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Research article

Do older parents do better? Relationships between parental age, chick body condition and migratory behaviour in a colonial-breeding waterbird

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Animals' performance of basic functional behaviours, such as foraging and movement, may improve with age as a result of past experiences. In migratory birds, for example, due to earlier or more efficient migration, older and likely more experienced individuals tend to arrive at breeding sites earlier and enjoy better breeding conditions than younger conspecifics, resulting in a higher reproductive success. Yet, despite the advantages of early arrival for breeding adults, the long-term effects of fledging early and/or with a higher body condition on chicks' future fitness prospects remain largely unexplored. In differential migration systems, low-quality or socially subordinate individuals may be constrained to sub-optimal migratory behaviours associated with lower demographic rates. Therefore, producing high-quality chicks may enhance the survival of offspring. In this study, we analysed data from the long-term ringing programme on the breeding population of Eurasian spoonbills in the Camargue (southern France) to investigate how breeder age may influence the timing of breeding and, in turn, how this may affect chick body condition and their subsequent migratory behaviour. Using breeding resightings of birds individually marked as a chick since 2008, combined with chick biometric measurements and subsequent winter resightings of offspring, we show that older spoonbills tend to breed earlier in the season than younger individuals, and that early breeders, regardless of age, are more likely to produce chicks with higher body condition than late breeders. Finally, migratory behaviour of juveniles appears to be influenced by the timing of breeding, with later-born juveniles tending to undertake less demanding migrations (without crossing major ecological barriers) than juveniles born earlier in the breeding season. Our study therefore highlights the relevance of long-term studies to better understand the complex breeding phenology of migratory species, which can lead to changes in population-level patterns and processes.

Keywords: breeding performance, ecological barriers, juvenile migratory behaviour, ontogeny, *Platalea leucorodia*, scale-mass-index

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Introduction

As animals age, past experience can improve their performance of basic functional behaviours (e.g. foraging and movement; Lecomte et al. 2010, Aikens et al. 2022, Acácio et al. 2024). This is often associated with relatively higher mortality rates of juveniles in comparison to adults (Sullivan 1989, Daunt et al. 2007, Corbeau et al. 2020). Furthermore, in addition to physiological changes (Robbins et al. 2006), accumulated experience may also explain why older individuals often outperform younger ones during the breeding season (Clutton-Brock 1988, Daunt et al. 1999). However, due to the difficulty of tracking individual animals throughout their annual cycle and lifetime (Brown et al. 2013, Riotte-Lambert and Weimerskirch 2013), comparisons of performance of complex behaviours (e.g. migration and timing of breeding) are often simplified to dichotomous comparisons between juveniles or immatures, and adults of unknown age or experience (Berthold 2001, Hake et al. 2003, Desprez et al. 2011, Pradel et al. 2012). Long-term marking programmes have enabled us to examine how certain behaviours (e.g. timing of breeding and migration at the individual level) and performance (e.g. survival and productivity) change over an individual's lifetime (Clark et al. 2009, Reichlin et al. 2009, Neate-Clegg and Tingley 2023).

In seasonal environments, birds that breed earlier in the season tend to achieve higher reproductive success (and produce better-quality chicks) than those that breed later (Klomp 1970, Drent et al. 2003, Smith and Moore 2005, Alves et al. 2019, Costa et al. 2021). Moreover, older individuals, with prior knowledge of migration challenges and habitat quality, may arrive earlier at breeding sites and select higher-quality habitats, leaving sub-optimal habitats for younger individuals arriving later (van de Pol and Verhulst 2006, McCleery et al. 2008, Zhang et al. 2015, Campioni et al. 2020).

In the case of migratory birds, arriving at the breeding sites earlier often means priority of access to better-quality sites, greater resource availability, higher-quality partners, and higher productivity (Ketterson and Nolan 1976, Gauthreaux 1978, Kokko 1999, Morrison et al. 2019). Thus, to maximise their reproductive success, migratory birds face the additional challenge of timing their spring migration to coincide with favourable local environmental conditions at their breeding sites, while being hundreds of kilometres away (Costa et al. 2021). For these species, accumulated experience gained during previous migrations plays a significant role in improving performance at stopover sites (Alerstam et al. 2003, Sergio et al. 2014, Rus et al. 2017). Experienced individuals are likely to achieve a more efficient migration (Hedenström and Alerstam 1997, Miller et al. 2016, Aikens et al. 2024) with shorter stopover durations (Péron and Grémillet 2013, McKinnon et al. 2014, Campioni et al. 2020) and faster refuelling times compared to inexperienced migrants (Lindström 2003, Sergio et al. 2014, Votier et al. 2017). This is the case for the black kite *Milvus migrans*, where individuals tend to migrate more efficiently with age, likely due to individual improvements and the selective disappearance of less efficient migrants (Sergio et al. 2014). Indeed, many studies reported that older, more experienced individuals arrived at the breeding sites earlier and had higher reproductive success than younger ones (Lack 1966, Crawford 1977, Balbontín et al. 2007, Neate-Clegg and Tingley 2023). Furthermore, it is also widely known that chicks can be affected by age or quality of the parents (Crawford 1977, Ricklefs 1983, Richner 1989). For example, in the European shag *Phalacrocorax aristotelis* system, younger adults may be less efficient at feeding and brooding their chicks (Snow 1960). These links between adult age and associated breeding performance can therefore produce variation in chick body condition, which may in turn influence chick survival and subsequent behaviour (e.g. dispersal and migration). Although the effects of adult age have been widely explored with regards to breeding performance (Sæther 1990, Forslund and Pärt 1995, Limmer and Becker 2010, Ortega et al. 2017), the potential effect of being raised by experienced parents on a chick's future migratory behaviour remains mostly unknown.

Individual-level processes such as migratory and dispersive behaviour have been reported to be influenced by several factors, as well as by variation in body condition (Ketterson and Nolan 1976, Kaitala et al. 1993, Barbraud et al. 2003, Chapman et al. 2011, Buchan et al. 2020). Peig and Green (2009) define body condition as the energy capital accumulated in the animal body due to food consumption and, as such, an indicator of an animal's general health and quality. Migratory and dispersive movements are energetically expensive and involve a high risk of mortality, thus, the acquisition of a good body condition prior to departure influences the extent to which an animal can disperse or migrate (Barbraud et al. 2003, Sanz-Aguilar et al. 2012). Therefore, producing higher-quality chicks likely contributes to the migratory behaviour and survival outcomes of offspring. In differential migratory systems, low-quality (body-size hypothesis, or foraging-limitation hypothesis; Boyle 2008) or socially subordinate individuals (dominance hypothesis) may be pushed to sub-optimal migration strategies, such as longer migration, to reduce the negative effects of competition and harsher environmental conditions during wintering (Ketterson and Nolan 1983, Cristol et al. 1999, Hegemann et al. 2015). Thus, it can be expected that larger individuals will adopt a resident behaviour due to their ability to withstand longer periods of food deprivation, while smaller individuals are presumed to be more likely to migrate as they are unable to compete with dominant individuals when food is scarce (Ketterson and Nolan 1983, Cristol et al. 1999, Hegemann et al. 2015). Assuming an inherent cost to wintering close to the breeding grounds, the arrival time hypothesis proposes that immature individuals migrate farther, shifting closer with age as reproductive benefits increase (Myers 1981). Nevertheless, the hypotheses regarding the mechanisms of differential migration were primarily based on passerine systems, and exceptions to the predictions of these hypotheses do exist. For example, juveniles of the greater flamingo *Phoenicopterus roseus* that presented higher body condition were more likely to migrate than those in poorer condition, which became residents (Barbraud et al. 2003).

The Eurasian spoonbill *Platalea leucorodia* (hereafter spoonbill) is a long-lived species which can live for up to approximately 30 years in the wild (Werkgroep Lepelaar 2022). The growing breeding population in the Camargue (southern France) has a relatively long breeding season (Ferreira et al. 2025a) with egg laying occurring between February and June. Since 2008, a colour-ring monitoring programme has been implemented in this population (Blanchon et al. 2019). Observations (i.e. resightings) of marked birds throughout the breeding and non-breeding distribution of this population have revealed diverse migratory behaviours, covering a wide range of migratory routes and distances (Blanchon et al. 2019, Ferreira et al. 2024b). Thus, this population presents a unique opportunity to assess variation in chick body condition over time (i.e. within breeding seasons and across years) and its potential influence on migratory behaviour. In addition, observations during the breeding season allowed for the identification and aging of the parents (as more than 5000 individuals were marked as chicks) and, in some cases, their respective nests.

Here, we monitored breeding spoonbills and their nests, measured biometrics of chicks, and recorded their subsequent migratory behaviour to investigate how breeder age may influence the timing of breeding and, in turn, how this may affect chick body condition and their subsequent migratory behaviour. We predicted that: 1) older, and likely more experienced, adults breed earlier than younger adults; 2) chick body condition declines during the breeding season due to increasing resource competition between breeders (Lack 1968, Gauthreaux 1978, Kokko 1999) and decreasing quality of the parents (potentially due to the late arrival and/or late breeding of less experienced birds); and 3) a chick's migratory behaviour is determined by timing of hatching and body condition. Considering that the majority of spoonbills in this population adopt a long-distance migratory behaviour (Ferreira et al. 2024b), we predict that, contrary to the body-size, dominance, and arrival hypotheses, higher-quality or earlier-born juveniles migrate longer distances than lower-quality or later-born juveniles. Spoonbills are social birds (de Goeij et al. 2012, Lok et al. 2019) and, as such, by the time later-born juveniles (previously termed chicks) are able to migrate, experienced individuals undertaking such migrations may have already left the breeding sites, thereby potentially limiting the ability to travel with adults to more distant sites (Gunnarsson 2006, Gill et al. 2014, 2019, Nightingale 2023).

Material and methods

Study site and population

Camargue is a semi-natural region of 180 000 ha, along the Mediterranean Sea in southern France, making it the largest wetland in France (Blondel et al. 2013, Galewski and Devictor 2016). Since 1998, the breeding population of spoonbills has increased from two breeding pairs to more than 400 since 2019 (Blanchon et al. 2019, Champagnon and Kralj 2023), nesting on the ground on small islets. Spoonbill chicks stay in their nest during at least the first three weeks of their life, where they are regularly fed by both parents (Cramp and Simmons 1977).

During the breeding seasons of 2009 to 2023, spoonbill colonies in Camargue were monitored (43°28'N, 4°28'E, Fig. 1). Resightings of Darvic rings (white ring with a unique black alphanumeric identification code) over the years have shown that the same individual can be seen in multiple breeding areas of Camargue. Therefore, hereafter, we considered Camargue as a single site.

Long-term monitoring programme

Since 2008, more than 5000 spoonbills chicks have been ringed at the nest, with a unique code-engraved Darvic ring allowing us to individually identify and age individuals. To minimize disturbance, ringing operations occurred in the early morning (avoiding heat stress) and only under favourable weather conditions (i.e. no precipitation and/or strong winds) between April and July of each year. In addition to resightings performed by experts at a distance using telescopes (from a hide), camera traps were deployed close to the nests since 2016, during the first weeks of incubation. Between one and three cameras were deployed simultaneously, randomly within the colony, programmed to take photos every 10 min. When possible, these cameras were rotated regularly across the colony every 10–15 days to maximise breeder identification until all chicks had left the colony.

Determining timing of breeding and breeders' age

Given that previously marked individuals return to the breeding site as breeders, it was possible to infer their age and to test if older individuals breed earlier in the season (data were available from 2014 to 2022; a single resighting from 2011 was excluded and data from 2023 were not available at the time of this analysis). Spoonbills have a delayed maturity, usually beginning to breed in their third or fourth calendar year, and lay clutches of 3–4 eggs (Cramp and Simmons 1977, Triplet et al. 2008). To ensure accurate identification of breeding activity, resightings of birds not confirmed as breeders (i.e. those seen at the colony but not recorded building a nest, incubating, or with chicks), and of birds younger than four calendar years (due to a higher chance of being misclassified as breeder) were excluded. A total of 451 marked breeders (*Breeder*) were identified. For each individual and year, the first day they were resighted as a confirmed breeder (*First_Obs*) was considered as their observation date. Age of each breeding adult in any given year was obtained as the time difference between the year of ringing (all breeding adults were individually ringed as chicks) and the year of sighting, resulting in a dataset of 968 cases, corresponding to 451 different breeders across eight years (hereafter referred as *Br_1st_Obs* dataset; Supporting information).

During the breeding seasons of 2021 and 2022, using the same camera traps, it was possible to determine the age of 121 marked breeding adults on a subset of 101 individually marked nests (i.e. using small, marked flags; *Nest*). For 49 of

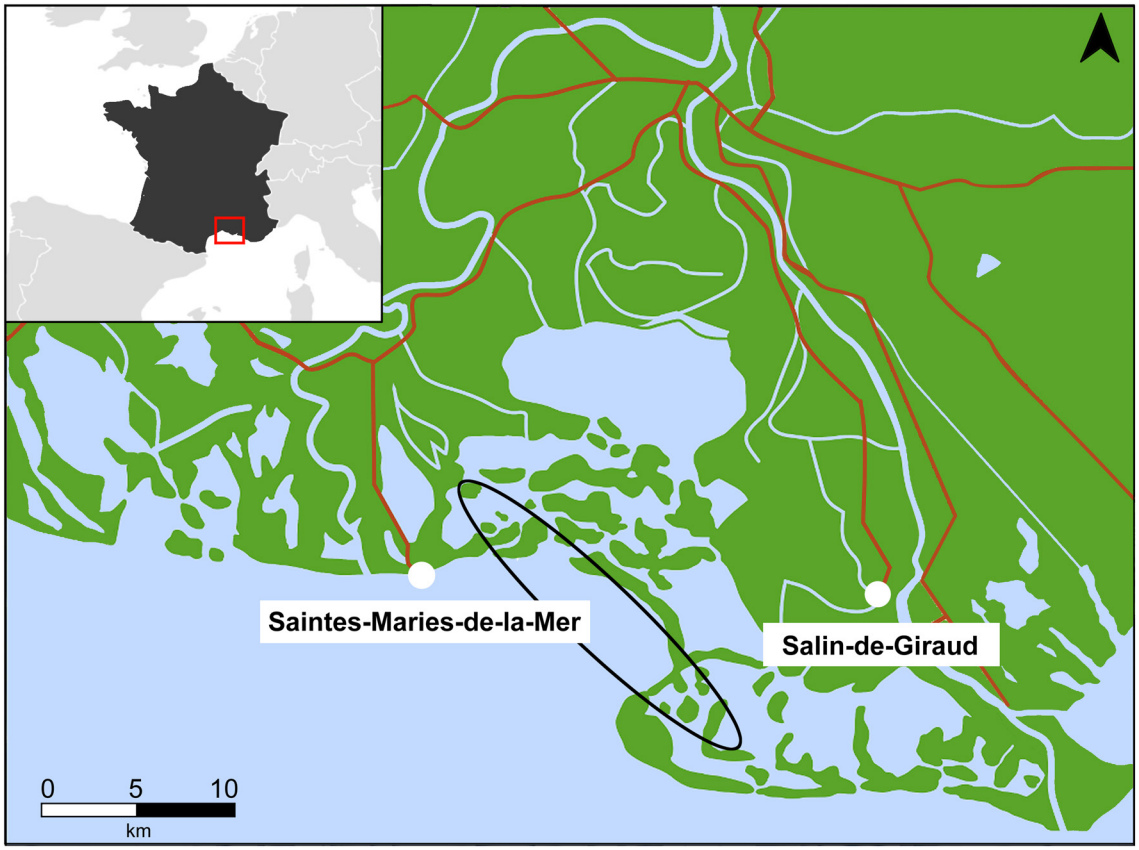

Figure 1. Map of Camargue (green) in the Mediterranean coast of France and approximate location of spoonbill colonies (black ellipse) where nests were monitored, and chicks were measured. Red lines represent the main roads and white dots the cities of Saintes-Maries-de-la-Mer and Salin-de-Giraud.

these nests, corresponding to 54 different marked breeders (*Breeder*), we were able to estimate the laying date (*Laying_day)* by measuring head-bill length of chicks younger than two weeks (associated error ± 2 days, using the species-adapted Gompertz growth curve from Lok et al. 2014) or by using the egg flotation method (associated error ± 3 days; Liebezeit et al. 2007). This dataset of breeders with known age and laying date (hereafter referred as *Br_Lay* dataset) included three breeding individuals which were three years old but were confirmed as breeders.

Since the colour-ringing programme in Camargue started in 2008, the oldest colour-ringed individuals are only 14 years old (Supporting information), with few exceeding 10 years of age, even though spoonbills can live up to 30 years in the wild (Werkgroep Lepelaar 2022). Therefore, a potential effect of senescence was not considered here.

Quantifying chick body condition

Due to changes in biometric measurements over time, two datasets were considered: one containing all individuals for which tarsus length (mm) and body mass (g) were measured, and a subset of this dataset that includes only individuals in which the eighth primary feather length was also measured (Table 1).

From 2009 to 2023 (*Year*), a total of 2461 spoonbill chicks were captured prior to fledging, at an age of ca 15–30 days, as part of a long-term ringing programme. Hereafter, ringing date will be referred to as *Session* when considered

Table 1. Data summary according to chick datasets. Age of chicks is given in days.

Variable	BC_SMI	BC_P8
No. of individuals	2382	409
Years	2009–2023	2016–2023 (except 2020)
Age of chicks	15–30	> 24
Tarsus	Yes	Yes
8th primary	No	Yes
Body mass	Yes	Yes
Hatch date	Could not be estimated, proxy *Session*	Estimated using 8th primary
Sex	No	Estimated using tarsus and 8th primary

as a categorical variable and *Ring_day* when considered as a continuous variable (*Day of the year*). During each *Session*, chicks' tarsus length and body mass were recorded using metal rulers (± 1 mm) and Pesola spring balances (± 10 g), respectively. The body condition of each chick was then calculated using the scale mass index (SMI) developed by Peig and Green (2009). SMI provides a reliable depiction of body condition as it standardises all individuals to their specific growth stage, thus accounting for the changing slope in the relationship between body mass and length measurements (Peig and Green 2009, 2010). Individuals fitted with a GPS logger were excluded from this analysis (n = 79), as older and heavier individuals were selected for GPS logger deployment and this likely biased the sampling of those individuals on those *Sessions*. A total of 2382 individuals were thus considered for this analysis (hereafter referred as *BC_SMI* dataset; Supporting information).

From 2016 to 2023, following the recommendation of Lok et al. (2014) to achieve more accurate estimates of body condition, in addition to the tarsus length and body mass as described above, the eighth primary feather length using metal rulers (± 1 mm) was also measured. With this additional biometric we were able to estimate chick age (days after hatching), using the estimated growth curves developed for this species (Lok et al. 2014). Then, by subtracting the estimated chick age from *Ring_day*, we calculated hatching date and the corresponding laying date (hereafter *Laying_day* estimated hatching date minus 25 days of incubation and 2 days between laying of first egg and start of incubation; Lok et al. 2014), thus obtaining the variable *Laying_day* for each individual. Furthermore, using the combination of the length of the eighth primary feather and tarsus length, we were able to determine the sex of each chick (Lok et al. 2014, Oudman et al. 2017). Differences in growth between sexes become pronounced after 25 days of age, so to avoid misclassifications of sex, only individuals estimated to be older than 24 days were included in this analysis (hereafter referred as *BC_P8* dataset; $n_{BC\_P8} = 411$; Supporting information). In 2020, only two individuals older than 24 days were recorded, which were subsequently excluded from the analysis due to the limited sampling in that year. Body condition of this subset of chicks, with estimated age (*Age of chicks*) and sex (*Sex*), was then calculated as the proportional deviation in body mass from the predicted sex- and age-specific body mass (Lok et al. 2014).

Determining juvenile migratory behaviour

Due to a large network of dedicated amateur and professional ornithologists, we were able to determine the first wintering site of 105 spoonbill juveniles for which body condition had been measured when they were chicks (hereafter referred as *Chick_W* dataset, consisting of chicks born between 2009 and 2023). We considered wintering as the period between October and February, and individuals were assigned a migratory behaviour according to the site where they were resighted during that period. Juvenile spoonbills do not migrate with their parents and there is little support for a genetic basis of migration tendency in spoonbills (Lok et al. 2011, 2013). Additionally, spoonbills remain at non-breeding sites until they reach maturity, after which they show high fidelity to breeding and non-breeding sites (Triplet et al. 2008, Lok et al. 2011, Pigniczki and Karcza 2013). There are only four cases (0.8%; Ferreira et al. 2024b) of juvenile spoonbills being recorded in two locations in the same non-breeding season, and in all of them the second record was at a more southerly location, which suggests they were likely still on migration in the first record. This is further confirmed by GPS tracking of juveniles (Blanchon et al. unpubl.). However, to prevent the potential misclassification of individual migratory behaviour due to a late-autumn or early-spring stopover resighting, we only considered winter resightings during the months of November to January from the individuals seen in France, Italy, Morocco, Portugal, and Spain (Navedo et al. 2010, Lok et al. 2011).

In the single case of an individual that was resighted at different sites within the same flyway (East Atlantic flyway), we selected its southernmost site as its wintering site. We classified three migratory behaviours, considering the country of resighting and the crossing of major ecological barriers (*Barrier*) as these are known to influence demography in this population (Ferreira et al. 2024b): None – migrants which do not cross any major ecological barrier (Portugal, Spain, and France, including Camargue, i.e. residents); Single – migrants which cross the Mediterranean Sea (Algeria, Italy, Morocco, and Tunisia); and, Multiple – migrants which cross the Mediterranean Sea and the Sahara Desert (Cape Verde, Gambia, Mauritania, and Senegal) (Supporting information).

Statistical analysis

An exploratory analysis (R package 'lattice'; Sarkar 2008) was first undertaken to ensure that the body measurements data met the requirements for the SMI calculation (specifically, a strong relationship between body mass and tarsus length) and to determine the scaling exponent of the power function (Peig and Green 2009). For the relationship between body mass and tarsus per *Session*, see the Supporting information.

To test if younger breeders (*Age*) tend to breed later in the season, generalised linear mixed models with a negative-binomial family and a log link function were used to account for the non-normality of the data. Day of the year (*First_Obs*, numerical), the day when an individual was first confirmed breeding in any given year in Camargue, was treated as the response variable, with *Age* as the predictor (numerical). In most cases, the sex of breeding birds was unknown, preventing the estimation of sex-specific effects and thus preventing an analysis of assortative mating by age. To incorporate the dependency among observations of the same individual in different years, *Breeder* was included as the random intercept. Additionally, *Year* was included as a random intercept to account for potential annual variation in the data.

To more precisely examine the relationship between age of breeder and timing of breeding, we also analysed the subset dataset (*Br_lay*) of nests with estimated laying date using negative-binomial mixed models. As this subset contained only

two years, this variable did not meet the required five levels to be considered as a random intercept. Therefore, *Laying_day* (numerical) was standardised to account for the relative laying date in each year and annual variation in breeding timing or data collection (i.e. the first sampling day of each year was set as day zero). Some marked birds (n = 4) were associated with multiple nests in the same or different breeding seasons, and in ten nests both individuals of a breeding pair were ringed. However, the inclusion of *Breeder* and/or *Nest* as random intercepts in these models led to convergence issues, so these two variables were excluded from the models.

To investigate whether chick body condition varied throughout the breeding season ($n_{BC\_SMI} = 2382$), generalized linear mixed models with a gamma family and a log link function were used to account for the non-normality of the skewed body condition data. Body condition (*BC_SMI*) was considered as the response variable and ringing day of the year (*Ring_day*, numerical) as a predictor. *Ring_day* was scaled by centring (mean = 0) and standardising (standard deviation = 1) across the entire dataset. To capture a potential non-linear relationship between body condition and *Ring_day*, a quadratic term of *Ring_day* was included. To account for the fact that multiple chicks' measurements originate from the same ringing session and to avoid results being driven by early sessions where a higher number of chicks are measured, we included *Session* as a random intercept. Additionally, *Year* included was a random intercept to account for potential annual variation. For the subset of chicks with known sex and age and their body condition estimated as deviation from the sex-specific body-mass growth curves (*BC_P8*), the models included an estimated laying date (*Laying_day*, numerical and standardised across the dataset), and a quadratic effect of *Laying_day*. *Session* and *Year* were considered as the random intercepts. However, the null model failed to converge, and the remaining models encountered difficulties in estimating the 95% confidence intervals for *Year*. Consequently, *Year* was treated as a fixed effect in these models.

Lastly, to explore if a chick's body condition (*BC_SMI*) or timing of breeding (*Ring_day*) influences its subsequent migratory behaviour as a juvenile, number of barriers (*Barrier*) was considered as a nominal response variable with three levels (None, Single, and Multiple) of a multinomial model (Venables and Ripley 2002). Both a linear and quadratic effect of body condition and laying date were included to account for a potential non-linear relationship between these variables and the probability of crossing barriers. Specifically, while lower-condition individuals or late-born individuals are expected to have a lower probability of crossing barriers, this probability is hypothesized to stabilize at certain levels. Once the most supported model was selected, model coefficients were then tested for significance between groups, using multiple Wald tests (Hayashi et al. 2011).

All analyses were carried out in the software R ver. 4.2.1 (www.r-project.org) and plots were created using the package 'ggplot2' (Wickham 2016) and 'sjPlot' (Lüdecke et al. 2023). For each full model presented, all possible reduced models were considered by excluding one or multiple predictor variables. Random intercepts were retained in all models, including in the null model. The different models developed were ranked and selected according to the Akaike information criterion adjusted for small sample size (AICc; Anderson and Burnham 2002). When there were multiple models within two AICc points of the top-ranking model, the model with the fewest number of parameters was selected (i.e. the most parsimonious model; Anderson and Burnham 2002). Generalized linear mixed models considering a negative-binomial distribution or gamma family were estimated using an *ML* and *nlminb* optimizer and the package 'glmmTMB' (Brooks et al. 2017). To assess model validity, homoscedasticity and linearity were examined by plotting residuals against fitted values and predictors. Overdispersion was evaluated using the *check_overdispersion* function from the R package 'performance' (Lüdecke et al. 2021).

Results

Breeders' age and timing of breeding

The model including an *Age* effect was much better supported than the null model ($\Delta_{AICc} = -20.2$), with younger individuals breeding later than older individuals (Beta = −0.02, 95% CI [−0.03, −0.01]; Fig. 2, Supporting information). A similar result was found for the data subset *Br_Lay*, where the model including *Age* was also supported over the null model ($\Delta_{AICc} = -3.31$; Supporting information).

Within- and between-year variation in chick body condition

When considering the *BC_SMI* dataset, the most supported model included an effect of *Ring_day* (Model 3, Table 2), implying a decreasing body condition as the breeding season progresses (Beta = −0.02, 95% CI [−0.02, −0.01]; Fig. 3, Supporting information). The model explained 8% of the total variance in body condition (conditional R^2), with fixed effects accounting for 3% (marginal R^2). The random effects of *Session* and *Year* explained low variance (ICC = 0.06).

When considering the smaller subset (*BC_P8*) comprising chicks with known laying date and sex ($n_{BC\_P8} = 409$), the most supported model (Model 4, Supporting information) confirmed an initial decreasing trend of body condition along the breeding season (Beta = −0.02, 95% CI [−0.03, −0.01]; Supporting information). However, this is followed by an increasing body condition towards the end of the breeding season (Fig. 4).

Migratory behaviour of juveniles

When testing the phenology on juvenile migratory behaviour, the most parsimonious model included an effect of *Ring_day* (Model 3, Table 3), implying that chicks born later in the season were less likely to cross an ecological barrier (None versus Single: Beta = −0.31, 95% CI [−0.25, −0.87]; None versus Multiple: Beta = −0.55, 95% CI [−1.03, −0.06]; Fig. 5). Due to the correlation detected between *Ring_day* and body condition in the previous analysis, the fact that body condition

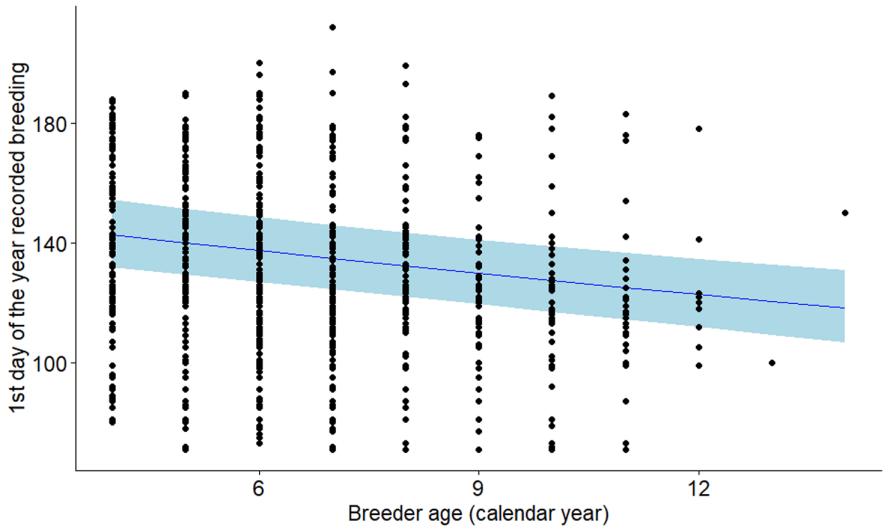

Figure 2. Variation in breeder age (n = 968) throughout the season according to model: *First_Obs ~ Age* (blue). *Year* and *Breeder* were considered as random variables. Black dots represent the actual age recorded and shaded blue area a 95% confidence interval.

is not present in the most parsimonious model implies that *Ring_day* better explains the variation in the migratory behaviour detected. A subsequent Wald test confirmed significant differences between migratory behaviours. Juveniles that did not cross any major barrier differed significantly from those crossing a single barrier ($z = -2.58$, $p = 0.010$) or multiple barriers ($z = -2.20$, $p = 0.028$). However, no significant difference was found between crossing a single barrier and multiple barriers ($z = -0.54$, $p = 0.590$).

Discussion

In this study we showed that older, likely more experienced, spoonbills tend to breed earlier in the season than younger individuals, and that early breeders are more likely to produce chicks with higher body condition than late breeders (regardless of age). There was limited annual variation in chick body condition. Finally, juvenile migratory behaviour seems to be influenced by timing of breeding, as later-born juveniles tend to undertake a less challenging migratory behaviour than early-born juveniles.

Breeders' age and timing of breeding

In bird species, older and more experienced individuals tend to arrive at breeding sites earlier and have higher reproductive success than younger ones (Lack 1966, Rowe et al. 1994, Neate-Clegg and Tingley 2023). Furthermore, better migratory performance could also mean that more experienced individuals arrive in better condition than inexperienced ones, and may therefore need less time to prepare for breeding, and consequently lay earlier than individuals in poorer condition (Bêty et al. 2003, Drent and Daan 1980, Drent et al. 2003, Lok 2013). Accordingly, our results show that older spoonbills tend to be seen breeding earlier in the season, and a subsample of nests with known laying date supported that the earliest nests tend to be associated with the oldest breeders. Spoonbills of the Dutch breeding population have previously been seen to advance their breeding timing with age, but this was mainly the case for the short-distance migrants (Lok et al. 2017). As with the Dutch population and other species (e.g. black kite; pied flycatcher *Ficedula hypoleuca*), a likely mechanism behind our result is an earlier departure from the wintering grounds or a faster and/or more efficient migration of the oldest individuals (Potti and Montalvo 1991, McCleery et al. 2008, Sergio et al. 2014, Lok et al. 2017). Nevertheless, given the long breeding season in Camargue, with the last breeders laying eggs in June, while long-distance migrants are already resighted in Camargue as early as February (Blanchon et al. unpubl.), it is unlikely that migratory performance can fully explain our results. Therefore, besides arriving later, it is possible that younger birds are also more susceptible to being pushed to breed later by dominant and/or older individuals (McCleery et al. 2008, Lok et al. 2017). For example, preliminary information suggested that young mute swans *Cygnus olor* spend more time fighting early in the season than older birds, which consequently delays their laying (McCleery et al. 2008).

Table 2. Generalised linear mixed models' selection for body condition ($n_{BC\_SMI} = 2382$). *Session* and *Year* were included as random predictors. Models were ranked according to the Akaike value, and the most supported model is indicated in bold.

Number	Model	K	LL	ΔAIC_c	Akaike weight
2	**Ring_day**	***5***	**−15209.3**	**0.0**	**0.65**
3	Ring_day + Ring_day^2	*6*	−15209.0	1.3	0.35
1	Constant	*4*	−15217.1	13.4	0.00

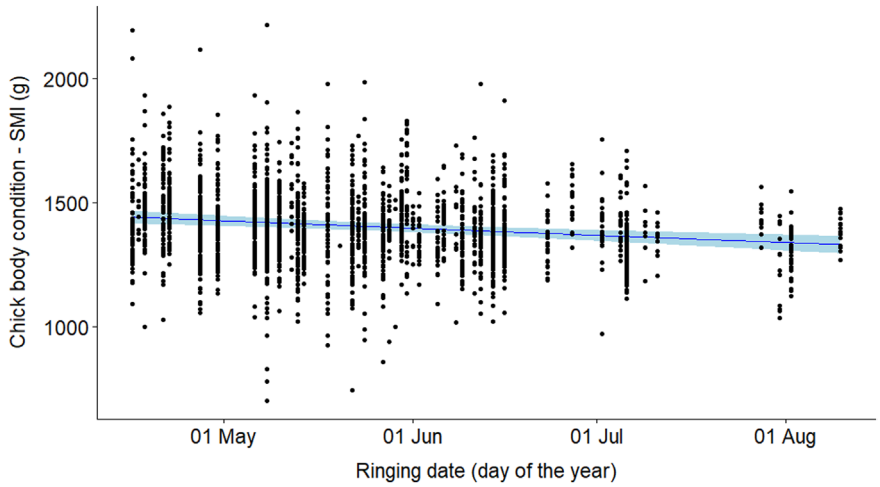

Figure 3. Variation in chick body condition (obtained using the SMI: $n_{BC\_SMI}=2382$) throughout the season predicted by the most supported model (Model 2, Table 2). Black dots represent the actual body measurements obtained using the SMI and shaded blue area the 95% confidence interval. In this plot, day of the year was not scaled for clarity of interpretation.

As spoonbills age, they seem to cope better with migratory challenges and wintering conditions, as suggested by the lack of differences between the survival rates of experienced individuals with different wintering strategies (Ferreira et al. 2024b). Thus, it is likely that spoonbills improve their migratory and breeding performance due to accumulated experience, which is in accordance with the constraint or experience hypothesis (Curio 1983, Wood et al. 2016). This hypothesis assumes that reproductive success may improve with age due to improved parental care activities such as brooding, foraging, protection of chicks from adverse weather conditions (e.g. wind and precipitation), and feeding (Curio 1983, Pyle et al. 2001, Limmer and Becker 2009). This was the case in European shags where, when breeding in similar environmental conditions, old pairs performed consistently better than young pairs due to intrinsic differences in brood-rearing capacity (Daunt et al. 1999). Detailed analysis of the reproductive success of western gulls *Larus occidentalis* showed that increased clutch size was related to female experience, and enhanced hatching success to the experience of both sexes (Pyle et al. 1991). Furthermore, fledging success was likely influenced by age-related improvements in foraging skills (Pyle et al. 1991). The impact of experience has also been widely reported in other groups, where reduced foraging skills of inexperienced individuals have been suggested to lead to low productivity in aerial insectivores such as tree swallow *Tachycineta bicolor* (Steven 1978) and bee-eater *Merops apiaster* (Costa et al. 2021). For several Passeriformes, an increase in foraging skills with age has also been documented (Enoksson 1988, Jansen 1990, Desrochers 1992, Franks and

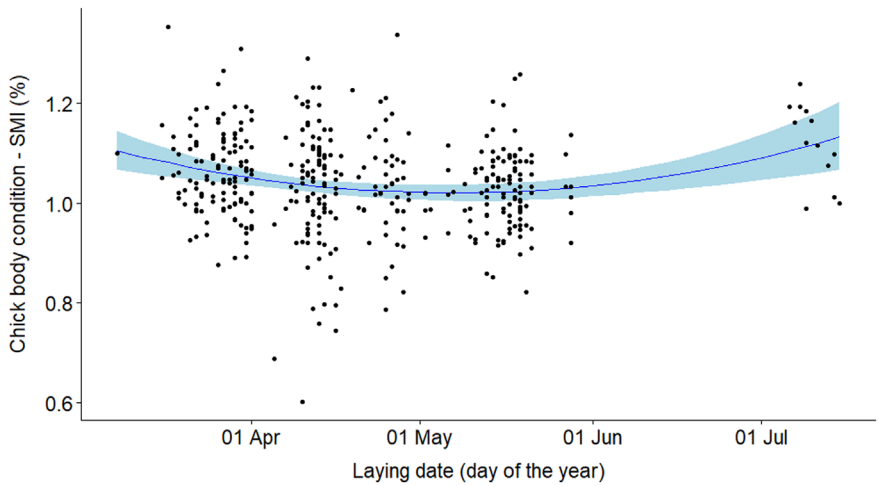

Figure 4. Variation in chick body condition (obtained using the BC_P8: $n_{BC\_P8} = 409$) throughout the season predicted by the most supported model (Model 2, Table 2). Black dots represent the actual body measurements obtained using the growth curves and shaded blue area the 95% confidence interval. In this plot, day of the year was not scaled for clarity of interpretation. Note that the cluster of dots at the end of the season result from a single Session.

Table 3. Multinomial model selection for explaining the recorded migratory behaviour of first calendar year spoonbills ($n_{Barrier}$ = 105). *Session* was included as a random variable. Models were ranked according to the Akaike value, and the most parsimonious model is indicated in bold.

Number	Model	K	LL	ΔAIC_c	Akaike weight
5	Ring_day + Ring_day^2	*6*	−105.1	0	0.26
3	**Ring_day**	***4***	**−107.4**	**0.19**	**0.24**
6	BC_SMI + Ring_day	6	−105.4	0.71	0.19
8	BC_SMI + Ring_day + Ring_day^2	8	−103.1	0.76	0.18
2	BC_SMI	4	−108.9	3.19	0.05
1	Constant	2	−111.5	4.10	0.03
7	BC_SMI + BC_SMI^2 + Ring_day	8	−105.4	5.33	0.02
9	BC_SMI + BC_SMI^2 + Ring_day + Ring_day^2	10	−103.0	5.45	0.02
4	BC_SMI + BC_SMI^2	6	−108.7	7.21	0.01

Thorogood 2018). Furthermore, younger breeders may suffer from reduced access to resources due to competition with older individuals (Emlen 1978, 1982, Curio 1983).

Within-year variation in chick body condition

Spoonbills in the Camargue breed in protected islets that are relatively undisturbed, except for opportunistic predation events by Eurasian wild boar *Sus scrofa* and red fox *Vulpes vulpes* (Champagnon et al. 2021). Furthermore, the abundance of food sources in the surrounding area (e.g. temporary and permanent marshes; Ferreira et al. 2024a), including the high abundance of red-swamp crayfish *Procambarus clarkii* (Ottonello et al. 2005, Poulin et al. 2007, Meineri et al. 2014, Rodriguez-Perez et al. 2014) are likely sufficient to meet the energetic needs of the Camargue spoonbill population and support its continued and ongoing growth (Champagnon and Kralj 2023). Although we did not conduct any diet analysis in our study, in Camargue, crayfish species are important prey for several waterbird species, such as the Eurasian bittern *Botaurus stellaris* (Poulin et al. 2007) and the glossy ibis *Plegadis falcinellus* (Champagnon et al. 2019). Furthermore, previous opportunistic sampling at the breeding sites by the Tour du Valat team in 2007 detected a dominance of crayfish remains in spoonbill regurgitates (Tour du Valat unpubl.).

Our analysis showed significant variation in chick body condition within years, indicating that early chicks have higher body condition than later-born chicks. This is commonly attributed to the fact that later-born chicks are likely to be more exposed to increased competition (i.e. adult individuals, plus the early chicks) and/or lower food availability (Lack 1968, Drent and Daan 1980, Verboven and Visser 1998, Evans et al. 2020). However, the fact that the population is still growing (Champagnon and Kralj 2023) and that the crayfish abundance peaks between April and June (Meineri et al. 2014), suggests that other factors may also influence chick body condition. In the case of the glossy ibis, no effect of hatching date on chick body condition was detected, suggesting that food availability in Camargue, particularly crayfish, as also consumed by spoonbills, is sufficient to satisfy the colony energetic demands throughout the breeding season (data collected from 2005 to 2017; Ferreira et al. 2019). Thus, if there is sufficient food available, the observed decline in chick body condition throughout the breeding season may be due to the potential lower quality of

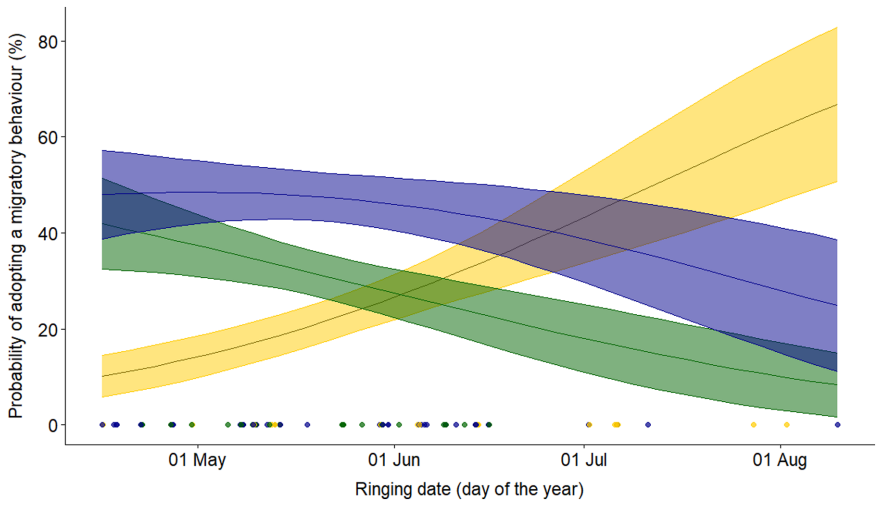

Figure 5. Probability of adopting a migratory behaviour as modelled by Model 3, Table 3. Each line represents the predicted probability of crossing no barrier (yellow – n_{None} = 25), one barrier (dark green – n_{Single} = 32) or multiple barriers (dark blue – $n_{Multiple}$ = 48) given the ringing day ($n_{Barrier}$ = 105). Shaded areas represent 95% confidence intervals.

later-breeding parents. Less experienced parents could lack the skills to feed the chicks as successfully, forage efficiently, and/or provide the needed thermal support (Marchetti and Price 1989, Sæther 1990, Wunderle 1991, Martin 1995).

The smaller subset (*BC_P8*) showed an increase in chick body condition at the end of the breeding season. However, this increase is driven by individuals from a single ringing session and is not supported by the main dataset (*BC_SMI*). Furthermore, nine of these chicks were associated with five breeders of six to eight years old, while only three were associated with two breeders of three years old, and one chick had no breeder identified. Therefore, this result should be interpreted with caution, as the effect of breeder experience in that ringing session is likely influencing this outcome.

Migratory behaviour of juveniles

In social species, the timing of hatching can have consequences for juvenile migratory behaviour, as experienced individuals may have left the breeding sites by the time later-born juveniles are able to migrate (Gunnarsson 2006, Cresswell 2014, Gill et al. 2014, 2019, Meyburg et al. 2017, Nightingale 2023). This may be the case for Camargue spoonbills, as our results suggest that later-born juveniles tend to undertake a less challenging migratory behaviour. Indeed, spoonbills are social birds (de Goeij et al. 2012, Navedo and Garaita 2012, Lok et al. 2019) that often migrate in mixed-age flocks (Lok 2013). Consequently, later-born juveniles are more likely to find themselves with fewer adults to follow in crossing a major ecological barrier such as the Mediterranean Sea and the Sahara Desert. This could potentially explain the number of juveniles that stay in France and Iberia for their first winter, but subsequently move to further locations in the following winter (Blanchon et al. unpubl.; Lok et al. 2011). Socially mediated migratory behaviour is also found in other species. For example, young oystercatchers *Haematopus ostralegus* are known to adopt the same migratory behaviour as their father, who waits for his offspring to be ready to migrate (Méndez et al. 2020, 2021). As for lesser spotted eagles *Clanga pomarina*, despite not following their parents, successful arrival at non-breeding sites was higher for individuals that migrated with adults, who are therefore likely to benefit from adult navigational cues (Meyburg et al. 2017). Finally, and potentially like the spoonbills, late-fledged juveniles of black-tailed godwits *Limosa limosa islandica* are more likely to join flocks dominated by juveniles, as adults depart from the breeding areas shortly after breeding, and are thus more likely to winter at northern sites (Gunnarsson 2006, Gill et al. 2019, Nightingale 2023). However, we cannot rule out the possibility that late-born juveniles also attempt to cross barriers but are more likely to die due to having fewer adults to follow, a higher probability of getting lost, a stopover in suboptimal wintering sites, or less time to prepare for migration than early-born juveniles. Despite a significantly lower probability of crossing major ecological barriers of individuals born at the end of the breeding season, it is still possible that later-born juveniles can follow experienced individuals that have left the breeding site later and still cross such barriers. This could happen because later-born juveniles may encounter such individuals, including those from other breeding populations (Ferreira et al. 2024b), at the stopover sites. This is the case for juveniles of short-toed snake eagles *Circaetus gallicus* which can learn detours to complete trans-Mediterranean migration from older individuals encountered during migrating (Agostini et al. 2017). Likewise, the departure date of continental black-tailed godwit *Limosa limosa limosa* juveniles from the Netherlands was related to hatching date, and while monitored juveniles all left the breeding grounds later than adults, they joined adult flocks at stopover sites around the Mediterranean (Verhoeven et al. 2022). Furthermore, such social learning can significantly increase the resilience of individual birds to cope with environmental change and extreme events, while also mitigating the need for juveniles to migrate synchronously with adults (Agostini et al. 2017).

Body condition could influence spoonbill migratory behaviour in two different ways: 1) like flamingos, higher-quality juveniles would be more likely to move away from the natal area (Dufty and Belthoff 2001, Barbraud et al. 2003) and thus be able to undertake more challenging migrations and cross major barriers (e.g. Mediterranean Sea); or 2) because Camargue is a high-quality site, birds in good condition could potentially remain over the winter (Ketterson and Nolan 1976, Gauthreaux 1978, Cristol et al. 1999, Boyle 2008) and potentially outcompete lower-quality birds to undertake a more challenging migration to distant wintering sites. Although the relationship between body condition and migratory behaviour was not retained in our most parsimonious models (despite being within one ΔAIC from that model), our results suggest that early-born juveniles tend to have higher body condition and are more likely to cross barriers. Migration is inherently risky, and it remains possible that lower-quality juveniles also attempted demanding migrations but experienced higher mortality rates, resulting in fewer resightings at the most distant non-breeding sites. This could explain the absence of a significant (or at least a weaker) relationship between body condition and migratory behaviour. However, in the case of Dutch juveniles, no relationship was found between chick body condition and survival during their first autumn/winter (Lok et al. 2017).

While previous studies of spoonbills have suggested improvements in migratory performance with age (Ferreira et al. 2024b), this study suggests that breeding performance may also improve as spoonbills age. Additionally, our results suggest that early-born chicks (with a tendency to have higher body condition) are more likely to undertake more challenging migrations. Therefore, even though older and more experienced adults breed earlier and raise chicks in better condition, these chicks are subsequently more likely to die as they undertake the riskiest migrations which are associated with lowest survival (at least during first return migration; Ferreira et al. 2024b). Our study therefore highlights the relevance of long-term studies to better understand the complex breeding phenology of a migratory species, which can lead to changes in population-scale patterns and processes (Gil et al. 2018, Nightingale 2023).

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Data availability statement

Data are available from the Zenedo Digital Repository: https://doi.org/10.5281/zenodo.13144093 (Ferreira et al. 2025b).

Supporting information

The Supporting information associated with this article is available with the online version.

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