



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, Eyer, 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

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