

# Familiarity drives social philopatry in an obligate colonial breeder with weak interannual breeding-site fidelity



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Repeated association between subsets of individuals is a common feature of species living in social groups. Because colonial breeding, an extreme case of group living, is associated with certain group behaviour, colonial species are interesting study models to explore the occurrence of social bonds between individuals. As colonial species are usually highly philopatric, disentangling the fidelity to a breeding site from the fidelity to a group of individuals is challenging. Slender-billed gull, *Chroicocephalus genei*, colonies, however, relocate almost yearly. This behaviour makes it possible to study individual associations over several years, i.e. associations between individuals breeding in the same colony in more than 1 year. To quantify and identify the mechanisms that favour repeated individual associations across years, we analysed data from 14 years of observations of 953 individually marked gulls. Our results showed that some individuals repeatedly bred together across breeding seasons despite the colony moving every year. The probability of an individual selecting a colony increased with an increase in the number of birds that had bred in the same colony as that individual the previous year and not the overall number at the colony. However, we found yearly variation in group tenacity levels and that colony breeding failure favoured splitting of the groups. We also found that association rates rapidly decreased across years but stayed higher than random associations during 2 consecutive years after the first observations. Moreover, over the entire study period, we plotted a bipartite network and found that all colonies and individuals in the population were fully connected. This study reveals group tenacity across years in a colonial bird. Evolutionary pressures as well as the mechanisms favouring social bond persistence across years in colonial birds, however, need further research.

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Of the different forms of group living, coloniality is one of the most extreme: colonies consist of hundreds, or sometimes thousands, of individuals (del Hoyo, Elliott, & Sargatal, 1996). Coloniality is a life history strategy in which individuals form large, dense groups exclusively during the breeding period; the breeding site does not encompass feeding resources (Danchin & Wagner, 1997; Rolland, Danchin, & Fraipont, 1998; Wittenberger & Hunt, 1985). In vertebrates, colonial breeding has mostly been studied in birds, among which approximately 13% of species are colonial (Lack

1968); however, it is also found in some species of mammal (Cantor et al., 2012) and reptile (Trillmich & Trillmich, 1984). Although coloniality has been the subject of hundreds of studies investigating its costs and benefits (e.g. Krause & Ruxton, 2002; Rolland et al. 1998), there has been much less focus on the social factors behind the maintenance of colony membership (Silk, Croft, Tregenza, & Bearhop, 2014), i.e. the recurrent association of the same individuals across years.

Social networks (the number and patterns of associations between an individual and its conspecifics) are known to have important consequences for fitness. For instance, it has been demonstrated in birds that an individual that is well connected or familiar with others in a breeding group may have, on average, greater reproductive success than more solitary individuals or

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individuals that are randomly associated with others (Beletsky & Orians, 1991; Schieck & Hannon, 1989; Silk et al., 2014). The number and quality of an individual's social bonds (Silk, Alberts, & Altmann, 2003; Silk et al., 2010), its position in the social network (Formica et al., 2012; Wey, Burger, Ebensperger, & Hayes, 2013) and, crucially, which individuals they are connected to (Farine & Sheldon, 2015; Formica et al., 2011) have been demonstrated to impact its survival and reproductive success. Because coloniality is associated with certain group behaviour, such as antipredator and foraging activity (Canova & Fasola, 1993; Evans, 1982; Lachmann, Sell, & Jablonka, 2000; Waltz, 1987), colonial species are interesting study models to explore the occurrence of social bonds between individuals and, as a result, group tenacity (i.e. the recurrent associations of individuals within a group). For example, black-headed gulls, *Chroicocephalus ridibundus*, from neighbouring nesting sites form stable groups of individuals that forage together over a breeding season (Prévot-Julliard & Lebreton, 1999). Similarly, neighbouring colonies of northern gannets, *Morus bassanus*, forage in mutually exclusive areas when population densities are high (Wakefield et al., 2013). Both examples suggest that an individual's foraging behaviour is related to its colony membership. If differences in these types of group-related behaviour result in differences in foraging or chick-rearing success, then an individual's fitness is also affected by its group membership, a factor that could promote the evolution of group philopatry (sensu Farine, Montiglio, & Spiegel, 2015).

A social group is defined as a pool of individuals that interact more together than with other individuals and whose associations persist over time (at different temporal scales; Krause & Ruxton, 2002; Silk et al., 2014). Colonies are often perceived as temporary aggregations (occurring only during one breeding period), and the importance of the formation and maintenance across years of social groups within a colony or when establishing a colony has rarely been explored. Moreover, as colonial species are often highly philopatric (Greenwood, 1980), it is difficult to disentangle the effect of simple passive spatial fidelity from the effect of an individual's choice to maintain associations with specific individuals across years (e.g. neighbours; Burger, 1984; Haymes & Blokpoel, 1978; McKinnon, Gilchrist, & Scribner, 2006; Prévot-Julliard & Lebreton, 1999). Little is known about the persistence of social groups from one year to the next independent of simple site fidelity.

Not all species that breed in colonies show strong site philopatry. Species that evolved in unstable environments tend not to be particularly faithful to their breeding sites (McNicholl, 1975). For instance, high breeding site turnover from year to year has been observed in colonial species such as terns and certain gulls (Erwin, Galli, & Burger, 1981; Erwin, Nichols, Eyler, Stotts, & Truitt, 1998; Kharitonov & Siegel-Causey, 1988). Species that breed in unstable environments are most of the time obligate colonial species sensu Siegel-Causey and Kharitonov (1990), i.e. they depend on the colony to breed. These authors predicted group tenacity in these species because forming associations of stable social groups could provide important benefits, such as favouring more efficient and rapid breeding-site selection. When colonies must relocate regularly, stable groups may also benefit by pooling information when choosing where to breed. Such collective decision making could improve accuracy via collective intelligence (Couzin, 2009), and maintaining associations with the same individuals over time could further facilitate decision making. Familiarity may also reduce intraspecific aggressiveness (Fisher, 1954; Temeles, 1994), thus allowing more rapid colony establishment.

In this study, we investigated whether the members of a breeding colony maintain associations across years independently of site philopatry. Following Siegel-Causey and Kharitonov's (1990) assumption, we predicted that in obligate colonial species with low

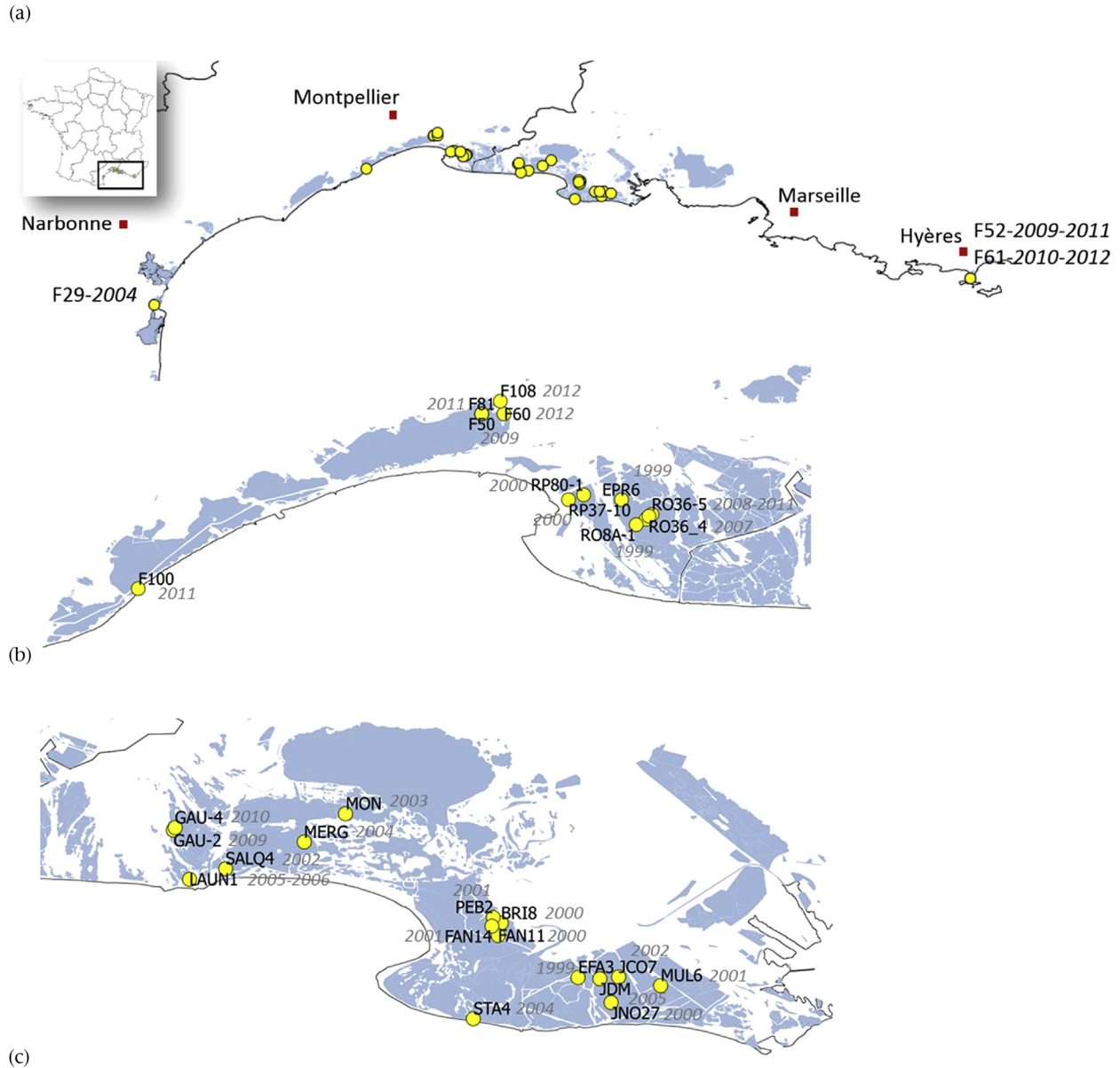
site fidelity, greater group tenacity should favour rapid breeder settlement at the colony site and common decision making. To investigate this, we used observations of the slender-billed gull, *Chroicocephalus genei*, a species that, in contrast to most colonial species, changes the location of its colony sites almost every year (Kharitonov & Siegel-Causey, 1988). By exhibiting such low breeding-site philopatry, the slender-billed gull is an ideal test case for detecting potential medium- or long-term group tenacity within a colony. Furthermore, since slender-billed gulls rear their young in crèches, the breeding success of an individual is closely related to the breeding success of the colony, allowing an examination of whether maintaining group tenacity depends on reproductive success. As shown in many bird species, breeding failure is often linked to dispersal and divorce (Dubois & Cézilly, 2002; Schmidt, 2004); we thus predicted that breeding failure would lead to the group splitting. Last, we evaluated the implications of social philopatry at the population level, i.e. how individual associations within a colony impact the dynamics of associations within an entire population. We tested whether maintaining colony membership, i.e. associating with the same individuals breeding in the same colony in more than 1 year, over time results in a fragmented social structure (i.e. breeding colonies that are isolated from each other rather than interconnected) at the population level.

## METHODS

### *Species, Area and Monitoring Programme*

The slender-billed gull is an obligate colonial species that rears its chicks in crèches (Besnard & Gimenez, 2002; Kharitonov & Siegel-Causey, 1988). This species exhibits several types of breeding behaviour that appear to be adaptations to habitats showing high spatiotemporal heterogeneity of nesting site availability on both inter- and intra-annual scales. It principally occupies lagoons and deltas (del Hoyo et al., 1996), rapidly establishing colonies after prospecting several sites at the beginning of the season. There is a very short interval between the establishment of a colony and laying, and this species spends a significantly shorter time at the colony site than similar species that breed in stable habitats such as the black-headed gull (Besnard, 2001). In addition, slender-billed gulls form high-density breeding colonies and exhibit a low level of interindividual aggressiveness (Besnard, Sadoul, & Lebreton, 2006); this may favour the development, or be the result, of social groups (Fisher, 1954).

Our study was based on data from a population of slender-billed gulls on the French Mediterranean coast. From 1970 to 2004, this population exclusively occupied the Camargue (the delta of the Rhône River), and then it progressively spread out along the coast (Fig. 1). Before 1985, the number of breeding pairs was around 20 (Isenmann & Sadoul, 1999), and then it rapidly increased to reach about 1000 pairs by 1995. Since 1995, the population has fluctuated between 299 and 877 breeding pairs, living in from one to five colonies depending on the year. We defined a colony as an aggregation of individuals at one site in one year. Since 1997, chicks have been captured before fledging and banded with PVC rings displaying a unique alphanumeric code to enable identification from a distance (Sadoul, 1996). In total, 4991 chicks were ringed over the study period (1997–2012), representing 72% of the chicks in the French population (N. Sadoul, personal observation). Ringed chicks were then resighted in breeding colonies over the following years and observed from when birds arrived in the breeding area (May) to the fledging of the last chicks (end of July). Observations were conducted from a hide using a telescope to avoid disturbance. Since 1997, resightings have been conducted each year at all breeding colony locations (except in 2003, when two colonies were present



**Figure 1.** Distribution of slender-billed gull colonies along the French Mediterranean coast from 1997 to 2012. (a) The two areas at the furthest extremes are La Palme in the west (Aude department) and Hyères in the east (Bouches-du-Rhône). However, most colonies were in two main areas: (b) Languedoc-Roussillon and (c) the Camargue. The name of the colony is written next to its location and the years the site was occupied are indicated in grey.

but only one could be monitored because the second was inaccessible; Table 1).

As we were interested in examining the stability of groups of breeders from year to year, we removed from the data resightings of ringed chicks just after fledging and those of first-year individuals, as recruitment at 1 year is very low in this species (Doxa et al., 2013). We also removed observations made outside the colony sites (during migration or the prospection phase early in the breeding season), and we restricted the data to observations made from mid-May to August as this corresponds to the peak of the breeding season for the French population of this species (Sadoul, n.d.). Slender-billed gulls usually start to lay eggs from the second half of May and leave the site between the end of July and mid-August (del Hoyo et al., 1996).

Individuals that were seen at only one colony in a specific year were considered as breeders in that colony (2139 events). Individuals observed at two different colonies in the same year (449

**Table 1**

Number of colonies and number of individual ringed slender-billed gulls resighted each year from 1999 to 2012 in the south of France

Year	Number of colonies	Number of individuals resighted
1999	3	82
2000	5	145
2001	3	230
2002	3	265
2003	1	234
2004	3	114
2005	2	204
2006	2	117
2007	3	134
2008	2	172
2009	3	219
2010	3	255
2011	4	250
2012	4	181

events) were deemed to breed at the site where they were observed closest in time to the colony breeding time. Individuals observed at more than two colonies in a specific year (<100 events) were removed from the data because they may have been nonbreeders or failed breeders and thus difficult to assign to a specific site. The resulting data included 12 036 observations of 953 individuals observed at 33 different colony sites.

#### *Ethical Note*

All ringing and resightings comply with current laws of France (permit granted by The Research Center by Ringing Bird Populations, Natural History Museum of Paris; programme no. 326). The entire crèche is slowly pushed into an enclosure made of soft reeds by several persons and kept there during the ringing. This operation takes place early in the morning to avoid high temperatures and sun. Once chicks are all ringed, they are then released together by opening the enclosure and pushing them slowly outside. The entire operation lasts less than 3 h for large crèches but usually only 1 h. After ringing, birds are not captured again and individual data are only resightings conducted with a telescope at large distances, so as not to disturb the colonies, either from a floating hide or a hide on the bank.

#### *Statistical Analyses*

Using these data, we investigated patterns of colony membership to address four main questions. (1) Are the associations of individuals between colonies from year to year random? If not, are the patterns of association linked to reproductive success? (2) Do individuals prefer to breed in colonies of conspecifics from the same breeding colony as the previous year? (3) If they do form stable groups, for how many years are these maintained? (4) Are groups stable enough over successive years that this results in a structured population with several communities within which individuals associate more often while they never associate with individuals from another community?

#### *Interannual patterns of movement between colonies*

To investigate the first question, for each year, we calculated the proportion of birds that were observed in a colony in one year and were then reobserved in another colony (noting which colony) in the next year. We then calculated the coefficient of variation (CV) of the resulting proportions. A high CV represented many individuals moving to certain colonies and not to others, while a low CV represented approximately equal movement to all future colonies (i.e. approximately  $1/K$ , where  $K$  is the number of colonies). We used these CVs, which are a measure of the dispersion of the data, to determine whether these movements in each pair of years formed a pattern or were random. They are a useful way to measure structure in social data (Farine & Whitehead, 2015; Whitehead, 2008). To evaluate whether a CV from our data was significantly larger than random, we constructed a simple null model in which individuals moved from one colony to another at random while maintaining the same number of individuals in each colony each year. If the value of the CV was higher than the 95% range drawn from 10 000 simulated movement patterns, it suggested that significantly more individuals moved together from one colony to another in that year than would be expected if the movement was random.

Next, we tested whether the propensity of a group of individuals to breed together again in the same colony was affected by reproductive success at the colony level. Each year, each colony was scored as either 1 (if any chicks fledged) or 0 if the colony failed entirely. We constructed a generalized linear mixed model (GLMM) with the colony level CV (i.e. the clustering of birds moving from a site from

one year to the next) as a function of the reproductive success at the colony level, with year as a random effect. We calculated the significance value ( $P_{\text{rand}}$ ) for the effect of reproductive success as the number of times the coefficient value was greater than the coefficient value generated using the same model fitted on data generated from the null model described above (see Boogert, Farine, & Spencer, 2014; Farine, 2013; Farine & Whitehead, 2015 for details on integrating null models within GLMMs). The estimated coefficient value of the GLMM is the effect of reproductive success on the CV.

Because the colonies were spatially widespread (see Fig. 1), the nonrandom movements of birds from one colony in one year to another in the following year could be simply explained by birds moving to the nearest colony site. To test whether distance between sites explained any patterns of movements we observed, we constructed a GLMM with the proportion of birds moving between sites from one year to the next as a function of the distance between these sites, including year as a random effect. To evaluate the significance of the result, we fitted the same GLMM model using the 10 000 simulated versions of the data created from the null model described above.

#### *Quantifying the strength of social philopatry*

To investigate the second question, we quantified the strength of attraction to previous colony members. We constructed a simple predictive model in which individuals observed in subsequent years chose a colony  $c$  with probability  $p_c = \frac{p'_c}{\sum p'_c}$ , where  $p'_c = \frac{1}{C} + \lambda_s \times N_{c,s} + \lambda_d \times N_{c,d}$ ;  $C$  is the number of colonies in that year,  $\lambda_s$  is the attraction to individuals that bred at the same colony in the previous year,  $N_{c,s}$  is the number of individuals that bred at the same colony in the previous year and have already settled in colony  $c$ ,  $\lambda_d$  is the attraction to individuals that did not breed in the same colony in the previous year and  $N_{c,d}$  is the number of individuals in colony  $c$  that did not breed in the same colony in the previous year. When no birds are present in colonies, individuals have an equal chance of choosing any colony ( $p'_c = \frac{1}{C}$ ). As individuals cumulatively choose a colony, the propensity for their presence to influence subsequent birds to make a decision is determined by the attraction parameters  $\lambda_s$  and  $\lambda_d$ . The term  $\frac{p'_c}{\sum p'_c}$  allows probability matching to ensure all probabilities sum to 1. We used a parameter scan across values of  $\lambda_s$  and  $\lambda_d$  to find the values that best fitted the data. These fits were found by simulating 1000 data sets from each pair of values and calculating the likelihood of observing the data given the simulated data. We used the CV of the proportion of birds that moved sites (as before) to quantify how well our model replicated the data (for each pair of  $\lambda_s$  and  $\lambda_d$  values). The resulting  $\lambda$  values with the maximum log-likelihood represent those for which the simulated CV values each year best encompassed the CV of the observed data.

#### *Quantifying the temporal stability of social bonds*

To investigate the third question, we used lagged association rates (hereafter, LARs) to assess the degree of reassociation across years of two individuals seen in the same colony in a given year. LARs calculate the probability that two individuals will be observed together  $\tau$  units of time after an observed association, given that at least one individual was observed (Whitehead 1995, 2008). In this case, the units of  $\tau$  is measured in years, and a LAR of 0.5 when  $\tau = 1$  would suggest that given an observation of two individuals together, there would be a 50% chance of observing them together in the next year if one of them was present. The LARs showed the association of two individuals over different time spans: between two consecutive years as well as for longer periods. This allowed us to determine how



long associations last. Jackknife errors were used to obtain the confidence intervals (Efron, 1981) by removing 1 year for each resampling. The calculated LARs were compared to a random association rate to test their departure from this. The random LAR was a null rate that was calculated by dividing the mean group size (number of individuals) by the mean binary degree (number of total associates for each individual) as described in Farine (2013).

#### Evaluating the population structure

Finally, to answer the fourth question, we tested how the patterns of colony co-membership across years scaled up to shape the overall structure of the French population of slender-billed gulls. In particular, we analysed whether the colonies in the population are connected or fragmented, and whether a few individuals disproportionately account for connecting otherwise disparate parts of the population. To do this, we constructed a bipartite network in which the nodes consisted of either individuals or colonies (a unique code represented each colony each year). Bipartite networks are simple representations of the connections between two different types of entities, typically individuals in locations. In these networks, edges occur only between different types of nodes rather than between nodes of the same type, and can be used to explore patterns of connection with explicit consideration of the phenomena that connect individuals (Dormann, Fründ, Bluthgen, & Gruber, 2009). In our case, nodes represented either individuals or breeding colonies in a given year, and edges were defined by whether the individual bred at that particular colony in that year. We then organized the data in subsets, incrementally removing the individuals seen in the most years to test at which point the network became disconnected. This allowed us to determine whether the colonies in the population were connected only by a few individuals.

All calculations were performed using R 3.0.2 (The R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org>). The LAR was calculated using the 'asnipe' package (Farine, 2013), the GLMMs were fitted using the 'lme4' package (Bates, Mächler, Bolker, & Walker, 2015) and the network structure was modelled using the 'igraph' package (Csardi & Nepusz, 2015).

## RESULTS

#### Interannual Patterns of Movement Between Colonies

The movement of individuals between colonies was significantly more clustered than would be expected by chance. In most years, the

observed CV of the proportion of birds that had moved was significantly larger than the null model (see Fig. 2). Visual examination of the patterns clearly shows that stable social groups among colony members were stronger after the first few years of the study, and this coincides with colonies that had greater reproductive success (whereas the mean probability of reproductive success in 1999, 2000 and 2001 was 54%, in all subsequent years it was 91%). Slender-billed gull movements were significantly more clustered (had a higher CV) when a colony was successful than when it was unsuccessful (GLMM results of  $CV \sim \text{success}$ :  $\beta \pm SE = 18.8 \pm 11.5$ ,  $t = 1.65$ ,  $P_{\text{rand}} < 0.001$ ). There was no significant effect of distance on the proportion of birds moving between colonies (GLMM results of  $\text{proportion} \sim \text{distance}$ :  $\beta \pm SE = -0.0006 \pm 0.0002$ ,  $t = -2.84$ ,  $P_{\text{rand}} = 0.98$ ).

#### Quantifying the Strength of Social Philopatry

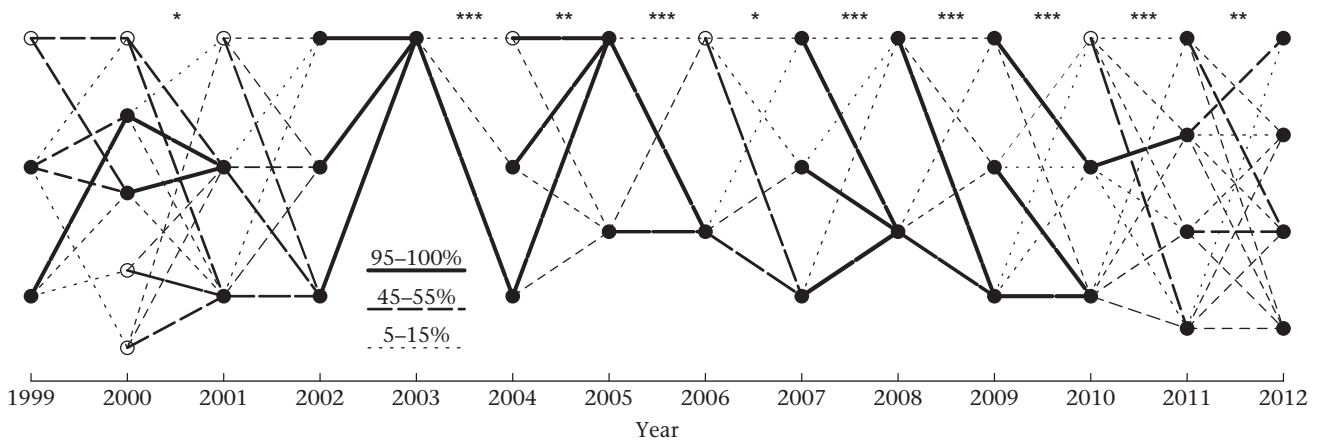
The simulated data that best fitted our observed data suggest that birds were significantly more attracted to co-members of their breeding colony from the previous year than to individuals that bred in other colonies the previous year (Fig. 3). Individuals that had previously bred in a colony and then settled in a new colony increased the likelihood that an individual from the previous colony would choose the new colony ( $\lambda_s = 0.85$ , 95% CI 0.7–1.2), whereas an individual that had previously bred in a different colony only marginally increased the probability of an individual choosing that colony ( $\lambda_d = 0.05$ , 95% CI 0–0.25). Thus, colony choice was impacted by the presence of individuals from the colony of the previous year, with only low attraction to individuals from other colonies.

#### Quantifying the Temporal Stability of Social Bonds

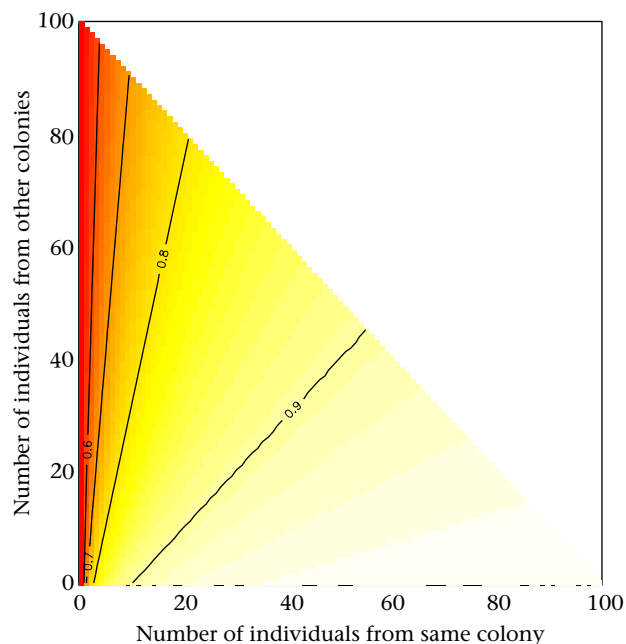
LARs showed that associations between individuals were higher than random for 2 consecutive years (Fig. 4). We found no evidence of stable associations between individuals longer than a 2-year time span. We observed a rapid decrease in LARs over time: the longer the time span, the smaller the probability of individuals being reassociated on a breeding site.

#### Evaluating the Population Structure

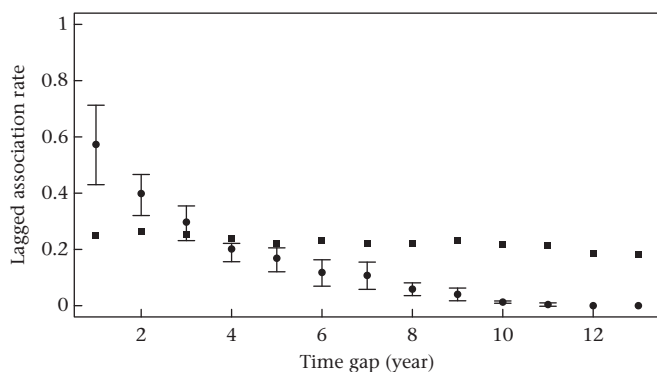
Our models of the population structure showed that the French population formed a fully connected social network over the 14 years of study. We found that the network formed by connecting



**Figure 2.** Representation of the exchange of individuals (lines) between sites (circles) in consecutive years. The thicker the line, the higher the percentage of individuals that moved from that colony to the colony the following year. Black circles represent successful colonies, and white circles colonies with complete breeding failure. Asterisks above each set of movements represent the significance level of the coefficient of variation (CV), which shows the propensity for birds to remain together: \* $P = 0.05$ ; \*\* $P = 0.01$ ; \*\*\* $P = 0.001$ .



**Figure 3.** The probability of choosing a colony given the number of individuals from the same colony in the previous year and the number of individuals from other colonies (or first-year breeders). The lighter colours represent a higher probability. The data assume two colonies, each with the same number of individuals present (but the alternative colony contains only individuals that previously bred in other colonies or are unknown to the focal individual). Thus, where all individuals are unfamiliar ( $x = 0$ ), the probability of choosing the focal colony is always 0.5. Where all individuals in the focal colony are familiar ( $y = 0$ ), the probability of choosing the focal colony ranges from 0.7 ( $N = 1$  in each colony) to 0.9 ( $N = 100$  in each colony).



**Figure 4.** Lagged association rates (LAR) of individuals sighted over 2 years. Squares indicate the random association rate while circles indicate the LAR associated with each time span, with error bars obtained by jackknifing.

individuals that bred in the same colony only required birds observed for a maximum of 3 years to create a fully connected component (Fig. 5). Furthermore, the network was almost fully connected when individuals observed in only 2 different years were included, which means that the French slender-billed gull population is almost completely connected with only the bare minimum of longevity required to create a connected network of breeding colonies.

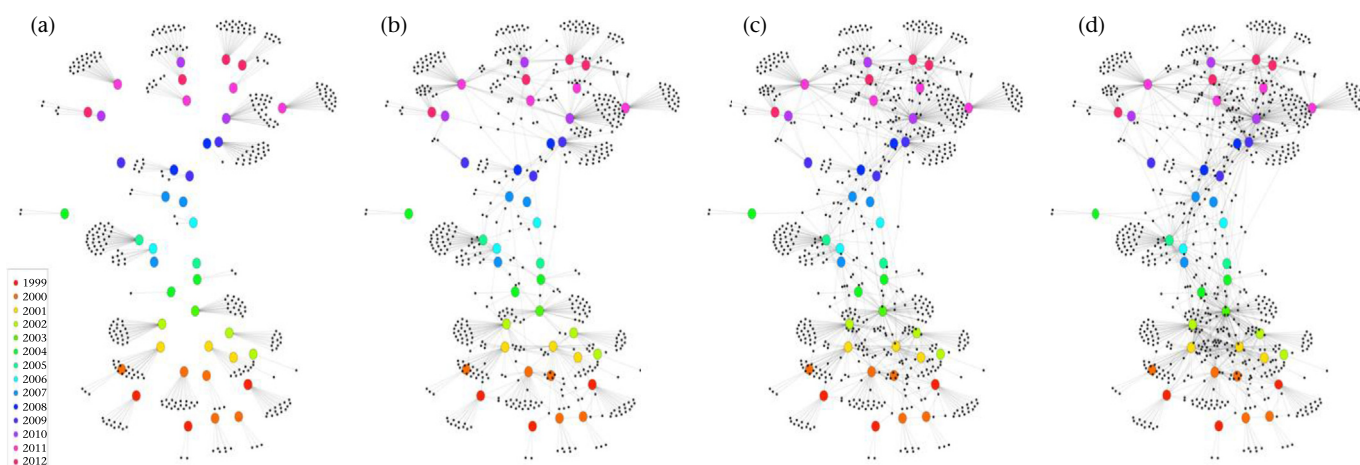
## DISCUSSION

We found extensive evidence that the slender-billed gull, an obligate colonial species, maintains significant colony cohesion

across years despite having very low breeding site philopatry. Our results showing group tenacity in an obligate colonial species adapted to unstable habitats are consistent with the predictions made by Siegel-Causey and Kharitonov (1990). Birds observed breeding in successive years were typically found with more co-members of their breeding colony from the previous year than would be expected by chance. Moreover, we found there was an effect of breeding success but not of distance between colonies on the coefficient of variation of these associations. A simple simulation model suggests that birds were significantly more likely to settle in a colony with individuals of the breeding colony from the previous year than in a colony with individuals that had bred in a different colony the year before, even when this colony was much larger. These patterns resulted in a continuation of colony membership across years despite annual colony relocation. However, the propensity to favour familiar individuals was affected by a colony's breeding success. Notably, we found that in colonies with failed breeding individuals did not preferentially reassociate the following year with individuals from the same colony. Furthermore, although we observed colony fidelity, with groups of individuals significantly more likely to reassociate over time (over 2 consecutive years) than could be explained by random colony choice, we also observed a sufficient exchange of individuals across colonies to maintain a fully connected breeding population over 14 years, which was partly driven by weak patterns of colony co-membership over longer time periods.

For colonial breeders, the more individuals are present on a site, the more attractive it is (Serrano, Forero, Donazar, & Tella, 2004; Tella, 1996). Moreover, the number of individuals in a bird colony is often a major factor in breeding success (Brunton, 1999), due to more efficient predator defence as well as higher foraging success in large colonies than in small ones (Jovani et al., 2015). Yet in slender-billed gulls it seems that the presence of familiar neighbours (individuals that bred in the same colony the previous year) is more important to an individual's choice of settlement than colony size itself as the number of unfamiliar individuals had a marginal impact on this choice of settlement. This suggests that familiarity between individuals might have more effect on fitness than colony size. To our knowledge, this is the first study to show evidence of group tenacity and familiarity over successive years in colonial breeding birds with such limited spatial philopatry. Groups of slender-billed gulls need to decide where to breed, and doing so as a group may improve decision-making accuracy in terms of colony location (Berdahl, Torney, Ioannou, Faria, & Couzin, 2013; Couzin, 2009; Couzin, Krause, Franks, & Levin, 2005; Simons, 2004). For species that breed in unstable habitats, in which resources such as food and potential breeding sites are unpredictable from one year to the next, increased familiarity could provide significant advantages (Piper, 2011), such as reducing aggressiveness (Fisher, 1954) and allowing more accurate decisions for selecting appropriate habitats or identifying a good foraging patch (Aplin, Farine, Mann, & Sheldon, 2014). Experienced or successful individuals could be identified and considered as 'leaders'. Energy saved by avoiding intraspecific aggressiveness could be used for other purposes such as defending the colony against predators. It would also allow nests to be close together on a site, a gain in time for laying eggs rather than defending a nesting territory. Slender-billed gull clutches have very high synchronized hatching (Besnard & Gimenez, 2002), so groups of birds need to choose a colony location in a way that enables them to commence breeding at the same time (in philopatric species, individuals simply need to return to their colony before reproduction starts). Making decisions as a group may facilitate synchronization during breeding.

Our results also highlight a link between group tenacity and a colony's reproductive success. When a colony failed to produce



**Figure 5.** The bipartite network connecting individuals to their breeding colony each year. In (a) 40% of all individuals were observed only in a single year, so they could not be connected to other breeding colonies. (b) However, adding individuals with two observations (21% of individuals) connected all but one colony, thus indirectly connecting most individuals in the population. (c) Adding individuals with three observations (13% of individuals) connected all colonies, and thus all individuals in the population. (d) When all individuals are included, the French population of slender-billed gulls is strongly connected.

chicks, colony members were found to distribute themselves randomly the following year. Birds from failed colonies disbanded their breeding social networks. In several species of colonial birds, individuals leave a colony when their breeding fails (a decision based on private information) or when the breeding success of the colony is low (a decision based on public information; [Danchin, Boulinier, & Massot, 1998](#); [Greenwood & Harvey, 1982](#)). This behaviour is expected when habitat quality is autocorrelated from one year to another, so that a failure one year would imply a failure the following year. The disbanding of groups observed in the slender-billed gull may be an equivalent strategy at a group scale instead of a site scale since this species changes colony location each year. If group quality is autocorrelated from one year to another (group quality could be affected, for instance, by a large number of individuals inexperienced in foraging or colony site selection), then individuals in a group with failed breeding may have better expected reproductive success by changing group than by staying in the same group. As a good indicator of fitness prospects, the breeding success or failure of a group may thus drive the maintenance or fission of a group.

Overall patterns of individual reassociations from one year to the next varied sharply depending on the period. Over the first period of the study (1999–2002), there was little clustering in the movement of individuals between colonies and associations were low (low CV). At that time, colonies remained in the eastern part of the Rhône delta and were very close to each other, which perhaps allowed the transfer of information between colonies and thus lowered the benefit of staying in the same groups. Over the 2002–2004 period, a mass emigration occurred, with about half of the breeding pairs leaving France, and then progressively returning after 2004 ([Doxa et al., 2013](#)). During and after this period, the breeding pairs colonized the western part of the Rhône delta (50 km away) as well as a small saltpan at La Palme, some 200 km further west ([Francesiaz et al., n.d.](#)). Over this period, the CVs were not relevant for our analysis, as in 2003 only one colony was monitored. Between 2004 and 2009, the CVs were higher than in the 1999–2002 period, meaning that group tenacity was higher after the western colonization. Group tenacity decreased again over the 2010–2012 period, corresponding to large-scale dispersal with the settlement of a colony at the Hyères salt pans some 300 km to the east.

Except for a low number of individuals in 1999, there was no tendency for the number of ringed individuals to increase during our study period ([Table 1](#)) which could have increased the power to detect associations. Associations between individuals seemed weak both when colonies were very close to each other and, in contrast, when the population undertook a largescale colonization of a new area. Thus, although we found that in general the distance between colonies did not influence group tenacity, massive emigration events seemed to break social bonds and result in population mixing. What induces these dispersal events, and why birds do not appear to move in social groups but rather create new groups, remains unknown.

Despite evidence of group tenacity within a colony, the social network across all the colonies in the population was fully connected over the entire study period. This is probably because the time span for group tenacity was relatively short (2 or 3 years), so beyond this duration individuals changed group frequently enough to be connected to the entire population. This relatively short group tenacity might have been the result of the high percentage of complete breeding failure in the population (20%).

Our results clearly show a form of social philopatry in the slender-billed gull. Yet exactly how these reassociations are formed between individuals that migrate over long distances remains unknown. Perhaps individuals stay together during the migration to and from the wintering grounds. They could also show a kind of regional philopatry (i.e. philopatry at a saltpan scale or an entire marsh scale rather than at a dyke or islet scale) that may favour group rebuilding at the beginning of the breeding season. At that time, slender-billed gulls are usually observed in the area where colonies were observed the previous year, moving in small groups between several potential breeding sites that are only used for a few days and then abandoned. During this phase, small groups seem to progressively aggregate to form larger ones and eventually form a colony. Regional philopatry may allow familiar birds to aggregate preferentially and then settle together. The wintering season as well as the precolony settlement phase in this species remains unexplored and merits further investigation. Tracking the social networks of birds over winter and at the onset of breeding would yield important insights into the role of social relations in the evolution of coloniality.



## Conclusion

Spatiotemporal variation in the strength of social bonds is widespread in the animal kingdom, but the links between associations of individuals and breeding colony structure remain poorly understood (Aureli et al., 2008; Jacobs, 2010). In this study, we found that colony membership tenacity (the propensity for colony members to reassociate across years) was relatively strong in a species whose colonies are relocated every year, and that this tenacity was affected by colony level breeding success. This finding suggests that group philopatry may be selected via the same drivers as spatial philopatry. Yet understanding exactly what drives an individual's decision to maintain strong social bonds across years, how these bonds are maintained and what drives individuals to change colonies between years are promising areas of research. Furthermore, studying how colonies form at the beginning of the breeding season or are maintained on wintering grounds would provide insight into how colony locations are chosen, which is a potentially fascinating case of collective decision making.

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