.89	0.370
Sibling presence	Yes	1.127	0.111	1.08	0.280	**1.297**	**0.118**	**2.21**	**0.027**
Group size		1.028	0.060	0.46	0.640	0.962	0.065	-0.59	0.550
Pair-bond tenure		0.997	0.057	-0.05	0.960	0.976	0.055	-0.44	0.660
Territory quality		0.897	0.058	-1.88	0.060	**0.889**	**0.058**	**-2.02**	**0.043**
Random effects		sd	N			sd	N		
Mum ID		0.312	272			0.016	289		
Dad ID		0.008	284			0.019	296		
Social mum ID		0.017	36			0.020	302		
Social dad ID		0.013	283			0.162	276		
Hatch season		0.178	263			0.156	37		

Table S11. Generalised linear mixed model results on the effect of parental pair-bond tenure and fidelity on offspring lifespan in the Seychelles warbler in (A) females (*N*=502) and (B) males (*N*=475) using a binary variable for pair-bond fidelity (yes/no). Significant fixed effects are in bold. Reference categories are pair-bond fidelity = yes (remain together), helper presence = no, sibling presence = no.

		A. Females				B. Males			
Fixed effects		Estimate	SE	z	p	Estimate	SE	z	p
Intercept		**0.870**	**0.136**	**6.410**	**<0.001**	**0.983**	**0.108**	**9.129**	**<0.001**
Pair-bond fidelity	No	-0.051	0.182	-0.278	0.781	-0.196	0.155	-1.613	0.107
Mum age		-0.032	0.072	-1.149	0.664	-0.004	0.066	-0.066	0.947
Helper presence	Yes	-0.258	0.170	-1.515	0.130	-0.023	0.142	-1.740	0.082
Sibling presence	Yes	0.022	0.140	0.159	0.874	-0.247	0.142	-1.740	0.082
Group size		-0.083	0.072	-1.149	0.251	-0.028	0.070	-0.395	0.693
Pair-bond tenure		0.029	0.071	0.410	0.682	0.037	0.065	0.568	0.570
Territory quality		0.085	0.065	1.307	0.191	0.018	0.060	0.301	0.763
Hatch season		**-0.351**	**0.068**	**-5.175**	**<0.001**	**-0.292**	**0.067**	**-4.287**	**<0.001**
Random effects		sd	N			sd	N		
Social mum ID		0.00004	233			0.00003	256		
Social dad ID		0.00002	247			0.00002	266		
Mum ID		0.00003	246			0.00004	265		
Dad ID		0.00003	231			0.00003	249		
Hatch season		0.00005	36			0.1257	36		
Breeding group		0.00001	464			0.00003	440		

Table S12. Zero-inflated generalised linear mixed model results on the effect of parental pair-bond tenure and fidelity on offspring lifetime reproductive success in the Seychelles warbler in (A) females (*N*=500) and (B) males (*N*=467) using a binary variable for pair-bond fidelity (yes/no). Significant fixed effects are in bold. Reference categories are pair-bond fidelity = yes (remain together), helper presence = no, sibling presence = no.

		A. Females				B. Males			
Fixed effects		Estimate	SE	z	P	Estimate	SE	z	p
Intercept		**1.051**	**0.109**	**9.677**	**<0.0001**	**0.520**	**0.226**	**2.297**	**0.021**
Zero-inflated intercept		0.100	0.141	0.708	0.479	-0.733	0.613	-1.197	0.231
Pair-bond fidelity	No	-0.310	0.182	-1.705	0.088	-0.226	0.253	-0.893	0.372
Mum age		-0.131	0.086	-1.528	0.127	0.077	0.103	0.742	0.458
Sibling presence	Yes	-0.013	0.143	-0.091	0.927	-0.283	0.251	-1.126	0.260
Group size		-0.091	0.081	-1.134	0.257	0.037	0.116	0.317	0.752
Helper presence	Yes	-0.356	0.204	-1.745	0.081	0.168	0.282	0.597	0.551
Pair-bond tenure		0.069	0.078	0.886	0.375	0.137	0.103	1.328	0.184
Territory quality		0.017	0.063	0.270	0.787	0.063	0.108	0.584	0.559
Hatch season		**-0.504**	**0.082**	**-6.171**	**<0.001**	**-0.587**	**0.133**	**-4.405**	**<0.001**
Random effects		sd	N			sd	N		
Social mum ID		0.0002	236			<0.00001	252		
Social dad ID		<0.00001	247			0.00001	264		
Mum ID		<0.00001	247			0.00001	260		
Dad ID		<0.00001	232			0.0001	247		
Hatch season		0.0001	36			0.3883	36		
Breeding group		0.00003	466			0.00008	433		

Bibliography

1. Lack D. Ecological adaptations for breeding in birds. London: Methuen; 1968. 409 p.
2. Emlen ST, Oring LW. Ecology, Sexual Selection, and the Evolution of Mating Systems. Science. 1977;197(4300):215–23.
3. Mariette MM, Griffith SC. The Adaptive Significance of Provisioning and Foraging Coordination between Breeding Partners. The American Naturalist. 2015 Feb;185(2):270–80.
4. Patrick SC, Corbeau A, Réale D, Weimerskirch H. Coordination in parental effort decreases with age in a long-lived seabird. Oikos. 2020;129(12):1763–72.
5. Black JM. Partnerships in birds. The study of monogamy. Oxford, UK: Oxford University Press; 1996.
6. Leach AG, Riecke TV, Sedinger JS, Ward DH, Boyd S. Mate fidelity improves survival and breeding propensity of a long-lived bird. Journal of Animal Ecology. 2020;89(10):2290–9.
7. Black JM. Fitness consequences of long-term pair bonds in barnacle geese: monogamy in the extreme. Behavioral Ecology. 2001 Sep 1;12(5):640–5.
8. Culina A, Firth JA, Hinde CA. Familiarity breeds success: Pairs that meet earlier experience increased breeding performance in a wild bird population: Pairs that meet earlier do better. Proceedings of the Royal Society B: Biological Sciences. 2020;287(1941).
9. Nicolai CA, Sedinger JS, Ward DH, Boyd WS. Mate loss affects survival but not breeding in black brant geese. Behavioral Ecology. 2012;23(3):643–8.
10. Culina A, Lachish S, Sheldon BC. Evidence of a link between survival and pair fidelity across multiple tit populations. Journal of Avian Biology. 2015 Sep;46(5):507–15.
11. Culina A, Radersma R, Sheldon BC. Trading up: the fitness consequences of divorce in monogamous birds. Biological Reviews. 2015 Nov;90(4):1015–34.
12. Love OP, McGowan PO, Sheriff MJ. Maternal adversity and ecological stressors in natural populations: the role of stress axis programming in individuals, with implications for populations and communities. Functional Ecology. 2013;27(1):81–92.
13. Wolf JB, Wade MJ. What Are Maternal Effects (And What Are They Not)? Philosophical Transactions: Biological Sciences. 2009;364(1520):1107–15.
14. Mousseau TA, Fox CW. The adaptive significance of maternal effects. Trends in Ecology & Evolution. 1998;13(10):403–7.
15. Kirkpatrick M, Lande R. The Evolution of Maternal Characters. Evolution. 1989;43(3):485–503.
16. Price T. Maternal and Paternal Effects in Birds. In: Maternal effects as adaptations. Oxford, UK: Oxford University Press; 1998. p. 202–26.
17. Moore MP, Whiteman HH, Martin RA. A mother’s legacy: the strength of maternal effects in animal populations. Ecology Letters. 2019;22(10):1620–8.

18. Clutton-Brock TH, Albon SD, Guinness FE. Parental investment and sex differences in juvenile mortality in birds and mammals. Nature. 1985;313(5998):131–3.

19. Arslan RC, Willführ KP, Frans EM, Verweij KJH, Bürkner PC, Myrskylä M, et al. Older fathers' children have lower evolutionary fitness across four centuries and in four populations. Proceedings: Biological Sciences. 2017;284(1862):1–9.

20. Bock MJ, Jarvis GC, Corey EL, Stone EE, Gribble KE. Maternal age alters offspring lifespan, fitness, and lifespan extension under caloric restriction. Sci Rep. 2019;9(1):3138.

21. Sparks AM, Hammers M, Komdeur J, Burke T, Richardson DS, Dugdale HL. Sex-dependent effects of parental age on offspring fitness in a cooperatively breeding bird. Evolution Letters. 2022 Dec 1;6(6):438–49.

22. Monaghan P. Early Growth Conditions, Phenotypic Development and Environmental Change. Philosophical Transactions: Biological Sciences. 2008;363(1497):1635–45.

23. Amato PR, Keith B. Parental divorce and the well-being of children: A meta-analysis. Psychological Bulletin. 1991;110:26–46.

24. Amato PR, Keith B. Parental divorce and adult well-being: a meta-analysis. Journal of Marriage and the Family. 1991;53(1):43–58.

25. Komdeur J. Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. Nature. 1992;358:493–5.

26. Wright DJ, Spurgin LG, Collar NJ, Komdeur J, Burke T, Richardson DS. The impact of translocations on neutral and functional genetic diversity within and among populations of the Seychelles warbler. Molecular Ecology. 2014;23(9):2165–77.

27. Speelman FJD, Burke TA, Komdeur J, Richardson DS, Dugdale HL. Causes and consequences of divorce in a long-lived socially monogamous bird. Authorea; 2024.

28. Komdeur J. Experimental evidence for helping and hindering by previous offspring in the cooperative-breeding Seychelles warbler Acrocephalus sechellensis. Behavioral Ecology and Sociobiology. 1994;34(3):175–86.

29. Komdeur J. Influence of helping and breeding experience on reproductive performance in the Seychelles warbler: A translocation experiment. Behavioral Ecology. 1996;7(3):326–33.

30. Komdeur J, Piersma T, Kraaijeveld K, Kraaijeveld-Smit F, Richardson DS. Why Seychelles Warblers fail to recolonize nearby islands: Unwilling or unable to fly there? Ibis. 2004;146(2):298–302.

31. Brouwer L, Richardson DS, Eikenaar C, Komdeur J. The role of group size and environmental factors on survival in a cooperatively breeding tropical passerine. Journal of Animal Ecology. 2006;75(6):1321–9.

32. Brouwer L, Barr I, Van De Pol M, Burke T, Komdeur J, Richardson DS. MHC-dependent survival in a wild population: Evidence for hidden genetic benefits gained through extra-pair fertilizations. Molecular Ecology. 2010;19(16):3444–55.

33. Sparks AM, Spurgin LG, Van Der Velde M, Fairfield EA, Komdeur J, Burke T, et al. Telomere heritability and parental age at conception effects in a wild avian population. Molecular Ecology. 2021;00:1–15.

34. von Zglinicki T. Oxidative stress shortens telomeres. Trends in Biochemical Sciences. 2002 Jul 1;27(7):339–44.

35. Spurgin LG, Bebbington K, Fairfield EA, Hammers M, Komdeur J, Burke T, et al. Spatio-temporal variation in lifelong telomere dynamics in a long-term ecological study. Journal of Animal Ecology. 2018;87(1):187–98.

36. Barrett ELB, Burke TA, Hammers M, Komdeur J, Richardson DS. Telomere length and dynamics predict mortality in a wild longitudinal study. Molecular Ecology. 2013;22(1):249–59.

37. Bebbington K, Spurgin LG, Fairfield EA, Dugdale HL, Komdeur J, Burke T, et al. Telomere length reveals cumulative individual and transgenerational inbreeding effects in a passerine bird. Molecular Ecology. 2016;25(12):2949–60.

38. Bebbington K, Kingma SA, Fairfield EA, Dugdale HL, Komdeur J, Spurgin LG, et al. Kinship and familiarity mitigate costs of social conflict between Seychelles warbler neighbors. Proceedings of the National Academy of Sciences of the United States of America. 2017;114(43):E9036–45.

39. Hammers M, Kingma SA, Spurgin LG, Bebbington K, Dugdale HL, Burke T, et al. Breeders that receive help age more slowly in a cooperatively breeding bird. Nature Communications [Internet]. 2019 [cited 2021 Apr 16];10(1301). Available from: https://doi.org/10.1038/s41467-019-09229-3

40. Brown TJ, Spurgin LG, Dugdale HL, Komdeur J, Burke T, Richardson DS. Causes and consequences of telomere lengthening in a wild vertebrate population. Molecular Ecology. 2022;31(23):5933–45.

41. van de Crommenacker J, Hammers M, Dugdale HL, Burke TA, Komdeur J, Richardson DS. Early-life conditions impact juvenile telomere length, but do not predict later life-history strategies or fitness in a wild vertebrate. Ecol Evol. 2022 Jul;12(6):e8971.

42. Boonekamp JJ, Simons MJP, Hemerik L, Verhulst S. Telomere length behaves as biomarker of somatic redundancy rather than biological age. Aging Cell. 2013 Apr;12(2):330–2.

43. Brown TJ, Hammers M, Taylor M, Dugdale HL, Komdeur J, Richardson DS. Hematocrit, age, and survival in a wild vertebrate population. Ecology and Evolution. 2021;11(1):214–26.

44. Arendt JD. Adaptive Intrinsic Growth Rates: An Integration Across Taxa. The Quarterly Review of Biology. 1997 Jun;72(2):149–77.

45. Labocha MK, Hayes JP. Morphometric indices of body condition in birds: a review. J Ornithol. 2012 Jan 1;153(1):1–22.

46. Brown TJ, Dugdale HL, Hammers M, Komdeur J, Richardson DS. Seychelles warblers with silver spoons: Juvenile body mass is a lifelong predictor of annual survival, but not annual reproduction or senescence. Ecology and Evolution. 2022;12(7):e9049.

47. Bebbington K, Kingma SA, Fairfield EA, Spurgin LG, Komdeur J, Richardson DS. Consequences of sibling rivalry vary across life in a passerine bird. Behavioral Ecology. 2017 Apr 1;28(2):407–18.

48. Brouwer L, Tinbergen JM, Both C, Bristol R, Richardson DS, Komdeur J. Experimental evidence for density-dependent reproduction in a cooperatively breeding passerine. Ecology. 2009;90(3):729–41.

49. Komdeur J. Cooperative breeding in the Seychelles warbler. University of Cambridge; 1991.

50. Richardson DS, Burke T, Komdeur J. Direct benefits and the evolution of female-biased cooperative breeding in Seychelles warblers. Evolution. 2002;56(11):2313–21.

51. Richardson DS, Burke T, Komdeur J. Grandparent helpers: The adaptive significance of older, postdominant helpers in the Seychelles warbler. Evolution. 2007;61(12):2790–800.

52. Kingma SA, Bebbington K, Hammers M, Richardson DS, Komdeur J. Delayed dispersal and the costs and benefits of different routes to independent breeding in a cooperatively breeding bird. Evolution. 2016;70(11):2595–610.

53. Richardson DS, Jury FL, Blaakmeer K, Komdeur J, Burke T. Parentage assignment and extra-group paternity in a cooperative breeder: The Seychelles warbler (Acrocephalus sechellensis). Molecular Ecology. 2001;10(9):2263–73.

54. Raj Pant S, Komdeur J, Burke TA, Dugdale HL, Richardson DS. Socio-ecological conditions and female infidelity in the Seychelles warbler. Behavioral Ecology. 2019;30(5):1254–64.

55. Hadfield JD, Richardson DS, Burke T. Towards unbiased parentage assignment: Combining genetic, behavioural and spatial data in a Bayesian framework. Molecular Ecology. 2006;15(12):3715–30.

56. R Core Team. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing; 2023.

57. Bates D, Maechler M, Bolker BM, Walker S. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software. 2015;67(1):1–48.

58. Brooks ME, Kristensen K, Benthem KJ van, Magnusson A, Berg CW, Nielsen A, et al. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal. 2017;9(2):378–400.

59. Lüdecke D, Ben-Shachar MS, Patil I, Waggoner P, Makowski D. performance: An R Package for Assessment, Comparison and Testing of Statistical Models. Journal of Open Source Software. 2021 Apr 21;6(60):3139.

60. Hartig F. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models [Internet]. 2022. Available from: https://CRAN.R-project.org/package=DHARMa

61. van de Pol M, Wright J. A simple method for distinguishing within- versus between-subject effects using mixed models. Animal Behaviour. 2009;77(3):753–8.

62. Hammers M, Kingma SA, Van Boheemen LA, Sparks AM, Burke T, Dugdale HL, et al. Helpers compensate for age-related declines in parental care and offspring survival in a cooperatively breeding bird. Evolution Letters. 2021;5(2):143–53.

63. Bouwhuis S, Vedder O, Becker PH. Sex-specific pathways of parental age effects on offspring lifetime reproductive success in a long-lived seabird. Evolution. 2015 Jul;69(7):1760–71.

64. Therneau TM. coxme: Mixed Effects Cox Models [Internet]. 2022 [cited 2022 Dec 22]. Available from: https://CRAN.R-project.org/package=coxme

65. Grambsch PM, Therneau TM. Proportional hazards tests and diagnostics based on weighted residuals. Biometrika. 1994 Sep 1;81(3):515–26.

66. Crean AJ, Bonduriansky R. What is a paternal effect? Trends in Ecology & Evolution. 2014 Oct 1;29(10):554–9.

67. Bried J, Pontier D, Jouventin P. Mate fidelity in monogamous birds: A re-examination of the Procellariiformes. Animal Behaviour. 2003;65(1):235–46.

68. Beamonte-Barrientos R, Velando A, Drummond H, Torres R. Senescence of Maternal Effects: Aging Influences Egg Quality and Rearing Capacities of a Long-Lived Bird. The American Naturalist. 2010 Apr;175(4):469–80.

69. Valcu CM, Scheltema RA, Schweiggert RM, Valcu M, Teltscher K, Walther DM, et al. Life history shapes variation in egg composition in the blue tit Cyanistes caeruleus. Commun Biol. 2019 Jan 4;2(1):1–14.

70. Groothuis TG, Kumar N, Hsu BY. Explaining discrepancies in the study of maternal effects: the role of context and embryo. Current Opinion in Behavioral Sciences. 2020 Dec 1;36:185–92.

71. Reinhold K. Maternal Effects and the Evolution of Behavioral and Morphological Characters: A Literature Review Indicates the Importance of Extended Maternal Care. Journal of Heredity. 2002 Nov 1;93(6):400–5.

72. Monteith KM, Andrews C, Smiseth PT. Post-hatching parental care masks the effects of egg size on offspring fitness: a removal experiment on burying beetles. Journal of Evolutionary Biology. 2012;25(9):1815–22.