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Benefits of Pair-Bond Duration on Reproduction in a Lifelong Monogamous Cooperative Passerine

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ABSTRACT: Long-term social and genetic monogamy is rare in animals except birds, but even in birds it is infrequent and poorly understood. We investigated possible advantages of monogamy in a colonial, facultative cooperatively breeding bird from an arid, unpredictable environment, the sociable weaver (*Philetairus socius*). We documented divorce and extrapair paternity of 703 pairs over 10 years and separated effects of pair duration from breeding experience by analyzing longitudinal and cross-sectional datasets. Parts of the colonies were protected from nest predation, thereby limiting its stochastic and thus confounding effect on fitness measures. We found that 6.4% of sociable weaver pairs divorced and 2.2% of young were extrapair. Longer pair-bonds were associated with more clutches and fledglings per season and with reproducing earlier and later in the season, when snake predation is lower, but not with increased egg or fledgling mass or with nestling survival. Finally, the number of helpers at the nest increased with pair-bond duration. Results were similar for protected and unprotected nests. We suggest that long-term monogamy is associated with a better capacity for exploiting a temporally unpredictable environment and helps to form larger groups. These results can contribute to our understanding of why long-term monogamy is frequently associated with unpredictable environments and cooperation.

Keywords: breeding experience, cooperative breeder, long-term monogamy, monogamous songbirds, pair-bond duration, predation pressure.

Introduction

Mating strategies in animals are very diverse, ranging from lifelong monogamy to polygamy. The advantages of mating systems with multiple mates have been the focus of many empirical and theoretical studies (Jennions and Petrie 1997; Jones and Ratterman 2009; Janicke et al. 2016) and are broadly explained as a result of sexual selection (Emlen and Oring 1977; Andersson and Simmons 2006). The fitness advantages of monogamy, however, remain less studied and understood (Kvarnemo 2018). This is partly because the term “monogamy” often refers to several mating systems (Mock and Fujioka 1990), encompassing social monogamy with genetic polygamy, social or genetic monogamy with successive partners over time (i.e., divorce), and long-term social and genetic monogamy. This broad definition leads to diverse expectations about the costs and benefits of monogamy (Griffith 2019).

Long-term social monogamy is rare but phylogenetically widespread across vertebrates, from sharks (Chapman et al. 2004) to skinks (Bull et al. 2017) and rodents (Syrůčková et al. 2015). In birds, social monogamy (over either the short or the long term) is by far the most common mating system, found in approximately 90% of 5,143 surveyed species (Cockburn 2006). However, in socially monogamous species, extrapair mating is frequent (Brouwer and Griffith 2019) and divorce is common, although with extremely variable rates (Jeschke and Kokko 2008). Hence, long-term social and genetic monogamy is an uncommon socioreproductive system

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even in birds (Mock and Fujioka 1990; Black and Hulme 1996), and the factors underlying its evolution and maintenance are still debated (Kvarnemo 2018).

The advantages of switching partners rely mainly on the possibility of mating with an individual of higher quality or with a more compatible partner (Choudhury 1995; Culina et al. 2015). This can also be achieved by extrapair paternity (Kvarnemo 2018). Nevertheless, in many species the value of keeping the same partner over consecutive breeding attempts appears to outweigh the benefits of divorce (Griffith 2019). The two frequently measured classes of benefits potentially arising from long-term monogamy are (i) improved reproductive timing and (ii) improved investment in parental care.

For the former (i), improving the timing of reproduction is closely linked to the ability to capitalize on suitable climatic conditions and thus resource availability. For temperate species, improving breeding timing is interpreted as earlier breeding, which is usually correlated with increased seasonal fitness (Verhulst and Nilsson 2008) and was found to correlate with breeding experience in several populations (Nol and Smith 1987; van de Pol et al. 2006; Jankowiak and Wysocki 2016). However, in environments where the climate is unpredictable, the breeding season onset and length are highly variable, and pairs can rear several consecutive clutches (Zann 1994; Mares et al. 2017). Hence, pairs need to make decisions about whether to reneest and the level of reproductive investment for each breeding event. Individuals that already have a mate might spare the costs of mate searching (Culina et al. 2015) and thus breed earlier (Real 1990) or reneest faster (Adkins-Regan and Tomaszycski 2007). Long-term monogamy can therefore be a particularly beneficial strategy for species living in highly variable environments by allowing already paired individuals to more efficiently exploit the conditions suitable for breeding (Rowley 1983).

For the latter (ii), improved parental care over time may result from increasing levels of within-pair cooperation and/or investment (Griffith 2019), also called the “mate familiarity effect” (Black and Hulme 1996), and/or from the improved parental skills and breeding competence of each parent at each breeding event (Kvarnemo 2018). In either case, improved parental care can affect clutch size or egg size and content, as larger eggs with higher nutritional content are more costly to produce (Nager et al. 2001) but positively correlate with offspring quality and survival (Krist 2011). Consistent with this, both egg and clutch size have been found to correlate with pair duration, individual experience, and/or age in several bird species (Fowler 1995; Bogdanova et al. 2006; but see Lv et al. 2016; van de Pol et al. 2006). Postnatally, long-term monogamy has been found to be positively correlated with fledgling mass, fledging success, and the number of chicks per season (Griggio and Hoi 2011; Sanchez-Macouzet et al. 2014; Wiley and Ridley 2018). Finally,

in cooperatively breeding species, staying together may increase the chances of retaining offspring from previous breeding attempts as helpers at the nest, which usually have beneficial effects on reproduction (Downing et al. 2020).

To identify the factors associated with the benefits or costs of monogamy, it is important to disentangle correlated effects of pair duration, individual reproductive experience, and age (Fowler 1995; Ens et al. 1996; Rebke et al. 2017). This is possible experimentally by forcing divorces (Remage-Healey et al. 2003; Crino et al. 2017), but it is also possible analytically, to a certain extent, by using a longitudinal dataset if the breeding history of the population is known and there is variation in the age of first reproduction and the number of sexual partners. Another possibility is to use a cross-sectional approach, where individuals of a certain age or experience are selected and, if re-pairing occurred during the life of such individuals, they will differ only in pair duration (Sanchez-Macouzet et al. 2014).

Here, we investigated the association between pair duration and fitness benefits while controlling for age and individual experience by using both longitudinal and cross-sectional datasets in the sociable weaver. Sociable weavers are facultatively cooperatively breeders, which means that breeding pairs can breed on their own or be assisted by adult individuals (known as helpers) that contribute to feeding and care for the nestlings (Covas et al. 2008). This species builds communally large structures (colonies) formed by compound nests where each pair (or group) occupies one or more separate nest chambers. This relatively long-lived bird is endemic to the Kalahari Desert of southern Africa (Maclean 1973a), which is characterized by an arid and unpredictable climate (Mares et al. 2017). These birds' reproductive activity is tightly linked to rainfall, and after abundant rainfall the birds continue re-laying for several months (Mares et al. 2017). We first characterized this species' type of monogamy by calculating levels of extrapair paternity and divorce. Having established that, relative to their reproductive life span, sociable weavers are long-term monogamous, we investigated the relationship between pair duration and seasonal reproductive success (number of eggs and clutches laid and fledglings produced), expecting a positive correlation (Griffith 2019). Next, we studied whether the expected advantages of long-term pairing resulted from improving the timing of reproduction and/or other breeding parameters (size of eggs and chicks and fledging success). To assess the effects of timing, we studied both the onset and the end of pairs' breeding activity, as well as inter-clutch interval (time between two breeding attempts). We expected that longer pair duration could allow individuals to more readily exploit the variable breeding conditions when they become favorable by starting to reproduce earlier, reneesting more rapidly after nest failure, and continuing to reproduce until later in the season. Given that this species

experiences high nest predation by snakes (up to 70% of all clutches; Covas et al. 2008), we examined how fledging probability changed across the year and expected to find benefits of reproducing early and late in the season, when temperatures are cooler and nest predation by snakes is lower (D'Amelio et al. 2022). To test the prediction that longer pair duration can improve parental investment or care, we studied female reproductive investment (egg mass), fledging mass, and fledging success, expecting to find positive correlations if pair duration played a role. In addition, we also tested a possible association between long-term monogamy and number of helpers at the nest, as in this species group size was found to have an overall positive association with reproduction (D'Amelio et al. 2022). Finally, sociable weavers often experience high levels of nest predation, and adults are ineffective against nest predators (D'Amelio et al. 2022). Hence, nest predation introduces stochasticity in the relationship between measures of success and pair duration or experience (because any pair can be equally affected), which can mask the effects of pair duration or experience on reproductive outcome. To better detect the influence of pair duration on reproductive parameters, we used a snake exclusion experiment that substantially reduced nest predation (D'Amelio et al. 2022). We expected to better identify the effects of pair duration on reproductive output in protected colonies than in colonies under natural conditions.

Material and Methods

Study Site, Model Species, and Data Collection

Sociable weavers are colonial cooperative breeders that build large communal colonies, ranging from 12 to 150 birds at our study site (fig. S2; figs. S1–S15 are available online). Within these colonies, pairs or groups use the individual nest chambers for roosting throughout the year and for reproduction (Maclean 1973b), and pairs were never found breeding in two different colonies within the same season and very rarely changed between seasons (4 of 703, 0.5%). Our study site is located within the Benfontein Nature Reserve in the Northern Cape province of South Africa (28°520S, 24°500E, ~15 km², 1,180 m asl). The area is semi-arid, experiencing low and unpredictable rainfall (annual average: 431 ± 127 mm; South African Weather Service, Pretoria). Regular captures at the colonies for bird ringing started in 1993, and from 2008/2009 to 2018/2019 detailed reproductive and behavioral data used in the present study were collected on individually marked birds at 10–14 colonies per season (“season” in this study is used to designate the entire year beginning from September 1, since it is often around this time that breeding activity starts). However, in this study, for the analyses of the variables quantified at the seasonal level (number of eggs, clutches, and fledglings) we

excluded the seasons until 2011/2012, as they were not monitored with the same level of detail of the following seasons. Every year, before the beginning of the breeding season (August–September), all of the birds at the study colonies were captured, and colony size was assessed. Birds were ringed with a unique numbered metal and color combination, bled for DNA analyses (sexing and genotyping; Paquet et al. 2015), weighed, and measured (wing, tarsus, plus intertarsal joint).

The breeding season usually takes place between September and June and can vary considerably in length (from 3 to 12 months; Covas et al. 2008; this study). Within each season females may lay several clutches (up to 13 in the present dataset), with an average clutch size of 3.17 ± 0.81 ($N = 4,407$). To monitor reproduction, all nest chambers were routinely checked every 3 days to detect new clutches, mark and weigh eggs, ring and bleed nestlings (at 9 days of age), measure (wing, tarsus, plus intertarsal joint), and weigh the nestlings before fledging (at 17 days of age, as later visits may induce premature fledging). The long-term breeding monitoring of sociable weavers at Benfontein and the yearly captures, ringing, and blood sampling of individual birds were conducted with permission from the Northern Cape Department of Environment and Nature Conservation and the Ethics Committee of the University of Cape Town, including blood sampling permission from the South African Veterinary council to R. Covas (latest used permit: FAUNA 0684/2019).

Pair and Helper Identification

Sociable weavers are facultative cooperative breeders (Covas et al. 2008), meaning that the pair (i.e., breeders) may be aided in raising the chicks by other individuals (i.e., helpers). Helpers are typically close relatives of the breeders, but 14.3% were unrelated ($R \leq 0.125$; A. C. Ferreira, R. Covas, C. Doutrelant, et al., unpublished manuscript). The mean group size in our dataset was 3.32 ± 1.28 ($N = 1,313$, max = 10). From 2011/2012 on, we determined how many birds attended each nest using either direct observations (before 2014) or video recordings (after 2014) of birds feeding nestlings (details in the supplemental PDF and in Silva et al. 2018; Fortuna et al. 2021). In brief, each nest was recorded or observed for at least 120 min, usually spread over multiple days, and individuals were identified through their unique color ring combination. We used as group size the average number of birds seen feeding the nestlings over all observations/videos of each breeding attempt. We included in the group size count only birds seen visiting the nest at least three times per breeding attempt, after excluding nonfeeding visits. Within the breeding group, we determined the “breeder” or “helper” status by integrating genetic parentage analysis (based on the method described in Fortuna

et al. 2021) with information about the frequency of nest attendance, age, breeding history, and the genetic relationships within the breeding group (full description of the genetic analysis and the algorithm used for breeder status identification provided in the supplemental PDF).

Experimental Treatment to Reduce Nest Predation

From 2010 to 2019, a predator-exclusion experiment was conducted to increase nestling survival in three to eight colonies per year. We excluded nest predators by wrapping tree trunks with plastic film (fig. S2), which generally prevented snakes from climbing up trunks and reaching the colonies (see the supplemental PDF for details and the full list of the protected colonies and predation rate each year; fig. S3). This treatment, by reducing the proportion of predated clutches, has been shown to markedly decrease nest failure and increase fledging success in our population (Fortuna et al. 2021; D'Amelio et al. 2022). Control and treatment colonies are hereafter respectively called “natural” and “protected.”

Disentangling Mate Familiarity Effects: Longitudinal and Cross-Sectional Datasets

Sociable weavers are a suitable system to attempt to disentangle effects of pair duration, age, and experience because while pairs usually breed together for several breeding attempts and seasons (figs. S4–S6), the disappearance of mates leads them to have multiple partners within their reproductive life (fig. S7). This allowed us, in the longitudinal dataset, to separate the effects of pair duration from each partner's breeding experience (Rebke et al. 2017). Individual breeding experience is defined here as the difference in days between the laying date of the first recorded breeding attempt for a given individual and the laying date considered in the analysis; likewise, pair duration has the same definition but for a specific combination of two individuals (see “Variables Studied and Statistical Analyses” for details on each analysis). Sociable weavers have a maximum recorded life span of 16 years and an average life span of 3.19 ± 1.56 years for females ($N = 211$) and 3.86 ± 2.06 years for males ($N = 301$; based on the used dataset, considering only individuals of known age and including the ones that may still be alive after the end of data collection). Sociable weavers start breeding at different ages (Doutrelant et al. 2004), and consequently it was possible to separate the effects of age from experience and, especially, pair duration. Additionally, we further attempted to separate the effects of pair duration from experience by selecting a cross-sectional dataset with equal breeding experience for all focal individuals (Sanchez-Macouzet et al. 2014). However, sociable weavers are a challenging system to standardize breeding experience at the seasonal level, as is usually done for seabirds

or temperate species (Sanchez-Macouzet et al. 2014). Seasons are difficult to compare because they can vary dramatically in length and thus number of breeding attempts, and we discovered that pairs can form throughout the season (fig. S8A). Therefore, we quantified breeding experience in number of days and restricted the analysis of the cross-sectional dataset to variables related to parental effort (egg mass, fledging mass, and nestling survival) that are calculated at each breeding attempt. To do this, we selected breeding attempts for which individuals had a breeding experience of 597 ± 90 days, which is the 66th percentile for the breeding experience (in days) for all of our breeders. The 66th percentile threshold was set to have a large enough sample size to work with—one-third of the total sample size. This allowed us to work with one breeding attempt of 243 focal birds with equal breeding experience but possibly differing pair duration if divorce or re-pairing occurred.

Variables Studied and Statistical Analyses

All analyses were performed in R version 4.1.2 (R Core Team 2021) using a Bayesian approach. We used the package *brms* (Bürkner 2017, 2019) with uninformative priors. In every model, we included explanatory variables based on our knowledge of the system and the literature. In a few cases, we used model comparison to determine the best-performing link function (without modifying the variables included in the model). For these, the best-fitting model was selected with Bayesian leave-one-out cross-validation information criteria (Vehtari et al. 2017) using the package *loo* (Vehtari et al. 2019). We ran four chains for at least 8,000 iterations with a burn-in period of 50%; no thinning was applied. To assess models' convergence, we visually examined the trace plots and checked posterior predictive plots comparing observed data to simulated data from the posterior predictive distribution. Finally, we computed a Bayesian version of R^2 for regression models using the package *sjPlot* (Lüdtke 2021). In the supplemental PDF, for each analysis we present the link function used, the number of iterations, the R^2 value, and the sample sizes—including the ones for each subset—together with the model structure and the estimated effects for all model variables (tables S1–S13, available online).

To study the seasonality of reproductive success and investigate whether there were specific periods when breeding success was higher, we described fledging success probability throughout the year for natural and protected colonies. We used generalized additive mixed models, with our dependent variable fledging probability scored as a binary variable for each egg (0: dead; 1: fledged) and including as independent variables the spline of the laying date as Julian days from the season beginning and colony size as fixed effects, alongside season, and pair ID nested within brood nested within colony as random effects.

For all other analyses performed we modeled as fixed effects the following explanatory variables: pair duration, breeding experience, and age of each partner, each in interaction with protection status. We also included colony size in all analyses. Additionally, the number of seasons of protection was included as an ordinal variable to control for potential directional cumulative effects of increased population density in protected colonies. In the cross-sectional dataset, we included sex of the focal bird but not its experience because it was the same for all individuals. Experience and age were calculated in days or seasons depending on the analysis (see below). To assign an age to breeders that were first captured as adults, we computed the minimum age by adding 258 and 237 days for females and males, respectively, as these were the youngest recorded breeding ages in this population (P. B. D'Amelio, R. Covas, C. Doutrelant, et al., unpublished data). All of the continuous explanatory variables were scaled and centered to allow comparisons between estimates (Schielezeth 2010). As random effects, we considered the following in all analyses: season, colony, and pair and breeder identities nested within colony. Furthermore, for the longitudinal dataset, since there are multiple measures per subject, besides random intercepts we included random slopes for the experience of partners' and pairs' duration (Schielezeth and Nakagawa 2022).

Pair duration longer than 4 years was extremely rare (fig. S4A), and this can be a statistical problem if correlations are driven by a few extreme points. It can also represent a biological problem if the benefits of long-term monogamy are achieved only by these few individuals paired for over 4 years and hence may not be evolutionarily relevant. Therefore, we ran all models excluding the extreme pair durations ($N = 8$ data points from six pairs). This led to nearly identical results, and we thus present only the results from full models.

The specific approach followed for each dependent variable is described below.

Number of Eggs, Clutches, and Fledglings. To estimate the relationship between pair duration and measures of seasonal fecundity and reproductive success, we estimated the number of eggs or clutches per season laid and chicks fledged relative to the number of seasons during which a pair was together (one value per pair per season).

Timing: Onset, End of Laying, and Interclutch Interval. To determine whether increasing pair duration allows pairs to better exploit the full length of the breeding season, we tested the correlation between breeding onset (or end) and pair duration. We considered the breeding season's start as the first breeding attempt of the monitored population and the breeding season's end as the last breeding attempt. We calculated the breeding onset of each pair each season as the difference (in days) between the pair's first

laying date and the season's start and used, as predictors, the pair duration, individual age, and experience (in days) at the moment of the pairs' first breeding attempt of the season. Since we found a moderate degree of overdispersion, we added to the model an observation-level random factor (i.e., a factor with the levels 1 to N , the sample size) to account for the extra variance in the data. As for breeding onset, we calculated the breeding end of each pair each season as the difference in the number of days between the pair's last laying date and the end of the season. We used, as predictors, pair duration, individual age, and experience (in days) of the pairs' last breeding attempt of the season.

We considered the possibility that, over time, pairs would have shorter re-laying intervals. We computed these by extracting the interval between two consecutive breeding attempts of the same pair in a season using the difference between the end of one attempt and the start of the next one, excluding periods longer than 80 days (because these were likely to belong to different breeding periods). To correct for the influence of the developmental stage at which the breeding attempt stopped on the interclutch interval, we included in the analyses three possible brood outcomes (of the first clutch) as categorical fixed effects: clutch failed at the egg stage, failed at the chick stage, or fledged.

Egg Mass, Fledging Mass, and Fledging Success. To analyze the link between pair duration and egg mass, we included female tarsus length (as a proxy of size), clutch size, and breeding attempt number of the female in that season (as an ordinal variable). In the cross-sectional analysis, only focal females (not males) were included. For the fledging mass analysis, we included the tarsus length of each parent, the chicks' wing length (as a proxy for hatching order), and the number of hatched chicks (brood size) among the explanatory variables. For the nestling survival analysis, we calculated nestling survival as a binary variable for each hatched chick, depending on whether they reached day 17 posthatch. Clutch ID or brood ID and nest ID were included as random factors in all of these analyses. Pair duration, experience, and age were scored in days.

Group Size. We investigated whether the number of helpers at the nest was associated with our explanatory variables using pair duration, mates' experience, and age calculated in days. Nest ID was included as a random factor.

Results

Social and Genetic Mating System

We obtained data from 703 pairs. We found that pairs tend to stay together for multiple seasons (mean \pm SD:

1.58 ± 0.94; max = 7; fig. S4A) and breeding attempts (3.92 ± 3.65; max = 21; figs. S5A, S6). These values were close to the maximum individuals' breeding experience (2.11 ± 1.5 seasons and 5.3 ± 4.9 breeding attempts for females [fig. S4B, S4C] and 2.37 ± 1.57 seasons and 5.9 ± 5.06 breeding attempts for males [figs. S5B, S5C, S6]). The observed overall divorce percentage (true divorces; i.e., percentage of pairs for which both birds were known to be alive after at least one paired with another individual) was relatively low at 6.4% (45 divorces among 703 pairs), and most birds had only one partner during their lifetime (71.7% of females and 65% of males; fig. S7).

Extrapair paternity was calculated as clutches with more than one father ($N = 66$) divided by the total number of clutches with more than one chick sampled and successfully assigned to a parent ($N = 1,275$), totaling 5.2%; in addition, we estimated (see the supplemental PDF) that 2.2% of young were from extrapair fathers. In seven broods different breeders (male and female) were assigned to chicks within the same nest (which may, e.g., suggest egg dumping).

Number of Eggs, Clutches, and Fledglings

The number of eggs and number of clutches per pair per season were positively associated with pair duration measured

in entire years in both natural and protected colonies, but with a clear effect only in the natural colonies (estimates [95% credible interval (CrI)] here and throughout are from models that control for age and experience; relationship of pair duration with the number of eggs: natural, 0.47 [95% CrI: 0.15 to 0.83]; protected, 0.25 [95% CrI: -0.16 to 0.70]; fig. 1; table S1; relationship of pair duration with the number of clutches: natural, 0.11 [95% CrI: 0.04 to 0.19]; protected, 0.06 [95% CrI: -0.03 to 0.15]; fig. S9; table S2).

Pair duration was positively associated with the number of fledglings per pair per year in both natural (0.09 [95% CrI: 0.00 to 0.19]), and protected (0.13 [95% CrI: 0.03 to 0.22]) colonies (fig. 2; table S3). These estimates predict that pairs at their average duration increase the number of fledglings in the following year by 0.18 and 0.57 in natural and protected colonies, respectively (estimates calculated using average values of the other factors considered here).

Seasonality of Reproductive Success

Breeding success probability across the year was more constant in protected colonies than in natural colonies (fig. 3). Specifically, in natural colonies fledgling success was considerably higher for clutches laid at the beginning and at the end of the breeding season compared with those laid

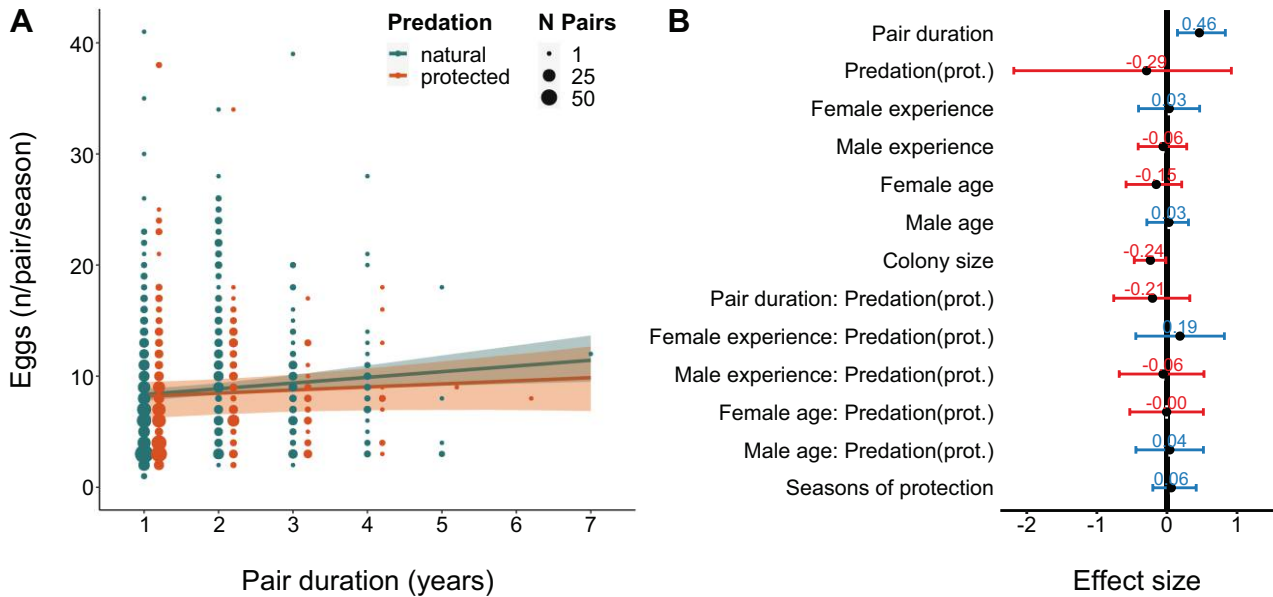


Figure 1: Effects of pair duration and other covariates on the number of eggs per pair per season. *A*, Correlation between number of eggs and pair duration. Points represent raw data, and lines and shaded areas represent estimated means with 95% credible intervals. Results from the two experimental conditions are depicted in green for colonies under natural conditions and in orange for colonies protected from predation. *B*, Forest plot including all analyzed fixed factors (all scaled). Bars represent 95% credible intervals, and the value of the effect size depends on the link function; positive and negative mean correlations are depicted in blue and red, respectively. Variable effects are for the reference level of the predator-exclusion experiment (“natural colonies”), and effects of protection from nest predation for the “protection colonies” level are represented with the label “Predation(prot.)” added to the variable name.

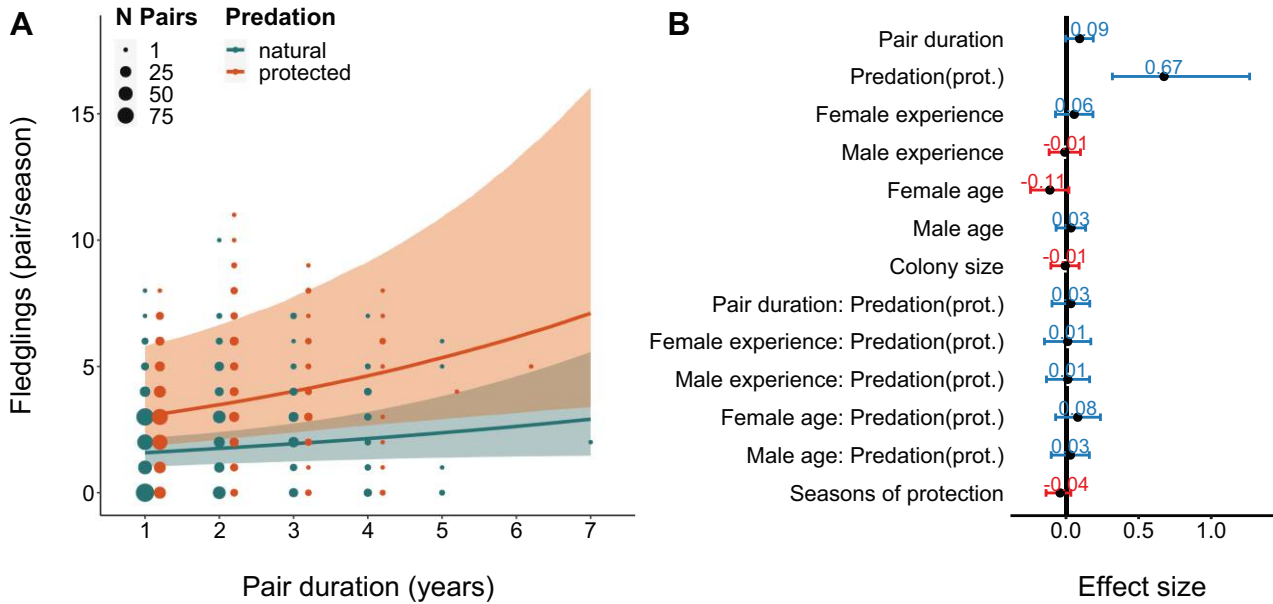


Figure 2: Effects of pair duration and other covariates on the number of fledglings per pair per season. **A**, Correlation between a measure of reproductive success (number of fledglings) and pair duration. Points represent raw data, and lines and shaded areas represent estimated means with 95% credible intervals. Results from the two experimental conditions are depicted in green for colonies under natural conditions and in orange for colonies protected from predation. **B**, Forest plot including all analyzed fixed factors (all scaled). Bars represent 95% credible intervals, and the value of the effect size depends on the link function; positive and negative mean correlations are depicted in blue and red, respectively. Variable effects are for the reference level of the predator-exclusion experiment (“natural colonies”), and effects of protection from nest predation for the “protection colonies” level are represented with the label “Predation(prot.)” added to the variable name.

in the middle (beginning: September 15, 0.41 [95% CrI: 0.14 to 0.77]; end: May 1, 0.87 [95% CrI: 0.63 to 0.97]; middle: December 15, 0.01 [95% CrI: 0.00 to 0.05]). In protected colonies, this difference was considerably lower, as fledgling success was 0.64 (95% CrI: 0.40 to 0.83) at the beginning (September 15) and 0.57 (95% CrI: 0.35 to 0.77) at the end (May 1) of the breeding season and was 0.46 (95% CrI: 0.27 to 0.67) in the middle of the season (December 15).

Potential Explanations for Increased Fecundity and Breeding Success Associated with Pair Duration

Breeding Onset. Breeding onset was strongly negatively correlated with pair duration, with longer pair duration being associated with laying earlier in both natural (-0.31 [95% CrI: -0.43 to -0.20]) and protected (-0.29 [95% CrI: -0.42 to -0.15]) colonies (fig. 4; table S4). The raw data suggested that this result was mostly driven by recently formed pairs that succeeded in breeding earlier in their second season (fig. S10). All other covariates being equal, increasing pair duration by 1 standard deviation (336 and 301 days in natural and protected colonies, respectively) advanced the laying date in the following breeding season by 27% in natural colonies and 25% in protected colonies.

Breeding End. We found a negative correlation between pair duration and pair last clutch (laying date) of the breeding season in both natural and protected colonies, indicating that pairs with longer duration bred until later in the season. However, this association was clear only in protected colonies (natural: -0.07 [95% CrI: -0.20 to 0.05]; protected: -0.21 [95% CrI: -0.34 to -0.08]; fig. S11; table S5).

Interclutch Intervals. We found no evidence that pair duration was correlated with interclutch intervals (natural: 0.00 [95% CrI: -0.98 to 1.00]; protected: -0.16 [95% CrI: -1.70 to 1.39]; fig. S12; table S6).

Egg Mass. We found no evidence that pair duration was correlated with egg mass (natural: 0.01 [95% CrI: -0.01 to 0.02]; protected: 0.00 [95% CrI: -0.02 to 0.02]; fig. S13A, S13B; table S7), and this was also the case in the cross-sectional dataset (fig. S13C, S13D; table S8).

Fledging Mass and Nestling Survival. We found no strong correlations between pair duration and fledging mass (natural: -0.05 [95% CrI: -0.34 to 0.25]; protected: 0.14 [95% CrI: -0.16 to 0.46]; fig. S14A, S14B; table S9),

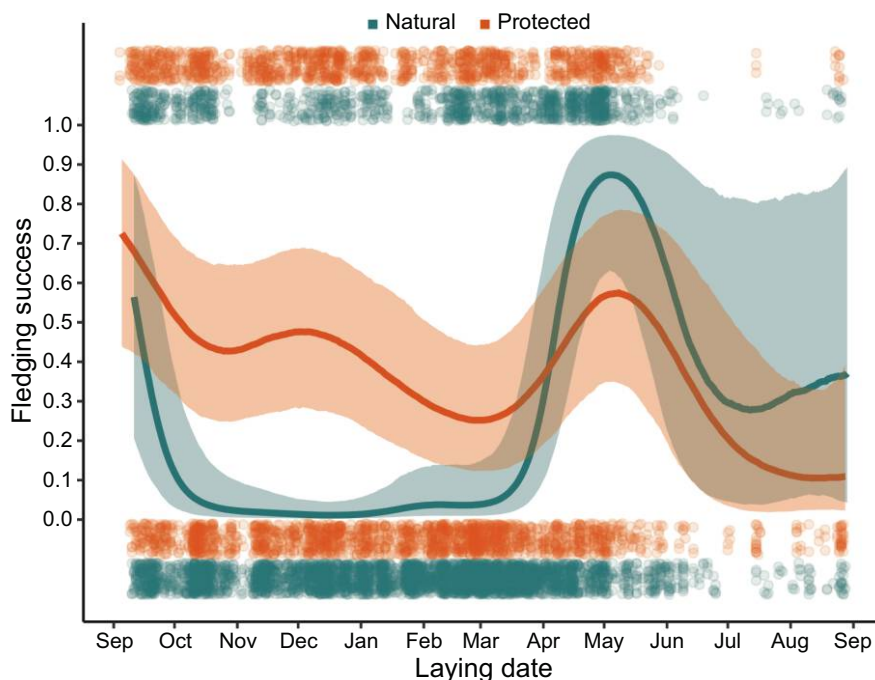


Figure 3: Fledging success probability during the year. Green shows natural colonies, and orange shows protected colonies. Lines are the predicted values of the generalized additive mixed model, shaded areas represent the 95% credible intervals, and circles represent the raw data with a binary outcome from each egg (bottom = failures; top = successes). The graph starts in September because this is usually the beginning of the breeding season for sociable weavers. This graph is based on 8,744 eggs from 2,741 breeding events of 702 pairs across 10 seasons.

and this was also the case in the cross-sectional dataset (fig. S14B, S14C; table S10).

We found that pair duration did not strongly correlate with nestling survival (i.e., number of fledged young/number of hatched) in either protected or natural conditions using the longitudinal (natural: 0.07 [95% CrI: -0.37 to 0.52]; protected: 0.20 [95% CrI: -0.29 to 0.71]; fig. S15A, S15B; table S11) and cross-sectional (fig. S15C, S15D; table S12) datasets. However, in all analyses means were estimated with large uncertainty.

Group Size. We found that pair duration was positively correlated with breeding group size in both natural (0.21 [95% CrI: 0.07 to 0.35]) and protected (0.12 [95% CrI: -0.03 to 0.29]) conditions (fig. 5; table S13). We estimated that at the average for all other covariates, group size would increase by 0.20 birds after a year of breeding together in natural colonies and by 0.14 birds in protected colonies.

Discussion

Sociable weavers tend to keep the same partner for consecutive breeding attempts and seasons, but re-pairing, al-

though most often due to adult mortality, is relatively frequent. Overall, we consider sociable weavers to be long-term monogamous, relative to their reproductive life span, both socially (only $\sim 6.4\%$ of all pairs divorced) and genetically (only $\sim 2.2\%$ were extrapair young). We investigated the benefits of long-term monogamous relationships, controlling for the effects of age and breeding experience, and found positive correlations between pair duration and the number of eggs, clutches, and fledglings produced per season as well as improved reproductive timing. Specifically, pair duration was associated with higher chances of breeding at the beginning and end of the breeding seasons, corresponding to cooler periods when nest predation by snakes is low (D'Amelio et al. 2022) and reproductive success is markedly higher (this study). On the other hand, we did not find associations between pair duration and egg mass, fledging condition, and nestling survival. Finally, we found that pair duration was positively associated with group size. Contrary to our expectation, we found only limited differences between natural and protected colonies. In general, pair duration was more consistently and frequently linked to the variables studied than individual experience or age. Taken together, these results indicate important fitness benefits of long-term monogamy and suggest that these

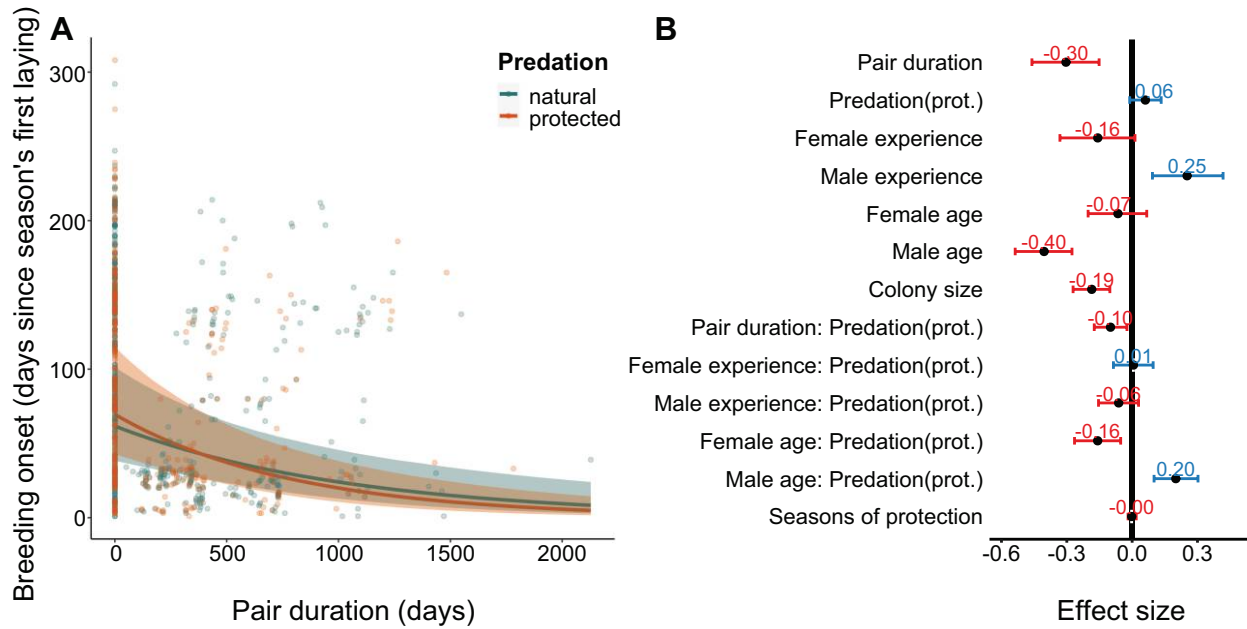


Figure 4: Effects of pair duration and other covariates on breeding onset. *A*, Correlation between breeding onset (a measure of readiness to breed early in the breeding season) and pair duration. Points represent raw data, and lines and shaded areas represent the estimated means with 95% credible intervals. Results from the two experimental conditions are depicted in green for colonies under natural conditions and in orange for colonies protected from predation. *B*, Forest plot including all analyzed fixed factors (all scaled). Bars represent 95% credible intervals, and the value of the effect size depends on the link function; positive and negative mean correlations are depicted in blue and red, respectively. Variable effects are for the reference level of the predator-exclusion experiment (“natural colonies”), and effects of protection from nest predation for the “protection colonies” level are represented with the label “Predation(prot.)” added to the variable name.

benefits are strongly linked to improving the timing of reproduction.

Having found that sociable weavers tend to keep the same breeding partner, we expected to find a positive association between pair duration and reproductive success (Kvarnemo 2018; Griffith 2019). We did find such positive correlations, and overall our results suggest that the effects of pair duration are biologically relevant. For example, a pair in their fourth year together would produce 0.6 more fledglings in natural colonies and 1.7 more in protected ones than during their first season together. This is considerable, given that for our entire dataset pairs in their first season fledged on average 1.7 and 2.7 chicks in natural and protected colonies, respectively. Protection from nest predation increased seasonal fitness as well as, moderately, the steepness of the positive correlation with pair duration. Notably, we found no clear associations between individual experience and age and number of eggs, clutches, and fledglings, stressing the relevance of pair-bond in this species.

Concurrently, we found that pair duration was associated with earlier breeding in both natural and protected colonies and with later end of breeding in protected colonies. There were limited differences between natural and protected colonies, indicating that the differences found in seasonal fitness cannot be explained simply by better timing. In addition,

age and experience of either sex were not strongly associated with breeding onset in both natural and protected colonies.

We suggest that being in a pair before the season’s onset may be a strong driver of long-term monogamy in this system, and we propose two possible non-mutually-exclusive explanations connected to breeding timing. First, being already in a pair before the breeding season might allow pairs to match the timing of reproduction with favorable conditions for breeding success. In north temperate bird species and seabirds, where most studies of breeding timing and the benefits of monogamy have been conducted, earlier breeding is usually connected to resource abundance (e.g., food, territories, and mates; Kokko 1999; Gilson et al. 2020) and is frequently positively correlated with pair duration (Fowler 1995; McGraw and Hill 2004; van de Pol et al. 2006; Sanchez-Macouzet et al. 2014; Jankowiak and Wysocki 2016). The correlation between pair duration and the breeding season end has been less investigated (but see Jankowiak and Wysocki 2016), as most of the studied species have one breeding attempt per year. Here, we argue that better timing of reproduction, both early onset and late end of breeding, may be advantageous in systems suffering temperature-dependent nest predation by snakes (Cox et al. 2013). If pairs are ready to start breeding or can continue breeding when

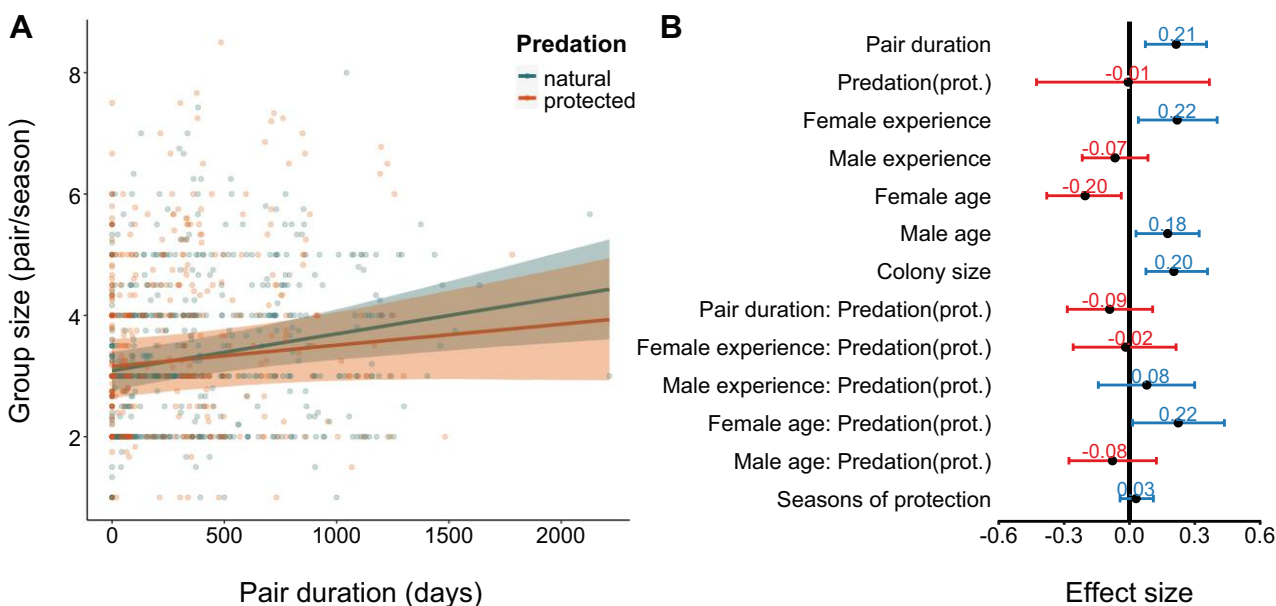


Figure 5: Effects of pair duration and other covariates on group size. *A*, Association between group size (number of birds, including the pair, feeding during a breeding attempt; noninteger values are because average numbers were used; see “Material and Methods”) and pair duration. Points represent raw data, and lines and shaded areas represent the estimated means with 95% credible intervals. Results from the two experimental conditions are depicted in green for colonies in natural conditions and in orange for colonies protected from predation. *B*, Forest plot including all analyzed fixed factors (all scaled). Bars represent 95% credible intervals, and the value of the effect size depends on the link function; positive and negative mean correlations are depicted in blue and red, respectively. Variable effects are for the reference level of the predator-exclusion experiment (“natural colonies”), and effects of protection from nest predation for the “protection colonies” level are represented with the label “Predation(prot.)” added to the variable name.

temperatures are lower, they can take advantage of periods when nest predation pressure is lower. Second, in unpredictable environments, reproductive periods differ in onset, end, length, and quality, and it can thus be advantageous to be ready to breed when conditions become suitable and spare the cost of mate searching (Culina et al. 2015). The link between environmental unpredictability and social monogamy has been based on the hypothesis that pairs that stay together are ready to quickly lay a clutch without having to invest time establishing a new relationship (Rowley 1983; Adkins-Regan and Tomaszycski 2007; Maldonado-Chaparro et al. 2021). Several Australian estrildids, such as zebra finches (*Taeniopygia guttata*), seem to follow this strategy (Goodwin 1982; Zann 1994), but studies including several breeding seasons and a complete record of the individuals’ breeding history were, until now, missing. Essentially, being in couples to breed early in the second season may be particularly valuable because it maximizes the number of breeding attempts—especially in species like sociable weavers that have pair formation spread along the season, relatively short breeding lifetimes, and long and unpredictable breeding seasons.

In contrast to the effects of pair duration on seasonal reproductive output, we did not find pair duration, nor individual experience or age, to be consistently associated with

egg and fledging mass and nestling survival, which can be interpreted as proxies of parental investment and care (Kokko and Jennions 2012). We did not detect an effect on these variables even when we experimentally removed the random chick mortality due to nest predation or when we analytically isolated the effect of pair duration in the cross-sectional datasets. Reproductive investment and parental care might be associated with individual condition or quality (van de Pol et al. 2006), which could be correlated with individual experience or age but also with other factors that we did not account for here, such as body condition during breeding and/or dominance. Parental competence has been found to increase with pair duration in diverse taxa—experimentally in Eurasian oystercatchers (*Haematopus ostralegus*; van de Pol et al. 2006) and bearded reedlings (*Panurus biarmicus*; Griggio and Hoi 2011) and correlatively in little penguins (*Eudyptula minor*; Nisbet and Dann 2009)—but this correlation has never been reported in zebra finches, a well-studied long-term monogamous species (Griffith 2019). Differences between species might be partially related to life span, as long-lived species can have more time for improving parental coordination and competence. However, we can also speculate that advantages related to parental competence might not be present in

species where offspring mortality is largely independent of individual quality of the parents—for example, when reproductive success is closely associated with weather conditions, such as in semiarid climates and/or when parents cannot deter nest predation (D'Amelio et al. 2022).

In cooperative species like sociable weavers, a further possible advantage of longer pair duration might come from increasing the number of helpers at the nest, since larger groups usually have a higher probability of fledging young in sociable weavers (D'Amelio et al. 2022) and other species (Downing et al. 2020). Here, we found a positive correlation between helpers' number and pair duration, with considerable effect sizes. Studies looking at the correlation between pair duration and success in cooperative species are rare (Wiley and Ridley 2018). In both pied babblers (*Turdoides bicolor*; Wiley and Ridley 2018) and pinyon jays (*Gymnorhinus cyanocephalus*; Marzluff and Balda 1988), longer-lasting pairs had higher reproductive success, but the correlation of pair duration with the number of helpers has, to our knowledge, not been previously reported. Interestingly, we also found that breeders' age in natural colonies was strongly associated with group size (the effect was comparable in strength to pair duration). However, fathers' age was positively correlated and mothers' age was negatively correlated with helpers' number. This result could be a consequence of helpers' tendency to help their brothers but not their sisters (which often migrate to reproduce), as most helpers that are feeding their nephews come from the father's side (A. C. Ferreira, R. Covas, C. Doutrelant, et al., unpublished manuscript). We also found that in females, individual experience, like pair duration, was positively correlated with group size. The opposite effects of individual experience and age can be explained if young females prefer to breed with males that already have helpers, but these patterns were not present in protected colonies, and further investigations about factors influencing mate choice and its timing are necessary to fully understand these results. The positive correlation between long-term monogamy and the number of helpers present is also in line with hypotheses describing the interlinked evolution of monogamy and cooperation, with one possibly leading to the evolution of the other or the two reinforcing each other (Cornwallis et al. 2010; Song and Feldman 2013; Dillard and Westneat 2016).

Conclusion

We found that sociable weavers are one of a few known long-term socially and genetically monogamous passerines and that pair duration in this species is associated with improved seasonal fitness and having more helpers at the nest. Our analyses indicated that the benefits of pair duration in this system arise from improving breeding timing, as pairs that were previously together can rapidly breed when con-

ditions are suitable and can fully exploit the breeding seasons' unpredictable length. In addition, early reproduction often matches the cool temperatures associated with low nest predation and high fledging success. These results are therefore tightly linked to the highly variable semiarid environment inhabited by this species and suggest that improved reproductive timing and, for cooperative breeders, increased group size are important mechanisms favoring long-term monogamy. As more long-term studies will be able to follow individuals over their lifetime, these findings may prove to be a common pattern in many subtropical long-term monogamous and cooperative species.

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Statement of Authorship

P.B.D., R.C., and C.D. conceived the study. R.C. and C.D. led the long-term data collection and together with

F.R. provided funding. R.C., C.D., P.B.D., R.F., L.R.S., A.C.F., and F.T. collected and stored the data. P.B.D., L.R.S., R.F., and A.C.F. processed the data. P.B.D. analyzed the data. P.B.D. wrote the manuscript. R.C., C.D., R.F., L.R.S., A.C.F., and F.R. commented on the manuscript. All authors read and approved the final manuscript.

Data and Code Availability

The data and code to reproduce all analysis and figures supporting the results have been archived and are publicly available on Figshare (<https://doi.org/10.6084/m9.figshare.24835803>; D'Amelio et al. 2024).

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