The number of strong social bonds is linked to survival in a cooperative bird

Gabriel Munar-Delgado[1,2,*], Matthieu Paquet[3], Babette Fourie[1,2], Franck Theron[1,2], André Ferreira[4], Claire Doutrelant[5,6], Rita Covas[1,2,6]

[1] CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto, Vairão, Portugal

[2]BIOPOLIS, Program in genomics, Biodiversity and Land Planning, Vairão, Portugal

[3]SETE, Station d'Écologie Théorique et Expérimentale, CNRS, Moulis, France

[4]Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland

[5]CEFE, CNRS, University of Montpellier, EPHE, IRD, Montpellier, France

[6]FitzPatrick Institute of African Ornithology, DST-NRF Centre of Excellence, University of Cape Town, Rondebosch, South Africa

Correspondence: gabriel.munar@gmail.com

SUMMARY

Recent evidence from large mammals, including humans, shows that the quality of social associations beyond general group size can positively influence health and survival. However, whether individuals in other taxa consistently differ in sociality in ways that affect fitness and thus provide a basis for selection remains largely unexplored. In this study, we examined how individual sociality relates to survival probabilities in a population of sociable weavers (*Philetairus socius*), a highly cooperative bird. We combined social network analysis with multi-state capture–recapture models to quantify the number of strong social bonds each individual had and to estimate survival probabilities. We found that sociality was positively associated with survival: individuals with medium and high sociality showed higher survival probabilities than those with low sociality. Additionally, individuals were more likely to remain in the same sociality category across years than to shift to another, and when transitions occurred, they followed a gradual pattern, with adjacent shifts more common than abrupt changes, supporting the idea of stable individual differences in sociality. These findings support a link between sociality and individual fitness, and suggest that stable social traits may provide a basis for evolutionary change.

INTRODUCTION

Living in groups is common across many taxa, from invertebrates to fish, birds and mammals, and has been shown to provide fitness benefits such as protection from predators and improved access to food or information (Krause *et al.* 2002). Much of the early work on animal sociality focused on the trade-offs associated with group size (Bilde *et al.* 2007; Koenig 1981). More recently, long-term social-network studies have revealed that individuals' interactions within groups (i.e. individual sociality) also play a key role in fitness (Formica *et al.* 2012; Silk *et al.* 2010).

The link between individual sociality and survival—a key fitness component—has become central to understanding the evolution of social behaviour. A growing body of research, initially focused on humans and later extended to other mammals, shows that sociality can markedly increase survival (reviewed in Snyder-Mackler *et al.* 2020), underscoring that not only group living *per se*, but also specific interaction patterns—such as strong, stable social bonds—shape selection on social traits (e.g. Archie *et al.* 2014; Silk *et al.* 2010). However, for social behaviours to evolve, their expression must be at least partly stable over time (Boake 1989). While some studies have reported consistent individual differences in social network traits such as degree or strength (e.g., Aplin *et al.* 2015; Blumstein *et al.* 2013), others found lower consistency or variation across metrics (e.g., Plaza *et al*. 2020; Evans *et al*. 2021). Yet, few studies have jointly assessed the temporal stability of social traits and their relationship with fitness within the same system, constraining our understanding of their evolutionary dynamics (but see Vander Wal *et al.* 2015).

In this study, we assessed whether individual sociality is consistent over time and whether it is associated with survival in the sociable weaver (*Philetairus socius*), a highly cooperative, colonial passerine. Sociable weavers live in relatively stable colonies, built communally usually on acacia (*Vachellia spp*.), which harbour multiple independent chambers used for breeding and for roosting year-round (Maclean 1973). These weavers have different levels of social organisation, with the whole colony cooperating to build a large communal nest and typically foraging in large flocks that include most colony members (Lloyd *et al.* 2018). Within colonies, birds typically roost in groups inside individual nest chambers, which are used throughout the year and also for breeding (Paquet *et al.* 2016). These groups often remain stable across contexts and frequently stay together for breeding as well (Paquet *et al.* 2016; Pacheco 2022) and their social associations are further reflected in strong bonds that persist outside the breeding season while foraging (Ferreira *et al.* 2024). Sociable weavers are cooperative breeders with non-breeding group members assisting in chick provisioning. In our study population, between 30% and 80% of breeding attempts are assisted by up to nine helpers (Covas *et al.* 2008, 2022). Helpers have been associated with improved survival of the breeders and the offspring they helped (Covas *et al.* 2008; D'Amelio *et al.* 2022; Paquet *et al.* 2015) an effect also found in other cooperatively breeding species (Downing *et al.* 2021; Paquet *et al.* 2015). Altogether, these features suggest that the social structure within colonies, built upon stable group composition and strong social bonds, may be an important determinant of individual fitness in this species.

To explore this idea, we quantified individual sociality as the number of top-ranked social connections in the network (hereafter: strong social bonds), and assessed its consistency over time and association with survival. To achieve this, we combined social network analysis with multi-state capture–recapture models. We collected sociality data for 497 free-ranging individuals in a foraging context using RFID-based feeder stations over five years, and combined this with annual mist-net captures. We predicted that individual sociality—measured as the number of strong bonds—would be relatively consistent over time (Ferreira *et al.* 2024), and that individuals with higher sociality would show increased probability of survival, reflecting the fitness value of cohesive subgroups within colonies.

METHODS

Site and study species

We studied a population of sociable weavers at Benfontein Nature Reserve in South Africa (28°52′S, 24°50′E). This population has been the focus of a long-term research program initiated in 1993. Since 2008, the population has been regularly monitored through annual captures (see below), and since 2010, breeding has been consistently monitored, with all nestlings that reached nine days of age being ringed and having blood samples taken for sexing and genotyping.

Since 2017, all birds (adults and fledglings) at five colonies have also been marked with a passive integrated transponder (PIT-tag) enclosed in a plastic leg ring (3.3mm; Eccel Technology) to allow detection at RFID feeders (see below). In 2021, a fire destroyed two of those colonies, but in 2022, an additional colony was PIT-tagged, bringing the total number of marked colonies to four.

Mist-nest captures

Resident and recently migrated birds from PIT-tagged colonies are captured annually in September (i.e., at the end of the Southern Hemisphere winter). This was done by placing mist nets around the colony's nest structure before dawn (when the birds were roosting inside the nests) and later flushing them into the nets. Individuals not born in the study population were fitted with a metal ring, PIT-tagged, and had a blood sample taken for sexing (see Supplementary Material for details on age and sex determination). All individuals were released at the site of capture. For this study we used data from 2018 to 2023 (except for 2020 due to COVID-19 restrictions)

RFID data collection and social network metrics

From 2018 to 2023 (except for 2020), we collected association data in a foraging context using RFID-based feeding stations located 80–205 m away from each colony (described in Ferreira *et al.* 2020). In short, feeding stations consisted of four feeding boxes, each equipped with four small standard plastic bird feeders and four perches fitted with an RFID antenna (Priority1rfid, Melbourne, Australia) connected to a data logger which recorded the birds' visits. Each perch and feeder was designed to only allow one bird to feed at a time. Data were collected from April to June, with data collection conducted usually every three days. This period was chosen to coincide with the end of breeding and the first winter months (which is the dry season, when resources are expected to drop and temperatures fall to below zero, making communal roosting more important; (Paquet *et al.* 2016).

We inferred social networks based on the time overlap between individuals at the feeders. Following Ferreira *et al.* (2020), the strength of the association between two individuals (i.e., the value of each edge) was calculated as the time two individuals spent feeding simultaneously in the same feeding box, divided by the sum of the times each individual was present at the RFID feeders. This method has been shown to capture the fine-scale social structure within a colony of sociable weavers (Ferreira *et al.* 2020) better than other more commonly used approaches in birds such as co-occurrences. This is because sociable weavers are colonial and tend to forage in cohesive flocks, usually co-occurring at the RFID feeders with most members of their colony.

To determine social strong bonds (e.g., Gero *et al.* 2005; Kern & Radford 2021), we grouped individuals from the same colony and classified the edges between them as either strong or non-strong bonds. For each colony and year, we ranked the edges in descending order based on their association weight. Edges with weight values greater than or equal to the 80th percentile were classified as strong bonds, while the remaining edges were classified as non-strong bonds (Fourie *et al*. unpublished results). Based on this categorization, we then calculated the number of strong bonds each individual had.

Finally, we classified individuals into three social status categories based on their number of strong bonds: low, medium, and high. For each year and colony, we determined the 33rd and 66th percentiles of the number of strong bonds each individual had. Individuals with strong bond counts above the 66th percentile were classified as having a high number of social bonds, those between the 33rd and 66th percentiles as having a medium number, and those below the 33rd percentile as having a low number of social bonds. This classification served as the social network metric for our analyses (See Supplementary material for yearly and colony-based classification).

We discretized the social network metric variable to enable the use of a multi-state capture-recapture model (Lebreton & Cefe 2002; Schaub *et al.* 2004; see below). This model allowed us to estimate the transition probabilities from one social status to another from one year to the next, along with specific-state survival probabilities. Additionally, this model also enabled the inclusion of individuals with missing social status data, as long as data had been recorded in at least one year.

Multi-state capture–recapture models

We estimated social status-specific survival, transitions, and detection probabilities of RFID-tagged sociable weavers using a Bayesian multi-state capture-recapture model. Each year (t), we conducted two capture/detection events: one using RFID-feeders (see above) and another with mist nets (see above). RFID-feeders allowed us to estimate individuals' social metrics (Figure 1), while mist-net captures ensured a higher and more consistent detection of individuals.

This setup enabled us to estimate survival probabilities based on social status during the intervals between these two events. On the one hand, we estimated the survival probability between the RFID-feeder data collection and the mist net captures within the same year, specifically from July to August (Figure 1). This period largely corresponds to the winter season; therefore, for simplicity, during the analysis, specifications, and results we refer to this estimate as the winter survival probability. On the other hand, we estimated the survival probability between the mist net captures and the RFID-feeder data collection of the following year (*t+1*), specifically from October to April (Figure 1). This period largely corresponds to the spring and summer seasons. For simplicity, and in contrast to the winter survival probability, during the analysis specifications and results we refer to this estimate as the summer survival probability.

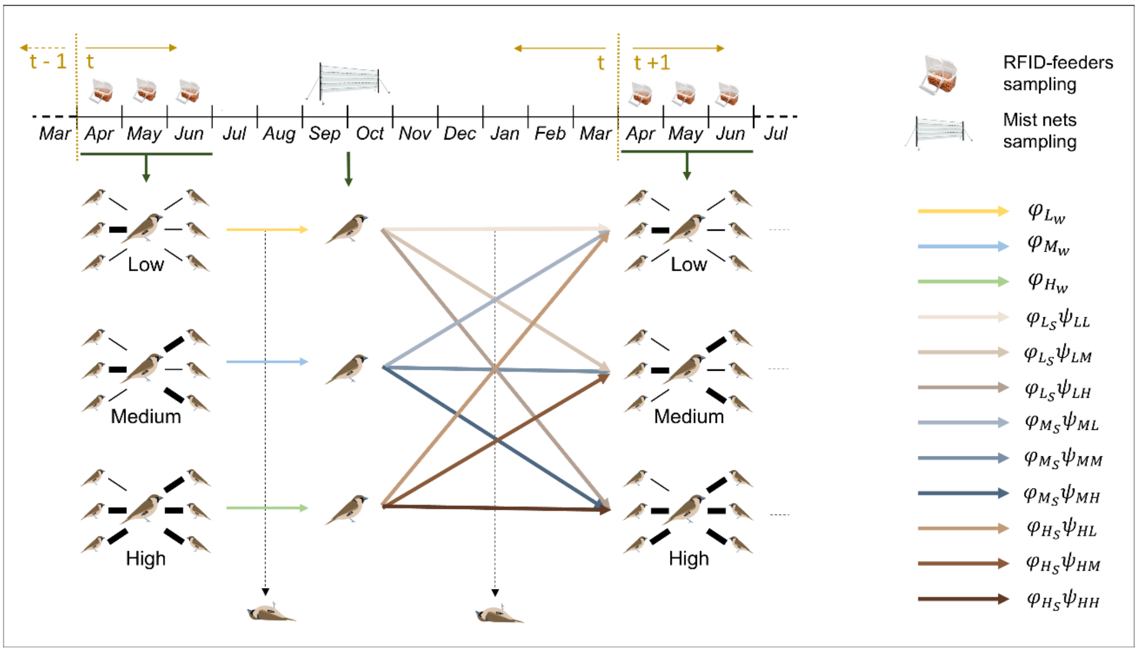

Figure 1. Schematic overview of yearly data collection and the multi-state capture-recapture model. Each yearly time period (t) begins in April with RFID data collection conducted from April to June and ends in March before the next year's RFID-data collection period. During the RFID data collection period, individuals' social status is estimated based on the number of strong social bonds that they have: low (L), medium (M) or high (H). Mist-net captures were conducted in September, at the end of the Southern Hemisphere winter. Between these two periods, individuals can either survive or not, and between consecutive RFID data collection periods, individuals can either remain in the same social status or transition to a different one, provided they survive. The capture-recapture model estimates two survival probabilities: (1) *winter* survival probability, from the RFID data collection period to the mist-net captures within the same year, for low, medium, and highly social individuals, and (2) *summer* survival probability of low, medium, and highly social individuals, conditional on their transition probabilities between social statuses, from the mist-net captures to the RFID data collection period. φ_{X_w} is the winter survival probability of an individual in state X; φ_{X_s} is the summer survival probability off an individual in state X and ψ_{XY} is the transition probability from state X to state Y from *t* to *t+1*.

With the same model, we also estimated the detection probability conditional on sociable weavers' social status (estimated from RFID-feeder data) at both the RFID feeder and mist-net captures, and the social-status transition probability from one year to the next. Multi-state capture–recapture models explicitly account for state-dependent differences in detection probabilities (Lebreton *et al.* 2009). This adjustment prevents the underestimation of survival probabilities in groups of individuals that are less likely to be detected due to their state (e.g., low-sociality birds may visit the RFID feeders infrequently; if their lower detection probability isn't modelled, an undetected bird could be wrongly assumed dead). In our study, this approach enabled us to assess the detection probabilities of birds with different sociality levels at both mist-nets and RFID feeders, allowing the model to adjust survival and transition-probability estimates accordingly.

These different survival, transition, and detection probabilities can be represented in the corresponding survival, transition, and detection probability matrices. In the survival and detection matrices, we can represent the different detection probabilities linking the state of an individual (in rows) to the possible observations (in columns) at each data collection occasion within an observation matrix (Θ). In the transition matrices, each row corresponds to the departure state, and each column corresponds to the arrival state of an individual. To improve clarity, we explicitly label the rows and columns of each matrix using the four possible states: L (low sociality), M (medium sociality), H (high sociality), and D (dead). Thus, in all matrices, the rows correspond to the individual's state at time *t*, and the columns represent either the observed state or the state at time *t+1*. In this way, for detection probabilities at the mist-net captures and winter survival probabilities, the matrices were:

$$\Theta_n = \begin{array}{ccccc} \mathrm{L}_{t+1} & \mathrm{M}_{t+1} & \mathrm{H}_{t+1} & \mathrm{D}_{t+1} & \\ p_{L_n} & 0 & 0 & 1-p_{L_n} & \mathrm{L}_t \\ 0 & p_{M_n} & 0 & 1-p_{M_n} & \mathrm{M}_t \\ 0 & 0 & p_{H_n} & 1-p_{H_n} & \mathrm{H}_t \\ 0 & 0 & 0 & 1 & \mathrm{D}_t \end{array} \qquad \Omega_w = \begin{array}{ccccc} \mathrm{L}_{t+1} & \mathrm{M}_{t+1} & \mathrm{H}_{t+1} & \mathrm{D}_{t+1} & \\ \varphi_{L_w} & 0 & 0 & 1-\varphi_{L_w} & \mathrm{L}_t \\ 0 & \varphi_{M_w} & 0 & 1-\varphi_{M_w} & \mathrm{M}_t \\ 0 & 0 & \varphi_{H_w} & 1-\varphi_{H_w} & \mathrm{H}_t \\ 0 & 0 & 0 & 1 & \mathrm{D}_t \end{array}$$

where θ_n is the observation matrix for mist-nets matrix and p_{X_n} is the detection probability at nets of an individual in state X. Ω_w is the winter survival matrix and φ_{X_w} is the winter survival probability off an individual in state X.

On the other hand, the detection probability matrix at feeders and transition-summer survival matrix were:

$$\Theta_f = \begin{array}{ccccc} \mathrm{L}_{t+1} & \mathrm{M}_{t+1} & \mathrm{H}_{t+1} & \mathrm{D}_{t+1} & \\ p_{L_f} & 0 & 0 & 1-p_{L_f} & \mathrm{L}_t \\ 0 & p_{M_f} & 0 & 1-p_{M_f} & \mathrm{M}_t \\ 0 & 0 & p_{H_f} & 1-p_{H_f} & \mathrm{H}_t \\ 0 & 0 & 0 & 1 & \mathrm{D}_t \end{array} \qquad \Omega_s = \begin{array}{ccccc} \mathrm{L}_{t+1} & \mathrm{M}_{t+1} & \mathrm{H}_{t+1} & \mathrm{D}_{t+1} & \\ \varphi_{L_s}\psi_{LL} & \varphi_{L_s}\psi_{LM} & \varphi_{L_s}\psi_{LH} & 1-\varphi_{L_s} & \mathrm{L}_t \\ \varphi_{M_s}\psi_{ML} & \varphi_{M_s}\psi_{MM} & \varphi_{M_s}\psi_{MH} & 1-\varphi_{M_s} & \mathrm{M}_t \\ \varphi_{H_s}\psi_{HL} & \varphi_{H_s}\psi_{HM} & \varphi_{H_s}\psi_{HH} & 1-\varphi_{H_s} & \mathrm{H}_t \\ 0 & 0 & 0 & 1 & \mathrm{D}_t \end{array}$$

where θ_f is the observation matrix for RFID-feeders and p_{X_f} is the recapture probability at RFID-feeders of an individual in state X. Ω_s is the summer survival-transition matrix,

φ_{X_s} is the summer survival probability of an individual in state X and ψ_{XY} is the transition probability from state X to state Y from *t* to *t+1*.

Detection probabilities for year 2020 (*t = 3*) were set to zero both for the mist-nets and RFID-feeders due to the lack of data collection for that year.

Model fitting

We used NIMBLE (version 1.1.0 of the *nimble* package; Valpine *et al.* 2017, 2022) to implement our multistate capture-recapture models in a Bayesian framework in Program R, version 4.0.2 (R Core Team, 2020). For all models, a logit link was used. We estimated parameters using vague priors (Table S2). Posterior samples from three independent Markov Chain Monte Carlo (MCMC) chains were based on 70000 iterations with a burn-in period of 35000 iterations and a thinning interval of 20, leading to 5250 posterior MCMC samples. We assessed model convergence both visually and by using the $\hat{R}$ Gelman–Rubin statistic (Gelman & Rubin 1992). Finally, we also performed posterior predictive checks (Figures S1 and S2). Mean differences between the state specific survival, transition, and detection probabilities (and their 95% credible intervals) were calculated from the posterior estimates. We considered differences statistically significant when their 95% credible intervals did not overlap zero.

Covariates and random effects

Our multistate model incorporated several individual covariates (see Supplementary Material for a detailed description) to account for their effects on social survival probabilities in both winter and summer, as well as on transition probabilities and detection probabilities at RFID-feeders. In contrast, we assumed that detection probability at mist nets was independent of covariates because of the mist-net capture method (see above).

For survival probabilities in winter and transition/survival probabilities in summer, we included individual age and sex as covariates, with year and the individual's colony as random effects. Age was included because we hypothesized that it could influence survival (Martin 1995). Sex was included because we hypothesized that survival may differ between males and females (Payevsky 2021). The individuals' colony and year were included to account for potential inter-colony and annual variation in survival. We allowed age and sex to have different effects on winter and summer survival, as these effects could vary between the two periods. Year and colony random effects were also allowed to differ between winter and summer. Age was centred by subtracting the mean of all observed ages across individuals and years. Sex was centred by subtracting the overall proportion of males across all individuals included in the model. This approach improves the efficiency of MCMC sampling and allowed us to interpret the model intercepts as the social status-specific survival probabilities of an individual with average age and sex ratio in the population (Table S3).

Finally, for the detection probability at RFID-feeders, we included the presence or absence of RFID-feeders at the individual's colony as a covariate since PIT-tagged individuals can migrate to colonies without RFID-feeders but are expected to be less likely detected if no feeders are present at their colony.

See Tables S1-S3 for the detailed models' description.

RESULTS

Data and model overview

We captured 661 individuals with mist nets over the study period. Based on RFID-feeders' detections, 430 individuals were included in the multi-state capture-recapture model, as they had RFID-feeder-based social status data for at least one year (excluding those with data only from the last year, since recapture data was not available for these individuals; see Supplementary material for exclusion criteria). Our RFID-feeder social status observation matrix consisted of 702 observations, with 36% corresponding to low, 33% to medium, and 31% to high sociality individuals.

We obtained satisfactory model performance (Figures S1 and S2)

Detection probabilities

We observed similar detection probabilities based on mist-net captures among individuals with low, medium, and high sociality (0.88 [95 % CI: 0.83–0.93], 0.84 [0.73–0.94], and 0.88 [0.81–0.93], respectively; Figure 2; Tables S5 and S6).

Similarly, at the RFID feeders we found no evidence of significant differences in detection probabilities among low-, medium-, and high-sociality individuals (0.51 [0.13–0.93], 0.29 [0.06–0.73], and 0.32 [0.08–0.77], respectively; Figure 2; Tables S5 and S6), although estimates show broad credible intervals, reflecting substantial uncertainty.

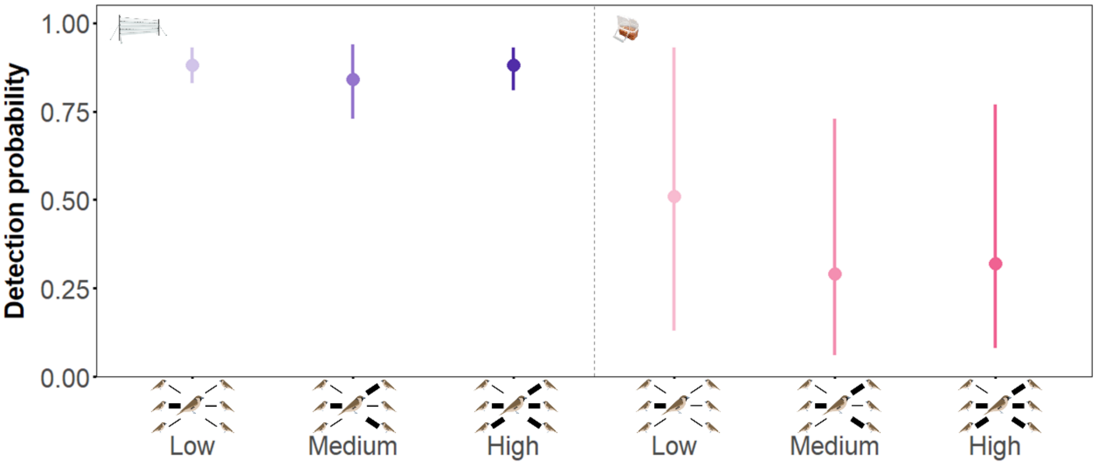

Figure 2. Detection probabilities. Model estimates of detection probabilities for low, medium and high sociality individuals at RFID-feeders (left) and mist-nets (right). Dots represent the posterior mean estimates and bars their 95% credible intervals

Transition probabilities

We found that low-sociality individuals were significantly more likely to remain in the low category (0.47 [0.34, 0.59]) than to shift directly to the high category (0.19 [0.10, 0.29]; Tables S5 and S6). The probability of transitioning from low to medium (0.35 [0.23, 0.48]) fell between those two values, and the differences between remaining low versus transitioning to medium and transitioning to medium versus transitioning to high did not reach statistical significance (Figure 3).

For medium-sociality individuals, we found that they were statistically significantly more likely to remain at the medium level (0.48 [0.36, 0.58]) than to transition to either the low level (0.27 [0.19, 0.36]) or the high level (0.25 [0.17, 0.35]; Tabled S5 and S6). However, there was no statistically significant difference between the likelihoods of transitioning to the low versus the high level (Figure 3).

Finally, for high-sociality individuals, we found that they were statistically significantly more likely to remain at the high level (0 .60 [0.49, 0.70]) than to transition to either the low level (0 .08 [0.04, 0.15]) or the medium level (0 .32 [0.22, 0.43]; Tables S5 and S6). Notably, they were also statistically significantly less likely to transition to the low than to the medium level, again highlighting that abrupt changes in sociality were less common (Figure 3).

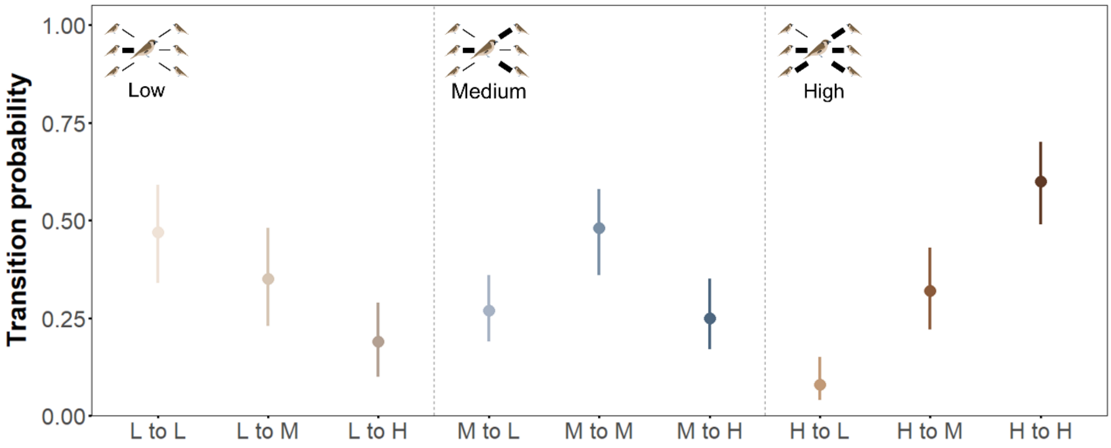

Figure 3. Transition probabilities. Model estimates of transition probabilities for low (L), medium (M), and high (H) social individuals. Dots represent the posterior mean estimates and bars their 95% credible intervals.

Survival probabilities

We found that, during the winter period, medium- and high-sociality individuals had statistically significantly higher survival probabilities (0.85 [0.71, 0.94] and 0.90 [0.78, 0.96], respectively) than low-sociality individuals (0.75 [0.56, 0.87]; Figure 4, Tables S5 and S6)—an average increase of about 13 %.

The same pattern emerged in summer: medium- and high-sociality birds again showed statistically significantly higher survival probabilities (0.72 [0.48, 0.88] and 0.67 [0.42, 0.84], respectively) than low-sociality birds (0.53 [0.28, 0.74]; Figure 4, Tables S5 and S6), representing an average increase of roughly 17 %. During both seasons, survival probabilities did not differ significantly between medium- and high-sociality individuals (Tables S5 and S6).

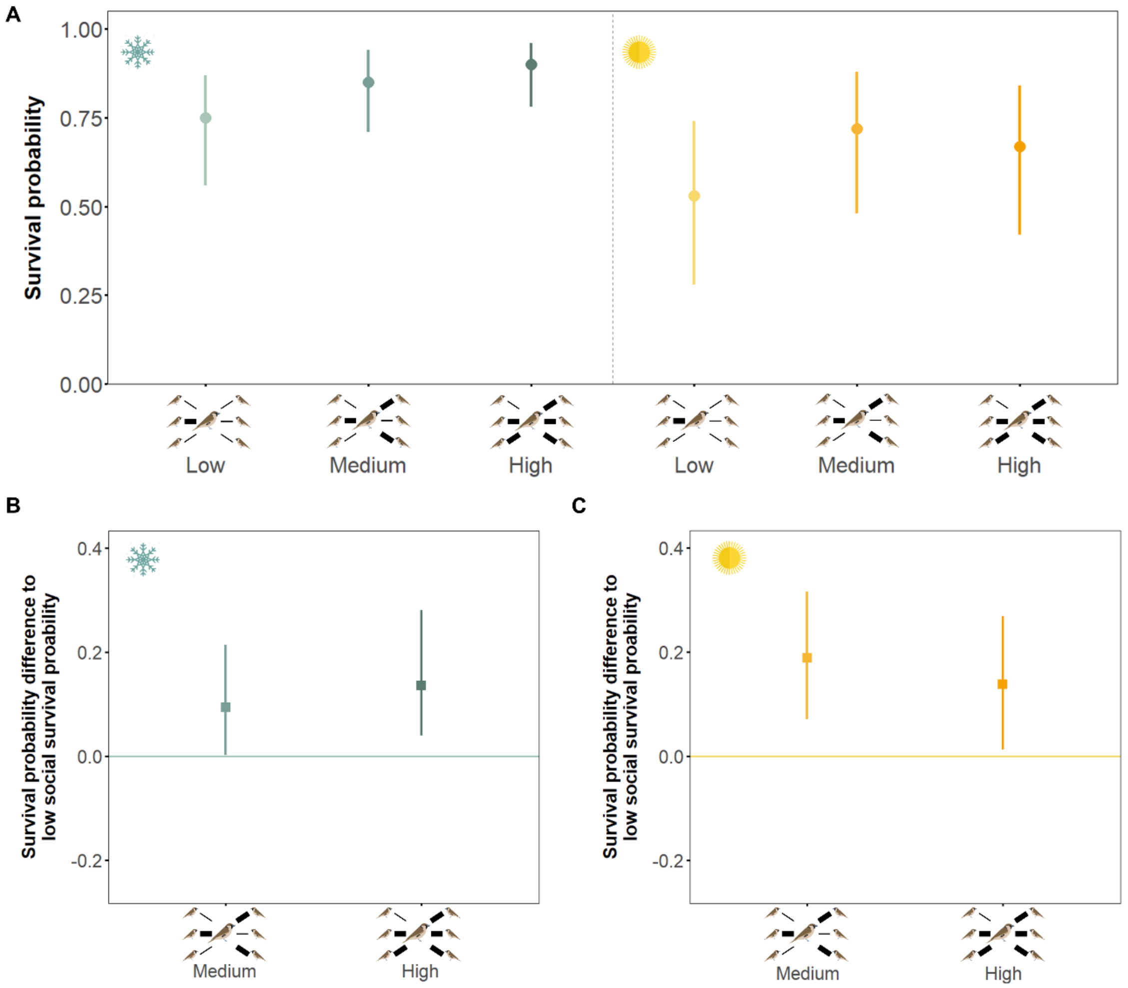

Figure 4. Survival probabilities. A) Model estimates of survival probabilities for low, medium and high sociality individuals for winter and summer intervals. Dots represent the posterior mean estimates and bars their 95% credible intervals. **B)** and **C)** Posterior mean differences in survival probabilities between low sociality individuals and medium and high sociality individuals for winter and summer, respectively. Squares represent the mean differences, and bars indicate the 95% credible intervals of the differences.

DISCUSSION

Our results show that sociable weavers tend to maintain consistent individual sociality levels, which are based on their number of strong social bonds. Furthermore, individuals with medium and high sociality levels exhibited a higher survival probability than those with a lower level of sociality. These findings suggest that, in our population, more social individuals should be favoured by natural selection.

By incorporating state-dependent individual detectability, our model explicitly accounted for detection probability differences across sociality levels, preventing biases from incomplete detections, and ensuring that variations in survival probabilities reflected biological differences rather than methodological artefacts.

Consistency of individual sociality across years

We found that, for sociable weavers, remaining in the same sociality category from one year to the next was the most likely outcome, although probabilities were close to 50% for low- and medium-sociality individuals. When transitions occurred, they tended to be between adjacent categories. The probabilities of moving from medium or high sociality to other categories were significantly lower than the probability of remaining in the same one. Low-sociality individuals showed the same general tendency, although the difference between remaining low and transitioning to medium was not statistically significant (Figure 3, Table S6).

The overall consistency in sociality levels observed in sociable weavers aligns with previous studies reporting individual-level stability in other social network metrics—such as degree, betweenness, strength, and closeness—in birds (Aplin *et al.* 2015; Dunning *et al.* 2023; Plaza *et al.* 2020; Shizuka *et al.* 2014; Thys *et al.* 2017), mammals (Blumstein *et al.* 2013; Evans *et al.* 2021; Tkaczynski *et al.* 2020; Vander Wal *et al.* 2015), and fish (Jacoby *et al.* 2014; Krause *et al.* 2017). This consistency also underscores the potential for sociality to evolve in sociable weavers. For a trait to evolve via natural selection, its expression must be consistent over time, at least to some degree (Boake 1989). This is particularly noteworthy in the case of sociality, which is influenced by a range of intrinsic and extrinsic factors that can promote or constrain changes in its expression (Schradin 2013), and which emerges through interactions among individuals, meaning that a given individual may not always be able to express their typical social behaviour, as it also depends on the behaviour of others (Niemelä & Santostefano 2015). If the expression of a social metric fluctuates randomly due to environmental or social factors, directional selection will be hindered, preventing evolutionary change in the trait at the population level, even if it has strong fitness consequences.

While overall patterns support consistency in individual sociality, our results also suggest that low-sociality individuals may be more prone to shifting their sociality level over time. Specifically, the difference between the probabilities of remaining low or transitioning to medium was not statistically significant (Figure 3, Tables S5 and S6), unlike the stronger stability observed in medium- and high-sociality individuals. This relative flexibility could reflect successful reproduction and the formation of new bonds with offspring, as discussed above. Alternatively, low-sociality individuals might actively attempt to increase their number of strong bonds—potentially through social niche construction (Trappes *et al.* 2022)—in order to gain access to the fitness benefits associated with stronger social integration, such as the higher survival probabilities observed in this study.

Individuals with higher sociality show increased survival

We found that medium and high sociality (reflecting their relatively higher number of strong social bonds) was associated with significantly higher survival probability than low sociality. This pattern was observed in both winter (July–August) and summer (October–March), indicating its consistency across seasons. This consistency could reflect persistent factors acting throughout the year, distinct mechanisms operating in each season, or a combination of both.

Although sociable weavers generally forage in cohesive colony groups—expected to provide foraging benefits to all members (Brown *et al.* 2003; Lloyd *et al.* 2018)—highly social individuals may gain additional advantages through nepotistic behaviours from group members (Rat 2015). Specifically, individuals may receive preferential access to food shared within their social group (Chiarati *et al.* 2011; Ekman *et al.* 2000), or benefit from enhanced information-sharing about novel food sources, which facilitates their discovery and exploitation (McMahon *et al.* 2024). Additionally, highly social individuals may experience nepotistic protection from predators, further increasing their survival (Griesser & Ekman 2004, 2005). Finally, being part of a larger and more cohesive group may reduce harassment from conspecifics, thereby lowering energy expenditure and stress (Cameron *et al.* 2009).

During winter, thermoregulatory benefits associated with access to roosting chambers and communal roosting are likely to play a crucial role in improving condition and survival. In sociable weavers, the communal nest provides significant insulation (Lowney *et al.* 2020; White *et al.* 1975), and night-time nest chamber temperatures are positively correlated with the number of birds roosting together, especially on cold nights (Paquet *et al.* 2016). Birds in larger roosting groups are therefore less exposed to extreme cold. If sociality influences group composition at night, medium- and high-social individuals may be more likely to roost in larger groups and thus benefit from improved thermoregulation, reduced energy expenditure, and lower risk of cold-related mortality.

During the breeding season, which coincides with the summer period, survival benefits may be linked to cooperative breeding behaviours. In sociable weavers, helpers-at-the-nest tend to form stronger associations strong bonds with breeders and other group members (Ferreira *et al.* 2020, 2024). Females with more helpers show higher survival, likely due to reduced parental effort (Paquet *et al.* 2015; see also Hatchwell 1999), and similar patterns are found in other cooperative breeders (Downing *et al.* 2021). This benefit may also extend to helpers, since helping incurs a physiological cost, particularly under high effort (Covas *et al.* 2022). Consequently, if individual sociality (i.e., number of strong bonds) is positively associated with the number of helpers received (Ferreira *et al.* 2024) and the amount of help provided (Covas *et al.* 2008), medium- and high-sociality individuals may experience increased survival, influenced by a life-history trade-off between investment in reproduction and self-maintenance.

Conclusions

Our results offer the first evidence of a positive association between the quality of social associations and survival in birds, suggesting that the evolutionary dynamics of sociality may be shared across taxa.

The consistency of individual sociality levels and its fitness effects suggests that this social trait is under directional selection, favouring more social individuals (i.e., those with a higher number of strong social bonds). While previous studies have demonstrated a link between sociality and survival (Archie *et al.* 2014; Barocas *et al.* n.d.; Blumstein *et al.* 2013; Campos *et al.* 2020; Ellis *et al.* 2017; Lehmann *et al.* 2016; Silk *et al.* 2010; Stanton & Mann 2012; Thompson & Cords 2018), few have explicitly examined the temporal consistency of social traits. Notable exceptions, such as Vander Wal et al. (2015), have addressed this by quantifying repeatability. Although our approach did not directly estimate repeatability, the transition probabilities suggest a degree of temporal consistency in individual sociality. Future studies should formally test repeatability in this and other species to better evaluate the evolutionary potential of sociality.

To further investigate these dynamics, future research should explore the heritability of sociality, disentangling the genetic and environmental components that shape its expression (Brent *et al.* 2013; Lea *et al.* 2010). This includes considering indirect genetic effects (Moore *et al.* 1997; Wolf *et al.* 1998) and the potential covariance between individual sociability and the surrounding social environment (Munar-Delgado *et al.* 2023). Such efforts will help evaluate the evolutionary potential of sociality and clarify why variation persists despite its apparent fitness benefits. The social niche specialization hypothesis suggests that individuals may exhibit consistent social differences when behaviours are linked to distinct trade-offs (Montiglio *et al.* 2013). Future studies could test whether low-social individuals outperform high-social ones under specific environmental conditions or for other key fitness components such as reproductive success or disease susceptibility. Finally, stochastic developmental factors—such as random early-life experiences or unpredictable environmental exposures—should also be integrated to gain a more comprehensive understanding of how sociality emerges, is maintained, and evolves.

ACKNOWLEDGEMENTS

We thank Annie Basson for her help building the RFID stations and all the field workers that helped collecting the data: Louis Bliard, Corisande Abiven, Tshianeo Melda, Lesego Moagi, Natasha Prindal, Paola Stefanini , Irene Baquero, Taylor Keet, and all persons who helped with the annual captures. De Beers Consolidated Mines provided access to Benfontein Reserve. This study was funded by an ERC Consolidator grant 866489 (EU) to R.C. and the ANR 19CE02-0014-01 OSU OREME and SEE-Life (CNRS, France) to CD. RC was funded by FCT (CEECIND/03451/2018).

ETHICAL STATEMENT

Birds were captured and handled in accordance with protocols approved by Northern Cape Nature Conservation (permits FAUNA 1338/2017, 0684/2019, 0059/2021, and 0775/2023) and the Ethics Committee of the University of Cape Town (2014/V1/RC, 2018/V20/RC, 2020/2018/V22/RC/A1, and 2023/V8/RC). All efforts were made to minimize handling time and disturbance, and to ensure that procedures caused the least possible stress to the animals.

DATA AVAILABILITY STATEMENT

Data (https://doi.org/10.5281/zenodo.16276322) and codes are available at Zenodo (https://doi.org/10.5281/zenodo.16276060).

REFERENCES

Aplin, L.M., Farine, D.R., Morand-Ferron, J., Cockburn, A., Thornton, A. & Sheldon, B.C. (2015). Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*, 518, 538–541.

Archie, E.A., Tung, J., Clark, M., Altmann, J. & Alberts, S.C. (2014). Social affiliation matters: both same-sex and opposite-sex relationships predict survival in wild female baboons. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20141261.

Barocas, A., Ilany, A., Koren, L., Kam, M. & Geffen, E. (2011). Variance in Centrality within Rock Hyrax Social Networks Predicts Adult Longevity. *PLOS ONE*, 6, e22375.

Bilde, T., Coates, K.S., Birkhofer, K., Bird, T., Maklakov, A.A., Lubin, Y., *et al.* (2007). Survival benefits select for group living in a social spider despite reproductive costs. *Journal of Evolutionary Biology*, 20, 2412–2426.

Blumstein, D.T., Petelle, M.B. & Wey, T.W. (2013). Defensive and social aggression: repeatable but independent. *Behavioral Ecology*, 24, 457–461.

Boake, C.R.B. (1989). Repeatability: Its role in evolutionary studies of mating behavior. *Evolutionary Ecology*, 3, 173–182.

Brent, L.J.N., Heilbronner, S.R., Horvath, J.E., Gonzalez-Martinez, J., Ruiz-Lambides, A., Robinson, A.G., *et al.* (2013). Genetic origins of social networks in rhesus macaques. *Scientific Reports*, 3, 1042.

Brown, C.R., Covas, R., Anderson, M.D. & Brown, M.B. (2003). Multistate estimates of survival and movement in relation to colony size in the sociable weaver. *Behavioral Ecology*, 14, 463–471.

Cameron, E.Z., Setsaas, T.H. & Linklater, W.L. (2009). Social bonds between unrelated females increase reproductive success in feral horses. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 13850–13853.

Campos, F.A., Villavicencio, F., Archie, E.A., Colchero, F. & Alberts, S.C. (2020). Social bonds, social status and survival in wild baboons: a tale of two sexes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 375, 20190621.

Chiarati, E., Canestrari, D., Vila, M., Vera, R. & Baglione, V. (2011). Nepotistic access to food resources in cooperatively breeding carrion crows. *Behavioral Ecology and Sociobiology*, 65, 1791–1800.

Covas, R., Lardy, S., Silva, L.R., Rey, B., Ferreira, A.C., Theron, F., *et al.* (2022). The oxidative cost of helping and its minimization in a cooperative breeder. *Behavioral Ecology*, 33, 504–517.

Covas, R., du Plessis, M.A. & Doutrelant, C. (2008). Helpers in colonial cooperatively breeding sociable weavers Philetairus socius contribute to buffer the effects of adverse breeding conditions. *Behavioral Ecology and Sociobiology*, 63, 103–112.

D'Amelio, P.B., Ferreira, A.C., Fortuna, R., Paquet, M., Silva, L.R., Theron, F., *et al.* (2022). Disentangling climatic and nest predator impact on reproductive output reveals adverse high-temperature effects regardless of helper number in an arid-region cooperative bird. *Ecology Letters*, 25, 151–162.

Downing, P.A., Griffin, A.S. & Cornwallis, C.K. (2021). Hard-working helpers contribute to long breeder lifespans in cooperative birds. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 376, 20190742.

Dunning, J., Burke, T., Hoi Hang Chan, A., Ying Janet Chik, H., Evans, T. & Schroeder, J. (2023). Opposite-sex associations are linked with annual fitness, but sociality is stable over lifetime. *Behavioral Ecology*, 34, 315–324.

Ekman, J., Bylin, A. & Tegelström, H. (2000). Parental nepotism enhances survival of retained offspring in the Siberian jay. *Behavioral Ecology*, 11, 416–420.

Ellis, S., Franks, D.W., Nattrass, S., Cant, M.A., Weiss, M.N., Giles, D., *et al.* (2017). Mortality risk and social network position in resident killer whales: sex differences and the importance of resource abundance. *Proceedings of the Royal Society B: Biological Sciences*, 284, 20171313.

Evans, T., Krzyszczyk, E., Frère, C. & Mann, J. (2021). Lifetime stability of social traits in bottlenose dolphins. *Communications Biology*, 4, 1–8.

Ferreira, A.C., Covas, R., Silva, L.R., Esteves, S.C., Duarte, I.F., Fortuna, R., *et al.* (2020). How to make methodological decisions when inferring social networks. *Ecology and Evolution*, 10, 9132–9143.

Ferreira, A.C., Farine, D.R., Silva, L.R., Fortuna, R., Doutrelant, C. & Covas, R. (2024). Foraging associations are related with helping interactions in a cooperatively breeding bird.

Formica, V.A., Wood, C.W., Larsen, W.B., Butterfield, R.E., Augat, M.E., Hougen, H.Y., *et al.* (2012). Fitness consequences of social network position in a wild population of forked fungus beetles (*Bolitotherus cornutus*). *Journal of Evolutionary Biology*, 25, 130–137.

Gelman, A. & Rubin, D.B. (1992). Inference from Iterative Simulation Using Multiple Sequences. *Statistical Science*, 7, 457–472.

Gero, S., Bejder, L., Whitehead, H., Mann, J. & Connor, R.C. (2005). Behaviourally specific preferred associations in bottlenose dolphins, *Tursiops spp*. *Canadian Journal of Zoology*, 83, 1566–1573.

Griesser, M. & Ekman, J. (2004). Nepotistic alarm calling in the Siberian jay, *Perisoreus infaustus*. *Animal Behaviour*, 67, 933–939.

Griesser, M. & Ekman, J. (2005). Nepotistic mobbing behaviour in the Siberian jay, *Perisoreus infaustus*. *Animal Behaviour*, 69, 345–352.

Hatchwell, B.J. (1999). Investment strategies of breeders in avian cooperative breeding systems. *The American Naturalist*, 154, 205–219.

Jacoby, D.M.P., Fear, L.N., Sims, D.W. & Croft, D.P. (2014). Shark personalities? Repeatability of social network traits in a widely distributed predatory fish. *Behavioral Ecology and Sociobiology*, 68, 1995–2003.

Kern, J.M. & Radford, A.N. (2021). Strongly bonded individuals prefer to forage together in cooperatively breeding dwarf mongoose groups. *Behavioral Ecology and Sociobiology*, 75, 85.

Koenig, W.D. (1981). Reproductive success, group size, and the evolution of cooperative breeding in the acorn woodpecker. *The American Naturalist*, 117, 421–443.

Krause, J., Ruxton, G.D., Krause, J. & Ruxton, G.D. (2002). *Living in Groups*. Oxford Series in Ecology and Evolution. Oxford University Press, Oxford, New York.

Krause, S., Wilson, A.D.M., Ramnarine, I.W., Herbert-Read, J.E., Clément, R.J.G. & Krause, J. (2017). Guppies occupy consistent positions in social networks: mechanisms and consequences. *Behavioral Ecology*, 28, 429–438.

Lea, A.J., Blumstein, D.T., Wey, T.W. & Martin, J.G.A. (2010). Heritable victimization and the benefits of agonistic relationships. *Proceedings of the National Academy of Sciences*, 107, 21587–21592.

Lebreton, J.D. & Cefe, R.P. (2002). Multistate recapture models: Modelling incomplete individual histories. *Journal of Applied Statistics*, 29, 353–369.

Lebreton, J.D., Nichols, J.D., Barker, R.J., Pradel, R. & Spendelow, J.A. (2009) Modeling individual animal histories with multistate capture–recapture models. In: *Advances in Ecological Research*, vol. 41. Ed. Caswell, H. Academic Press, New York, 87–173.

Lebreton, J.D. & Cefe, R.P. (2002). Multistate recapture models: Modelling incomplete individual histories. *Journal of Applied Statistics*, 29, 353–369.

Lehmann, J., Majolo, B. & McFarland, R. (2016). The effects of social network position on the survival of wild Barbary macaques, Macaca sylvanus. *Behavioral Ecology*, 27, 20–28.

Lloyd, K.J., Altwegg, R., Doutrelant, C. & Covas, R. (2018). Factors affecting the foraging distance and duration of a colonial bird, the sociable weaver, in a semi-arid environment. *African Journal of Ecology*, 56, 659–663.

Lowney, A.M., Bolopo, D., Krochuk, B.A. & Thomson, R.L. (2020). The large communal nests of sociable weavers provide year-round insulated refuge for weavers and pygmy falcons. *Frontiers in Ecology and Evolution*, 8, 570006–07.

Maclean, G.L. (1973). The Sociable Weaver, Part 2: Nest architecture and social organization. *Ostrich*, 44, 191–218.

Martin, T.E. (1995). Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs*, 65, 101–127.

McMahon, K., Marples, N.M., Spurgin, L.G., Rowland, H.M., Sheldon, B.C. & Firth, J.A. (2024). Social network centrality predicts dietary decisions in a wild bird population. *iScience*, 27.

Montiglio, P.-O., Ferrari, C. & Réale, D. (2013). Social niche specialization under constraints: personality, social interactions and environmental heterogeneity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368, 20120343.

Moore, A.J., III Brodie, E.D. & Wolf, J.B. (1997). Interacting phenotypes and the evolutionary process: I. Direct and indirect genetic effects of social interactions. *Evolution*, 51, 1352–1362.

Munar-Delgado, G., Araya-Ajoy, Y.G. & Edelaar, P. (2023). Estimation of additive genetic variance when there are gene–environment correlations: Pitfalls, solutions and unexplored questions. *Methods in Ecology and Evolution*, 14, 1245–1258.

Niemelä, P.T. & Santostefano, F. (2015). Social carry-over effects on non-social behavioral variation: mechanisms and consequences. *Frontiers in ecology and evolution*, 3, 49.

Pacheco, L. (2022) Roosting dynamics: assessing the ‘pay-to-stay’ hypothesis using a social network approach. MSc thesis, Universidade do Porto, Portugal.

Paquet, M., Doutrelant, C., Hatchwell, B.J., Spottiswoode, C.N. & Covas, R. (2015). Antagonistic effect of helpers on breeding male and female survival in a cooperatively breeding bird. *Journal of Animal Ecology*, 84, 1354–1362.

Paquet, M., Doutrelant, C., Loubon, M., Theron, F., Rat, M. & Covas, R. (2016). Communal roosting, thermoregulatory benefits and breeding group size predictability in cooperatively breeding sociable weavers. *Journal of Avian Biology*, 47, 749–755.

Payevsky, V.A. (2021). Sex Ratio and sex-specific survival in avian populations: a review. *Biology Bulletin Reviews*, 11, 317–327.

Plaza, M., Burke, T., Cox, T., Flynn-Carroll, A., Girndt, A., Halford, G., *et al.* (2020). Repeatable social network node-based metrics across populations and contexts in a passerine. *Journal of Evolutionary Biology*, 33, 1634–1642.

R Core Team (2020) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: https://www.R-project.org/

Rat, M.E.T. (2015) Dominance, social organisation and cooperation in the sociable weaver (*Philetairus socius*). PhD thesis, University of Cape Town, South Africa.

Schaub, M., Gimenez, O., Schmidt, B.R. & Pradel, R. (2004). Estimating survival and temporary emigration in the multistate capture–recapture framework. *Ecology*, 85, 2107–2113.

Schradin, C. (2013). Intraspecific variation in social organization by genetic variation, developmental plasticity, social flexibility or entirely extrinsic factors. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368, 20120346.

Shizuka, D., Chaine, A.S., Anderson, J., Johnson, O., Laursen, I.M. & Lyon, B.E. (2014). Across-year social stability shapes network structure in wintering migrant sparrows. *Ecology Letters*, 17, 998–1007.

Silk, J.B., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R., et al. (2010). Strong and Consistent Social Bonds Enhance the Longevity of Female Baboons. Current Biology, 20, 1359–1361.

Snyder-Mackler, N., Burger, J.R., Gaydosh, L., Belsky, D.W., Noppert, G.A., Campos, F.A., *et al.* (2020). Social determinants of health and survival in humans and other animals. *Science*, 368, eaax9553.

Stanton, M.A. & Mann, J. (2012b). Early Social Networks Predict Survival in Wild Bottlenose Dolphins. PLOS ONE, 7, e47508.

Thompson, N.A. & Cords, M. (2018). Stronger social bonds do not always predict greater longevity in a gregarious primate. *Ecology and Evolution*, 8, 1604–1614.

Thys, B., Eens, M., Aerts, S., Delory, A., Iserbyt, A. & Pinxten, R. (2017). Exploration and sociability in a highly gregarious bird are repeatable across seasons and in the long term but are unrelated. *Animal Behaviour*, 123, 339–348.

Tkaczynski, P.J., Mielke, A., Samuni, L., Preis, A., Wittig, R.M. & Crockford, C. (2020). Long-term repeatability in social behaviour suggests stable social phenotypes in wild chimpanzees. *Royal Society Open Science*, 7, 200454.

Trappes, R., Nematipour, B., Kaiser, M.I., Krohs, U., van Benthem, K.J., Ernst, U.R., *et al.* (2022). How Individualized Niches Arise: Defining Mechanisms of Niche Construction, Niche Choice, and Niche Conformance. *Bioscience*, 72, 538–548.

Valpine, P., Paciorek, C., Turek, D., Michaud, N., Anderson-Bergman, C., Obermeyer, F., Wehrhahn Cortes, C., Rodríguez, A., Temple Lang, D. & Paganin, S. (2022) NIMBLE: MCMC, particle filtering, and programmable hierarchical modeling. R package version 1.1.0. Available at: https://r-nimble.org

Valpine, P., Turek, D., Paciorek, C.J., Anderson-Bergman, C., Lang, D.T. & Bodik, R. (2017) Programming with models: writing statistical algorithms for general model structures with NIMBLE. *Journal of Computational and Graphical Statistics*, 26: 403–413. https://doi.org/10.1080/10618600.2016.1172487

Vander Wal, E., Festa-Bianchet, M., Réale, D., Coltman, D.W. & Pelletier, F. (2015). Sex-based differences in the adaptive value of social behavior contrasted against morphology and environment. *Ecology*, 96, 631–641.

White, F.N., Bartholomew, G.A. & Howell, T.R. (1975). The Thermal Significance of the Nest of the Sociable Weaver *Philetairus Socius*: Winter Observations. *Ibis*, 117, 171–179.

Wolf, J.B., Iii, E.D.B., Cheverud, J.M., Moore, A.J. & Wade, M.J. (1998). Evolutionary consequences of indirect genetic effects. *Trends in Ecology & Evolution*, 13, 64–69.

The number of strong social bonds is linked to survival in a cooperative bird

Gabriel Munar-Delgado[1,2,*], Matthieu Paquet[3], Babette Fourie[1,2], Franck Theron[1,2], André Ferreira[4], Claire Doutrelant[5,6], Rita Covas[1,2,6]

[1] CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto, Vairão, Portugal

[2]BIOPOLIS, Program in genomics, Biodiversity and Land Planning, Vairão, Portugal

[3]SETE, Station d'Écologie Théorique et Expérimentale, CNRS, Moulis, France

[4]Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland

[5]CEFE, CNRS, University of Montpellier, EPHE, IRD, Montpellier, France

[6]FitzPatrick Institute of African Ornithology, DST-NRF Centre of Excellence, University of Cape Town, Rondebosch, South Africa

Correspondence: gabriel.munar@gmail.com

SUPPLEMENTARY MATERIAL

Parameters description as in Nimble code

Parameter	Description
phiLw	survival probability state L (Low sociality) during winter
phiMw	survival probability state M (Medium sociality) during winter
phiHw	survival probability state H (High sociality) during winter
phiLs	survival probability state L during summer
phiMs	survival probability state M during summer
phiHs	survival probability state H during summer
psiL[1]	transition probability from L to L, i.e. stay in state L
psiL[2]	transition probability from L to M
psiL[3]	transition probability from L to H
psiM[1]	transition probability from M to L
psiM[2]	transition probability from M to M i.e., stay in state M
psiM[3]	transition probability from M to H
psiH[1]	transition probability from H to L
psiH[2]	transition probability from H to M
psiH[3]	transition probability from H to H i.e. stay in stare H
pLn	recapture probability L at nets in sep
pMn	recapture probability M at nets in sep
pHn	recapture probability H at nets in sep
pLf	recapture probability L at feeders
pMf	recapture probability M at feeders
pHf	recapture probability H at feeders
betaLw	intercept of winter survival probability for state L (logit scale)
betaMw	intercept of winter survival probability for state M (logit scale)
betaHw	intercept of winter survival probability for state H (logit scale)

betaw[1]	coefficient for the effect of sex on winter survival probability
betaw[2]	coefficient for the effect of age on winter survival probability
epstw[]	random effect of year (t) on winter
epscw[]	random effect of colCNA on winter
betaLs	intercept of summer survival probability for state L (logit scale)
betaMs	intercept of summer survival probability for state M (logit scale)
betaHs	intercept of summer survival probability for state H (logit scale)
betas[1]	coefficient for the effect of sex on summer survival probability
betas[2]	coefficient for the effect of age on summer survival probability
epsts[]	random effect of year (t) on summer
epscs[]	random effect of colCNA on summer
betaDL	intercept of detection probability at RFID-feeders for state L (logit scale)
betaDM	intercept of detection probability at RFID-feeders for state M (logit scale)
betaDH	intercept of detection probability at RFID-feeders for state H (logit scale)
betaD	coefficient for the effect of RFID_at_Col on detection probability
age_centered	age matrix (in years)
sex_centered	centered sex vector
colCNA	colony matrix, represent to what colony each individual belonged each year
RFID_at_Col	matrix of RFID feeder presence at colonies

Table S1. Description of parameters used in the Bayesian multi-state capture–recapture model, as implemented in Nimble. Notation used in the code, along with a brief explanation of each parameter's biological or modelling meaning.

Specification of priors

Parameter	Prior	Description of prior values
psiL[1:3], psiM[1:3], psiH[1:3]	ddirch(alpha[1:3])	Dirichlet prior with concentration parameters 1, 1, 1 (i.e., equal weight to all transitions)
pln, pmn, phn	dunif(0, 1)	Uniform prior between 0 and 1 for detection probabilities
epstw[t], epsts[t]	dnorm(0, sd = sdepstw) dnorm(0, sd = sdepsts)	Normal prior with mean 0 and standard deviation sdepstw/ sdepsts
epscw[j], epscs[j]	dnorm(0, sd = sdepscw) dnorm(0, sd = sdepscs)	Normal prior with mean 0 and standard deviation sdepscw/sdepscs
sdepstw, sdepscw, sdepsts, sdepscs	dexp(1)	Exponential prior with rate 1
betaw[1], betaw[2]	dnorm(mean = 0, sd = 1.5)	Normal prior with mean 0 and standard deviation 1.5
betaLw, betaMw, betaHw	dnorm(mean = 0, sd = 1.5)	Normal prior with mean 0 and standard deviation 1.5
betas[1], betas[2]	dnorm(mean = 0, sd = 1.5)	Normal prior with mean 0 and standard deviation 1.5
betaLs, betaMs, betaHs	dnorm(mean = 0, sd = 1.5)	Normal prior with mean 0 and standard deviation 1.5

Table S2. Specification of prior distributions used in the Bayesian multi-state capture–recapture model. Parameter notation corresponds to that described in Table S1. For each parameter, the prior distribution and its characteristics are provided.

Model description

	Model
Survival in winter	logit(phiLw[i,t]) <- betaLw + betaw[1] * sex_centered[i] + betaw[2] * age_centered[i,t] + epstw[t] + epscw[colCNA[i,t]]
	logit(phiMw[i,t]) <- betaMw + betaw[1] * sex_centered[i] + betaw[2] * age_centered[i,t] + epstw[t] + epscw[colCNA[i,t]]
	logit(phiLw[i,t]) <- betaLw + betaw[1] * sex_centered[i] + betaw[2] * age_centered[i,t] + epstw[t] + epscw[colCNA[i,t]]
Survival in summer and transitions	logit(phiLs[i,t]) <- betaLs + betas[1] * sex_centered[i] + betas[2] * age_centered[i,t] + epsts[t] + epscs[colCNA[i,t]]
	logit(phiMs[i,t]) <- betaMs + betas[1] * sex_centered[i] + betas[2] * age_centered[i,t] + epsts[t] + epscs[colCNA[i,t]]
	logit(phiHs[i,t]) <- betaHs + betas[1] * sex_centered[i] + betas[2] * age_centered[i,t] + epsts[t] + epscs[colCNA[i,t]]
Detection at RFIDs	logit(pLf[i,t]) <- (betaDL + betaD * RFID_at_Col[i,t]) * captured[t] - (1 - captured[t]) * 15
	logit(pMf[i,t]) <- (betaDM + betaD * RFID_at_Col[i,t]) * captured[t] - (1- captured[t]) * 15
	logit(pHf[i,t]) <- (betaDH + betaD * RFID_at_Col[i,t]) * captured[t] - (1- captured[t]) * 15

Table S3. Model equations used in the Bayesian multi-state capture–recapture analysis. All models used a logit link**.** Parameters are defined in Table S1 and priors in Table S2. See main text for rationale and code for implementation. *captured* is a dummy variable used to fix detection probability to 0 in 2020 due to missing RFID data.

Covariates and random effects

- Age: For most birds (81%), we determined their exact age through breeding monitoring. For immigrant birds first captured as adults within the studied population (sociable weavers can disperse between colonies; van Dijk *et al.* 2015), we estimated their age based on the average age of dispersal observed within our population. According to this, we assumed that immigrant individuals were 709 days old at the date of first capture (the average minimum dispersal age in our population; Silva *et al.* 2025).

- Sex: During mist-nets samplings, individual blood samples were taken to determine sex through genetic sexing (Griffiths *et al.* 1998).

- Individual's colony: Birds were sometimes registered at RFID-feeder stations from different colonies. To assign each bird to a colony, we used mist-net sampling data, associating individuals with the colony where they were captured, which corresponds to their roosting location. If an individual was not captured at mist-nets in a specific year (*t*) but was registered at feeders, we used mist-net data from the following year to determine its colony identity. In cases where the individual was not captured the next year either, we relied on mist-net data from the previous year. Using this approach, we were able to assign a colony identity to every individual with social status data.

Individual exclusion criteria for multi-state capture–recapture analyses

We excluded individuals from the multi-state capture–recapture model based on three criteria. First, individuals were excluded if they only had RFID-feeder data from the last year of the study, as no recapture data could be obtained for them. Second, individuals for which sex could not be determined were excluded from the analysis, as sex was included as a covariate in the survival and transition components of the model. Third, only individuals from PIT-tagged colonies were retained. This is because social status estimates are calculated relative to the social structure of each colony, and individuals residing in non-tagged colonies could not be accurately assigned a social status. Individuals that ever migrated from PIT-tagged to non-tagged colonies were entirely excluded from the analysis, as their social status could not be determined after migration and the missing data could be wrongly interpreted by the model as mortality. Conversely, individuals that migrated from non-tagged to PIT-tagged colonies were retained, but only social status data from after migration were included.

Sociality levels classification

Year	Colony	Sociality level	Minimum strong bonds	Maximum strong bonds
2018	11	Low	0	3
		Medium	4	6
		High	7	16
	20	Low	0	3
		Medium	4	7
		High	8	16
	27	Low	0	3
		Medium	4	8
		High	9	16
	43	Low	0	1
		Medium	2	6
		High	7	11
	71	Low	0	5
		Medium	6	9
		High	11	24
2019	11	Low	0	2
		Medium	3	6
		High	7	12
	20	Low	0	0
		Medium	1	1
		High	3	4
	27	Low	0	1
		Medium	2	3
		High	4	9
	43	Low	0	0
		Medium	1	1
		High	2	6
	71	Low	0	2
		Medium	3	4
		High	5	12

2021	11	Low	1	5
		Medium	6	10
		High	11	16
	20	Low	0	2
		Medium	3	5
		High	8	10
	27	Low	0	3
		Medium	4	8
		High	9	15
	43	Low	0	2
		Medium	3	4
		High	5	9
	71	Low	0	6
		Medium	7	8
		High	9	19
2022	11	Low	0	1
		Medium	2	5
		High	6	11
	20	Low	0	2
		Medium	3	3
		High	4	6
	21	Low	0	0
		Medium	1	1
		High	2	2
	71	Low	0	1
		Medium	2	4
		High	5	10
2023	11	Low	0	4
		Medium	5	12
		High	13	23
	20	Low	0	4
		Medium	5	7
		High	9	20
	21	Low	0	3
		Medium	4	5
		High	6	9
	71	Low	0	3
		Medium	4	7
		High	10	15

Table S4. Classification of sociality levels by year and colony. For each year-colony combination, the table shows the minimum and maximum numbers of strong social bonds observed within each category (see main text for classification criteria).

Posterior predictive checks of the model

We assessed the goodness-of-fit of our model using Bayesian p-values (Gelman et al., 2014), a model-checking procedure that measures the dissimilarity between observed data and model predictions. We evaluated the dissimilarity between the observed and model-predicted means and coefficients of variation (CV) for the total number of re-detections per individual at mist nets and RFID-feeders. The reported Bayesian p-values indicate the proportion of simulated data generated from the model in which the distance between this simulated data and the expected mean (or CV) exceeds the distance between observed data and the expected mean (or CV). Values close to 0 or 1 (commonly below 0.05 or above 0.95) suggest a lack of fit.

To perform this analysis for detections at RFID-feeders, we transformed the observed data and model-prediction matrices (which contained four states: three social-status states and non-observation) into binomial matrices with observation (any social-status) and non-observation.

We obtain Bayesian p-values of 0.33 for mean of detections at the mist-nets, 0.47 for CV of detection at mist-nets, 0.26 for mean of detections at the RFID-feeders, 0.32 for CV of detection at RFID-feeders (Figure S1) showing no evidence for a lack of fit of our model to estimate the mean, and CV of the number of detections per individual.

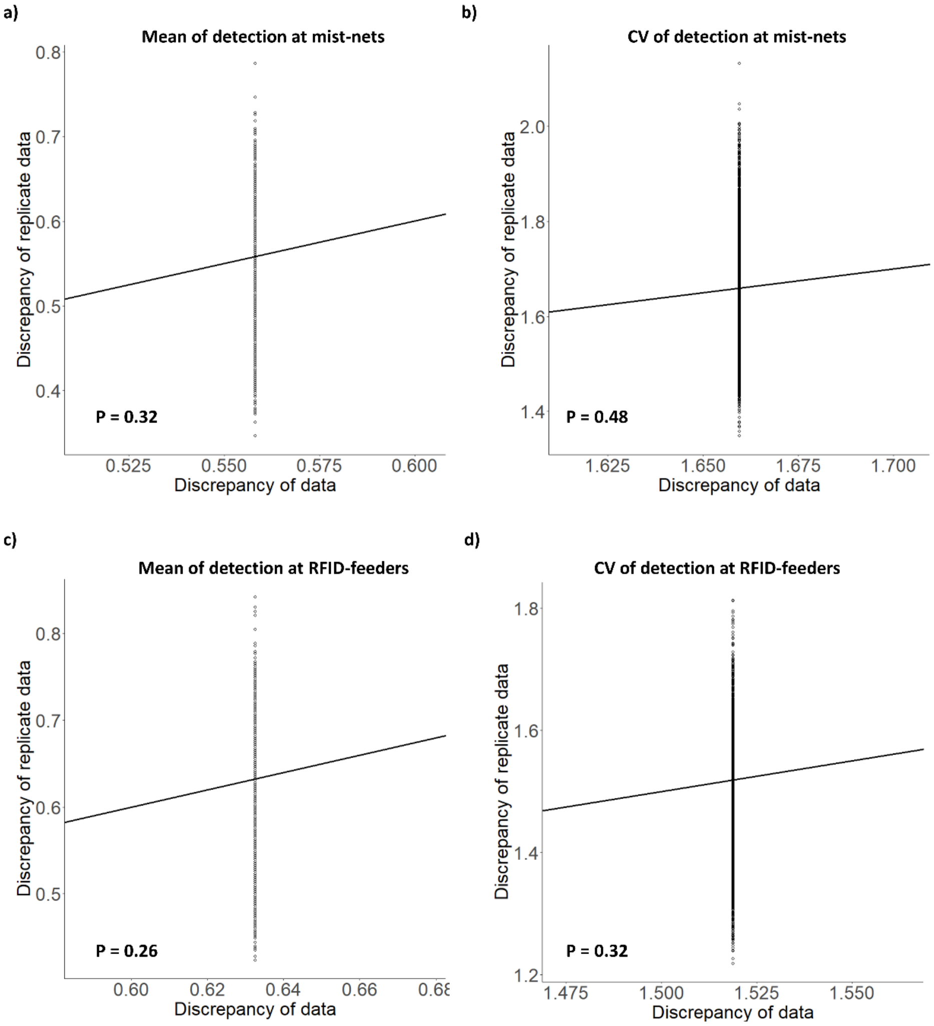

Figure S1. Posterior predictive checks of detection probabilities. P-values represent Bayesian p-values. a) Mean detection at mist-nets, b) coefficient of variation (CV) of detection at mist-nets, c) mean detection at RFID-feeders, and d) CV of detection at RFID-feeders.

Model convergence and mixing of chains

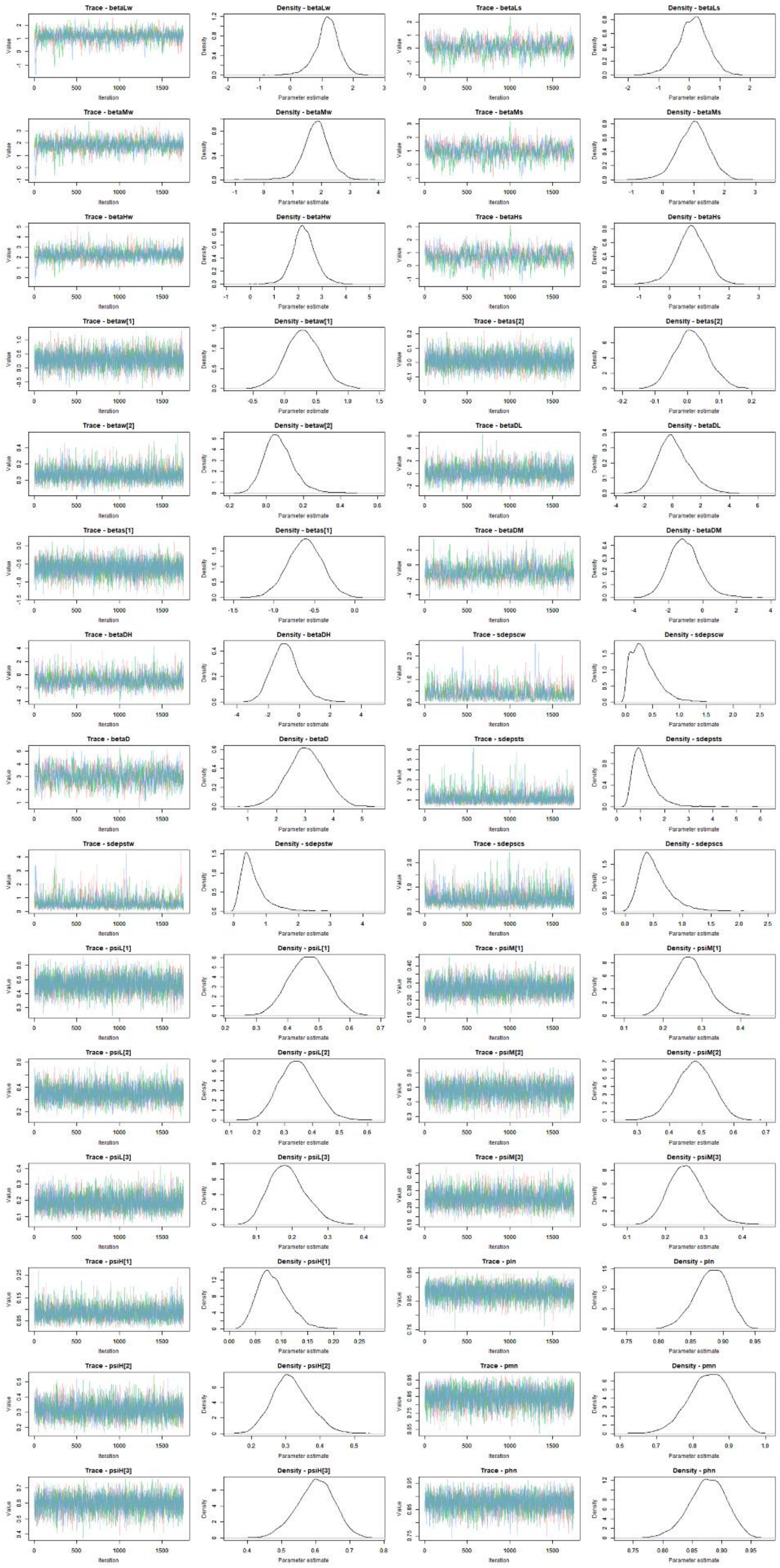

Figure S2. Trace plots and posterior density distributions for monitored parameters in the Bayesian multi-state capture–recapture model. Parameter notation corresponds to that described in Table S1

Model estimated values

		mean	SD	2.50%	97.50%	$\hat{R}$	n.eff
Survival in winter	$Intercept_{\varphi_{L_w}}$	1.16	0.41	0.24	1.89	1.00	799
	$Intercept_{\varphi_{M_w}}$	1.82	0.46	0.89	2.74	1.00	888
	$Intercept_{\varphi_{H_w}}$	2.24	0.51	1.29	3.30	1.00	1151
	β_{Sex_w}	0.29	0.28	-0.25	0.85	1.00	4436
	β_{Age_w}	0.07	0.08	-0.07	0.26	1.00	3224
	$SD_{\varepsilon_{t_w}}$	0.61	0.43	0.11	1.71	1.01	726
	$SD_{\varepsilon_{Col_w}}$	0.36	0.27	0.02	1.02	1.02	910
Survival in summer	$Intercept_{\varphi_{L_s}}$	0.11	0.51	-0.95	1.06	1.03	547
	$Intercept_{\varphi_{M_s}}$	0.98	0.51	-0.08	1.96	1.02	590
	$Intercept_{\varphi_{H_s}}$	0.73	0.51	-0.33	1.69	1.02	520
	β_{Sex_s}	-0.62	0.21	-1.05	-0.21	1.00	5250
	β_{Age_s}	0.01	0.05	-0.09	0.12	1.00	4495
	$SD_{\varepsilon_{t_s}}$	1.15	0.52	0.53	2.42	1.00	2194
	$SD_{\varepsilon_{Col_s}}$	0.52	0.28	0.14	1.23	1.00	1831
Detections at RFIDs	$Intercept_{p_{L_f}}$	0.06	1.13	-1.89	2.55	1.00	2210
	$Intercept_{p_{M_f}}$	-1.04	0.94	-2.73	1.01	1.00	1396
	$Intercept_{p_{H_f}}$	-0.86	0.94	-2.50	1.23	1.00	1356
	β_{RFID_f}	3.04	0.64	1.75	4.29	1.00	928
Detect. at nets	p_{L_n}	0.88	0.03	0.83	0.93	1.00	4034
	p_{M_n}	0.84	0.06	0.73	0.94	1.00	3290
	p_{H_n}	0.88	0.03	0.81	0.93	1.00	4018
Status Transitions	ψ_{LL}	0.47	0.06	0.34	0.59	1.00	4497
	ψ_{LM}	0.35	0.06	0.23	0.48	1.00	3894
	ψ_{LH}	0.19	0.05	0.10	0.29	1.00	4730
	ψ_{ML}	0.27	0.05	0.19	0.36	1.00	4987
	ψ_{MM}	0.48	0.06	0.36	0.58	1.00	3728
	ψ_{MH}	0.25	0.05	0.17	0.35	1.00	4246
	ψ_{HL}	0.08	0.03	0.04	0.15	1.00	4943
	ψ_{HM}	0.32	0.05	0.22	0.43	1.00	3655
	ψ_{HH}	0.60	0.05	0.49	0.70	1.00	3735

Table S5. Multi-state capture-recapture model estimates. φ_{X_z} is the survival portability of an individual in state X (L low; M medium, H high) and time interval Z (W winter or S summer). β_{C_z} is the effect of the covariate C (Sex or Age) at time interval Z. $SD_{\varepsilon_{t_s}}$is the standard deviation of random effect (ε_{r_z}) where r is the identity of the random effect (t year; Col colony) for the time period Z. p_{X_n} is the recapture probability at nets of an individual in state X. p_{X_f} is the recapture probability at RFID-feeders of an individual in state X. ψ_{XY} is the transition probability from state X to state Y from *t* to *t+1*. Columns represent mean, standard deviation (SD), lower (2.5%) and upper (97.5%) values of 95 confidence intervals, $\hat{R}$ and effective sample size (n.eff).

Posterior mean differences

	2.5%	50%	97.5%	Significance
$p_{H_f} - p_{M_f}$	-0.508	0.031	0.550	NO
$p_{H_f} - p_{L_f}$	-0.675	-0.180	0.335	NO
$p_{M_f} - p_{L_f}$	-0.727	-0.217	0.347	NO
$p_{H_n} - p_{M_n}$	-0.088	0.030	0.158	NO
$p_{H_n} - p_{L_n}$	-0.087	-0.005	0.072	NO
$p_{M_n} - p_{L_n}$	-0.157	-0.036	0.076	NO
$\varphi_{H_w} - \varphi_{M_w}$	-0.047	0.041	0.149	NO
$\varphi_{H_w} - \varphi_{L_w}$	0.040	0.135	0.280	YES
$\varphi_{M_w} - \varphi_{L_w}$	0.002	0.094	0.213	YES
$\varphi_{H_S} - \varphi_{M_S}$	-0.172	-0.051	0.065	NO
$\varphi_{H_S} - \varphi_{L_S}$	0.012	0.138	0.269	YES
$\varphi_{M_S} - \varphi_{L_S}$	0.071	0.188	0.316	YES
$\psi_{LL} - \psi_{LM}$	-0.112	0.122	0.337	NO
$\psi_{LL} - \psi_{LH}$	0.091	0.283	0.455	YES
$\psi_{LM} - \psi_{LH}$	-0.033	0.162	0.349	NO
$\psi_{ML} - \psi_{MM}$	-0.374	-0.209	-0.019	YES
$\psi_{ML} - \psi_{MH}$	-0.131	0.014	0.154	NO
$\psi_{MM} - \psi_{MH}$	0.03	0.225	0.393	YES
$\psi_{HL} - \psi_{HM}$	-0.367	-0.230	-0.096	YES
$\psi_{HL} - \psi_{HH}$	-0.642	-0.518	-0.371	YES
$\psi_{HM} - \psi_{HH}$	-0.476	-0.290	-0.063	YES

Table S6. Posterior mean differences. Mean differences between the survival, transition, and recapture probabilities of the different social states (and their 95% confidence intervals) calculated from the posterior estimates. See Table S5 for parameters description.

REFERENCES

van Dijk, R.E., Covas, R., Doutrelant, C., Spottiswoode, C.N. & Hatchwell, B.J. (2015). Fine-scale genetic structure reflects sex-specific dispersal strategies in a population of sociable weavers (*Philetairus socius*). *Molecular Ecology*, 24, 4296–4311.

Gelman, A., Carlin, J.B., Stern, H.S., Dunson, D.B., Vehtari, A. & Rubin, D.B. (2014). BayesianData Analysis. 3rd edn. CRC Press, Boca Raton, FL.

Griffiths, R., Double, M.C., Orr, K. & Dawson, R.J.G. (1998). A DNA test to sex most birds. *Molecular Ecology*, 7, 1071–1075.

Silva, N.J., Ferreira, A.C., Silva, L.R., Perret, S., Tieo, S., Renoult, J.P., *et al.* (2025). Deep learning approach to detect and visualize sexual dimorphism in monomorphic species. *Animal Behaviour*, 225, 123223.