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LIFE-HISTORY DECISIONS OF LARIDS IN SPATIO-TEMPORALLY VARYING HABITATS: WHERE AND WHEN TO BREED

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Foreword

This thesis in *ecology, biodiversity and evolution* was funded with a doctoral allocation provided by the French Ministry of Higher Education and Research and granted by the doctoral school Sciences Ecologiques, Vétérinaires, Agronomiques, Bioingénieries (SEVAB, Toulouse) in 2013. This work also benefited from support granted by the laboratory Evolution & Diversité Biologique (UMR 5174 EDB, Toulouse), the Centre d'Ecologie Fonctionelle et Evolutive (UMR 5175 CEFE, Montpellier), the TULIP Laboratoire d'Excellence (Toulouse), the Université Fédérale Toulouse Midi-Pyrénées, and Paul Sabatier University (Toulouse III).

The different studies which are the subject of this manuscript were conducted with several collaborators: Emmanuelle Cam (supervisor of the thesis), Aurélien Besnard (co-supervisor of the thesis), Jean-Yves Monnat, Michael Schaub, Charlotte Francesiaz, Arnaud Béchet, Nicolas Sadoul, Kate Lessells, and Agata Pijl. These studies are based on analyses of data from long-term wildlife monitoring programs. I would not have had the opportunity to work on these precious datasets without the tenacious involvement of program managers (counted among my collaborators). These monitoring programs also benefited from the help provided by many field assistants, financial supports granted by multiple funders, and the goodwill of several institutions (acknowledged at the end of each article).

The manuscript is composed of four chapters: a general introduction, three articles, and a general discussion. Appendices containing supporting information to the different chapters (i.e. technical details, secondary results, and additional discussion) are also provided.

The public defense was held on March 30, 2017 at Paul Sabatier University in Toulouse. The jury was composed of: Pr. Gilles Gauthier, Dr. Etienne Prévost, Dr. Giacomo Tavecchia, Dr. Blandine Doligez, Dr. Aurélien Besnard, and Pr. Emmanuelle Cam.

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General introduction

1.1 Ecology and evolution of life histories

Evolutionary ecology is the field which studies the causes and consequences of biological variability on the light of interactions between organisms and their biotic and abiotic environment (Pianka 1974). Evolutionary ecologists aim at identifying phenotypic traits that differ between individuals, and at explaining how they evolve, that is, how trait frequencies are modified over time in given environments. One of the raw materials of evolutionary ecologists is the variability in major events occurring over the life of individuals (e.g. growing, mating, breeding, dispersing, and dying) which yields a diversity of *life histories* (Stearns 1992, Roff 1992). Life-history diversity forms a basis of differentiation between individuals, populations, or taxa, and may be regarded from multiple perspectives such as behavior (Krebs and Davies 1978), genetics (Lande 1982), demography (Charlesworth 1994), or physiology (Zera and Harshman 2001). The study of life histories is thus fundamental to understand and depict the drivers of biological diversity.

To understand the evolution of life histories, evolutionary ecologists focus on 'life-history traits', that is, phenotypic traits underlying the realization of individual life histories (e.g. growth rate, survival rate, breeding rate, fecundity rate, dispersal rate, etc.). Variation in phenotypic traits in a given population may arise from mutation (i.e. modification in a trait, e.g. via alteration of a DNA strain) and migration (i.e. incoming and outgoing of trait variants, e.g. via gene flow) and may persist over generations or disappear by drift (i.e. stochastic variation of trait frequencies in finite populations), and natural selection (i.e. differential fitness among heritable trait variants). Further, the same genotypes may yield different phenotypes through a plastic response of trait expression to environmental conditions.

Natural selection is of primary interest for evolutionary ecologists because it shapes traits − including reaction norms setting the extent of plasticity − for a maximal fitness in the environment, given the phylogenetic history of organisms which constrains trait expression (Stearns 1992, Roff 1992). The evolution of life-history traits is thus governed by necessary tradeoffs arising because organisms have a limited amount of resource (e.g. energy, time, and space) they can allocate to either of the traits influencing the two components of fitness: survival and reproduction (Stearns 1992, Roff 1992). For example, there is a major tradeoff between current reproduction and future reproduction or survival (namely, 'the cost of reproduction'), notably because individual expenditure for reproductive processes cannot be allocated to somatic processes (Williams 1966). There are other fundamental tradeoffs such as between growth and reproduction or survival, between offspring number and offspring size. More generally, tradeoffs may be expected among any set of traits as far as they conflict in resource allocation (Stearns 1992, Roff 1992).

Fitness maximization given life-history tradeoffs may be handled in various ways: some species have evolved a short-lived life cycle whereas others species are long-lived, some are semelparous whereas others are iteroparous, some have high fecundity whereas others have low fecundity, etc. (Pianka 1974). To a lower extent, life-history differences also exist between populations of the same species (Berven 1982, Blondel et al. 1993). Moreover, individuals of the same population may differ in the way they deal with tradeoffs and in their ability to acquire, or monopolize resources which determines the strength of tradeoffs they have to face (due to genetic variation or plasticity; van Noordwijk and de Jong, 1986, McNamara and Houston 1996). Life-history differences may thus exist between obvious individual-state categories such as sex, age, or life stage, but also within deeper strata of obvious states, e.g. depending on competitiveness, experience, body condition, social dominance, parasite load, microhabitat features (McNamara and Houston 1996, Gross 1996), which may all co-vary (Wilson and Nussey 2010). Accordingly, individual life-history trajectories are adjusted to a unique set of internal and external circumstances influencing fitness prospects. This dissertation focuses on major decisions underlying life-history adjustment: where and when to breed.

1.2 Breeding in spatio-temporally varying environments

In natural populations, the external factors influencing the fitness of individuals (i.e. habitat attributes) are heterogeneous in space and time. Conditions in the breeding habitat are of pivotal importance because they determine the reproductive success.

Variation in the reproductive output between breeding habitats may stem from spatiotemporal variation in, e.g. predation (Stokes and Boersma 1998, Spencer 2002), parasitism (Fitze et al. 2004, Arriero et al. 2008), food resources (Wauter and Lens 1995, Creighton et al. 2009), (micro)climatic features (Wilson 1998, Warner and Shine 2008), competition (Lewis et al. 2001, Clutton-Brock and Huchard 2013), etc. Moreover, habitat conditions experienced by offspring during early development may have important consequences on their lifetime fitness (Lindström 1999, Monaghan 2008, Cam and Aubry 2011). Spatio-temporal heterogeneity in breeding habitat quality thus produces variability in life trajectories between individuals: some succeed in settling in good habitats where they achieve high reproductive success (and produce offspring which are likely to have high lifetime fitness), while others do not.

Not only habitat quality is decisive for immediate fitness of a breeder, but it has also a crucial influence on the breeder's future life history. Consequences of a single breeding event on the rest of the reproductive career may notably arise due to the tradeoff between current and future reproduction or survival (e.g. Creighton et al. 2009). Indeed, individuals breeding in a low-quality habitat (e.g. where resource availability is low or competition is strong) may incur a higher reproductive cost than if they bred in a high-quality habitat (Erikstad et al. 1998, Barbraud and Weimerskirch 2005, Nicolaus et al. 2012). This cost is physiological when poor conditions imply a lower allocation to somatic maintenance and repair, but it may also stem from strong social constraints on breeding opportunities. For example, breeding failure in socially monogamous birds often triggers divorce and dispersal (Dubois and Cézilly 2002, Naves et al. 2006), while re-mating and acquiring a new nest site requires time or costly contests (Danchin and Cam 2002, Bruinzeel 2007). Accordingly, breeding failure may destabilize individuals and cause a phenomenon of 'spiral of failure' inducing a long-term decrease in fitness prospects (Cam et al. 2004a). Natural selection is thus expected to favor phenotypes that manage to take advantage of good breeding conditions.

On the one hand, spatial heterogeneity experienced at each breeding occasion induces a selective pressure on mobile organisms that promotes the evolution of dispersal mechanisms to escape bad conditions (Clobert et al. 2001, Bowler and Benton 2005, Ronce 2007). Spatio-temporal variability of the environment thus favors the evolution of mechanisms of *habitat selection* by which individuals achieve joining the highest-quality habitats (i.e. where fitness is maximized; Levins 1968, Cody 1985). This view underlies all ecological and evolutionary thoughts on the spatial distribution of individuals. As a reference model of habitat selection, one would assume that all individuals are equivalent, have perfect knowledge of the environment, similar access to the resource, and preferentially occupy the highest-quality habitat. This would lead to the 'ideal free distribution' (Fretwell and Lucas 1970, Fretwell 1972) according to which the highest-quality habitat is occupied first but progressively devaluated by the increase in competition for the local resource. Individuals then start to occupy habitats that were initially of lower quality but that eventually provide identical fitness prospects.

On the other hand, sessile and mobile organisms may adjust their reproductive investment to habitat conditions (Nichols et al. 1976, Creighton et al. 2009). This is expected to result from life history evolution (Stearns et al. 2012, Roff 1992). The 'restraint hypothesis' states that a decrease in reproductive effort under poor conditions is an adequate response to maximize fitness, due to the tradeoff between current reproduction and future reproduction or survival (Curio 1983, Forslund and Pärt 1995). As an extreme case, individuals may avoid the costs of breeding under poor conditions by skipping the reproductive attempt (Erikstad et al. 1998, Cubaynes et al. 2011, Cayuela et al. 2014). Such an adaptive intermittent reproduction is particularly relevant in long-lived species because their fitness is more sensitive to changes in adult survival than fecundity (Roff 1992, Erikstad et al. 1998).

Reproductive costs are a central assumption underlying the theory of life history evolution (Stearns 1992). The idea that costs may vary according to the individual state and that allocation decisions leading to the highest possible fitness payoff may also vary according to the individual state has considerably enriched life history studies (e.g. see McNamara and Houston 1992 for an early example). The individual state encompasses several intrinsic and extrinsic features that can affect reproductive costs and the fitness prospect of reproductive decisions, such as the quality of the breeding habitat (e.g., predation risk; Mangel and Clark 1986). In this framework, individual reproductive decisions should be considered together with habitat selection and associated decisions (Ens et al. 1995, Frederiksen and Bregnballe 2001).

It is however crucial to note the importance of constraints exerted on these two decisions. The restraint hypothesis implies refraining from breeding even though reproduction is not impossible. Reproductive costs may have shaped the evolution of such tactics if refraining from breeding in a given occasion yields higher lifetime fitness than breeding in that occasion. Similarly, reproductive costs may have shaped the evolution of tactics where refraining from breeding in a given occasion yields higher lifetime fitness than breeding in that occasion in a risky or low-quality habitat. However, in observational studies it is notoriously difficult to assess whether several possibilities are opened for individuals (whether breeding is impossible or not), and if individuals refrain from breeding or if they are constrained to skip a breeding opportunity. Given that settling in a breeding site is a necessary condition to attempt to breed, similar constraints are exerted on the decision of *where* to breed and on the decision of *when* to breed. Consequently, skipped breeding may also, if not only, result from the inability to acquire a breeding position (Danchin and Cam 2002), as stated by the so-called 'constraint hypothesis' (Curio 1983, Reed et al. 2015). In the same vein, dispersal patterns may be studied in the light of fitness maximization and the corresponding adaptive mechanisms of habitat selection. Nonetheless, one must bear in mind that constraints (e.g. competition, environmental uncertainty) may lead to apparently sub-optimal habitat choices, even though they reflect the result of a state-dependent fitness maximization process.

In this work I will not attempt to draw conclusions about whether the restraint or the constraint hypothesis is likely to have dominated the evolution of individual breeding decisions. The nature of this work and the statistical analyses of empirical data that I will present do not allow such inferences. Rather, I will attempt to consider individual decisions in a context integrating classical theory of life-history evolution and habitat selection theory, and I will put a particular emphasis on the identification of the set of constraints involved in this complex framework.

1.3 Constraints and mechanisms of habitat selection

Individuals may not be 'free' to join a given breeding habitat and acquire a breeding position. Rather, they are likely to differ in their access to the resource they compete for. Notably, territorial behavior (i.e. defense of a limited resource; e.g. in birds, Brown 1964) leads to the pre-emption of high-quality territories by some individuals (the first arrived or the more competitive ones), so that others are despotically excluded from the highest-quality habitats (Brown 1969, Fretwell 1972). Adding this process to the assumptions of an ideal distribution (see above) implies that some individuals achieve better fitness than others who are forced to settle on lower-quality habitats : this is the 'ideal despotic distribution' (Fretwell 1972). Such kind of distribution has been described, for instance, in many bird studies (e.g. Andrén et al. 1990, Ens et al. 1995, Zimmerman et al. 2003, Kokko et al. 2004, Oro 2008), bringing a considerable understanding of the strong constraint that competition puts on breeding opportunities.

However, habitat selection behavior may not be 'ideal' in the sense that each individual "selects the habitat best suited to its survival and reproduction" (as stated by Fretwell and Lucas, 1970). Individuals are more likely to face perceptual constraints inducing a deviation from the ideal assumption that they have perfect information on habitat quality (Abrahams 1986). In reality, individual use environmental clues to assess habitat quality (Cody 1985, Clobert et al. 2001, Clobert et al. 2009) which are necessarily imperfect. This imperfection stems from the fact that individuals cannot assess all the interacting factors determining habitat quality (and their joint effect), and have to face uncertainty due to temporal unpredictability in these factors (Danchin and Wagner 1997, Dall et al. 2005, Schmidt et al. 2010). Nevertheless, imperfect information may very often be better than none (Koops and Abrahams 1998).

Individuals may thus cue on proximate factors that are indicative of their fitness prospects and thus determine habitat preferences (e.g. vegetation structure, microclimate, food abundance, predation risk; Cody 1985, Orians and Wittenberger 1991, Martin 1998, Chalfoun and Martin 2007, Chalfoun and Schmidt 2012). Nonetheless, relatively few studies have provided unambiguous examples that choices are guided by a given proximate factor under study, and many have reported a mismatch between preferences and fitness (Chalfoun and Martin 2007, Chalfoun and Schmidt 2012). Such a mismatch may indicate that evolved preferences have become maladaptive due to rapid (often human-induced) environmental changes ('ecological traps'; Battin 2004, Robertson and Hutto 2006). The mismatch may also indicate that researchers have failed in identifying the right proxies for preferences or the individual choice processes leading to the apparent preferences (Chalfoun and Martin 2007, Chalfoun and Schmidt 2012). In addition, any (combination of) proximate factor provides information on habitat quality that is likely to be inaccurate and incomplete (Bollman et al. 1997, Storch and Frynta 2000, Giraldeau et al. 2002). Furthermore, many authors have reported that animals often leave apparently suitable habitats unoccupied while clumping their territories (e.g. in Stamps 1988, Reed and Dobson 1993) – an extreme but common example being colonial species (Danchin and Wagner 1997, Evans et al. 2015).

Breeding aggregations are probably the by-product of social information use in breeding habitat selection (Danchin and Wagner 1997, Wagner and Danchin 2003, Nocera et al. 2009) such as the presence, abundance, and breeding success of conspecifics, or even heterospecifics sharing the same fitness requirements (i.e. same use of resource; e.g. Kivelä et al. 2014). Patterns of conspecific and heterospecific attraction have been shown in many studies (Reed and Dobson 1993, Ward and Schlossberg 2004, Mönkkönen and Forsman 2002, Seppänen et al. 2007). These patterns may be explained by the fact that the presence of conspecifics may be indicative of habitat quality (and more readily assessed than a bunch of proximate factors; Stamps 1988), and by positive density dependence in fitness ('Allee effects'; Allee et al. 1949, Courchamp et al. 1999). For example, individuals might benefit from the presence of others through predator defense or dilution (Clutton-Brock et al. 1999) or mating opportunities (Fletcher and Miller 2006).

Nonetheless, individuals may also avoid breeding aggregations when fitness is negative density-dependent due to competition (Sillett et al. 2004, Matthysen 2005). It is likely that a switch from attraction to avoidance at a given density evolve when there is a threshold above which the costs of competition outweigh the benefits of attraction, as suggested by recent empirical studies (Fletcher 2007, Kim et al. 2009). However, alternatively to conspecific presence or abundance, individuals may directly cue on the outcome of habitat quality: breeding success in the target habitat (Switzer 1993, Danchin et al. 2001, 2004). Such information integrates the effect of all habitat attributes on reproductive success: abiotic, biotic, social or non-social (Danchin and Wagner 1997, Danchin et al. 1998). Contrary to conspecific density, reproductive success should enable individuals to accurately assess the quality of a formerly-good environment that attracted many individuals but has finally deteriorated (Danchin and Wagner 1997).

This feature notably provides a mechanism for a switch from conspecific attraction to conspecific avoidance.

It has indeed been very often shown, and has been experimentally evidenced, that animals decide to leave their breeding habitat after their personal breeding failure (the 'win-stay/lose-switch strategy'; Switzer 1993, 1997, Hoover 2003, Schaub and von Hirschheydt 2009). Many empirical and some experimental studies have shown that individuals also use conspecific success as a proxy of habitat quality for habitat selection, and that it may overcome personal information because it is more reliable (e.g. Danchin et al. 1998, Doligez et al. 2002, Brown et al. 2000, Parejo et al. 2007, Aparicio et al. 2007; and see literature census in Appendix A.1). Other studies have shown that such public information may also reach heterospecifics sharing similar fitness requirements (e.g. Parejo et al. 2005). Nonetheless, to be efficient, the use of reproductive success in habitat selection requires that individuals assess habitat quality at a given breeding occasion (*t*) for an effective choice in the next breeding occasion (*t+1*), and thus that the environment is predictable from *t* to *t+1* (Switzer 1993, Boulinier and Danchin 1997, Doligez et al. 2003). In agreement, studies conducted in unstable habitats have failed in confirming the occurrence of such mechanism (e.g. Erwin et al. 1998, Cam et al. 2004b, Parejo et al. 2006).

1.4 Ensuing and pending issues concerning individual decisions

As detailed above, a large body of research has described fundamental aspects of processes governing individual decisions of where and when to breed in spatio-temporally varying environments. These decisions are framed by the species characteristics and subject to life-history tradeoffs, they are constrained by social features involving competition, and they may be made by individuals informed about habitat quality. Because natural selection favors the evolution of life histories that maximize fitness, patterns of variation in the decisions of where and when to breed should reflect the tension between gaining the benefits of breeding under the best conditions and avoiding the costs brought by mechanisms involved to achieve such goal. This tension may be highlighted through comparisons between individual states that vary according to characteristics making them more or less able to overcome the costs.

For example, in birds, males are often more involved in territory acquisition and defense than females (Greenwood 1980, Clarke et al. 1997). It is thus more costly for males to abandon their breeding site for another one, while females benefit from dispersal through mating opportunities, which explains why female birds are usually more dispersal-prone (Greenwood 1980, Clarke et al. 1997). Also, young or inexperienced individuals are often less competitive, less skilled (e.g. for foraging and parental care) than older or more experienced ones. It may thus be more costly for young or inexperienced individuals to acquire a territory (Doligez et al. 1999, Serrano and Tella 2007, Oro 2008) or to attempt breeding (Charlesworth 1994, Desprez et al. 2014), notably under harsh environmental conditions when limitation in resource occurs (Viallefont et al. 1995, Barbraud and Weimerskirch 2005, Genovart et al. 2013). As suggested by the literature cited here, this may be part of the explanation why younger individuals tend to occupy lower-quality habitats or delay their recruitment beyond age at maturity.

Among pending questions concerning the decisions of where and when to breed, one is: to what extent competition is necessary to yield such state-dependent differences? Regarding arguments exposed above, competition for holding the same territory over the years is a cornerstone in explanations for sex- and age-dependent variations in dispersal propensity and age at first reproduction. However, in (rarely studied) species that occupy unstable, ephemeral habitats, individuals are forced to change breeding site from one reproductive occasion to another (e.g. McNicholl 1975, Oro et al. 2010). In this context, settlement before breeding is often quick and opportunistic (McNicholl 1975) and there is no benefit from occupying the same territory over the years, which should largely relax the strength of competition for breeding sites. In these species, sex- and age-dependent variations in the decision (of where and when) to breed would thus be reduced. If one or the other effect is not reduced (e.g. if there are large delays in recruitment) or changes direction (e.g. if males disperse more than females), this would indicate that other costs than competition for territories exert a pressure on individual decisionsand that they might have been obscured in stable habitats by costs associated with the constraint of competition.

Beyond sex- and age-dependent differences, other sources of variation in habitat choices are likely to occur and remain to be highlighted and investigated in depth.

Studies of information use in individual choices of breeding habitats have mostly focused on the decision to leave but relatively few have addressed the decision to join a new site (e.g. Brown et al. 2000, Grosbois and Tavecchia 2003, Citta and Lindberg 2007). Most of these studies concerned relatively small spatial scales and focused on local individuals (i.e. individuals already established in the study area) which are readily able to gather information. Almost none has addressed immigration from another, distant population (Szostek et al. 2014). Can immigrants assess reproductive prospects to target their new habitat? Are they rather attracted by the abundance of conspecifics? Also, many studies have ignored the decisions made by nonbreeders. Why do they attend sites where they do not breed and where should they go next (Danchin and Cam 2002, Bruinzeel and van de Pol 2004)? Do they use social information on reproductive prospects in their decision not to breed (Oro and Pradel 2000, Frederiksen and Bregnballe 2001)? Are social constraints such as competition influencing this decision (Danchin and Cam 2002, Bruinzeel 2007)? Such questions might be extended to other individual states (e.g. prebreeders). Addressing these questions would provide valuable insights on the constraints on habitat selection and the costs and benefits they involve.

One essential cost that has often been absent in theoretical and empirical studies concerning habitat selection is the cost of dispersal (Morris 2003, Burgess et al. 2012). Surprisingly, dispersal and habitat selection have long progressed as two separate scientific fields, despite the many fundamental concepts they share (Baguette et al. 2013). Indeed, dispersal is the essential mechanism by which individuals are distributed across space. Dispersal has thus to be fully integrated to habitat selection studies attempting to explain why individuals breed somewhere. For example, ideal views of habitat selection are based on the assumption that individuals choose the best option among habitats, at least according to available information and given that territorial pre-emption potentially makes higher-quality habitats inaccessible (see above). Nonetheless, costs of dispersal (and conversely benefits of philopatry) may prevent individuals from doing so regardless of habitat quality, and they may result in the evolution of mechanisms leading to non-ideal patterns of habitat selection (see rare developments in Stamps et al. 2005, Piper et al. 2011).

Dispersal kernels always feature a limitation of dispersal by distance, resulting from distance-dependence in the cost of dispersal (Hovestadt et al. 2012). The spatial distribution of animals – and thus the way they select their habitat – must involve distance-dependent dispersal costs. However, very few studies have addressed the issue of spatial-scale in habitat selection, and variation in the causes of dispersal across scales remains poorly understood (Bowler and Benton 2005, Matthysen 2012). This issue may be challenging because it requires monitoring individuals within a relatively extended area that may be best represented with a hierarchical structure of habitat patches (Kotliar and Wiens 1990). To date, most individual-based studies of breeding habitat selection that benefited from such a set-up have focused on identifying the spatial scale at which it was possible to best explain individual choices (e.g. Doligez et al. 1999, Kivelä et al. 2014). However, because these studies could not differentiate a single spatial scale at which some factor inflected habitat choices, they finally analyzed and discussed habitat selection patterns at the largest scale available. Nonetheless, this might indicate that individuals are indeed making choices at several spatial scales (see Orians and Wittenberger 1991) and thus that scale-dependence in habitat selection is likely to occur. To be addressed, this issue requires studies on scale-dependent habitat selection accounting for dispersal costs in theoretical interpretations.

1.5 The black-legged kittiwake and the slender-billed gull

Long-term monitoring studies on long-lived colonial birds are particularly well suited to address variability in the motivations underlying the decisions of where and when to breed. Many animals can be easily monitored within discrete patches where they breed in high densities (i.e. the colonies). Further, long iteroparous trajectories provide the opportunity to record how the same individuals react to changes in external or internal circumstances (features constitutive of the individual state; Mangel and Clark 1988). Such species are a fruitful material for biologists willing to work on individual variation in life history. The work presented in this dissertation is based on data collected in two populations of two colonial seabirds which are the subject of long-term ringing programs: the black-legged kittiwake (*Rissa tridactyla,* hereafter named 'kittiwake') and the slender-billed gull (*Chroicocephalus genei*). Both species belongs to the family Laridae and have about the same size and same life span. The kittiwake has been well-studied all over its distribution range (e.g. in Frederiksen et al. 2005, Coulson 2011), whereas much challenges are still pending to depict the biology of the slender-billed gull

(Doxa et al. 2013, Sanz-Aguilar et al. 2014). Both species have contrasted life histories, part of which will be examined in studies composing this dissertation.

The black-legged kittiwake has been monitored since 1979 in the Cap Sizun (Brittany, France; Monnat et al. 1990, Danchin and Monnat 1992), at the southern edge of the current species range in Europe (the core of the species range is at the Arctic Circle; del Hoyo et al. 1996). Kittiwakes are pelagic birds that nest on cliffs, feed offshore and winter at sea (Coulson 2011). More than 15000 individuals have been ringed as chicks in the six colonies of the area (located a few kilometers apart on the mainland coast of Cap Sizun). The presence, location, reproductive success and behavior of marked individuals have been monitored each year from first arrivals at the breeding cliffs to last departures (January–September). Much effort is being made to record individual activities in May–August to get detailed information on the reproduction (Cam et al. 1998, Cam and Monnat 2000). The age and sex of almost all individuals is known and no breeding attempt within the study area is missed. Once recruited in the population, virtually all ringed birds (breeding or nonbreeding) are resighted each year until they die or permanently emigrate from the population (Cam et al. 1998). This system allows observation of complete life histories of individuals. In addition, the content of all nests (whether or not they are occupied by a ringed bird) is recorded throughout the breeding season (Cam and Monnat 2000). Therefore, the reproductive success is known with much precision all over the study population. Breeding population size can be derived from these data as the annual number of nests whose construction reached the completion criterion (Maunder and Threlfall 1972).

Much work has already been done in this population to understand life histories, and notably the decisions of where and when to breed. Important flows of individuals between colonies follow episodes of intense predation, and immigration is suspected to sustain the population (Monnat et al. 1990, Danchin and Monnat 1992, Frederiksen et al. 2005). At the beginning of the breeding season, males compete to pre-empt nest-sites, then females perform acceptance behavior (Danchin 1987, 1990). Prospection at the end of the season, and notably squatting (i.e. attendance of nests owned by others, occurring preferentially in productive patches), plays a key role in the competitive process of territory acquisition (Monnat et al. 1990, Cadiou 1993, Cadiou et al. 1994, Cam et al. 2002a). Local first-time breeders and experienced breeders select their breeding cliff and nest site according to their own success and the success of conspecifics in the cliff (Danchin et al. 1998, Naves et al. 2006, Aubry et al. 2009, Bled et al. 2011). Breeding failure may destabilize individual reproductive trajectories by triggering dispersal and nonbreeding (Danchin and Cam 2002, Cam et al. 2004a). Further, there is considerable unobserved heterogeneity and a positive co-variation between life-history traits. Some individuals do consistently better than others: they have better survivorship, higher breeding propensity and higher reproductive success (Cam et al. 2002b, Cam et al. 2013).

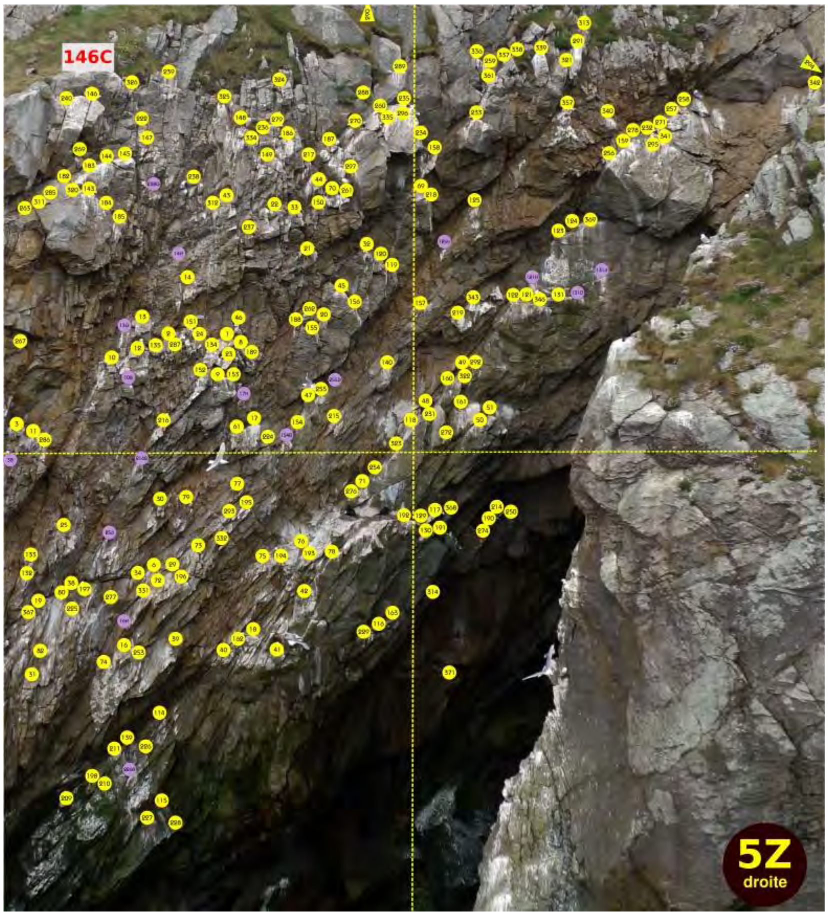

Plate 1.1. Cartography of the right side of the '5Z' cliff wall at the Pointe du Raz (Cap Sizun, Brittany, France). 5Z is a cliff face located in the fifth colony of the area which has been active since 1984 and carries the largest number of nests among all cliff faces in the population. Each yellow point indicates a nest site.

The slender-billed gull has been monitored since 1997 along the entire French Mediterranean coast, at the western edge of the species range. Slender-billed gulls nest on the ground and colony sites are located on islets or dykes in temporary wetlands, brackish lagoons and saltpans. More than 4000 individuals have been ringed as chicks within all colonies present in the study area, that is, almost all birds born in France since the beginning of the program (Besnard 2001, Doxa et al. 2013). Each year, all colonies present along the French Mediterranean coast (2−10 colonies) are detected. Resightings are conducted every day from colony settlement to bird departure and each resighting is accompanied with a behavioral observation indicating the current activity of the bird. The breeding status of the birds can be inferred from these observations with capture-recapture methods taking uncertainty in status assignment into account, but a direct translation into a reproductive life history is not possible. Because nests are too close to one another and chicks quickly amalgamate into crèches, it is not possible to assess the individual breeding success. However, colony success is derived from the number of nests and the number of chicks alive at the end of the season.

Plate 1.2. "DNL" accompanying two chicks. "DNL" is a male slender-billed gull ringed in 1998, thus aged 16 at the time this photo was taken. *Photo credit: Charlotte Francesiaz.*

The ecology of the slender-billed gull remains poorly known, though considerable progress has been made. The species recently expanded in the western Mediterranean (the core of the species range is the coast of the Black Sea; del Hoyo 1996): the number of breeding pairs in Italy, France, Tunisia and Spain has grown from ca. 750 to >8000 in 1980-2000; Isenmann and Goutner 1993, Sanz-Aguilar et al. 2014). Local population dynamics in this area rely more on immigration and emigration than intrinsic growth rate (Doxa et al. 2013, Sanz-Aguilar et al. 2014). Colony sites are often shared with other species and they change almost every year (Fasola et al. 1993, Sadoul et al. 1996, Besnard 2001, Oro 2002). Birds arrive in the breeding area in March. Courtship and copulation happen on ‘clubs’ away from the colony sites and before colony formation (Oro 2002). Breeding activities are highly synchronous: birds form a new colony and build rudimentary nests that are closely packed (10−30 cm between immediate neighbors) within a few days, and females lay eggs within ten days (Isenmann 1976, Fasola and Canova 1992, Besnard 2001). Three or four days after hatching, chicks join into crèches in which parents only feed their own brood (Isenmann 1976, Besnard 2001). Crèching behaviour has probably evolved as an adaptation to within-year habitat instability (Besnard et al. 2002). Intraspecific aggression is reduced (Besnard et al. 2006). Colony sites are not selected on the basis of conspecific success in the area, due to unpredictability in habitat quality (Simon et al. *in prep*).

1.6 Objectives of the dissertation

This dissertation focuses on the life-history patterns arising from the decisions concerning where and when to breed in natural populations. I was primarily interested in assessing the motivations which underlie these decisions depending on the individual state (e.g. sex, age, breeding status, breeding success) and discuss them in an evolutionary context. To address these issues, I focused on patterns of dispersal, recruitment and intermittent breeding in the black-legged kittiwake and the slender-billed gull. My dissertation is composed of three articles on three empirical studies conducted with the help of several collaborators. The first study (Chapter 2) focuses on scale-dependence in the strategy of habitat selection in the kittiwake. The second study (Chapter 3) focuses on the decision to breed taken by immigrants and locals of different breeding status in the kittiwake population considered as whole. The third study (Chapter 4) focuses on sex- and age-dependent variation in recruitment and dispersal probabilities in the slender-billed gull.

In the first study, I suggest a synthetic hypothesis that integrates the benefits of dispersal through information use on habitat quality and distance-dependence in the cost of dispersal. According to this hypothesis, animals should use a habitat selection strategy of ‘sequential proximity search’. More precisely, they should first assess habitat quality in their own territory and decide whether or not to leave this territory; then, if they decided to leave, they should assess habitat quality in their neighborhood and decide whether or not to leave their neighborhood; and so on expending their search area until they choose a suitable breeding site. I examine the spatial scale-dependent patterns of the decision to leave the previous breeding habitat while taking into account a hierarchical structure of habitat patches in the kittiwake. In this purpose, I developed mixed sequential models (or ‘continuation-ratio’ models Agresti 2010) in a Bayesian framework to analyze the spatial magnitude of dispersal as an ordinal response. I confirm that the general scale-dependent pattern of habitat selection fit the sequential proximity search hypothesis. I discuss how variation according to the individual state reflects differences in the ability to overcome a distance-dependent cost of dispersal in order to settle in farther, higher-quality habitats.

In the second study, I draw inferences about the multi-strata dynamics of the Cap Sizun kittiwake population by means of an integrated population model (Schaub and Abadi 2011) which jointly analyses capture-recapture data, nest count data, and fledgling productivity data. Specifically, I estimated annual numbers and rates characterizing immigration, recruitment and intermittent breeding. I assess the relative contribution of these demographic phenomena to population growth. I address the importance of social factors (competition, attraction and conspecific productivity) in the motivation underlying the decisions to breed in this population, made either by immigrants, prebreeders, breeders or skippers. I show that the population would not be viable in absence of the large immigration flows I estimated. I show that the decision to breed is positively associated with offspring productivity in the population and negatively associated with the number of breeders or nonbreeders. However, these associations were not always confirmed in each class of individuals: each class might have its own motivations to breed regarding competition with the other classes and habitat quality in the population. I attempt to discuss these findings in a life-history context, and considering habitat selection mechanisms. I also discuss population functioning at the edge of the species range.

In the third study, I suggest that species occupying unstable, ephemeral habitats, and hence nomadically breeding, should have low variation in recruitment and dispersal according to age and sex because they lack the constraint of competition for holding breeding territories over the years. I address this hypothesis in the slender-billed gull with multi-event capture-recapture models (Pradel 2005) taking uncertainty in state assignment into account. These models include temporary emigration and allow studying dispersal as movements in and out the population. As expected, recruitment age was only slightly delayed; the variation in recruitment age was small, and the sex bias in dispersal is very small. However, males recruited earlier than females and there was some evidence of male-biased dispersal. I discuss how the results are consistent with the idea that the lack of competition for holding a territory over the years cancels a major constraint driving age- and sex-dependent variation in recruitment and dispersal. I suggest other constraints and associated costs that may have generated the remaining observed variation.

Plate 1.3. Rappelling down the cliff to ring a kittiwake chick

1.7 Literature cited

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2

Breeding habitat selection across spatial scales: is grass always greener on the other side?

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In revision for Ecology

2.1 Abstract

A cornerstone of habitat selection theory is that natural selection should favor mechanisms allowing individuals to track habitats associated with the highest fitness prospects. A long-standing problem has been to identify the sources of information on habitat quality that individuals use to choose their breeding habitat. Another one has been to identify dispersal costs that may prevent individuals from joining the highest-quality sites. To date, the literature lacks a synthetic view integrating dispersal costs and habitat selection mechanisms across space.

Because the cost of dispersal is generally distance-dependent, we suggest that a habitat selection strategy of *sequential proximity search* (SPS) can be favored by natural selection. This strategy consists in two decisions: first, deciding whether to stay or leave the previous breeding site, depending on reproductive success. Then if the individual chooses to disperse, deciding whether to stay in or leave the neighborhood, depending on information on habitat quality in this neighborhood, and expanding the search area until the nearest suitable site is chosen. This would minimize distance-dependent dispersal costs while maximizing benefits of gaining a better habitat.

We confirmed the existence of such a strategy in a kittiwake population stratified into colonies, social groups, cliffs and nest sites (in descending order of spatial scale magnitude). We used mixed sequential regressions designed for the study of dispersal decisions over 32 years, and 10702 habitat choice events by 2558 individuals. The response was treated as an ordinal variable whose modalities represented the magnitude of breeding dispersal movement. Moreover, we found differences in scale-dependent dispersal propensities according to breeding status, breeding experience, sex and individual identity.

Distance-dependent dispersal costs result from strong competition among kittiwakes for nesting sites. Individual decisions regarding dispersal (whether to leave or not, and where to go) depend on nesting habitat quality as well as the competitive ability required to keep territory ownership in a previous site, or to acquire a new site; this ability varies according to distance between sites and individual characteristics.

This study calls for investigations in other species to assess the generality of the SPS in habitat selection, and identify the dispersal costs involved.

Keywords: habitat selection, informed dispersal, habitat quality, public information, life history, spatial scales, colonial species, seabird, ordinal response, shrinkage prior.

2.2 Introduction

For most species, the distributions of conspecifics and heterospecifics (i.e. competitors, cooperators, prey, predators, parasites, etc.) and the physicochemical properties of breeding habitats are spatiotemporally variable at several scales. These ecological characteristics strongly influence the fitness of breeders and their offspring (*e.g.* Wilson 1998, Stokes and Boersma 1998, van de Pol et al. 2006a, Nussey et al. 2007, Creighton et al. 2009). From an evolutionary viewpoint, breeding habitat quality has thus to be defined as fitness prospects related to local ecological features (Johnson 2007). In such context, mechanisms allowing animals to select the best option among habitats of varying quality are expected to evolve (Cody 1985).

Early influential models of habitat selection assume that individuals have perfect knowledge of habitat quality in different locations when deciding whether to leave a breeding habitat and settle in another (i.e. whether and where to disperse). They are assumed to be free to distribute themselves according to habitat quality, and achieve equal realized fitness among habitats of different initial quality because negative density-dependent effects cause a discrepancy between expected and realized fitness – the ‘ideal free’ distribution (see Fretwell 1972). Alternatively, competition is assumed to constrain individuals so that some preempt higher-quality habitats and force others to settle in lower-quality habitats – the ideal ‘despotic’ distribution (see Fretwell 1972). Although these models provide a useful departure point to investigate animal distributions, they lack consideration of behavioral mechanisms by which individuals assess habitat quality and achieve dispersal.

To assess breeding habitat quality, individuals may cue on abiotic or biotic factors (e.g. microclimate: Martin 2001, food supplies or vegetation structure: Orians and Wittenberger 1991, predation risk: Fontaine and Martin 2006, con- or heterospecific density: Fletcher 2007). However, each of these factors provides only partial information on habitat quality and might be unreliable (Bollmann et al. 1997, Danchin and Wagner 1997, Giraldeau et al. 2002). It may be more reliable and parsimonious to cue on the breeding success of individuals that previously bred in a location, which integrates the consequences of all factors on breeding habitat quality (Danchin and Wagner 1997), providing sufficient environmental predictability (Switzer 1993, Doligez et al. 2003). Individuals may use personal information, i.e. their own success which results from habitat quality and own individual characteristics, to decide *whether* to disperse (Switzer 1997, Schaub and von Hirschheydt 2009). They may also use public information, i.e. the success of conspecifics (Danchin et al. 1998, Doligez et al. 2002, Ward 2005) or even heterospecifics (Parejo et al. 2005), which provides a greater sampling power to accurately assess the quality of any habitat (Schmidt et al. 2010), to decide *whether* and *where* to disperse.

One might deduce from what precedes that individuals should disperse anywhere in space toward the best habitats when they are able to do so, provided that they know the location and have access to information on the quality of potential breeding habitats. Nonetheless, if all individuals from an area select the same location (the highest-quality habitat), this may lead to competition increase and thus post-choice devaluation of habitat quality (Lima and Zollner 1996). Further, dispersal entails costs (reviewed in Bonte et al. 2012) that have been widely neglected in habitat selection studies (Morris 2003, Burgess et al. 2012). These costs may be incurred while searching for, or simply moving to a new habitat (e.g. predation risk, energy and time spent in movement or information gathering and establishment in a competitive context; Stamps et al. 2005). There may also be opportunity costs due to loss of familiarity advantages when dispersing (e.g. knowledge of foraging areas and routes, efficient predator escape, territorial dominance, pacified neighborhood interactions; Piper 2011). Refinements of habitat selection theory and empirical studies acknowledging the potential for such costs are required (Morris 2003, Stamps et al. 2005, Piper 2011, Burgess et al. 2012).

An issue which has received little attention is that the spatial scale of analyses determines our perception of individual decisions (Kotliar and Wiens 1990, Bowler and Benton 2005). For instance, a bird changing nest site might also change woodland or not. The factors influencing the dispersal movement might differ according to whether the individual decision concerns the nest, the woodland, or both. A hierarchical framework considering a nested spatial structure of habitat patches (e.g. nest sites within woodlands within a given area) is needed to disentangle the scales over which information might be gathered and understand how individuals make decisions (Kotliar and Wiens 1990, Orians and Wittenberger 1991, Boulinier and Lemel 1996, Bowler and Benton 2005).

For instance, a breeding bird might face poor conditions at the nest site because of high accessibility to predators, its surrounding neighborhood might not be accessible to predators, but the woodland might face strong predation, and overall the woodlands in the area might experience good conditions if predation is localized. This example illustrates that multiple optimal choices are often conceivable in situations where information is contradictory across scales with some scale-dependent degree of uncertainty (Boulinier and Lemel 1996). Such a habitat selection dilemma is likely to be commonplace for animals. However, habitat selection and dispersal studies scarcely considered multiple spatial scales; how individuals adjust habitat choices across scales remains poorly known (Lima and Zollner 1996, Bowler and Benton 2005, Schmidt et al. 2010, Chalfoun and Schmidt 2012, Matthysen 2012).

Integrating costs and constraints on habitat selection across spatial scales can solve the dilemma exposed above. Indeed, whereas high-quality habitats might maximize fitness anywhere, dispersal costs are expected to increase with distance to the previous habitat (van der Jeugd 2001, Baker and Rao 2004, Bowler and Benton 2005, Bonte et al. 2012). Natural selection should favor a strategy balancing dispersal costs and benefits by settling in the closest habitat which maximizes fitness (see also Lima and Zollner 1996). We suggest that natural selection should favor the following strategy: a 'sequential proximity search' (SPS) consisting in a suite of conditional choices of leaving the previous habitat at an increasing magnitude of spatial scale starting from own breeding site (e.g. a territory). Thereby, individuals first assess the quality of their own site and decide whether to resettle on the same site, then, if they leave this site, they assess habitat quality in their closest neighborhood and decide whether or not to resettle in this neighborhood, then expend their decision to an enlarged neighborhood and so on until a habitat is accepted.

When considering the costs associated with a movement of a given magnitude (e.g. changing woodland), it is important to account for the fact that individuals might not incur identical costs depending on their own state (Matthysen 2012). For instance, breeders face a strong trade-off between time allocated to habitat selection and time allocated to parental care, which may be relaxed by breeding failure and is not incurred by nonbreeders (Danchin and Cam 2002). The territorial sex (e.g. generally males in birds) have higher costs of establishing in an unfamiliar habitat and leaving the breeding site on which dominance was acquired (Greenwood 1980). More experienced (or older) individuals might be more competitive and thus able to preempt breeding sites, but they might also have gained more familiarity advantages in a previous location (Greenwood 1980, Matthysen 2012). Static individual differences in competitiveness and other dispersal-related traits that might shape personalities are also likely to yield additional heterogeneity in dispersal motivations (Matthysen 2012).

The present study aimed to test for the SPS strategy and to investigate spatial-scale dependency in habitat-selection behavior in a metapopulation of kittiwakes (*Rissa tridactyla*) composed of colonies subdivided into ‘social groups’, themselves subdivided into several ‘cliffs’ containing nest sites (see Materials and Methods). We used 10702 observations of individual location in two successive breeding seasons involving 2558 banded birds from first reproduction to last resighting over 32 years. We defined breeding dispersal as an ordinal response with five possible outcomes according to the scale at which individuals resettled (i.e. staying in or leaving the nest site, cliff, social group and colony). We used mixed sequential binary regressions (Agresti 2010) to account for the hierarchical nature of habitat patch structure. We assessed how public information, individual state (i.e. sex, previous breeding experience, status and own performance) and spatial, individual and annual heterogeneities influenced dispersal probability at each spatial scale, conditional on departure at lower scales.

In this kittiwake population, several studies have shown that individuals use conspecific success in the cliff to decide whether to leave the nest or cliff and found differences in dispersal motivations according to personal success, status, experience and sex (Danchin et al. 1998, Danchin and Cam 2002, Naves et al. 2006, Bled et al. 2011). These studies support assumptions of information use and dispersal costs at small spatial scales but ignore the hierarchy of scales and do not address the SPS hypothesis.

Here we expected that each conditional decision to leave the previous habitat at a given scale will be motivated by habitat quality evaluated at that scale but not at larger scales. If the SPS hypothesis does not hold, there will be an influence of public information evaluated at all spatial scales on each dispersal decision (regardless of scale) because individuals will be attracted by the highest-quality habitats anywhere in space.

2.3 Materials and Methods

2.3.1 Study population and data collection

The study (meta)population is located in the Cap Sizun (Brittany, France, 48°03'N, 4°39'W; Appendix B.1). Each year from 1979 on, hundreds of chicks were color-banded. Mainland colonies were visited at least once a week from first arrivals to first fledging (January-June), and then once a day until bird departure (July-August). We recorded information about the life history of banded birds and the history of reproductive success at every nest site (Cam and Monnat 2000, Bled et al. 2011). In the present study, we used data from 1982 to 2012. We excluded the first three years when the monitoring design was in development and resulted in uncertainty concerning reproductive success.

Resighting probability is virtually equal to one once birds recruit to the mainland breeding population (0.998 in Cam et al. 1998). Thus, individuals which do not come back to the colonies after recruitment can be considered dead or permanently emigrated (Cam and Monnat 2000). We categorized birds as inexperienced the year of first reproduction and experienced the following years. Each year, birds were classified as nonbreeders if they had bred in the past but did not complete nest building in the current year (i.e. a platform of mud and grass with a deep cup; Cullen 1957, Maunder and Threlfall 1972, Cam et al. 1998). Individuals were considered as unsuccessful breeders if they completed nest building but did not raise any chick to fledging. They were classified as successful breeders if they raised at least one chick to fledging (Cam and Monnat 2000). Chicks were considered as fledged if they either left the nest site and came back to be fed by parents, or were seen alive in the nest before fledging with folded wings several centimeters longer than tail. Sex was identified through behaviour (Cam et al. 1998, Naves et al. 2006).

The annual location (i.e. nest site) was known for every breeder. Each nonbreeder that built an incomplete nest at a given site was assigned to this location. Alternatively, nonbreeders were assigned to the location where they were the most involved in breeding activities (site attendance, territorial and sexual behavior; Cam and Monnat 2000). Data from nonbreeders that were evenly involved at different sites (36% of nonbreeder cases) were not considered in this study. We focused on breeding dispersal, thus we only kept data from individuals that were seen at least on two breeding seasons from first reproduction. We excluded data from individuals with unknown state (i.e. unknown sex and/or unknown breeding status, 1% of individual-year observations) when addressing the relationship between individual characteristics and their decision regarding habitat selection.

2.3.2 Spatial scales of the habitat

We considered kittiwake breeding habitat in the study area as nested spatial units which have straightforward physical and biological interpretations. The first unit is the nest site, which is the elementary settlement area for an individual during the reproductive season. The second is the ‘cliff’: a cliff wall containing nest sites and separated from other cliffs by rocky ridges or coastal segments without nesting birds (Naves et al. 2006). The third is the ‘social group’: a set of cliffs constitutive of a cove where birds may be connected by direct visual and vocal contacts. The fourth is the colony: a set of social groups separated from other colonies by at least 500 m (max. 12 km; Cam et al. 2004, Aubry et al. 2009). Over 1982-2012, the study area hosted annually 2-5 colonies (mean 4.5±0.7 standard deviation), 5-18 social groups (14.0±2.8), 20-44 cliffs (31.0±7.2) and 658-1201 nests (935.0±118.0) (see details in Appendix B.1). Hereafter we will designate spatial units above the elementary nest site (i.e. cliffs, social groups or colonies) as "patches", regardless of the spatial scale considered.

2.3.3 Breeding habitat quality

We used the annual proportion of nests with successful reproduction in a given patch (hereafter ‘patch success’) as a measure of breeding habitat quality in that patch. The breeding attempt outcome of an individual settled in a patch and the patch success of this patch cannot be considered as independent. Consequently, when analyzing the decision of an individual regarding habitat selection, we excluded the reproductive outcome of this individual from data used to calculate patch success. We kept only individual data from patches including more than 10 nests (we thus removed 4% of individual-year observations) because demographic stochasticity may result in a large mismatch between patch quality and success in patches with very few nests and might imply peculiar forms of habitat selection. The same approach was employed by Danchin et al. (1998), Cam and Monnat (2000) and Naves et al. (2006).

Uncertainty concerning reproductive success arose when nest content could not be assessed or chicks could not be confirmed to have fledged. The former cases were excluded from patch success calculation but the latter were included. In such cases, we corrected for prefledging survival from the last observation of the chicks to 35 days old (i.e. the age at which chicks are expected to be able to fly) by using survival estimates obtained from chicks that were observed up to 35 days of age, to calculate patch success. We then excluded data when the number of nests used for patch success calculation was lower than 80% of the number of nests in the patch (0.3% of individual-year observations), considering that the targeted value might be flawed by too many missing data.

As mentioned earlier, an important ecological prerequisite for the use of public information in breeding habitat selection is that patch quality is heterogeneous in space and time but predictable from one reproductive event to the next (Danchin et al. 1998, Doligez et al. 2003). We used visual assessment to evaluate spatiotemporal heterogeneity at the cliff, social-group and colony scale (Appendix B.2). We addressed habitat predictability in a time-series analysis framework, by inspecting the sample autocorrelation function of patch success at each spatial scale (Appendix B.2).

2.3.4 Individual dispersal events

We considered breeding dispersal, i.e. the movement between breeding locations (Fig. 2.1), as a variable (Y) with five possible modalities depending on spatial scales of departure: coming back to the previous nest site (Y=1), leaving the nest site but staying in the cliff (Y=2), leaving the cliff but staying in the social group (Y=3), leaving the social group but staying in the colony (*Y*=4), leaving the colony (*Y*=5). These modalities are ranked from 1 to 5 according to the movement magnitude (from none to dispersal among colonies). Note that our variable 'dispersal' also includes fidelity to the previous site. We used 10702 observations of dispersal events (*Y*=1: 7814, *Y*=2: 2059, *Y*=3: 293, *Y*=4: 131, *Y*=5: 405) concerning 2558 individuals, 2376 nest sites, 43 cliffs, 21 social groups, 6 colonies and 32 years.

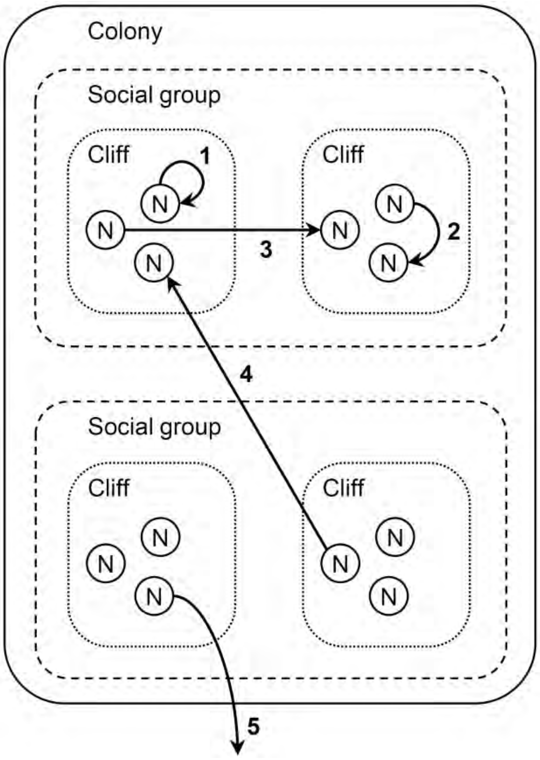

Figure 2.1. Schematic representation of the five possible dispersal events. Modalities are ordered according to the scale of the movement: (1) staying in the nest, (2) leaving the nest but staying in the cliff, (3) leaving the cliff but staying in social group, (4) leaving the social group but staying in the colony, (5) leaving the colony.

2.3.5 Modeling approach

To study the relationship between patch success and decisions in breeding habitat selection, we used a regression model for ordinal variables, more precisely a sequential model (or 'continuation-ratio model'; Agresti 2010). Such a model integrates the sequence of an ordinal response by splitting the probability space into a suite of conditional probabilities following the response ordering. It is a parallel modeling of z-1 binary responses (where z is the number of categories in the ordinal variable) that contrast each category (Y=j) with the grouping of higher-order categories {(Y=j+1),...,(Y=z)}.

We considered the departure phase in dispersal as a habitat selection process involving successive decisions of whether to leave the breeding patch at each spatial scale, conditional on having left at lower scales. Each dispersal event Y_{it} concerned one individual i in two consecutive years: t (the year of departure) and $t+1$ (the year of arrival). We built a joint model for four levels of dispersal probability $P_{it}^{(j)}$: (j=1) the probability of leaving the nest site occupied at t, (j=2) the probability of leaving the cliff occupied at t given that the individual has left its nest site occupied at t, (j=3) the probability of leaving the social group occupied at t given that the individual has left the cliff occupied at t, (j=4) the probability of leaving the colony occupied at t given that the individual has left its social group occupied at t (Eq. 1).

$$P_{it}^{(j)} \;=\; Pr(Y_{it} > j \mid Y_{it} \geq j) \;=\; 1 - Pr(Y_{it} = j \mid Y_{it} \geq j), \tag{1.1}$$

$$\begin{cases} Pr(Y_{it} = 1) = 1 - P_{it}^{(1)} \\ Pr(Y_{it} = \; k) \; = \left(\prod_{j=1}^{k-1} P_{it}^{(j)}\right)(1 - P_{it}^{(k)}) \qquad k = 2,\ldots,5. \end{cases} \tag{1.2}$$

In our model, each of the probabilities $P_{it}^{(j)}$ was expressed as a function of variables characterizing the individual state (sex, experience, breeding status and individual identity in the year of departure t), the location of origin (nest site, cliff, social group or colony identity, and patch success at the three spatial scales in year t), and year of departure (year identity: t). We also considered interaction effects between breeding status and patch success. Individual identity, year and patch identity were treated as random effects (except colony identity because there were only 6 colonies, which is too small for variance parameter estimation; Gelman 2006). Other variables were treated as fixed effects.

For each of the probabilities $P_{it}^{(j)}$, patch success at lower scales than the scale of the focal dispersal movement was excluded from the set of linear regressors (e.g. for the probability $P_{it}^{(3)}$ of leaving the social group in individuals that left their cliff, patch success at the cliff scale was not considered). We thus assumed that individuals did not refer anymore to information concerning spatial units once they had decided to leave these units. Further, we took spatial heterogeneity in dispersal probability into account only at the scale of the focal dispersal movement (i.e. only nest site identity was included at the nest-site scale, only cliff identity was included at the cliff scale, etc.).

We used the robit link function, a robust alternative to logit or probit links for binary regressions which is less sensitive to outlying observations (Liu 2004). The inverse function of the robit link is the cumulative distribution function of the standard Student's t-distribution. We used 7 degrees of freedom and scale parameter 1.5484, which offer an excellent approximation of the logistic model (Liu 2004).

Our model was thus the following (Eq. 2.1 to 2.4):

$$\begin{aligned} robit(P_{it}^{(1)}) = {} & \mu^{(1)} + \alpha_s^{(1)} + \alpha_e^{(1)} + \alpha_r^{(1)} + (\beta_W^{(1)} + \gamma_{Wr}^{(1)})L_{Wit} + (\beta_G^{(1)} + \gamma_{Gr}^{(1)})L_{Git} \\ & + (\beta_C^{(1)} + \gamma_{Cr}^{(1)})L_{Cit} + u_i^{(1)} + u_t^{(1)} + u_n^{(1)} \end{aligned} \tag{2.1}$$

$$\begin{aligned} robit(P_{it}^{(2)}) = {} & \mu^{(2)} + \alpha_s^{(2)} + \alpha_e^{(2)} + \alpha_r^{(2)} + (\beta_W^{(2)} + \gamma_{Wr}^{(2)})L_{Wit} + (\beta_G^{(2)} + \gamma_{Gr}^{(2)})L_{Git} \\ & + (\beta_C^{(2)} + \gamma_{Cr}^{(2)})L_{Cit} + u_i^{(2)} + u_t^{(2)} + u_w^{(2)} \end{aligned} \tag{2.2}$$

$$\begin{aligned} robit(P_{it}^{(3)}) = {} & \mu^{(3)} + \alpha_s^{(3)} + \alpha_e^{(3)} + \alpha_r^{(3)} + (\beta_G^{(3)} + \gamma_{Gr}^{(3)})L_{Git} + (\beta_C^{(3)} + \gamma_{Cr}^{(3)})L_{Cit} \\ & + u_i^{(3)} + u_t^{(3)} + u_g^{(3)} \end{aligned} \tag{2.3}$$

$$robit(P_{it}^{(4)}) = \mu^{(4)} + \alpha_s^{(4)} + \alpha_e^{(4)} + \alpha_r^{(4)} + \alpha_c^{(4)} + (\beta_C^{(4)} + \gamma_{Cr}^{(4)})L_{Cit} + u_i^{(4)} + u_t^{(4)} \tag{2.4}$$

where μ stands for intercepts, α for fixed effects of categorical variables (i.e. fixed deviations from the intercept), β for fixed effects of continuous variables (i.e. fixed regression slopes), γ for interactions, u for random effects of categorical variables (i.e. random deviations from the intercept). L stands for patch success (continuous variables for the different spatial scales). Subscripts in capital letters indicate the spatial scale of the parameter or variable: W for cliff wall, G for social group and C for colony. Subscripts in italics indicate the object of the parameter or variable: s is the sex, e is the experience (first-time breeder or experienced), r is the reproductive status (nonbreeder, failed breeder or successful breeder), n is the nest site, w is the cliff wall, g is the social group and c is the colony - of the focal individual i in year t.

For individuals that left their social group (j=4), there were too few cases in the successful breeder category (8 observations) to consider a separate breeding status, we thus grouped them with unsuccessful breeders (478 observations). There were also very few observations in colony 6 (5 out of 536 observations) to consider a separate spatial unit, we thus grouped them with observations from colony 5 (the closest colony, 153 observations).

The random effects in our model account for non-independence in the data induced by individual, spatial and temporal pseudoreplication. They also provide opportunity to explore how deviations from the mean model can be partitioned into consistent influences of the individual, spatial and temporal contexts that are not captured by the fixed effects (i.e. heterogeneity in dispersal probabilities). Further, we used a quadrivariate normal distribution with mean 0 and a different variance-covariance matrix for individual identity and year to consider correlations between individual random effects and between year random effects over the four submodels (Appendix B.3). This correlation structure was notably helpful to improve Bayesian sampling. Also, this model feature provides opportunity to assess whether individuals are characterized by a propensity to consistently leave or stay across spatial scales (i.e. to disperse systematically to close or remote locations). We might expect positive correlations between year effects that would indicate a tendency for short- or long-distance dispersal in certain years. This might be due to the fact that dispersal magnitude in our models is only a rough approximation of dispersal distance. Indeed, the spatial structure of breeding success varied widely in the study population: depending on the year there were distant or close colonies with similar or opposite success (Appendix B.1, B.2). However, we would lack further biological explanations concerning such correlation between year effects.

2.3.6 Parameter estimation

Inference was based on a Bayesian approach using Gibbs sampling, i.e. a Markov Chain Monte Carlo (MCMC) algorithm, with the program JAGS 3.4.0 (see model code in Appendix B.3; Plummer 2003) called from R (R Core Team 2016) with the *rjags* package (Plummer 2013). We ran 20 chains with different sets of initial values. We used an adaptive phase (i.e. a period during which the samplers modify their behavior to reach adequate efficiency) of 100 iterations. We discarded the first 5000 iterations (burn-in period) and used the subsequent 40000 iterations for exploration of posterior distribution samples (monitoring period), yielding a total of 8×10^5 samples. Chains were not thinned (to keep all the information they contain; Link and Eaton 2012). Every continuous variable was standardized, making all effect sizes comparable.

2.3.7 Prior distributions

We performed variable selection and parameter estimation all at once in a single model. To do so, we used a shrinkage prior (see Hooten and Hobbs 2015), the horseshoe prior (Carvalho et al. 2010, Appendix B.3), for all fixed effects in the model. Such prior is weakly informative and heavy tailed, which ensures to *a priori* penalize model coefficients through effective shrinking towards zero, unless there is strong signal for non-zero in the data. This is a robust, conservative approach that separates strong signals from noise and avoids overestimating effects. The horseshoe prior has been shown to yield closely similar results to those obtained with the "gold standard" (but rapidly impracticable): Bayesian model averaging across discrete mixture models (Carvalho et al. 2010).

We did not include the intercepts in the set of parameters considered for variable selection (i.e. $\mu^{(j)}$, j=1...4 in Eq. 2.1 to 2.4), consequently, we specified weakly informative normal priors with mean 0 and variance 10^4. Similarly, we used a weakly informative uniform prior on the range (0,10) for standard deviation of patch random effects (i.e. $u_n^{(1)}$, $u_w^{(2)}$,$u_g^{(3)}$ in Eq. 2.1 to 2.4; Gelman 2006). For individual and year effects, we used the Choleski decomposition of the variance-covariance matrix of correlated random effects introduced by Chen and Dunson (2003). The priors used (following Chen and Dunson 2003) reflected reasonable doubt on variance parameters and shrinked covariance parameters towards zero (see Authier et al. 2012; and all prior distributions in Appendix B.3).

2.3.8 Posterior distributions

Post-processing of MCMC chains was performed in R (R Core Team 2016; Appendix B.4). Preliminary analyses allowed us to target optimal length of the burn-in and monitoring period. Convergence was assessed using the Brooks-Gelman-Rubin diagnostic $\hat{R}$ for each parameter (Brooks and Gelman 1998). We achieved convergence with all $\hat{R}<1.01$. Further, all effective sample sizes were larger than 4000. According to Raftery and Lewis (1992), this is sufficient for well-behaved posterior to provide the 2.5% quantile within

±0.005 with probability 0.95 (i.e. reported 95% credible intervals then have posterior probability within [0.94,0.96]). The Monte Carlo standard error (MCSE) would then be less than 1.5% of the posterior standard deviation. It was usually enough to report posterior means with 2 or 3 decimal place precision (Appendix B.4).

To assess if effects were different from zero, we calculated 95% posterior credible intervals (hereafter 95%CI) using the highest posterior density method. We classified the effects as robust when their 95%CI excluded zero. Among non-robust effects, those having a posterior effectively shrinked on zero could be clearly considered as nil. However, other effects were more equivocal, i.e. they were not robust but might have notably appeared to influence the mean model and general uncertainty. For these effects, a conservative approach is to disregard them: more data would be needed to draw clear conclusions. We foremost discussed robust effects and only discussed equivocal effects when they modified expectations arising from the sole robust effects. We considered that there was some support for heterogeneity captured by random effects when the 95%CI of their standard deviation excluded zero (at three decimal place precision, i.e. 0^+) and a strong support when the 95%CI of their variance excluded zero (0^+).

2.3.9 Posterior checks

For each submodel, we used posterior predictive checks (Gelman et al. 1996) to assess the overall goodness of fit. We referred to χ^2 discrepancy metrics (Gelman et al. 1996) to compute the posterior predictive p-value, which quantifies the proportion of samples in which the distance of observed data to the model is greater than the distance of replicated data to the model (a value close to 0.5 suggests a fitting model, whereas a value close to 0 or 1 indicates substantial lack of fit; Appendix B.5). Predictive power was assessed with contingency tables of true/false positives/negatives derived from replicated data, and a detailed visual assessment of model fit by means of separation plots (Greenhill et al. 2011, Appendix B.5). In addition, we inspected the behavior of the mean Pearson residuals, especially residuals plotted against predictors. These checks allowed us to identify where the model was well or poorly performing.

2.4 Results

2.4.1 Spatiotemporal heterogeneity and predictability

At each spatial scale, patch success plotted against year clearly showed that habitat quality varied in space and time so that the quality of a given patch relative to the others was varying over years (Appendix B.2). Temporal autocorrelation was moderate and increased with increasing spatial scale (at the time lag of 1 year, it was 0.47 at the cliff scale, 0.52 at the social-group scale and 0.64 at the colony scale) and estimates were different from expectations under assumptions of non-autoregressive processes (Appendix B.2).

2.4.2 Leaving the nest site

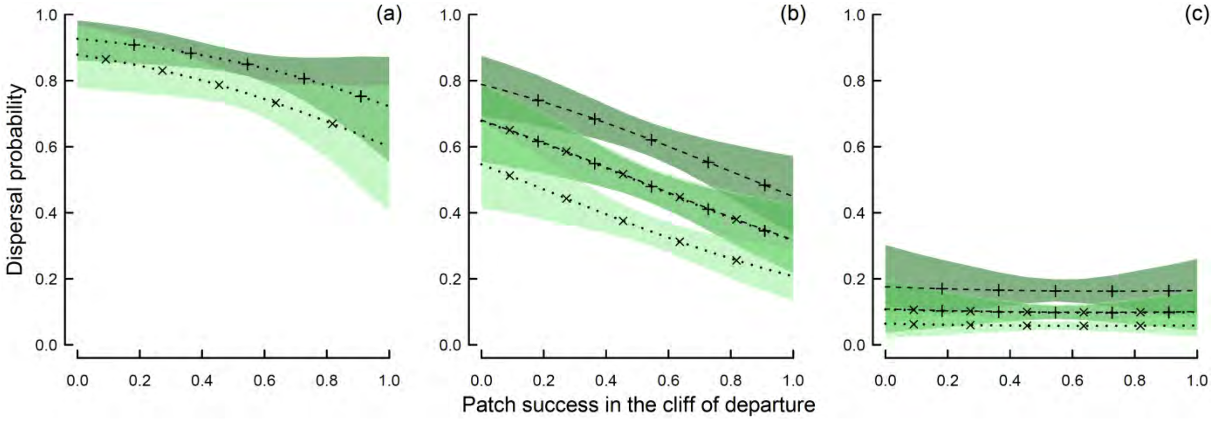

Figure 2.2. Estimated dispersal probability at the nest-site scale in (a) nonbreeders, (b) unsuccessful breeders, and (c) successful breeders according to sex and experience. The mean relationship was plotted with '×' crosses for males, '+' crosses for females, dotted lines for experienced individuals and dashed lines for inexperienced ones. Background transparent bands indicate 95% credible intervals of the relationships (see details in Appendix B.4). We considered the average situation regarding the other predictors (i.e. they were set to zero, the mean value of standardized variables and random effects). Additional graphics for the relationships for variables of patch success that had non-robust effects on dispersal probabilities are provided in Appendix B.4.

For the probability of leaving the nest site, the effects of sex, experience, breeding status and conspecific success in the cliff of departure had 95% credible intervals (95%CI) excluding zero (Appendix B.4: Table B.4.1). The lower bound of the 95%CI of the effect of cliff success was relatively close to zero. The interaction effect between successful breeding and cliff success was equivocal, but other effects (i.e. conspecific success in the social group and colony, and their interaction with breeding status) were null. Females and inexperienced individuals had a higher probability of dispersing than males and experienced individuals (Fig. 2.2). Dispersal probability of unsuccessful breeders was intermediate and decreased linearly with cliff success. Dispersal probability of nonbreeders was quite high and decreased with cliff success to a lesser extent than for unsuccessful breeders. Dispersal probability of successful breeders was quite low and did not appear to be modulated by cliff success (Fig. 2.2). In fact, the equivocal interaction effect between cliff success and individual successful breeding compensated for the sole effect of cliff success (Appendix B.4: Table B.4.1). In addition, there was strong support for moderate spatial heterogeneity (i.e. random effect of nest site identity) in dispersal probability (Appendix B.4: Table B.4.5) and for small annual heterogeneity (Appendix B.4: Table B.4.7), but not for individual heterogeneity (Appendix B.4: Table B.4.6).

2.4.3 Leaving the cliff (conditional on leaving the nest site)

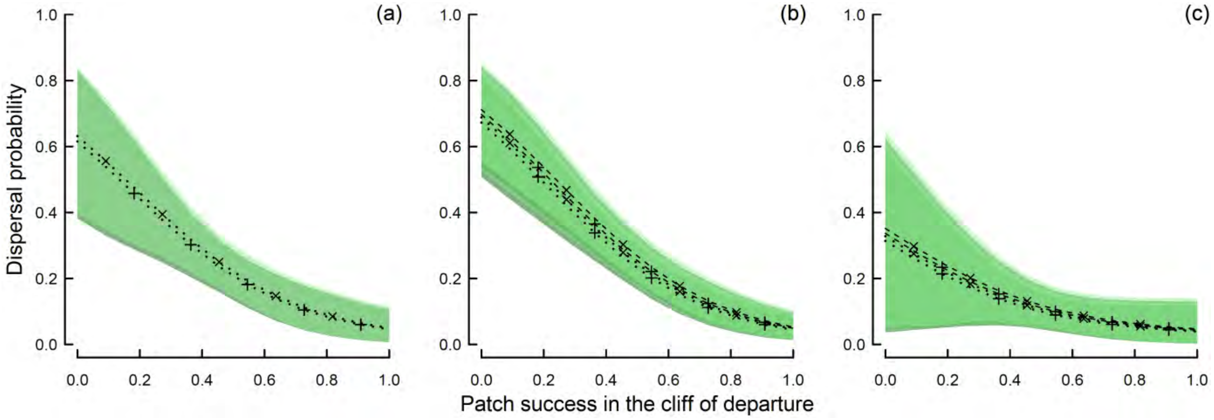

Figure 2.3. Estimated dispersal probability at the cliff scale (conditional on having left the nest site) according to sex and experience (a) in nonbreeders, (b) unsuccessful breeders, and (c) successful breeders. Specifications are the same as for Fig. 2.2.

For the probability of leaving the cliff, the effects of breeding status and conspecific success in the cliff of departure were the only ones to have 95%CIs excluding zero (Appendix B.4: Table B.4.2). Successful breeders had a lower probability of dispersing than unsuccessful breeders and nonbreeders. The latter categories had identical probabilities of dispersing. Dispersal probability decreased with cliff success, and this effect was clearly stronger at this scale than at the nest site scale (Fig. 2.2, 2.3). For unsuccessful breeders and nonbreeders, the probability of leaving the cliff was quite high when cliff success was null and decreased quasi-linearly to approach zero when cliff success was 100%. For successful breeders, the decrease in dispersal probability with the increase in cliff success was equivocal and this trend was only detectable when cliff success was lower than 50 or 60%; under better conditions, dispersal probability of successful breeders was stable (Fig. 2.3). In addition, there was strong support for moderate spatial heterogeneity (i.e. random effect of cliff identity) in dispersal probability (Appendix B.4: Table B.4.5), some support for moderate individual heterogeneity (Appendix B.4: Table B.4.6) and strong support for small annual heterogeneity (Appendix B.4: Table B.4.7).

2.4.4 Leaving the social group (conditional on leaving the cliff)

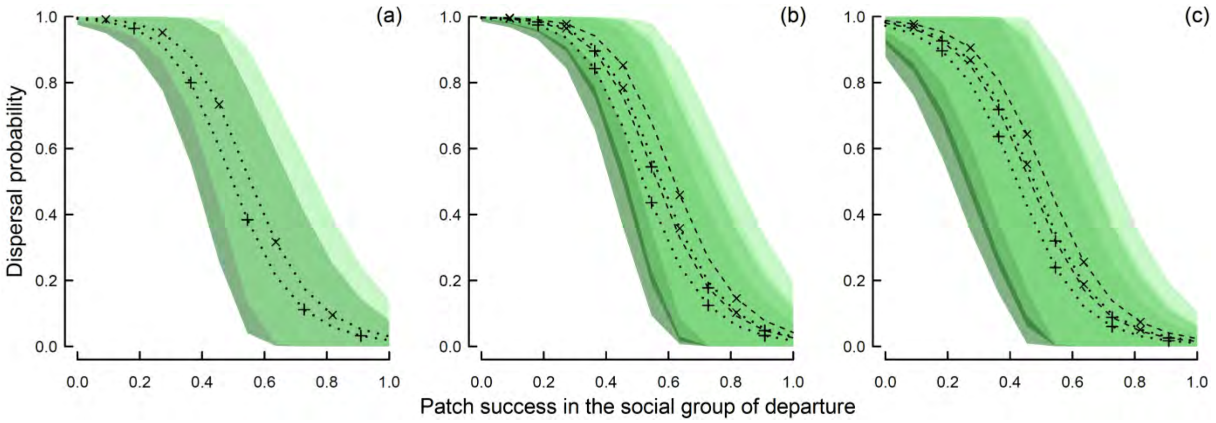

Figure 2.4. Estimated dispersal probability at the social group scale (conditional on having left the cliff) according to sex and experience in (a) nonbreeders, (b) unsuccessful breeders and (c) successful breeders. Specifications are the same as for Fig. 2.2.

For the probability of leaving the social group, only the effect of patch success in the social group of departure had a 95%CI excluding zero (Appendix B.4: Table B.4.3). Dispersal probability decreased with conspecific success in the social group, following a sigmoid pattern from 1 to 0 (Fig. 2.4). Disregarding random effects, for low values of social-group success (0-30%) almost all the individuals were dispersing. Within the range of intermediate values of success, dispersal probability rapidly decreased. Finally, virtually no individuals were dispersing for high values of success (70-100%). In addition, there was strong support for large spatial heterogeneity (i.e. random effect of social group identity) in dispersal probability (Appendix B.4: Table B.4.5), large individual heterogeneity (Appendix B.4: Table B.4.6) and large annual heterogeneity (Appendix B.4: Table B.4.7).

2.4.5 Leaving the colony (conditional on leaving the social group)

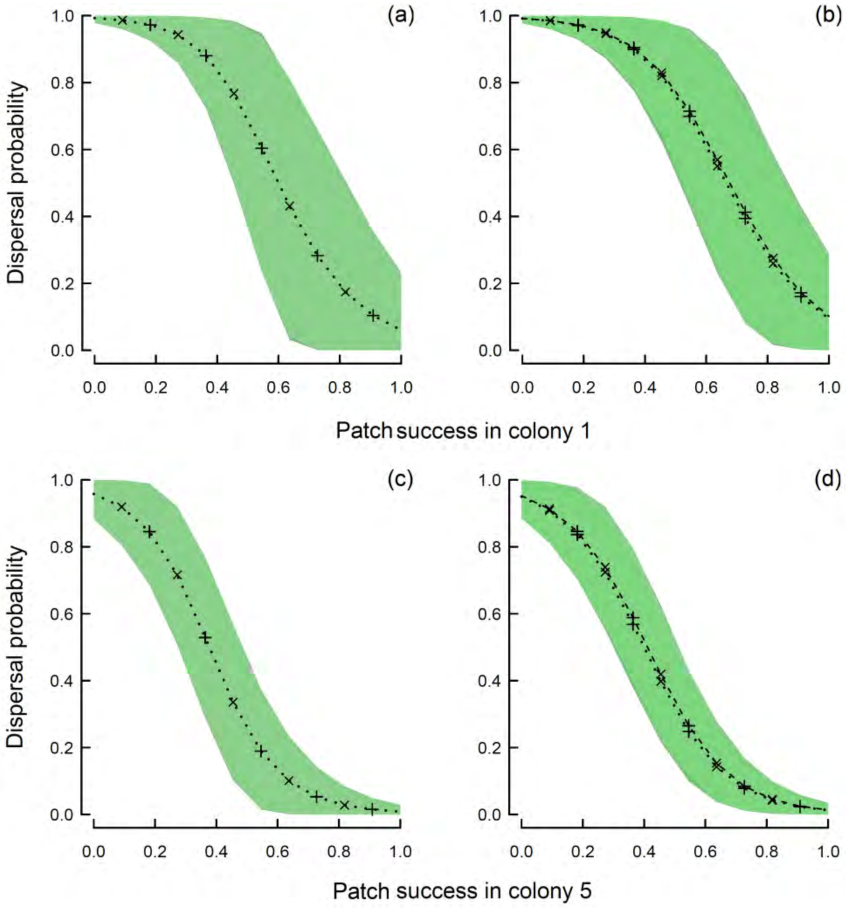

Figure 2.5. Estimated dispersal probability at the colony scale (conditional on having left the social group) according to sex and experience in (a) nonbreeders of colony 1, (b) breeders (mainly unsuccessful) of colony 1, (c) nonbreeders of colony 5 and (d) breeders (mainly unsuccessful) of colony 5. Figures for the relationships in colony 2, colony 3 and colony 4 are provided in Appendix B.4. Specifications are the same as for Fig. 2.2.

For the probability of leaving the colony, only the effect of conspecific success in the colony of departure had a 95%CI excluding zero (Appendix B.4: Table B.4.4). Dispersal probability followed a similar sigmoid pattern as for the probability of leaving the social group (Fig. 2.5). There was no equivocal effect. In addition, the probability of leaving colony 5 was lower than that of colony 1, with a 95%CI of the difference that excluded zero. Other spatial differences were equivocal, but as colony 1 was the reference category, some differences between other colonies might be different from zero. In detail: the mean dispersal probability from colony 2 and 3 was also lower than that of colony 1 and half that of colony 5; the mean dispersal probability from colony 4 was higher than that of colony 1, with the same difference than to the mean probability of dispersal from colony 2 and 3. There was no support for individual or year random effects on the probability of leaving the colony (Appendix B.4: Table B.4.6, B.4.7).

Table 2.1. Summary of the results.

Dispersal	Effect									
scale	Individual state				Patch success			Additional context		
(submodel)	Sex	Experience	Breeding status		Cliff	Group	Colony	Individual	Patch	Year
	Male	Experienced	Nonbreeder	Successful						
Nest site	Y−	Y−	Y+	Y−	Y−	N	N	N	Y	Y
Cliff	N	N	N	Y−	Y−	N	N	Y	Y	Y
Social group	N	N	N	N	/	Y−	N	Y	Y	Y
Colony	N	N	N	/	/	/	Y−	N	Y	N

"N" stands for "no" and indicates non-robust (nil or equivocal) effects, "Y" stands for "yes" and indicates robust effects. For the latter, "+" indicate positive effects and "−" indicate negative effects. For effects of the "additional context" (individual identity, patch, year) we were interested in the among-effects variance but not the direction of each effect. Below categorical fixed variables are indicated the non-reference categories for which an effect was estimated. The reference category was female for sex, first-time breeder for experience and unsuccessful breeder for breeding status. No interaction effect between breeding status and local success was robust in the model and they are not included in this table. "/" indicates that the effect was not included in the model. The detailed results are given in Appendix B.4.

2.4.6 Correlations of random effects

Two correlations between year effects among the four conditional dispersal probabilities (between those of nest-site and cliff scales, and between those of cliff and social-group scales) had 95%CIs that excluded zero and were positive (Appendix B.4: Table B.4.6, B.4.7). Speculating on possible biological meanings of these correlations is beyond the scope of this paper (see *Materials and Methods*). No other correlation between random effects had a 95%CI that excluded zero. The absence of robust correlations between individual random effects suggested that individuals that were prone to disperse at a given scale were not particularly prone to disperse at another scale.

2.4.7 Posterior checks

The posterior predictive p-value indicated a decent fit at the nest scale (0.35) and a very good fit at larger scales (cliff: 0.46, social-group: 0.48, colony scale: 0.51, Appendix B.5). Overall, diagnostics of predictive accuracy were quite good at the nest-site and cliff scales (75% of correct predictions) to almost excellent at the social-group and colony scales (85% of correct predictions). Predictive power for observations of actual philopatry was very good, with a small decrease at the colony scale. For observations of actual dispersal, predictive power was moderate at the nest-site and cliff scales to excellent at the social-group and colony scales (see details in Appendix B.5). Residuals inspection indicated that much of poor predictions concerned observations of actual dispersal at the nest-site and cliff scale in successful (and generally experienced) breeders in good-quality cliffs (Appendix B.5).

2.5 Discussion

In this study, we defined nested spatial units in the breeding habitat of kittiwakes and addressed hypotheses about factors influencing dispersal decisions at different spatial scales, conditional on having left at lower scale(s). Note that hereafter the conditionality will not be systematically specified. We showed that individuals relied on their own success only to decide whether or not to leave the nest site, and then the cliff, but not for subsequent decisions concerning dispersal of greater magnitude. They relied on conspecific success to make decisions at all scales. Importantly, they relied only on conspecific success evaluated at the smallest scale among all possible scales of increasing dispersal magnitude. For example, individuals leaving their cliff may also leave their social group or not: their decision might be motivated by the quality of their social group (smallest scale) or colony of origin (larger scale). However, only group success, influenced the probability of leaving the group, not colony success. Further, we found sex- and experience-dependence in dispersal probability at the nest-site scale and individual heterogeneity at the cliff and social-group scale. These findings (Table 2.1) are in agreement with the 'sequential proximity search' (SPS) hypothesis.

2.5.1 SPS and distance-dependent costs of dispersal

Under the SPS hypothesis, individuals sequentially expand their search area starting from their own previous breeding site until they choose the nearest suitable site according to information on habitat quality. Such strategy minimizes dispersal costs increasing with distance to the previous habitat and maximizes fitness prospects in the future habitat.

Costs often accumulate with distance travelled during the 'transfer' phase of dispersal due to predation risk, time spent, energetic expenditure and damages incurred (Baker and Rao 2004, Smith and Batzli 2006, Bonte et al. 2012). However, in species with great movement capacities such as the kittiwake, transfer *per se* is unlikely to be costly at the spatial scales we considered (≤ 12 kilometers, Appendix B.1). Indeed, daily foraging trips of kittiwakes during the breeding season are usually tens of kilometers and may expand to hundreds of kilometers (Ponchon et al. 2014). However, 'opportunity costs' due to familiarity loss and habitat selection constraints (Piper 2011, Bonte et al. 2012, reviewed in Appendix B.6), may also increase with distance (Heinze et al. 1996, van der Jeugd 2001, Péron et al. 2010).

In kittiwakes, the competition for nesting territories is strong. Our study system presents no limitation in nest-site availability (Bled et al. 2011) but social information use in habitat selection induces attraction to occupied (good-quality) habitats, which triggers aggregations (Stamps 1988, Danchin and Wagner 1997, Nocera et al. 2009) and thus territory contests. During the breeding season, and especially after failure, kittiwakes are seen attending nest sites they do not own, which is mainly interpreted as a prospecting behavior involved in the acquisition of a breeding position (Cadiou 1993, Cadiou et al. 1994). As exposed below, the balance between acquiring a new nest site farther and defending the currently owned nest site – to keep an insurance on philopatry – may bring a potential cost of dispersal which is distance-dependent.

A clear advantage for nest-site owners is the dominance in territory contests (Cullen 1957, Cadiou 1993): a 'prior resident effect' found in many species (Kokko et al. 2006, Sherratt and Mesterton-Gibbons 2015). Additionally, owners have a 'dear enemy' agreement of nonaggression with their immediate neighbors once accepted as dominant on their breeding site (Danchin 1987, Coulson 2011; and see Ydenberg et al. 1988, Eason and Hannon 1994, Booksmythe et al. 2010). It is common that established breeders defend a neighboring site against intrusion (Danchin 1987, Cadiou 1993), which fits theoretical expectations on dear-enemy relationships (Getty 1987, Mesterton-Gibbons and Sherrhat 2009) and resembles cases of territory-defense coalitions (Elfström 1997, Backwell and Jennions 2004). On the other hand, kittiwakes suffer aggression by nest-site owners as soon as they leave their immediate neighborhood (Cullen 1957, Danchin 1987, Cadiou 1993, Coulson 2011). Gaining familiarity and dominance on a nest site is costly. This requires prospecting habitats, assiduous attendance of a target area, intrusions on territories owned by others and defended by neighbors, repeated fights for males, and acceptance attempts for females (Danchin 1988, Cadiou et al. 1994, Danchin et al. 1998, Cam et al. 2002). Similar logics of territory acquisition hold in many species (Stamps and Krishnan 1999, Sergio et al. 2009, Ens et al. 2014). It is thus costly to leave a defended territory and to acquire a new one.

Dispersal decision is a big bet on future reproductive success because dispersers cannot be certain to obtain a suitable position for the next breeding occasion(s) and may be forced to nonbreeding if they do not (Danchin and Cam 2002, Cam et al. 2004, Bruinzeel 2007, Sergio et al. 2009). Individuals may lower this bet by keeping a property insurance on their current nest site. This implies to divide their time budget between breeding activities, acquiring a new site or mate, and maintaining ownership in their previous site. Successful breeders necessarily do so because parental duties constrain them to nest-site securing. The fact that unsuccessful and nonbreeder kittiwakes continue to attend their site along the prospecting period (after failures; Hatch and Hatch 1988, Danchin 1988, JYM and EC *personal observations*) also supports the idea that they maintain current territory ownership while prospecting. Distance-dependence in dispersal cost may arise because keeping an eye on the nest site is more difficult when the individual is farther. The efficiency in deterring intruders is higher for individuals in their neighborhood, than for those prospecting elsewhere in the social group, than for those prospecting a nearby social group, than for those prospecting another colony. As a corollary, intruders are more likely to acquire a nest site owned by individuals prospecting farther.

Other opportunity costs might exist in the kittiwake and induce scale-dependence in dispersal costs, but they remain speculative for the present study. For instance, kittiwakes may exhibit individual fidelity to foraging areas, suggesting a familiarity benefit (Irons 1998), which has growing support in colonial species (Bailys et al. 2012, Wakefield et al. 2015). An individual dispersing relatively far away (e.g. to another colony) might need to learn new foraging routes (e.g. in a juvenile seabird: Riotte-Lambert and Weimerskirsch 2013). Additionally, social familiarity may facilitate mating through the assessment of individual quality by eavesdropping (Doutrelant and McGregor 2000). Such facilitation might come into play in social groups of kittiwakes due to promiscuity, and is even more probable with immediate, dear-enemy neighbors (e.g. in Bried and Jouventin 2002).

2.5.2 Modulation of habitat selection behavior by the individual state

Successful breeders were very unlikely to leave their nest site and were not influenced by public information. In line with the SPS hypothesis, this site is their nearest best option. They were also very unlikely to leave their cliff. Parental duties prevent them from gathering extended public information and invest in nest-site acquisition in an unfamiliar neighborhood (Boulinier et al. 1996, Doligez et al. 1999). For the rare cases in which they have to change nest site (e.g. partner death, divorce, territory eviction or nest-site destruction; Harris and Wanless 1995, Naves et al. 2006, Bruinzeel 2007), they may either re-nest in their immediate neighborhood, or remain elsewhere in the cliff as nonbreeder after losing their breeding commodities. The latter is likely to be preponderant given that nonbreeding propensity of successful breeders is ca. 10% (Danchin and Cam 2002), which is very close to their probability of leaving the nest site (Fig. 2.2).

Unsuccessful breeders had an intermediate propensity to leave the nest site and their decision was affected by public information in the cliff. Consistently with the SPS hypothesis, their failure provides them with personal information encouraging dispersal and they assess how much it is attributable to habitat quality via public information (Danchin et al. 1998, Doligez et al. 1999, Bled et al. 2011). They had territorial dominance and parental duties until failure, which limits their motivation to prospect for a new nest site (and thus ultimately leave their previous nest site). This is in agreement with a previous study which demonstrated that failure timing negatively correlated with the probability of leaving the nest site; late failed kittiwakes behaving like successful ones (Naves et al. 2006).

Nonbreeders were very likely to leave their nest site. They may be forced to occupy these sites due to the preemption of high-quality sites (Bruinzeel and van de Pol 2004, Bruinzeel 2007, Sergio et al. 2009). Their site (assigned on the basis of attendance) may be their roost site in the cliff where they invest the most to acquire a nest site, perhaps queuing for it (Kokko and Sutherland 1998, van de Pol et al. 2007). Alternatively, nonbreeders might have not settled on these sites by default, but nonbreeding might be seen as extreme case of failure (Danchin and Cam 2002) perceived as such by individuals on these sites. The absence of differences between nonbreeders and unsuccessful breeders in dispersal decision at the cliff, social-group, and colony scale indicates that both follow a similar time allocation between an initial location (i.e. target cliff for nonbreeders, nest site for unsuccessful breeders) and potential higher-quality habitat(s) found farther.

Sex influenced only the decision of leaving the nest site, which was female-biased. This sex difference is typical in many birds: males incur more dispersal costs because they are more territorial and benefit from retaining their nest site, whereas females benefit from dispersal through mating (Greenwood, Pärt 1995). Once the decision to leave the territory taken, the absence of sex-bias in dispersal decision whatever the spatial scale suggests that male costs of territory acquisition and female costs of mate acceptance are balanced.

First-time breeders were more likely to leave their nest site than experienced breeders. The probability of leaving the nest site in our population is known to decrease with prior residence and previous successes on this site (Naves et al. 2006). Experienced breeders are likely to have accumulated familiarity with their nest site over several years, decreasing dispersal motivation (Lewis et al. 2006, Limmer and Becker 2010). Conversely, first-time breeders may have been subordinated to lower-quality sites they wish to leave (Aubry et al. 2009, Péron et al. 2010). However, one reproductive season might be sufficient to enhance competitiveness for nest-site defense and acquisition, as suggested by the absence of differences between first-time breeders and experienced breeders in dispersal probability at larger scales.

In short, an individual's time budget depends on its breeding effort, with a continuum from no time allocated to offspring production in nonbreeders, through partial allocation in failed breeders, to maximal allocation in successful breeders. The time that is not allocated to offspring production can be allocated to prospection for a new territory and mate. This explains why notable state-dependent differences were found in this study concerning small-scale dispersal decisions. Then, at larger scales, the effect of the individual state disappears and public information prevails against the distance-dependent ability to acquire a new breeding position.

2.5.3 Heterogeneity in dispersal behavior and missing predictors

We found evidence of static individual differences in the probability of leaving the cliff and social group, suggesting consistent differences in the ability to cope with dispersal costs. Such differences may relate to behavioral syndromes (i.e. 'personalities'; Sih et al. 2004). It is often evidenced that more aggressive individuals are also bolder, more active, exploratory, and dispersal-prone in a variety of ecological contexts (Cote et al. 2010). In kittiwakes, this would induce differences in capacities of social insertion and territorial dominance, and thus differences in how far individuals can afford to disperse for a better-quality habitat. Such differences might drive habitat selection tactics by which individuals achieve their reproductive careers (e.g. evicting from, or queuing for good-quality territories, or even occupying lower-quality ones; Kokko and Sutherland 1998, Cam et al. 2002, 2004, Heg et al. 2000, van de Pol et al. 2007). This issue could be addressed by relating individual differences in the probability of leaving the cliff and social group with the components of such lifetime tactics (e.g. age at first reproduction, individual propensity to perform eviction, undergo eviction, attempt breeding, and succeed in breeding attempts).

The model also indicated spatial and annual heterogeneity in dispersal probability at the different spatial scales considered. Both are relatively difficult to interpret because we had no *a priori* ecological hypothesis about variations in dispersal behavior among individuals in the same year or spatial unit, independently of individual state and patch success. Spatiotemporal heterogeneity was modeled as deviations around average dispersal levels over the study period, spatial units, and subsets of individuals: all these components have arbitrary limits constrained by the population history. For example, this system has been characterized by nest-sites, cliffs, social-groups and colonies varying in number, size, shape or spatial repartition over time (Appendix B.1), which certainly yields spatiotemporal heterogeneity in observations of dispersal. This heterogeneity may further stem from variations regarding missing predictors (e.g. due the activity and distribution of predators, and see below).

Overall our results are supported by a good model fit; our model indicates clear effects and accounts for much of the variability in the observations. Nonetheless, lower model performances at small scales, especially to predict actual dispersal of successful breeders in poor quality cliffs, indicated that we failed to include some predictor(s) of individual decisions at these spatial scales in our model. For instance, individuals may refer to finer-scale public information (e.g. success in the close neighborhood) for dispersal decisions (Bled et al. 2011). Partner death, territory eviction and nest-site destruction may also trigger dispersal. Pair features (e.g. arrival date and synchrony, or mate familiarity) are related to divorce rate and may thus explain dispersal propensity (van de Pol et al. 2006b, Naves et al. 2006). Moreover, individuals may use more detailed personal and public information than those we took into account, e.g. timing and causes of failure (Danchin et al. 1998, Naves et al. 2006), prior occupation and memory of past successes (Naves et al. 2006), offspring number and condition (Doligez et al. 2002), or conspecific density (Doligez et al. 1999, Bled et al. 2011). Since we are able to identify these missing predictors, it would be interesting to assess their relative weight across spatial scales to clarify their role in the SPS strategy.

2.6 Conclusion

Breeding habitat selection is a crucial process underlying dispersal, variability in life-history trajectories, population dynamics, spatial repartition and gene flow (Clobert et al. 2001). This study is among the very few providing evidence of spatial scale-dependence in breeding habitat selection (Bowler and Benton 2005, Matthysen 2012). We proposed a habitat selection mechanism balancing costs and benefits of dispersal, the sequential proximity search (SPS), which integrates the use of information on breeding habitat quality and positive distance-dependence in dispersal costs. Given the ubiquity of the two latter in animals (Bowler and Benton 2005, Schmidt et al. 2010), we defend the idea that the SPS should be a widespread strategy. The SPS hypothesis may help understand dispersal patterns in other species: tests of this hypothesis in a variety of taxa are necessary to evaluate its degree of generality. Other study systems may also allow extending this framework to arrival decisions, and studying fitness consequences of habitat choices and covariation with other traits.

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3

Population maintenance at a species range edge: why do immigrants and locals breed there?

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In preparation

3.1 Abstract

The numbers of immigrants and nonbreeders are notoriously difficult to estimate because data from these individuals are usually not collected. However, recent models enable to estimate these quantities, to investigate the contribution of all classes of individuals to population growth, and to address hypotheses about the underlying drivers of population dynamics. These models can help understand how and why populations persist at species range edges.

We used an integrated model to study a kittiwake population located at the southern edge of the current species distribution in Europe. We applied this model to a large dataset composed of nest counts, capture-recapture histories, and breeding-pair productivities collected over 28 years. We estimated all demographic rates and numbers necessary to fit the observed breeding population fluctuations. We assessed the relationships betwen (i) population productivity, breeding and nonbreeding numbers on the one hand, and (ii) the decision to breed made by immigrants, prebreeders, and individuals that bred or skipped a breeding opportunity in the previous year on the other hand.

We demonstrated that the population was sustained by large amounts of immigrants. Apparent survival and breeding propensities of former breeders and skippers also contributed to breeding population growth, but the contribution of local recruitment was negligible. Immigration was negatively associated with the number of nonbreeders. Local recruitment rate and breeding propensity of former breeders were positively influenced by population productivity. The breeding propensities of former breeders and skippers were negatively influenced by the number of breeders.

The substantial immigration is very likely to result from desertion of colonies elsewhere at the range edge due to predation pressure, a process that also occured within the study population. In the same vein, the low apparent survival might reflect emigration triggered by low reproductive prospects within the population. Nonetheless, the decision to breed in this population is probably governed by attraction to and competition for good-quality patches: high-quality habitats have coexisted with low-quality ones and have continued to motivate decisions made by immigrants and locals.

Keywords: dispersal, recruitment, intermittent breeding, social information, density-dependence, species range, seabird, Bayesian inference, integrated modeling.

3.2 Introduction

Fluctuations in breeding population sizes result from fluctuations in the numbers of births, deaths, emigrants and immigrants (Pulliam 1988, Sibly and Hone 2002), but also from the decision to attempt breeding, either in first time breeders or experienced breeders (Jenouvrier et al. 2003). Such fluctuations are generally attributable to environmental and demographic stochasticity, as well as to density-dependent processes (e.g. Grøtan et al. 2009, Crespin et al. 2006). The contribution of survival and reproduction to population dynamics have been relatively well studied (e.g. Gaillard et al. 2000, Coulson et al. 2001, Ozgul et al. 2010). However, the role of immigration, emigration and breeding decisions have often been left aside in empirical studies of local population dynamics (Abadi et al. 2010a, Lee et al. 2016). This is largely owed to methodological difficulties in estimating these demographic parameters. Nevertheless, immigration, emigration and breeding decisions can have a substantial influence on local dynamics (Jenouvrier et al. 2003, Panteriani et al. 2011, Fernández-Chacón et al. 2013, Szostek et al. 2014, Sanz-Aguilar et al. 2016).

Robust methods have flourished during the past twenty-five years for the purpose of analyzing longitudinal data from marked individuals in order to estimate fecundity, survival, dispersal, as well as recruitment and breeding propensities (Thomson et al. 2009). Yet, nonbreeders are commonly ignored because they are often floaters and not readily detectable (Sanz-Aguilar et al. 2011), or not present in breeding locations. Immigration is also rarely assessed because it is usually impossible to mark all individuals in all breeding locations to differentiate natives from immigrants (Abadi et al. 2010a). However, the estimation of the number of immigrants and nonbreeders was recently eased by integrated population models allowing the joint analyze of individual capture-recapture histories, offspring productivity data and breeding population counts (Schaub and Abadi 2011).

We used this approach to study the population dynamics in a cliff-nesting colonial gull, the black-legged kittiwake (*Rissa tridactyla*), and to address hypotheses about factors associated with breeding decisions of immigrants and individuals born or already established in the study population. We focused on the Cap Sizun population (Brittany, France) located at the southern edge of the current species range in Europe (Monnat and Cadiou 2004). The range core is at the Arctic Circle where colonies often exceed 100,000 pairs (del Hoyo et al. 1996). Compared to populations closer to the core, the number of breeding pairs in the Cap Sizun (about a thousand) has always remained small (Monnat and Cadiou 2004, and e.g. Frederiksen et al. 2005b, Nyeland 2004, Bakken et al. 2006, Labansen et al. 2008) and apparent adult survival is very low, while offspring productivity falls just below the average (Frederiksen et al. 2005a). These values suggested that this population was not self-sustainable and that apparent population stability was likely due to immigration (Frederiksen et al. 2005a).

Species ranges can be seen as spatial expressions of realized niches (Guo et al. 2005, Sexton et al. 2009). In this framework, edge populations are expected to experience greater ecological stress than core populations, which explains why they are generally smaller, more variable in size over time and less viable, although many exceptions exist (Sexton et al. 2009, Gaston 2009). High emigration from populations located at range edges might occur as a response to strong variability in habitat suitability (Holt 2003). Besides, high immigration from the core might sustain edges in a source-sink fashion, especially in highly mobile species (Pulliam 1988, Guo et al. 2005). Assessing demographic drivers of edge population dynamics and identifying motivations underlying the decision to breed at range edges is of pivotal interest for the understanding of the evolution and maintenance of species range limits (Gaston 2009, Hardie and Hutchings 2010, Kubisch et al. 2014).

To choose a breeding place, individuals may use proximate information on habitat attributes that correlate with fitness (e.g. climate, food, predation; Chalfoun and Martin 2007). Further, social information in a breeding season may provide integrative clues on habitat quality in the following season when the environment is temporally autocorrelated (Doligez et al. 2003). It has been suggested that conspecific reproductive success is a particularly appropriate cue for individuals to assess the potential fitness associated with a location because conspecific success provides information on the fitness realized in a local ecological and social setting (Danchin and Wagner 1997, Doligez et al. 2003). Individuals may also rely on conspecific abundance, and be either attracted or repulsed by high abundance (e.g. Fletcher 2007). Indeed, this information positively correlates with fitness when Allee effects occur (e.g. mate availability increases with abundance; Teichroeb et al. 2011) or simply when more individuals are in good-quality habitats (Stamps 1988), assuming that a sufficient number have relied on proper cues (Doligez et al. 2003). Conversely, conspecific abundance negatively correlates with habitat quality when competition is strong (e.g. Kim et al. 2009). In the Cap Sizun, previous studies have shown that kittiwakes choose breeding sites according to conspecific success at multiple spatial scales (Danchin et al. 1998, Naves et al. 2006, Aubry et al. 2009, Bled et al. 2011, Acker et al. *in prep.*). Here we extended the framework of previous studies by drawing inferences about immigration and nonbreeding using an analytical approach that uses data from marked and unmarked individuals in order to assess the relative support for (i) the hypothesis that the decision to breed is associated with conspecific success, (ii) and the hypothesis that this decision is associated with conspecific abundance.

Most previous studies of habitat selection focused on the decision to leave a habitat, but only a few explicitly addressed the decision to settle in a new habitat (e.g. Brown et al. 2000, Grosbois and Tavecchia 2003, Doligez et al. 2004). Moreover, these studies have usually been conducted at the scale of patches of a subdivided population, which generally confines to the area where individuals can prospect for breeding sites at low cost (Doligez et al. 2004). Consequently, little is known about how immigrants decide to join another population they are unfamiliar with. Here we addressed the above hypotheses in immigrants. Immigrants might use social information if they can afford to visit distant populations, which may be true in mobile species for individuals without parental duties (Doligez et al. 2004, Ponchon et al. 2013). To our knowledge, only two studies have addressed the two questions above in immigrants, and both have found that immigration positively correlated with conspecific abundance but not with reproductive success (Fernández-Chacón et al. 2013, Szostek et al. 2014). Notably, the authors of these two studies suggested that conspecific abundance is preferred because this information may be rapidly assessed, and because current reproductive success might not be a good predictor of future habitat quality in their study systems (Fernández-Chacón et al. 2013, Szostek et al. 2014).

Individual decisions regarding *where* to breed are intrinsically related to decisions regarding *when* to breed (Ens et al. 1995). The evolution of mechanisms underlying those decisions is governed by the same requirements: obtaining a mate and a breeding site of as high quality as possible. The mechanisms underlying habitat selection and site acquisition may be involved in the decision to breed for the first time (i.e. recruitment; Oro and Pradel 2000, Frederiksen and Bregnballe 2001, Crespin et al. 2006, Cubaynes et al. 2011) or for experienced breeders (i.e. breeding propensity; Kokko et al. 2004, Piper et al. 2006, Bruinzeel 2007, Moreno 2016). Here we assessed the relative contribution of recruitment and breeding propensity to the dynamics of a wild population using approaches accounting for imperfect detection of individuals *in natura*, which has rarely been done (Jenouvrier et al. 2003, Lee et al. 2016). We further addressed the factors motivating these breeding decisions and those motivating immigration within a common framework. We expected social information on habitat quality to be associated with the decisions to breed in our study population, because habitat selection processes underlie the acquisition of a breeding position.

Our first aim was to estimate immigration, recruitment and breeding propensity rates as well as numbers of individuals concerned. Second, we assessed the importance of these demographic processes in the breeding population dynamics, to gain insight into how the study population is maintained. Last, we tested the above versions (i and ii) of the hypothesis of social information use in breeding decisions made by immigrants, and by locals of different status (i.e. former prebreeders, skippers or breeders). For this, we considered social information on breeding habitat quality (in the year preceding the breeding decision) provided by offspring productivity, number of breeders, and number of nonbreeders present at the breeding habitat. These analyses were based on an integrated population model applied to 28 years of monitoring over 6 close colonies, about 1000 active nests in each year, and more than 12000 capture-resighting histories.

The distinctive feature of integrated population models is that they allow estimating demographic rates for which no explicit data are collected such as the number of unmarked immigrants, skippers and pre-breeders. For this reason, estimates of demographic rates may differ from previous work. Nevertheless, we expected to identify demographic features that are already known or highly suspected in our study population, and typically predicted at species range edges: substantial immigration sustaining the population, low apparent adult survival, and large fluctuations in population sizes and productivity (see Frederiksen et al. 2005, and Gaston 2009). Further, we expected a negative relationship between the number of breeders or nonbreeders and breeding decisions, because strong competition for high-quality nest sites occurs in our study population (see Cadiou et al. 1994, and e.g. Newton and Rothery 2001). Moreover, we expected a positive association between productivity and the decision to breed, due to a positive link between availability of productive patches and population productivity, and attraction to productive patches (see Danchin et al. 1998, and e.g. Frederiksen and Bregnballe 2001). We expected the same associations with immigration, because kittiwakes can prospect hundreds of kilometers away from their current population (McCoy et al. 2005). Thus, immigrants should rely on similar habitat selection mechanisms as observed in locals.

3.3 Materials and Methods

3.3.1 Study population and data collection

The study population is located in the Cap Sizun (Brittany, France, 48°03'N, 4°39'W). The present paper focuses on the 1985-2012 period, during which the population simultaneously hosted 4 to 5 colonies separated from one another by about 0.5–12 kilometers (Appendix C.1). Each year since 1979, hundreds of chicks have been color-banded. Further, the content of every nest site has been recorded throughout each breeding season (Cam et al. 1998, Bled et al. 2011), regardless of whether owners were marked or not. Colonies were visited at least once a week from first arrivals to first fledging (January-June), and then once a day until bird departures (July-August).

Resighting probability is virtually equal to one once birds have recruited to the breeding population (0.998 in Cam et al. 1998). We were thus able to identify the first breeding event of every banded bird in the Cap Sizun colonies. Individuals were considered as breeders when they completed nest building in the current year (i.e. a platform of mud and grass with a deep cup; Cullen 1957, Maunder and Threlfall 1972, Cam et al. 1998). Individuals were considered as skippers when they had bred in the past but did not complete nest building in the current year. The reproductive success in every nest of the population was assessed using the number of chicks fledged in the nest, regardless of whether owners were marked or not. Breeding population count was derived as twice the number of complete nests in the current year. This approach slightly overestimates the actual number of active nests because pairs of unmarked individuals can build two nests successively; for marked individuals, successive nests can be assigned to a unique pair.

Information from this monitoring was used to generate three datasets: count data, capture-recapture data and productivity data. Count data consisted of the annual breeding population sizes, ranging from 1316 to 2402 breeders with important fluctuations (Fig. 3.2a). Capture-recapture data consisted of the assemblage of multistate capture-resighting histories indicating the age and annual breeding status of each banded bird when resighted. This capture-recapture dataset was composed of 12091 individuals among whom some were marked as chicks in 1979–1984. In the present study (over 1985–2012), there were 11449 individuals entering the dataset as nestling, 474 as prebreeder, 89 as first-time breeder, 70 as experienced breeder, and 9 as skipper. Productivity data consisted of annual numbers of fledglings produced and the corresponding numbers of nests, belonging to a pair of either (i) first-time breeders – both banded (1962 breeding attempts), (ii) experienced individuals – both banded (8785 breeding attempts), or (iii) at least one unbanded individual or banded individuals with different levels of breeding experience (25366 breeding attempts).

3.3.2 Integrated population model

We developed an integrated population model (Besbeas et al. 2002, Schaub and Abadi 2011) for the joint analysis of the three datasets. This model allowed the estimation of parameters for which no explicit data were collected such as the number of immigrants, unmarked skippers and prebreeders that cannot be directly counted in the field.

The core of the integrated model is a projection matrix model (Caswell 2001). The life cycle (Fig. 3.1) and the corresponding matrix (Appendix C.2) were constructed according to prior knowledge of kittiwake life history (Cam et al. 1998, 2002, 2005, Link et al. 2002) and considering a pre-breeding census. We defined nine life-history states:

yearlings, pre-breeders of age 2, ..., prebreeders of age 6, first-time breeders, experienced breeders and skippers (Fig. 3.1). The number of individuals in each state in year *t* is a function of the number of individuals in each state in year *t-1* and demographic rates (Fig. 3.1, Appendix C.2). The number of first-time breeders in year *t* also stems from a pulse of immigrants in year *t* (i.e. non-native breeders that have never bred in the population before year *t* are added to local recruits in year *t*; Fig. 3.1).

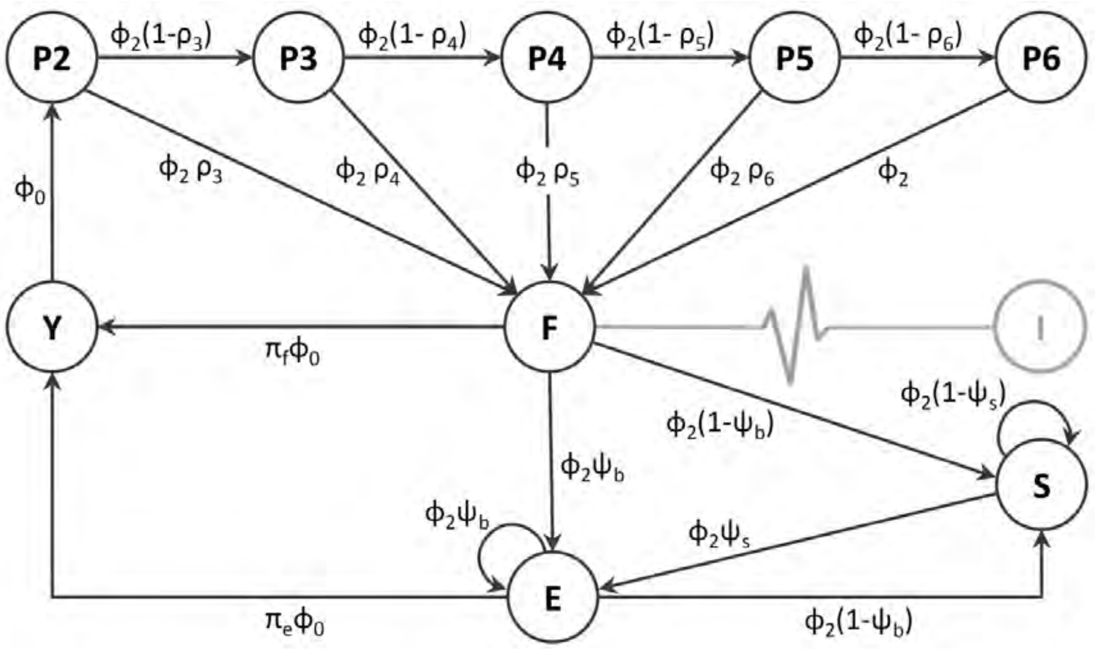

Figure 3.1. Kittiwake life cycle graph underlying the integrated population model. Black circles indicate elementary population classes: yearlings (Y), prebreeders of age *i* (P*i*), first-time breeders (F), experienced breeders (E), and skippers (S). Black arrows indicate transitions between classes along with transition rates, which are function of the demographic parameters: survival at age 0 and 1 (ϕ_0) and from age 2 (ϕ_2), recruitment probability at age *i* (ρ_i, which is 0 at age 1 and 2, and 1 at age 7), breeding propensity of former breeders (ψ_b) and former skippers (ψ_s), productivity rate of first-time breeders (π_f) and experienced breeders (π_e). Obviously, individuals that do not survive go in the dead state: they are not counted and thus not represented here. The grey part symbolizes the annual pulse of immigrants (I) into first-time breeders.

We considered two age classes for survival probability (from age 0 to age 2, and older than 2 years, cf. Link et al. 2002), five age classes for recruitment probability (i.e. the probability that a prebreeder decides to breed in year *t*: age 3, ..., age 6; Cam et al. 2005, Aubry et al. 2009), status-dependent breeding propensity (i.e. the probability of breeding in year *t* for individuals that bred in year *t-1*, or individuals that skipped a breeding opportunity in year *t-1*; Cam et al. 1998), and experience-dependent *per capita* productivity (first-time breeders, and experienced ones; Link et al. 2002, Naves et al. 2006). All these demographic rates were modeled as time-dependent. To account for demographic stochasticity, the numbers of individuals in each state were drawn from Poisson or Binomial distributions parameterized by expectations from the projection equation.

Because the very low resighting rate of yearlings prevents from identifying survival between age 0 and age 1, survival rate was assumed to be the same at age 0 and 1. In the data, very few individuals bred for the first time at age 2 (ca. 0.06‰) or between age 8 and 14 (ca. 3‰). For the sake of simplicity, we ignored these cases and assumed that no recruitment occurs before age 3 and after age 7. Further, we assumed equal productivity for immigrants and local first-time breeders: it has previously been shown that this assumption has a negligible impact on parameter estimates of the integrated population model in the common tern (*Sterna hirundo*), which has a very similar life cycle (Szostek et al. 2014).

We also assumed that immigrants have the same local survival rate as natives, which is necessary because immigrants are not individually monitored. If this assumption does not hold, the estimated number of immigrants is negatively (or positively) biased when immigrants have a lower (or higher) survival than natives. We have no *a priori* hypothesis concerning the ranking of survival probabilities in natives and immigrants (see Appendix C.2). Therefore we must assume equal survival between immigrants and natives. One should thus regard our immigration estimates as *effective immigration sizes* representing the amount individuals identical to natives necessary to yield the observed dynamics.

3.3.3 Likelihood of the model

The joint likelihood of the integrated population model is the product of the likelihoods of three models for the three datasets, provided that we can assume independence among these datasets. As often in practice, the assumption of independence was not completely fulfilled, but simulations for the same type of models have shown that its violation has a very limited effect on parameter estimates (Abadi et al. 2010b, Schaub and Fletcher 2015).

First, the likelihood from count data was formulated as that of a state-space model (de Valpine and Hastings 2002). The state process was defined by the matrix population model in which fluctuations in breeding population size (i.e. first-time breeders plus experienced breeders) are described (see Appendix C.2). We assumed a log-normal distribution for the breeding population counts, with a constant error over time.

Second, the likelihood from individual capture-resighting histories was formulated as that of a multistate capture-recapture model. More specifically, we used an individual-based state-space formulation (Gimenez et al. 2007, Appendix C.2). The state process is readily deductible from the life cycle (Fig. 3.1, Appendix C.2). The annual state of an individual depends on its previous state and is drawn from a categorical distribution parameterized by the vector of transition rates towards all possible states (including a dead state). Observations are drawn from a Bernoulli distribution following the resighting rate. We assumed different time-varying resighting rates for yearlings and pre-breeders, equal constant resighting rate for breeders and skippers, and no error in state assignment at resighting (Cam et al. 2002).

Third, the likelihood from productivity data was formulated as that of three Poisson regressions of the total number of fledglings produced as a function of the number of nests, and the *per capita* productivity involved (i.e. twice the *per nest* productivity). One regression was for pairs of first-time (inexperienced) breeders, one for pairs of - experienced breeders, and another for pairs of individuals of unknown or different levels of experience. For the latter, because we used *per capita* productivity rates and ignored pair characteristics, we made the assumption that the productivity rate was an average of productivity of inexperienced and experienced breeders weighted by their respective proportion among breeders in the model.

3.3.4 Parameter estimation

Inference was conducted by analyzing the joint likelihood of the integrated population model in the Bayesian framework (Kéry and Schaub 2012). We specified vague prior distributions with reasonable bounds for all parameters (Appendix C.2). We used the uniform distribution over [-5,1000] as prior for the number of immigrants. The inclusion of negative values enables to test whether there is immigration at all (Schaub and Fletcher 2015). We performed Markov Chain Monte Carlo (MCMC) simulation with software JAGS 3.4.0 (Plummer 2003; see model code in Appendix C.2) run from R (R Core Team 2016) with the *rjags* package (Plummer 2015). We ran 20 chains, discarded the first 15000 iterations and used the subsequent 35000 iterations for posterior exploration (7×10^5 samples). Chains were not thinned to keep all information they contained (Link and Eaton 2012). Convergence was assessed using the Brooks-Gelman-Rubin diagnostic $\widehat{R}$ (Brooks and Gelman 1998) and was satisfactory (all $\widehat{R}$<1.02). Monte Carlo standard errors were always small enough to report posterior means of demographic rates with three decimal place precision (Appendix C.3, Lunn et al. 2012). Each 95% posterior credible interval was calculated as the highest posterior density interval (i.e. the shortest interval containing 95% of the posterior samples).

3.3.5 Model assessment

We used posterior predictive checks (Gelman et al. 1996) to evaluate the fit of the state-space model for count data and the Poisson regression models for productivity data, over the complete time series and separately at each time step. We computed posterior-predictive p-values that quantify the proportion of samples in which the distance of observed data to the model is greater than the distance of predicted data (i.e. replicates from each posterior sample) to the model (i.e. each posterior sample of the parameters; Appendix C.4). We also inspected the distribution of predicted values (i.e. posterior predictive distributions) in regard with observed values (Appendix C.4).

Classical posterior predictive checks are harder to handle for sequences of categorical data (such as capture-recapture histories) analyzed with a state-space model (Kéry and Schaub 2012). Instead, we computed the proportion of correct predictions for each observation event in all the capture-recapture histories (i.e. the proportion of replicates from posterior samples that matched the observation; Greenhill et al. 2011; see Appendix C.4).

3.3.6 Contributions of demographic processes to population dynamics

We assessed how fluctuations in key demographic parameters contributed to fluctuations in the annual breeding population growth rate by inspecting partial correlations between population growth rate and either survival rate, breeding rates of former breeders (i.e. individuals that bred in the previous year) and former skippers (i.e.

individuals that skipped breeding in the previous year), integrative local recruitment rate (see below), or immigration rate (cf. Robinson et al. 2004, Schaub et al. 2013).

- The annual breeding population growth rate was calculated as the number of breeders in year *t* divided by the number of breeders in year *t-1* (see Appendix C.5).
- The integrative recruitment rate was calculated as the proportion of first-time breeders among the individuals of all age classes (3, ..., 6) alive and available for recruitment in the current year *t* (i.e. that have never bred before year *t*; Appendix C.5). This is thus the age-independent local recruitment rate.
- The immigration rate was calculated as the proportion of immigrants among breeders in the current year *t* (Appendix C.5).

Moreover, we calculated the average breeding population growth rate over the study period as the back-transformed slope from a simple regression of the log breeding population size against year (Schaub et al. 2013, Appendix C.5). We then calculated the hypothetical average growth rate over the study period in absence of immigration. For this purpose, we derived additional population projections in each posterior sample without the pulse of immigrants (Appendix C.5). We also calculated the proportion of former breeders, former skippers, local first-time breeders, and immigrants among breeders in the current year.

Posterior distributions of derived parameters (including correlations) were calculated from all posterior samples (Appendix C.5). Because there was insufficient information in the first year of the study to properly estimate the number of individuals in classes that could not be counted (unmarked individuals), we considered all parameter time series from the second year onwards to calculate partial correlations.

3.3.7 Correlates of immigration, local recruitment and breeding propensities

We used partial correlation analyses to assess whether there was a relationship between the decisions to breed in the population in a given year *t* and social information on breeding habitat quality in the previous year *t-1*. We considered the decisions to breed made by immigrants, pre-breeders, former breeders, and former skippers. We thus related immigration rate, integrative recruitment rate, breeding propensity of former breeders and of former skippers in a given year *t* with either the average productivity, the number of breeders, or the number of nonbreeders (i.e. prebreeders plus skippers) present at the breeding cliffs (in the previous year *t-1*). We also used autocorrelation analyses to check whether each type of social information was predictable from one year to the next (Appendix C.5). We further used correlations to check whether the number of breeders in year *t-1* was predictive of the number of former breeders among breeders in year *t* (i.e. individuals breeding in two consecutive years). We also checked whether the number of nonbreeders present in year *t-1* was predictive of the number of local recruits, and former skippers among breeders in year *t*.

3.4 Results

A detailed posterior summary of the complete set of parameters from the integrated population model is given in Appendix C.3. Summaries of the derived parameters are given in Appendix C.5. Hereafter, all estimates are reported as the posterior mean with the 95% credible interval (95%CI) in brackets.

3.4.1 Demographic parameters and model assessment

Estimates of breeding population size from the integrated model closely matched the count data (Fig. 3.2a). Overall, posterior checks indicated a very good fit (see Appendix C.4).

Mean *per capita* productivity rate was 0.163 [0.139,0.187] for first-time breeders and 0.358 [0.325,0.393] for experienced breeders, and both productivity rates fluctuated greatly over time (see Appendix C: Fig. C.3.4). Mean local survival rate was 0.649 [0.587,0.710] in the first and second years of life, and 0.805 [0.783,0.827] afterwards. Mean resighting rate was 0.050 [0.035,0.065] for yearlings, and 0.810 [0.776,0.844] for older pre-breeders. Resighting rate of individuals once recruited was 0.998 [0.997,0.999]. Mean recruitment rate at age 3, 4, 5, and 6 was 0.128 [0.082,0.179], 0.405 [0.342,0.471], 0.533 [0.479,0.586], and 0.674 [0.583,0.764], respectively. Mean breeding propensity was 0.895 [0.874,0.915] for former breeders and 0.685 [0.624,0.747] for former skippers. These values were highly consistent with those reported in previous studies that did not rely on integrated population modeling (e.g. Cam et al. 1998, 2005, Link et al. 2002).

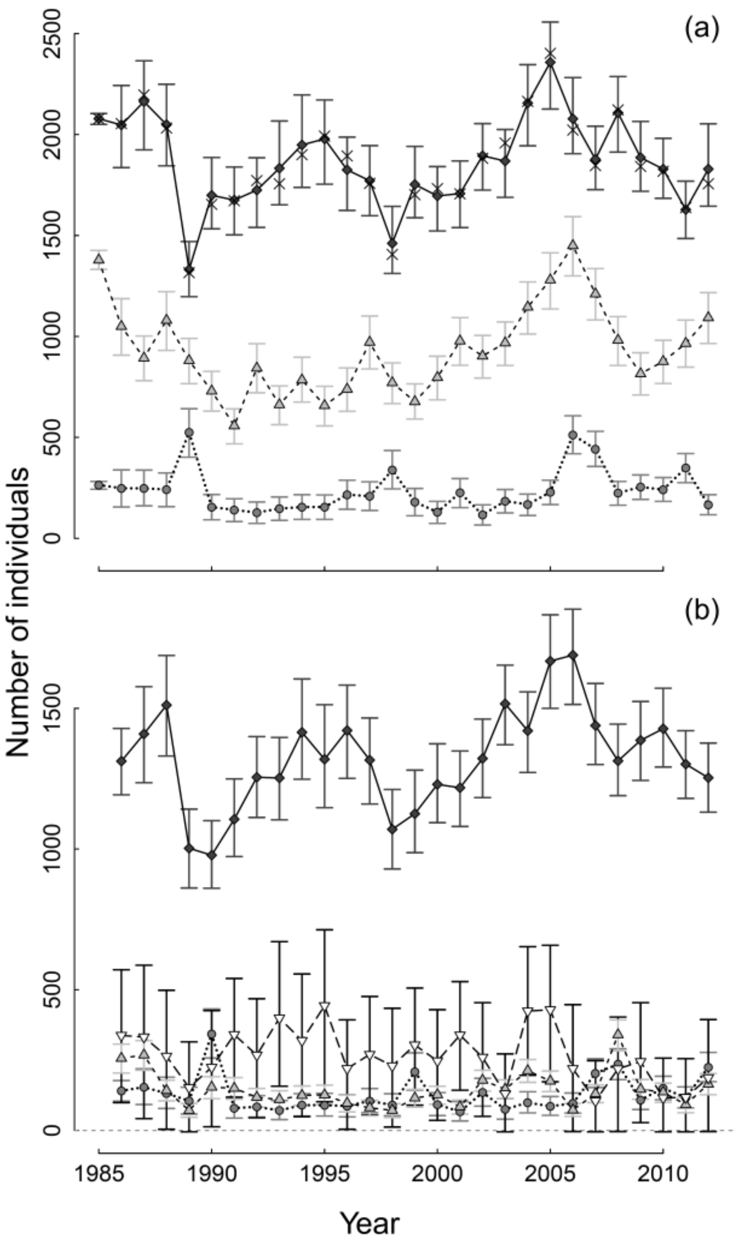

Figure 3.2. Dynamics of the kittiwake population at Cap Sizun over 1985–2012. Panel (a) provides estimates of the numbers of yearlings and prebreeders (triangles, dashed line), skippers (circles, dotted line) and breeders (diamonds, solid line) along with count data ('x' crosses). Panel (b) provides estimates of the numbers individuals from different origins among breeders: immigrants of the year (downward triangles, long-dashed line), local first-time breeders (upward triangles, short-dashed line), former skippers (circles, dotted line), former breeders (diamonds, solid line). Points indicate the posterior mean and vertical segments indicate 95% credible intervals.

3.4.2 Demographic contributions to population dynamics

The average breeding population growth rate was 1.001 [0.999,1.004] (Appendix C.5). This indicated that the breeding population was stationary at the scale of the study period. Without the annual pulse of immigrants, the average breeding population growth rate would have been 0.859 [0.843,0.875] (Appendix C.5). Therefore, the population would have declined from 2078 [2050,2104] in 1985 to 37 [18,56] in 2012, suggesting that a few more years would have resulted in extinction. This clearly shows that the population is not self-sustainable.

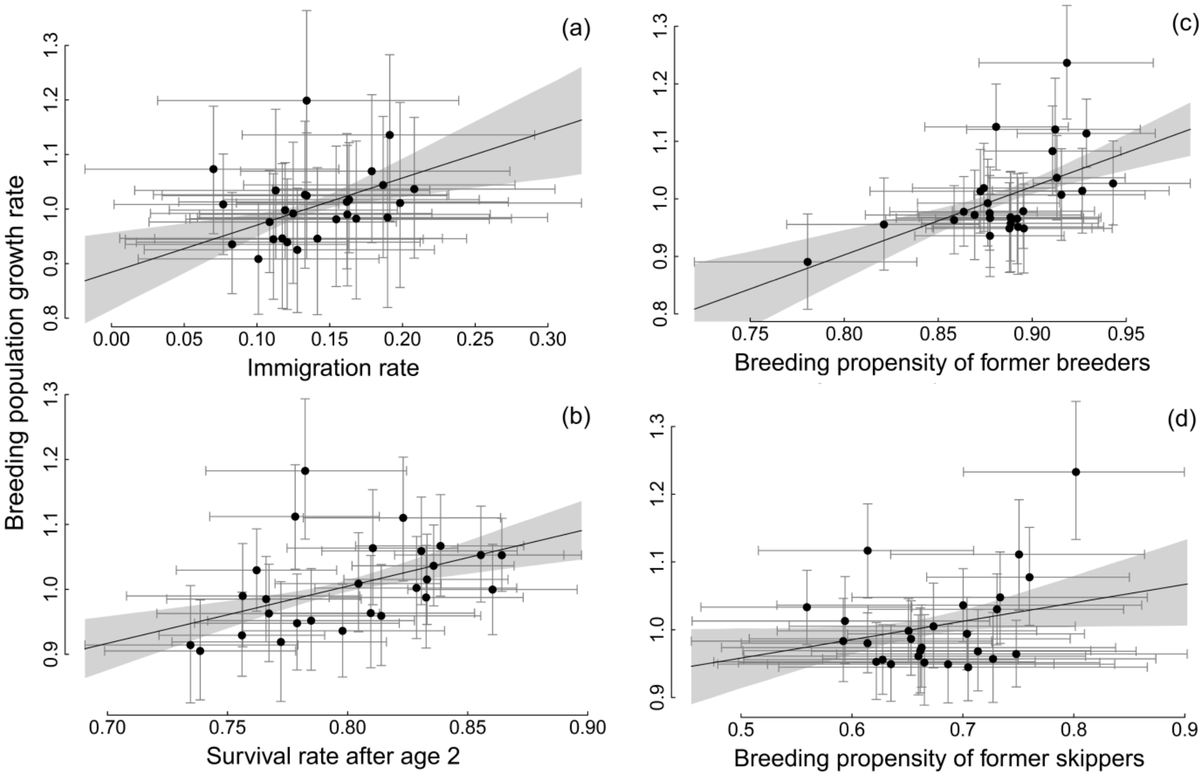

Figure 3.3. Relationships between breeding population growth rate and (a) immigration rate, (b) survival rate from age 2, (c) breeding propensity of former breeders and (d) breeding propensity of former skippers. Given are partial residual plots representing partial correlations with growth rate (while controlling for the set of remaining covariates). Each plot shows residuals from an ordinary least squares (OLS) regression with growth rate as the response, against residuals from an OLS regression with the focal covariate as the response; explanatory variables of the OLS regressions are the set of control variables. Residuals were centered on the variable mean to rescale variation within the original range. Points indicate posterior means and segments indicate 95% credible intervals. The solid line is the posterior mean of the corresponding OLS regression line, along with the 95% credible interval in grey background.

In average over 1985-2012, the breeding population was composed of 14.0% [12.9,15.0] of immigrants, 7.6% [7.2,8.0] of local first-time breeders, 71.4% [70.4,72.3] of former breeders, and 7.0% [6.5,7.5] of former skippers (Fig. 3.2b). Nonetheless, 95%CI of the number of immigrants included negative values in 8 out of the 27 years:

1989, 2003, 2006–2008, and 2010–2012, suggesting that immigration was absent or very weak in these years. Except for the integrative recruitment rate, 95%CIs of partial correlations between breeding population growth rate and key demographic rates excluded zero, which provides evidence of positive contributions to breeding population growth. The partial correlation was 0.593 [0.286,0.873] for immigration rate, 0.082 [-0.197,0.356] for recruitment rate, 0.474 [0.266,0.672] for survival rate after age 2, 0.562 [0.361,0.745] for breeding propensity of former breeders, and 0.322 [0.051,0.587] for breeding propensity of former skippers (Fig. 3.3).

3.4.3 Social information use in immigration and breeding decisions

Table 3.1. Partial correlations between a breeding rate (first variable), and an information component on breeding habitat quality (second variable), while controlling for the set of remaining second variables.

First variable (year *t*)	Second variable (year *t-1*)		
	Productivity rate	Number of breeders	Number of present nonbreeders
Immigration rate	0.072 [-0.205,0.347]	-0.260 [-0.517,0.014]	-0.353 [-0.593,-0.092]
Integrative recruitment rate	0.339 [0.203,0.475]	-0.184 [-0.366,0.008]	-0.041 [-0.179,0.101]
Breeding propensity of former breeders	0.380 [0.212,0.545]	-0.457 [-0.635,-0.265]	0.002 [-0.175,0.180]
Breeding propensity of former skippers	-0.092 [-0.394,0.214]	-0.399 [-0.644,-0.151]	-0.113 [-0.368,0.152]

Estimates are given as the posterior mean with 95% credible interval between brackets. Scatter plots of the relationships are provided in Fig. 3.4 when the 95%CI excludes zero, and in Appendix C.5 when the 95%CI includes zero.

Immigration rate (proportion of immigrants among breeders in the current year* t*)— As indicated by mean estimates and 95%CIs (Table 3.1, Fig. 3.4a), there was evidence of a negative partial correlation between the immigration rate and the number of nonbreeders present (i.e. prebreeders plus skippers) in the previous year. This result was also found when replacing immigration rate by the number of immigrants (Appendix C.5). There was no evidence of association between immigration rate and the other quantities considered (i.e. productivity and number of breeders in the previous year, Table 3.1).

Integrative recruitment rate (age-independent local recruitment rate in year* t*)— For the integrative recruitment rate, there was only evidence of a positive partial correlation with productivity rate in the previous year (Table 3.1, Fig. 3.4b).

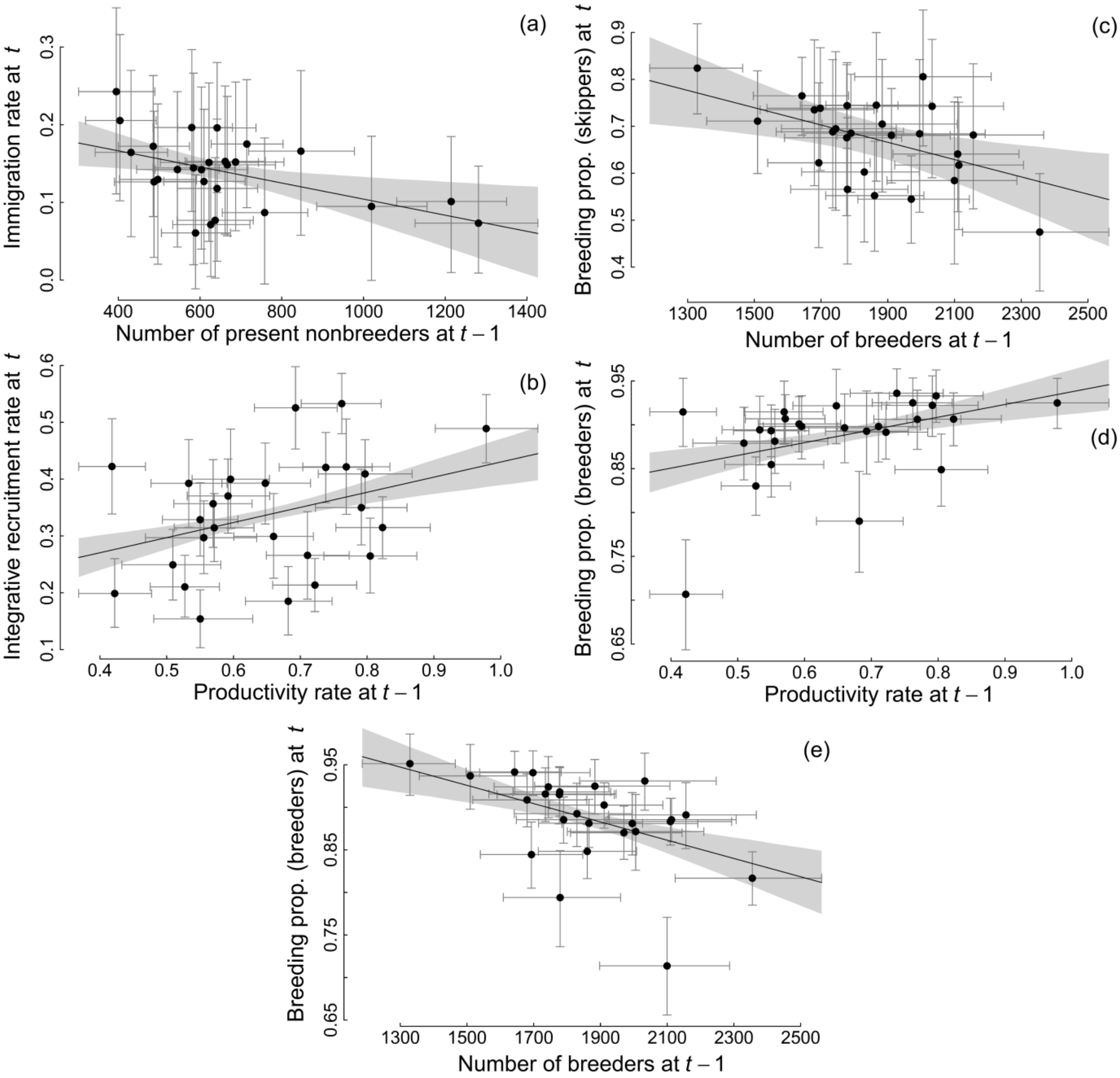

Figure 3.4. Relationships between breeding rates and social information components on breeding habitat quality: (a) immigration rate at time *t* against the number of potential recruits at *t-1*, (b) integrative recruitment rate at time *t* against productivity at *t-1*, (c) breeding propensity of former breeders at time *t* against productivity at *t-1*, (d) breeding propensity of former breeders at time *t* against the number of breeders at *t-1*, (e) breeding propensity of former skippers at tme *t* against the number of breeders at *t-1*. Given are partial residual plots as specified for Fig. 3.3.

Breeding propensity of experienced breeders (breeding probability in year* t *of individuals that bred or skipped breeding in year* t-1*)— For the breeding propensity of former breeders, there was evidence of a positive partial correlation with productivity in the previous year and a negative partial correlation with the number of breeders in the previous year (Table 3.1, Fig. 3.4c,d). For the breeding propensity of former skippers, there was only evidence of a negative partial correlation with the number of breeders in the previous year (Table 3.1, Fig. 3.4e).

Predictability in social information— Autocorrelation analyses suggested that the population productivity, number of breeders, and number of prebreeders plus skippers present, are predictable from one year to the next (autocorrelation coefficients at lag one year were 0.428 [0.339,0.516], 0.396 [0.204,0.552] and 0.559 [0.465,0.647], respectively; but see limitations in Appendix C.5). Correlations showed that the number of former breeders deciding to breed in year t were strongly predictable from the number of breeders in year $t-1$ (for breeders, correlation: 0.747 [0.646,0.841]). The number of former skippers and prebreeders deciding to breed in year t were both predictable from the number of prebreeders present plus skippers also present in year $t-1$ (for skippers: 0.735 [0.646,0.821], and for prebreeders: 0.494 [0.381,0.602]).

3.5 Discussion

This study investigated the dynamics of a kittiwake population at the edge of the current distribution of the species in Europe, and the decision to breed there, with an integrated population model. Breeding numbers showed no trend over the study period but fluctuated strongly, as well as productivity rates. Apparent adult survival was low, and the breeding population was sustained by immigration. Fluctuations in breeding numbers were explained by variations in immigration rate, apparent adult survival and breeding propensities of established individuals, but not by local recruitment. These results provide a rare example of population functioning at a species range edge, and fit usual expectations for this ecological context. Moreover, immigration was negatively associated with the number of nonbreeders in the preceding year. Local recruitment and breeding propensity of former breeders were positively associated with population productivity in the preceding year. Breeding propensities of former breeders and skippers were negatively associated with the number of breeders in the preceding year.

These patterns likely result from individual decisions governed by processes of habitat selection involving attraction to and competition for good-quality breeding habitats.

3.5.1 Variation in apparent adult survival rate

Local adult survival was the demographic rate exhibiting the largest correlation with population growth, which is expected for long-lived iteroparous species (Sæther and Bakke 2000). The local adult survival rate was quite low (over the study period: 0.81) compared to other kittiwake populations (e.g. maximum reported value: 0.93 in two Alaskan populations; Frederiksen et al. 2005a). We cannot assess the contribution of permanent emigration to apparent survival. If we consider that 0.93 is the survival prospect of kittiwakes (under good conditions), then 12% of breeders is the (maximum) adult emigration rate out the Cap Sizun. However, we cannot exclude the hypothesis that unfavorable local factors lead to higher mortality in the Cap Sizun. For example, it has been suggested that kittiwakes can suffer higher mortality due to a decrease in food supplies (e.g. Oro and Furness 2002, potentially due to higher temperatures: Frederiksen et al. 2004), and marine pollution (e.g. Goutte et al. 2015). Moreover, adults are regularly resighted with hooks and pieces of line in the bill, which suggests that bycatch mortality from longline fisheries occurs in the Iroise Sea where they forage (JYM and EC *personal observations*).

The breeding success of kittiwakes in the Cap Sizun is known to be particularly vulnerable to predation (Danchin and Monnat 1992, Cam et al. 2004, 2013). This may be explained by the small colony sizes that prevent dilution effects (Foster and Treherne 1981, Wrona and Dixon 1991). Massive predation on eggs by a few ravens (*Corvus Corax*) or crows (*Corvus corone*) has led to complete desertion of several colonies since 1979; one of these episodes is included in the present study, as well as a quasi-extinction of one colony followed by re-colonization several years later (Danchin and Monnat 1992, Monnat and Cadiou 2004, Appendix C.1). Infestation by ticks (*Ixodes uria, Ornithodoros maritimus*) might also have a non-negligible role in spatiotemporal variability of reproductive prospects (Danchin and Monnat 1992, Danchin et al. 1998). Further, massive dispersal events have been observed from lower-productivity patches in the population to higher-productivity ones (see Danchin and Monnat 1992, Danchin et al. 1998, Cam et al. 2004, Acker et al. *in prep.*). Permanent emigration associated with poor breeding prospects is thus likely to partly explain variations in apparent survival and breeding population size.

3.5.2 Variation in the amount of immigration

Theory predicts high immigration rates at the range edges of highly mobile species, under the assumption of identical survival across the range, and density-dependence yielding dispersal from the crowded core (Guo et al. 2005). Here immigration rate was a leading factor of breeding population fluctuations; which is consistent with the above prediction. Based on averages among first-time breeders of ca. 14% of immigrants against ca. 7.5% of local recruits, ca. 65% of established individuals in the population would be born elsewhere over the study period. Such proportions are similar to those assessed in other seabird populations not identified as located at range edges (e.g. in black guillemots, *Cephus grylle*: Frederiksen and Petersen 2000; in common terns, *Sterna hirundo*: Szostek et al. 2014). This suggests that substantial flows between seabird colonies are commonplace. However, here the population would have declined close to extinction without immigration, and thus appears as a sink (Pulliam 1988); though it might be a source for the species if emigration outweighs immigration (Runge et al. 2006). In fact, both features may be expected for edge populations in particular, because natural selection should favor high dispersal propensity at range edges due to the high spatiotemporal variability in habitat quality (Holt 2003).

In addition to density-dependent dispersal in the crowded core which is relatively far, immigration to the Cap Sizun might be driven by habitat desertion when reproductive prospects become too low in nearby colonies. Genetic data from ticks across the range indicate a stepping-stone pattern of dispersal, which suggests that kittiwakes rarely prospect for new colonies beyond ca. 200 kilometers (McCoy et al. 2005). Colonies that provided immigrants to the Cap Sizun are thus likely to be located within this limit, such as island colonies in the Iroise Sea (adjacent to the Cap Sizun), and in the Bay of Biscay (farther south; Monnat and Cadiou 2004). Some of these colonies have hosted up to ca. 150 pairs and all went extinct before 2012 (the end of our study period), which is thought to have resulted from strong predation followed by massive emigration (e.g. in Groix: 60 pairs, in Crozon: 135 pairs and in Ouessant: 158 pairs in 1987-1988, in Belle-Île: 146 pairs in 2000; Monnat and Cadiou 2004). Colonies that provided individuals to the Cap Sizun could also be located within the ca. 200 km limit in Cornwall, England, but we are lacking information about this area. The maintenance of the kittiwake range edge with small, sparse colonies probably follows a dynamic loop: colonization of suitable habitats, then predation without dilution effect (because colonies are small), and finally desertion when predation is excessive, and so on.

3.5.3 Variation in breeding probabilities

Our results provided evidence of a ranking of sensitivities of the growth rate to the breeding propensity of different categories of individuals: former breeders, then former skippers, and last former prebreeders. Recently, Lee et al. (2016) provided theoretical conclusions on sensitivity of the growth rate to the breeding propensity based on matrix population models depicting life cycles resembling ours (i.e. long-lived species with a lower breeding probability in prebreeders than in former skippers, and a lower breeding probability in former skippers than in former breeders). Interestingly, our results are consistent with their expectations in the following situation: when survival probability is the lowest in prebreeders, intermediate in skippers, and the highest in breeders, and when nonbreeder frequency negatively affects breeders' fecundity. The ranking of survival probabilities among states has been documented in this population (Cam et al. 1998, Cam et al. 2005, this study). Moreover, the hypothesis of a negative effect of nonbreeders on breeders' fecundity (e.g. via harassment, Bonebrake and Beissinger 2010) is realistic: intrusions by nonbreeders cause a risk of breeding failure to nest owners (Cadiou et al. 1994).

The above lines point toward the importance of competition in the regulation of breeding population sizes. Spatiotemporal heterogeneity and temporal autocorrelation in habitat quality is likely to yield competition for territory acquisition in patches where productivity was high (Danchin and Monnat 1992, Cadiou et al. 1994, Danchin et al. 1998). The attraction to good spots within the population might explain the intriguing fact that a number of immigrants and locals continue to breed there, despite strong but localized impacts of predation on breeding success. Individuals may efficiently escape bad conditions by using social information on habitat quality, but they have to face competition for the good spots.

3.5.4 Population patterns from social processes in breeding decisions

At the end of the reproductive season, kittiwakes planning to disperse prospect for a new breeding site. Their breeding status is determined by the outcome of a severe competition for territory acquisition, and mate acceptance (Cadiou et al. 1994). Within the population, individual choices of breeding habitat (observed in year *t*) rely on social information on habitat quality in year *t-1*. Kittiwakes decide *where* to breed according to offspring productivity (Danchin et al. 1998) but also competitive intensity in the different patches (Aubry et al. 2009, Bled et al. 2011). Here, we addressed patterns resulting from breeding decisions without explicitly considering habitat selection: we investigated the relationship between social information on habitat quality (productivity, numbers of breeders and nonbreeders) and breeding decisions at the population scale. Nevertheless, relationships between breeding decisions and productivity or numbers of individuals in the previous year can hardly be interpreted independently of habitat selection mechanisms (Ens et al. 1995, Frederiksen and Bregnballe 2001): *when* to breed is conditioned by nest-site acquisition or retention.

Good-quality sites are associated with a higher reproductive success; not only in the current year, but also over the years thanks to temporal autocorrelation of environmental factors (e.g. predation or parasitism; Boulinier and Lemel 1996, Danchin et al. 1998). Conversely, poor-quality sites lead to breeding failure, which triggers dispersal to escape poor habitat conditions (Switzer et al. 1993, Danchin et al. 1998). Moreover, dispersal is associated with increased probability of nonbreeding: acquiring a new breeding position implies targeting a nest site, and getting involved in competitive contests that are costly and of uncertain outcome (Cadiou et al. 1994, Danchin and Cam 2002). Nonbreeding is sometimes observed in several consecutive years in the same individual (Cam et al. 2004). Some individuals may be prone to nonbreeding, as the consequence of an active investment in uncertain attempts to acquire a good breeding position. In this framework, an obstinate strategy to acquire a higher-quality nest site may be associated with a higher fitness than a strategy based on acquisition of lower-quality sites and breeding on such sites. Some authors have described a ‘queuing’ strategy by which individuals sacrifice breeding opportunities not only waiting for, but acquiring dominance on a nest site (Zack and Stuchbury 1992, Ens et al. 1995).

Assuming a tight link between habitat selection strategies and decisions regarding breeding activity, breeding decisions should be positively associated with habitat quality in the previous year. Indeed, when population productivity is higher, there may be more patches of good quality and thus more opportunities to get a good breeding position (under the assumption that higher population productivity is achieved via productivity increase in multiple patches and not via a substantial increase in a few patches). In the same vein, years with higher breeding failure rate – lower productivity – should be associated with increased dispersal probability and thus a decrease in breeding propensity in former breeders. Our results concerning recruitment rate, and breeding propensity of former breeders are in line with these expectations. Moreover, the competition for good-quality sites should be higher when there are more individuals prospecting (typically, nonbreeders) or when there are more individuals occupying nest sites (breeders). Our results concerning immigration and the breeding propensity of former breeders and formers skippers are also consistent with these expectations.

However, our expectations recalled above were not always supported by the results for each breeding status (see Table 3.1). This might stem from a small sample size for the correlations: only 26 observations-years. Nonetheless none of the results were opposite to our expectations (Table 3.1). It is also possible that different life-history circumstances yield deviations from the general expectation. For instance, prebreeders tend to breed on intermediate-quality patches rather than high-quality ones: either they avoid competition, or they are unable to have access to higher-quality sites (Aubry et al. 2009). Skippers are sometimes individuals that did not acquired a breeding position, often after failure and dispersal (Danchin and Cam 2002). Perhaps skippers do not efficiently use information provided by conspecific success. Further, immigrants might not have the opportunity to gather social information in the year preceding immigration because they previously attended another, distant population. They might still incur competition with nonbreeders at their arrival. Immigrants might also be attracted by good quality patches within the population, independently of the whole population context. Analyses conducted at the scale of the whole population may not be able to identify the process operating at finer scale.

Additional studies are needed to address these hypotheses. We could notably switch to the individual level while controlling for confounding factors (e.g. individual success, conspecific success in the neighborhood, timing of failure; Naves et al. 2006). This is currently impossible for immigrants, but properly designed electronic tracking might become practicable to investigate the fate of immigrants in detail (Ponchon et al. 2013). It would however be more feasible to refine our model and estimate immigration to the different colonies in the population, together with dispersal between these colonies. This would allow us to address whether immigrants settle in high quality patches within the population based on information from the previous year, or if settlement patterns are inconsistent with the use of such information.

3.6 Conclusion

Integrated population modeling allowed us to show that the Cap Sizun kittiwake population received many immigrants over 1985-2012. Immigrants prevented population extinction despite a presumably high permanent emigration in response to localized deterioration of reproductive prospects. Attraction to good-quality habitats and competition may explain the decision to breed of several classes of individuals in this population, and population maintenance at the species range edge, but our results were not conclusive for all classes of individuals. However, we only looked at the tip of the iceberg: the population scale, whereas distinct colonies occupied by the population have grown and gone extinct during the study period, as it happened in other locations at this species range edge. Individuals might permanently emigrate due to low breeding habitat quality in some patches, and at sea mortality in foraging areas might occur in this population during the breeding season. At the same time, immigrants might be attracted by some good-quality patches in the population that also retain locally born and established individuals. Getting the full picture will now imply to investigate the dynamics of each colony in parallel, inter-colony movements and colony-specific immigration together with colony-specific apparent survival.

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4

Insights on dispersal and recruitment paradigms: sex- and age-dependent variations in a nomadically breeding bird

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4.1 Abstract

Sex- and age-dependence in recruitment and dispersal are often explained by costs arising from competition for holding a breeding territory over the years – a typical feature of species living in stable habitats. For instance, long-lived birds with male territoriality often exhibit large variation in recruitment age and higher dispersal in females and young individuals.

As a corollary, we expected that species with ephemeral habitat suitability, and hence nomadic breeding, would show weak age- and sex-dependence in dispersal and low variation in recruitment age because territory ownership is not maintained over the years. Also, males might recruit earlier due to a higher cost of reproduction in females which would not be (over)compensated for by costs of territoriality in males.

We explored these variations using multievent capture-recapture models applied to mark-resighting data collected over 13 years on 3479 (2393 sexed) slender-billed gulls (*Chroicocephalus genei*) in 45 colony sites along the French Mediterranean coast.

As expected, variability in recruitment age was low with males recruiting earlier than females. Dispersal in and out the study area decreased with age and was slightly male-biased.

Decreased dispersal with age might result from foraging benefits associated with increased familiarity with the area. Male-biased dispersal might be explained by a male-biased sex ratio or higher benefits of philopatry in females (arising from their higher cost of reproduction). Sex- and age-dependent dispersal and recruitment may thus occur in absence of year-to-year breeding territory ownership, which stresses the importance of considering other processes in shaping recruitment and dispersal patterns.

Keywords: life history, unstable habitats, sex differences, age dependence, colonial species, temporary emigration, capture–recapture, multievent models, larid, crèching.

4.2 Introduction

When and where animals breed are ‘two sides of the same coin’ (Ens et al. 1995) that shape short- and long-term fitness prospects (Charlesworth 1994, Lindström 1999, Clobert et al. 2001, Bowler and Benton 2005, Cam and Aubry 2011). Recruitment to a breeding population and movement between a natal and first-breeding location (‘natal dispersal’) or between successive breeding locations (‘breeding dispersal’) are thus important and intimately linked processes in life histories. They also have major consequences on population dynamics and gene flow (Clobert et al. 2001, Caswell 2001, Lebreton et al. 2003, Bowler and Benton 2005).

Early recruitment is favored by natural selection, notably because it maximizes the expected number of reproductive events over the lifespan (Charlesworth 1994). However, delaying recruitment may provide benefits that limit the costs of first reproduction (e.g. Desprez et al. 2014). For example, behavioural maturation (i.e. gains in competitive, foraging and parental care skills) implies to postpone first reproduction and may lower the reproductive effort needed to ensure offspring production or increase the chance of acquiring a good-quality habitat (Charlesworth 1994, Aubry et al. 2009). Prospecting, competing and queuing for good-quality habitats – which are constrained by maturation and breeding density – may also result in recruitment delays (Ens et al. 1995, Boulinier and Danchin 1997).

Heterogeneity in individual tactics may yield substantial variations in recruitment age; this is, for instance, commonly observed in long-lived species (Lebreton et al. 2003, Hadley et al. 2006, Descamps et al. 2006, Becker and Bradley 2007, Bowen et al. 2007, Aubry et al. 2009, Martin and Festa-Bianchet 2012). The optimal recruitment age thus depends on the quality of the individual (i.e. its competitive abilities), the quality of the breeding habitat (which may depend on the density of conspecifics or heterospecific competitors, food availability, etc.) and the interaction between the two (Komers et al. 1997, Frederiksen and Bregnballe 2001, van de Pol et al. 2007, Gaillard et al. 2000, Aubry et al. 2009, Fay et al. 2016). In addition, due to asymmetric costs of reproduction (Clutton-Brock 1991), sex differences in recruitment age might evolve through different optimal ages of behavioural maturation (Tavecchia et al. 2001, Kim et al. 2011). Such costs are expected in polygamous species in which one sex invests more in territoriality and parental care, while the other invests more in multiplying mating occasions (e.g. Michener and Locklear 1990). Such costs might also arise in monogamous species since some initial costs of reproduction are paid only by females (e.g. egg production; Monaghan and Nager 1997), but male territoriality may compensate (or even overcompensate) for this initial disequilibrium (Tavecchia et al. 2001, Becker and Bradley 2007, Kim et al. 2011). Empirical tests of sex differences in recruitment are scarce and equivocal (mostly concerning birds, e.g. in Pradel et al. 1997, Becker and Bradley 2007, Mills et al. 2008, Kim et al. 2011); this issue would thus deserve attention.

Dispersal is expected to be a beneficial response to inbreeding risk, competition and spatiotemporal variability in breeding habitat quality (Clobert et al. 2001, Bowler and Benton 2005). However, dispersal entails costs (reviewed in Bonte et al. 2012) such as energetic expenditure during movements (e.g. wing development, long-distance travel), time spent in activities related to dispersal (e.g. prospection, transfer movement), risks resulting from movement (e.g. predation, damage of dispersal organs and tissues) or opportunity costs incurred by choosing another habitat (e.g. maladaptation, loss of familiarity – including the loss of dominance on a territory).

These costs and benefits of dispersal may also depend on individual characteristics (Bowler and Benton 2005, Bonte et al. 2012). For instance, higher natal than breeding dispersal evolves when philopatry at recruitment brings higher costs than at later breeding attempts due to inbreeding or kin competition (Greenwood 1980, Clobert et al. 2001, Bowler and Benton 2005). A decrease in dispersal propensity with age generally results from increased competitiveness and increased advantages from territory ownership and familiarity with age and experience (Greenwood 1980, Greenwood and Harvey 1982, Bowler and Benton 2005, Piper 2011). Further, when dispersal is more costly (or more beneficial) for one of the sexes, sex-biased dispersal is expected to evolve (Greenwood 1980, Lawson Handley and Perrin 2007). In resource-defence systems that feature monogamy (e.g. most birds), female-biased dispersal is usually observed because males are more involved in territoriality and benefit more from acquiring and maintaining a familiar breeding territory. This pattern is reinforced by the fact that a female chooses a male based on his territory and benefits from dispersal through mating opportunities (Greenwood and Harvey 1982, Clarke et al. 1997). In mate-defence systems featuring polygyny (e.g. most mammals), males disperse more than females as they benefit from multiplying mating opportunities with females, which are the territorial sex (Greenwood 1980, Lawson Handley and Perrin 2007).

To date, most recruitment and dispersal studies have focused on species that have evolved in relatively stable environments in which the quality of breeding patches does not vary much over the timescale of an individual's life. Such environments provide sufficient habitat predictability to favour fidelity to breeding patches and year-to-year territory ownership within the patch (McNicholl 1975, Burger 1982, Switzer 1993). This brings familiarity advantages to breeding territory owners which accumulate over years of ownership (Greenwood 1980, Piper 2011) and favour the despotic pre-emption of (good-quality) sites (Ens et al. 1995, Rendón et al. 2001, van de Pol et al. 2007) alimenting a context of harsh competition for territories (e.g. Cadiou et al. 1994). The competition for acquiring and maintaining ownership on a good-quality territory to achieve a fruitful reproductive career thus yields a major constraint inducing asymmetry in the costs of dispersal or recruitment. This drives sex- and age-dependent variations exposed above.

In contrast, such cost asymmetry may be relaxed when there is no advantage in breeding on the same patch over the years: that is, in unstable, ephemeral environments where year-to-year predictability of habitat quality is weak, such as temporary wetlands which availability depends on precipitation thresholds or sedimentary dynamics (McNicholl 1975, Oro et al. 2011, Béchet et al. 2012). High dispersal propensity is expected in species that evolved under such selective pressures (McNicholl 1975, Greenwood and Harvey 1982, Travis and Dytham 1999, Friedenberg 2003). This may notably lead to the evolution of 'nomadic breeding', which involves the frequent dispersal of all individuals from a breeding patch (Greenwood and Harvey 1982, Blanco and Bertellotti 2002, Mariette and Griffith 2012). Individual-based studies on nomadic species are scarce, owing to inherent difficulties in monitoring them. Nonetheless, they might provide valuable insights on life-history evolution.

In nomadic breeders, the costs of dispersal and early recruitment associated with competitive ability or local familiarity for territory maintenance over the years should be largely relaxed. Though individuals still have to obtain a mate and defend a breeding territory, ownership is not maintained over the years and thus territories do not bear any long-standing value (see Piper 2011). Further, the high dispersal propensity of these species should induce low risk of inbreeding and kin competition. If competition for holding a breeding territory over the years has indeed a prevailing role as emphasized above, age or sex differences in dispersal propensity might therefore be attenuated and perhaps absent in these species (see e.g. in Greenwood and Harvey 1982). We would further expect low recruitment delays and low variation in age at recruitment. We would also expect sex-biased recruitment driven by asymmetry in costs of reproduction rather than by asymmetry in costs of territoriality. For instance, females might recruit later in monogamous species with biparental care due to the costs of egg production or gestation that would not be compensated for in males in the absence of costs associated with the competition for year-to-year territory ownership.

Here, we assessed the extent of individual variation in dispersal and recruitment in a colonial bird with a nomadic breeding strategy. In avian colonial species, breeding territories are generally reduced to the nest site and are separated from foraging resources which are not defended (Evans et al. 2015) but they are still heterogeneous in quality. Indeed, they offer different fitness prospects depending on their location, e.g. due to predator accessibility, risks of deterioration or parasite infestation (Boulinier and Lemel 1996, Kokko et al. 2004, Bled et al. 2011). The most dispersal-prone colonial species are typically found breeding in unstable habitats such as islets or banks in lagoons and rivers where droughts or floods frequently occur (McNicholl 1975, Burger 1982, Erwin et al. 1998, Oro et al. 2011). We studied one of these species, the slender-billed gull (*Chroicocephalus genei*), a socially monogamous bird with biparental care (Besnard 2001). This species is characterized by high inter-annual colony-site turnover and high dispersal propensity (Oro 2002, Doxa et al. 2013, Sanz-Aguilar et al. 2014) resulting in the absence of territory maintenance over the years.

We analysed the life histories of 3479 slender-billed gulls that were ringed as chicks, of which 2392 were genetically sexed, over a 13-year period in colonies along the French Mediterranean coast. We used multievent capture–recapture models to estimate demographic rates while taking imperfect detection as well as breeding-status uncertainty into account (Pradel 2005, Gimenez et al. 2008). We investigated the effect of breeding status (pre-breeder or breeder), age, and sex on local survival, dispersal and recruitment at a regional scale (i.e. over all the breeding colonies in the study area).

4.3 Materials and Methods

4.3.1 Study area and species

The slender-billed gull is a colonial larid which distribution extends from Senegal to Western India, the Mediterranean, Black and Caspian Seas (del Hoyo et al. 1996). In the Western Mediterranean, strong immigration and emigration drive local population dynamics and generate important regional variations in annual breeding numbers (Doxa et al. 2013, Sanz-Aguilar et al. 2014). Slender-billed gulls breed on isolated islands in temporary wetlands, brackish lagoons and saltpans. Just after hatching, chicks leave the nest and amalgamate into crèches, a behaviour considered to be an adaptation to the unpredictability of water levels throughout the breeding season (Besnard et al. 2002). Because chick rearing takes place in the crèche and nests are closely packed (Fasola and Canova 1992), any difference in nest-territory quality is reduced to its simplest expression: different risk levels during the incubation period from the margin to the core of the nesting area (e.g. due to predation; Brunton 1997).

Each year from 1998 to 2010, exhaustive survey of the French Mediterranean coast allowed locating all slender-billed gull colonies. We defined a 'colony' as the group of breeding gulls at a single island site in a given year. During the study period, between 2 and 10 colony sites were occupied each year. A total of 60 colonies were recorded breeding on 45 different colony sites, with a high colony-site turnover rate (i.e. change in occupied colony sites resulting from establishment or desertion between years; Erwin et al. 1981) of 0.82 (Appendix D.1). Most colonies were located in the Camargue wetlands (the Rhône Delta), but some were found further to the east and west (Fig. 4.1). Because almost all colony sites were abandoned from one year to the next, it was impracticable to consider individual variation from site-specific dispersal rates. We thus decided to combine all colonies and considered the study area as a single breeding location to explore recruitment and dispersal in and out this area. The annual breeding population size in the study area varied between 209 and 877 pairs and reproductive success varied between 0.11 and 1.26 fledged chicks per nest (average: 0.72; Appendix D.1: Fig. D.1.1; Doxa et al. 2013). Such variations are one par with those reported elsewhere (Oro 2002, Sanz-Aguilar et al. 2014).

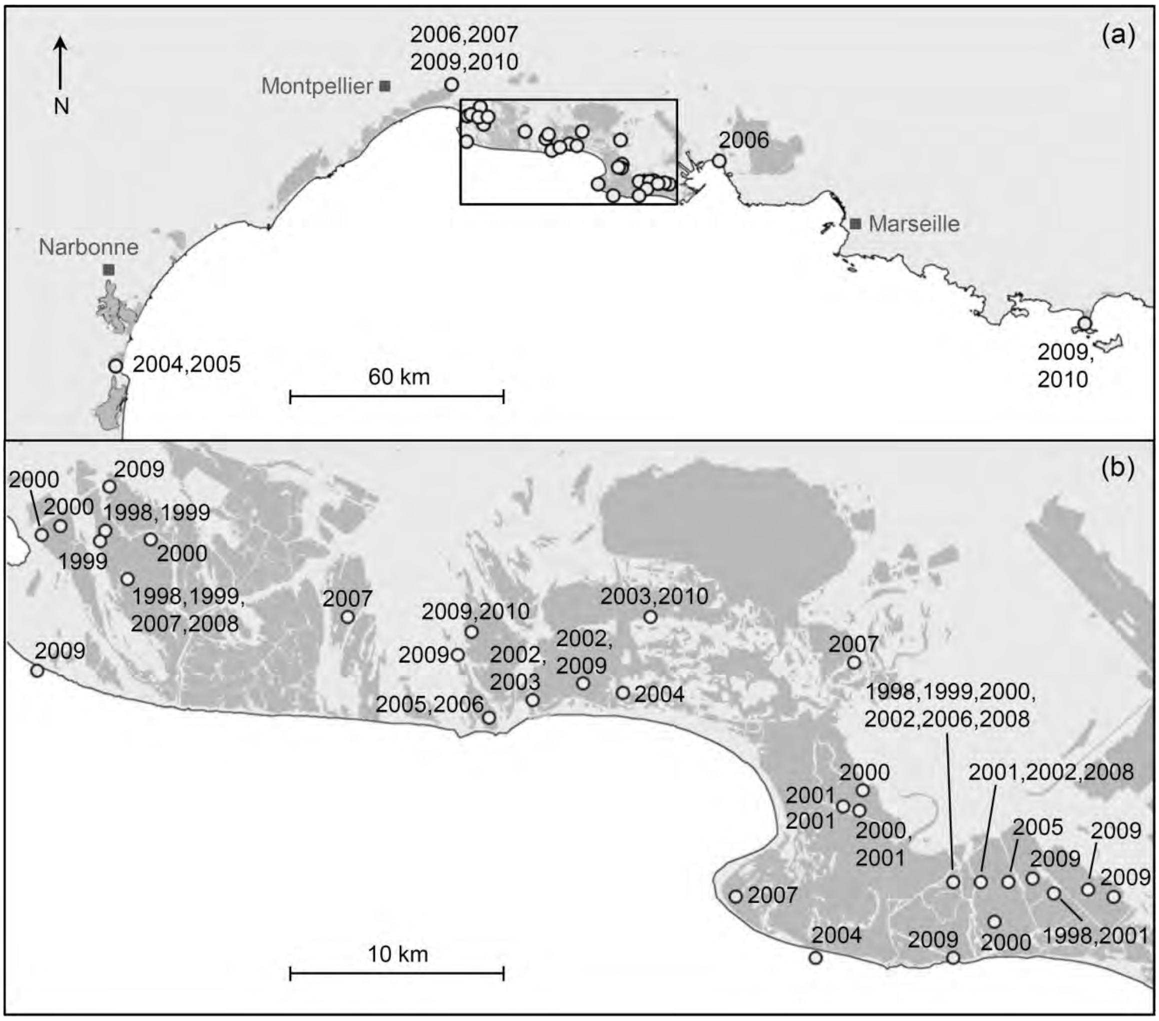

Figure 4.1. Locations of slender-billed gull breeding colonies in France during the study period (1997–2012). Panel (b) is a zoom of the boxed area in panel (a): the Camargue wetlands. The white zone is the Mediterranean Sea. Circles indicate colony sites, labelled with the (set of) year(s) in which they were occupied. Shaded zones indicate marshes. Scaling and approximation of spatial coordinates made several sites undistinguishable, which explains why less than 45 sites appear here and why the same year sometimes appears more than once next to a single point. Squares indicate main cities.

4.3.2 Data collection

From 1997 on, more than 90% of slender-billed gull chicks born in France have been marked just before fledging with rings bearing an alphanumeric code (easily readable with a telescope up to a distance of 100 meters; Doxa et al. 2013). Sex was genetically determined from a down or feather sample taken at ringing using standard molecular techniques (Griffiths et al. 1998). Each year, resightings including behavioural observations were conducted from blinds at each colony every day during several hours throughout the breeding season (from the arrival to the departure of the birds). Apart from one colony in 2003, each colony was intensively monitored during the study period. An individual may have been resighted several times throughout one season, but all these observations were collapsed into a single annual resighting in the study area. To complete the capture–recapture histories, each resighting was accompanied by the behavioural observation providing the highest level of information on its breeding status (Appendix D.2: Table D.2.1).

Each annual occasion in an individual's capture–recapture history was coded as one of five possible observation events, reflecting to some extent its underlying breeding status. These corresponded to different degrees of certainty regarding breeding or non-breeding in the study area: (i) 'not resighted', (ii) 'certain nonbreeder' (i.e. fledgling chick at ringing), (iii) 'uncertain breeder' (i.e. individual observed alive but without any of the expected breeding behaviours), (iv) 'possible breeder' (i.e. individual either manipulating nest material, attempting copulation, begging to, being fed by, or feeding another adult, or being begged by or accompanying a chick) and (v) 'certain breeder' (i.e. individual incubating, replacing its partner at the nest or feeding a chick) (Appendix D.2: Table D.2.1; and see Fig. 4.2).

4.3.3 Modelling approach

We used multievent capture–recapture models (Pradel 2005) to investigate both recruitment to the study area and dispersal through temporary emigration (i.e. dispersal was modelled as the probability of leaving and coming back to the study area where ringing and resighting occurred; Schaub et al. 2004; Fig. 4.2, Appendix D.2).

Each year, an individual was distinguished as being one of the following five states: (i) pre-breeder (i.e. an individual that has not yet reproduced) inside the study area, (ii) pre-breeder outside the area, (iii) breeder inside the area, (iv) breeder outside the area, or (v) dead (or permanently emigrated). We then sequenced the inter-annual transition between states into three successive steps (i.e. transition probability was expressed as a product of conditional probabilities) following the natural order of a post-breeding census: (i) local survival, (ii) movement (i.e. temporary emigration) and (iii) local recruitment (see Fig. 4.2 for a schematic summary of these transitions). Multievent models allow dealing with uncertainty in the assessment of an individual's breeding state during field observation and imperfect detection (Pradel 2005). Within this framework, individual states are unobserved (at least partly) but can be inferred from observation events (see above, below and Fig. 4.2).

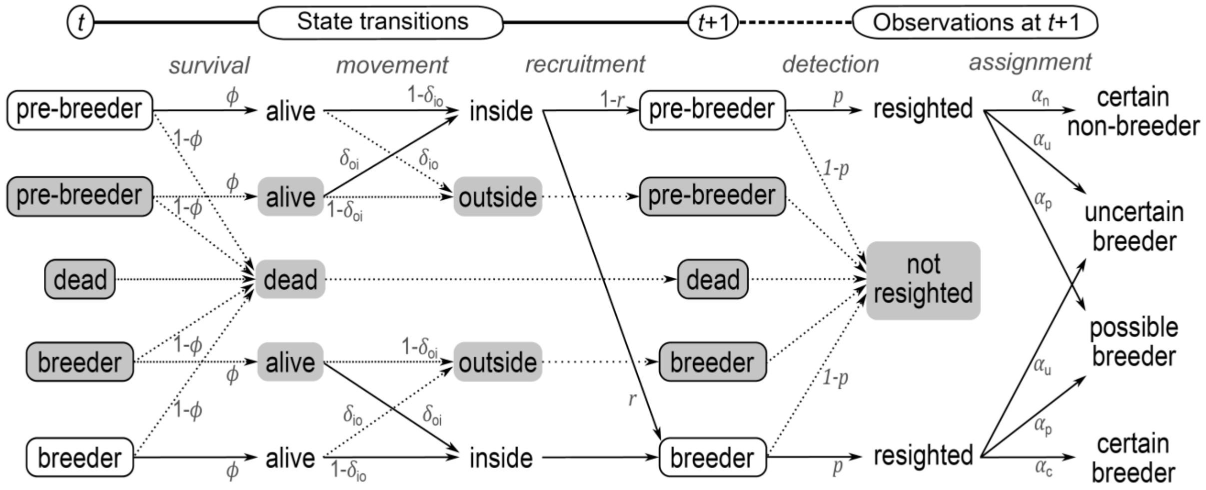

Figure 4.2. Diagram of animal fates from one breeding season (t) to the next ($t+1$) as considered in multievent capture–recapture models including local recruitment and temporary emigration for the slender-billed gull. Unobservable states (i.e. dead or outside the study area) are indicated in grey boxes. Observable states (i.e. inside the study area) are indicated in white boxes. Dotted arrows and grey backgrounds refer to (portions of) paths leading to the absence of resighting. Filled arrows and white backgrounds refer to paths leading to the assignment of a category of assessed breeding status. Arrow subscripts specify the associated probability (no subscript indicates a probability of 1). Survival rate is ϕ, emigration rate is δ_{io}, immigration rate is δ_{oi}, recruitment rate is r, detection probability is p, assignment probability is α_e (where the letter ‘e’ depends on the observation event). Further details are provided in *Materials and Methods* and Appendix D.2.

To cope with identifiability issues due to the absence of resightings outside the study area (Sanz-Aguilar et al. 2011), we considered an individual had an equal chance of local survival in step (i) whatever its location during the breeding season. In step (ii), an individual may stay in, emigrate from, stay outside or immigrate to the study area, depending on its previous location. In step (iii), pre-breeders may become breeders from age 2 (no individual in this species has ever been observed breeding before that age). They could only recruit locally or remain a pre-breeder (i.e. we did not model recruitment outside the study area). Once recruited, individuals remain in the breeder state (i.e. we did not model reproductive skipping and thus assumed that already recruited individuals breeding or skipping the breeding attempt make similar decisions concerning attendance of breeding grounds inside or outside the area).

For each individual state, the probability of each observation event was modelled as a product of conditional probabilities: (i) detection (i.e. resighting probability) and (ii) assignment (i.e. probability of being assigned to one of the four categories regarding breeding status assessment; see Fig. 4.2 which details the observation process). All capture–recapture histories started when the chick was ringed just before fledging within the study area. Obviously, dead individuals and those outside the study area cannot be resighted. In the years following ringing, an individual in any state can no longer be observed as a 'certain non-breeder', because this observation event only refers to individuals that were born that year. An individual in the pre-breeder state cannot be observed as a 'certain breeder' because, by definition, it does not attempt to breed and thus does not have behaviours that can be related to breeding with certainty.

4.3.4 Goodness of fit

Because goodness-of-fit tests are not currently available for multievent capture–recapture models, we tested the goodness of fit of the Cormack-Jolly-Seber model (i.e. full time dependence on survival and detection probability without reference to different states and events; Pradel et al. 2005) to our data using the software U-CARE v2.3.2 (Choquet et al. 2009a; Appendix D.3). As in previous analyses (Doxa et al. 2013), we found strong heterogeneity in our data. This heterogeneity may be due to transience (if there is age-dependent local survival; Pradel et al. 2005) and non-random temporary emigration (if the probability to be outside or inside the area depends on an individual's previous location, because detection is null outside the study area; Schaub et al. 2004). The disparities from the Cormack-Jolly-Seber hypotheses were handled using age-dependent survival and the model structure taking temporary emigration into account (Pradel et al. 2005, Schaub et al. 2004, and see Fig. 4.2, Appendix D.2, D.3).

There was no reason for heterogeneity in detection probability due to spatial position in the colony site. Indeed, there is no vegetation on the colony sites that obstructs resighting. Further, individuals hang at the periphery of the colony when they do not incubate (nest sites are too close from each other to allow individuals to stay near their nests; see Fasola and Canova 1992), they are very active around the crèche and feed chicks outside the crèche (Mathevon et al. 2003), which makes resighting very easy.

One might also question whether dispersal decisions may be taken by groups of individuals from the same colony and how it might bias dispersal estimates. This issue remains unconsidered in the literature on capture-recapture modelling and falls beyond the scope of this paper. Nonetheless, such a bias might exist if groups are assorted according to a variable of interest. There is obviously no colony assorted by sex or breeding status. However, colonies might be assorted by age but this effect would probably be diluted among the many cohorts and colonies constituting the dataset. Further, analyses of dyadic associations with the same dataset suggest that group tenacity is relatively low (Francesiaz et al. *in press*).

4.3.5 Inference and model selection

Analyses were conducted using E-SURGE v1.8.19 (Choquet et al. 2009b). Model selection was performed according to the corrected Akaike Information Criterion (AICc; Johnson and Omland 2004). Model building followed a step-wise approach. First, we conducted the analyses on the complete dataset (3479 individuals) to select the best structure of age dependence with constant parameters throughout the study period, taking advantage of the largest statistical power as possible. Then we conducted analyses on a reduced dataset containing only individuals of known sex (2392 individuals). We fitted the time-constant model structure previously selected and started from this model to select sex effects. The complete list of models involved is given in Appendix D.4.

At each step of model selection we also selected time-varying models to check whether or not temporal variations revealed major differences that would have called into question the results from the time-constant models (see Appendix D.5).

When analyzing the complete dataset, depending on the model, we considered two to four age classes in survival rates (e.g. two age classes: age 1, ≥ age 2; three age classes: age 1, age 2, ≥ age 3; etc.), two to four age classes in dispersal (which also depends on the breeding status and location; see above) and one to five age classes in recruitment (excluding yearlings, which do not recruit). The numbers of age classes were chosen following the conclusions from goodness of fit tests (see above and Appendix D.3), prior analyses (Doxa et al. 2013) and in an attempt to extend the test for age-dependence to a similar number of classes over which differences were shown in other larids of similar size and lifespan (e.g. Aubry et al. 2009, Szostek et al. 2014). We first assumed equal detection for pre-breeders and breeders (note: age-dependent temporary emigration account for the absence of individuals from the study area, as often observed for yearlings in larid species; e.g. Aubry et al. 2009, Szostek et al. 2014). However, after having compared all possible combinations of age dependence, we tested for a difference in detection probability between pre-breeders and breeders with a subset of best models (Appendix D.4) because they could be characterized by different degrees of colony attendance inducing differences in detection. Because survival estimate between birth and the first year (i.e. first-year survival) was fairly imprecise and was higher (0.77, with 95% confidence interval = [0.30,0.96]) than what is commonly found in other larids of the same size (around 0.5–0.6; e.g. black-headed gull, *Chroicocephalus ridibundus* [Prévot-Julliard 1996]; kittiwake, *Rissa tridactyla* [Link et al. 2002]; common tern, *Sterna hirundo* [Szostek et al. 2014]), we ran two complementary models in which first-year survival was fixed at 0.5 and 0.95 to assess how this may affect other parameter estimates.

With the reduced dataset containing only sexed individuals, first-year survival was very poorly estimated (see *Results*). We thus investigated how its value impacted other estimates with a model in which juvenile survival was fixed at the value obtained with the best time-constant model fitted to the complete dataset. To select sex-dependent variations, we compared multiple models, considering additive or multiplicative effects of sex on biologically relevant groupings of age classes (Appendix D.4).

4.4 Results

All AICc values and comparisons are given in Appendix D.4. Parameter estimates from the best models obtained in each selection step are provided in Appendix D.5, D.6. Time-varying models indicated strong temporal variations in survival and movement, but not in recruitment probabilities. However, they provided the same conclusions on state-dependent variations, which are the focus of this study. For clarity, we thus only present results from time-constant models in the main text (see Appendix D.5 for results of time-varying models). Hereafter, parameter subscripts indicate age class and estimates are given with 95% confidence intervals.

Table 4.1. Summary of time-constant model selection.

Data	Step	Covariates included	Model	Parameter variation				K	ΔAICc	wAICc
				ϕ	δ	r	p			
I	i	Age	1	$A_{1,\geq 2}$	$\Sigma\times A_{1,2,3,\geq 4}$	$A_{2,3,\geq 4}$	.	19	0	0.23
			2	$A_{1,\geq 2}$	$\Sigma\times A_{1,2,3,\geq 4}$	$A_{2,3,4,\geq 5}$	.	20	1.32	0.12
			3	$A_{1,\geq 2}$	$\Sigma\times A_{1,2,3,\geq 4}$	$A_{2,3,\geq 4}$	Σ	20	1.43	0.11
			4	$A_{[1,2],\geq 3}$	$\Sigma\times A_{1,2,3,\geq 4}$	$A_{2,3,\geq 4}$	.	19	1.78	0.10
			5	$A_{1,2,\geq 3}$	$\Sigma\times A_{1,2,3,\geq 4}$	$A_{2,3,\geq 4}$	.	20	1.99	0.09
II	ii	Age	6	$A_{1,\geq 2}$	$\Sigma\times A_{1,2,3,\geq 4}$	$A_{2,3,\geq 4}$	.	19	9.49	0
	iii	Age, Sex	7	$A_{1,\geq 2}$	$\Sigma\times(A_{1,2,3,\geq 4}+S)$	$A_{2,3,\geq 4}+A_{[2:3]}\times S$	.	21	0	0.39
			8	$A_{1,\geq 2}$	$\Sigma\times(A_{1,2,3,\geq 4}+S)$	$A_{2,3}\times S+A_{\geq 4}$	.	22	1.66	0.17
			9	$A_{1,\geq 2}$	$\Sigma\times(A_{1,2,3,\geq 4}+S)$	$A_{2,3,\geq 4}+S$	.	21	2.57	0.11
			10	$A_{1,\geq 2}$	$\Sigma\times(A_{1,2,3,\geq 4}+S)$	$A_{2,3,\geq 4}\times S$	.	23	3.05	0.08
			11	$A_{1,\geq 2}$	$\Sigma\times(A_{1,2,3,\geq 4}+S)$	$A_{2,\geq 4}+A_3\times S$	.	21	3.61	0.06

Only the 5 best models in each selection step are given. This summary indicates how survival (ϕ), movement (δ), local recruitment (r) and detection (p) probabilities vary with the covariates considered (A: age, S: sex) and individual states (Σ: pre-breeder inside the area, pre-breeder outside the area, breeder inside the area and breeder outside the area). '.' indicates no variation. With the complete dataset containing all individuals (I), 73 models were compared (step i). With the reduced dataset containing only sexed individuals (II), 40 models were compared: we first (step ii) fitted the best age-dependent structure selected in step i (Model 1), then (step iii) selected the best sex-dependent model. '×' designates interactions, '+' designates additive effects. Subscripts after 'A' specify age class divisions and combinations. K is the number of parameters, ΔAICc is the difference in corrected Akaike Information Criterion to the best model for each dataset, wAICc is the corresponding AICc weights. Complete model lists with AICc values are given in Appendix D.4.

4.4.1 Complete dataset containing sexed and unsexed individuals

The best model without time variation (Model 1, Table 4.1) had two age classes for survival (first year and older), four for dispersal and three for recruitment. Detection was independent of breeding status.

Survival probability was lower during the first year of life (ϕ_1=0.77 [0.30,0.96]) than for older individuals (ϕ_2=0.83 [0.79,0.86]). When juvenile survival was fixed at 0.5, the probability of emigrating in the first year of life (i.e. at age 1) decreased and pre-breeder immigration increased at age 2 and 3. When juvenile survival probability was fixed at 0.95, the opposite happened (Appendix D.6). However, other parameters were not impacted so our conclusions on age-dependent dispersal and recruitment remain unchanged.

The emigration probability of pre-breeders was very high for first-year individuals ($\delta^{\mathrm{P}}_{\mathrm{io},1}$=0.87 [0.80,0.92] but then decreased until the age of 3 ($\delta^{\mathrm{P}}_{\mathrm{io},2}$=0.20 [0.12,0.30], $\delta^{\mathrm{P}}_{\mathrm{io},3}$=0.07 [0.02,0.20], $\delta^{\mathrm{P}}_{\mathrm{io},\geq 4}$=0.95 [0.36,1.00]). Pre-breeder immigration probability was low and continuously decreased from age 2 to age 4 and older ($\delta^{\mathrm{P}}_{\mathrm{oi},2}$=0.25 [0.14,0.41], $\delta^{\mathrm{P}}_{\mathrm{oi},3}$=0.13 [0.06,0.27], $\delta^{\mathrm{P}}_{\mathrm{oi},\geq 4}$=0.03 [0.01,0.07]). It should be noted from these estimates that pre-breeders present in the area but not recruiting at age 3 were most likely to leave and almost never come back. Accordingly, for pre-breeders that survived, the probability of being inside the study area increased from 0.13 to 0.39 from age 2 to age 4, then fell to 0.04 and stabilized at 0.03 at age 6 and older (Fig. 4.3, see Appendix D.7 for calculation details).

A quarter of pre-breeders alive and present in the study area at age 2 recruited at that age (r_2=0.24 [0.18,0.32]), this recruitment rate was much higher at age 3 (r_3=0.89 [0.81,0.94]) and similar at age 4 and older ($r_{\geq 4}$=0.24 [0.13,0.41]). However, these latter recruitment rates are conditional on being alive and inside the study area (Fig. 4.2), which is a key point to understand their meaning. Accordingly, they must be integrated with temporary emigration to properly figure recruitment of locally born individuals. Indeed, a substantial number of individuals are outside the study area and thus cannot recruit within the study area (see above). Given temporary emigration, the probability of recruiting in the natal area for any pre-breeder alive at age 2, 3, 4 and older was 0.08, 0.34 and 0.01 respectively. As a result, given survival probability, the probability of being alive and recruiting in the natal area for any (pre-breeder) individual in the dataset was 0.05 at age 2, 0.20 at age 3, falling to 0.005 at age 4 and continuing to decrease from then on (Appendix D.7).

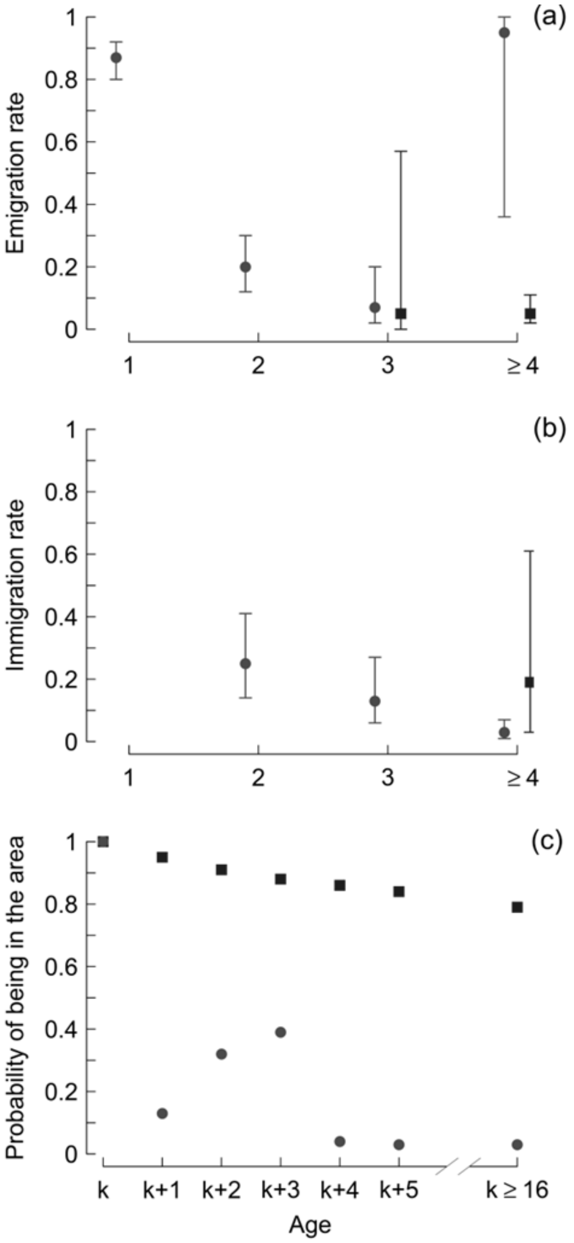

Figure 4.3. Age-dependent annual (a) emigration rate, (b) immigration rate and (c) probability of being inside the study area for slender-billed gulls over 1998–2010. Movement rates are the probability of changing location (i.e. inside or outside the study area) from one breeding season to the next, which is conditional on survival. Because all capture-recapture histories start at age 0 in the study area, pre-breeders emigration occurs only from age 1, pre-breeder immigration from age 2, breeder emigration from age 3 and breeder immigration from age 4. The probability of being inside the study area is also conditional on survival. Pre-breeders are plotted with circles and breeders with squares. For panel (c), age was expressed as a function of birth (i.e. age 0) for pre-breeders or recruitment age for breeders (labeled 'k' on abscissa for both). Segments indicate the 95% confidence intervals for parameter estimates. Estimates were obtained with the best time-constant model using the complete dataset (Model 1, Table 4.1, Appendix D.6) and probabilities of being inside the study area were derived from this model (Appendix D.7).

The emigration rate of breeders (i.e. individuals that have already recruited in the study area where they were ringed as chicks) was much lower ($\delta^{\mathrm{B}}_{\mathrm{io},3}$=0.05 [0,0.57], $\delta^{\mathrm{B}}_{\mathrm{io},\geq 4}$=0.05 [0.02,0.11]) than their immigration rate ($\delta^{\mathrm{B}}_{\mathrm{oi},\geq 4}$=0.19 [0.03,0.61]). For breeders that survived, the probability of being inside the study area was concave down, monotonically decreasing with age, from 0.95 the year after recruitment, 0.86 four years after recruitment, to the asymptotic value of 0.79 reached sixteen years after recruitment (Fig. 4.3, Appendix D.7).

Detection was very high (p=0.86 [0.83,0.88]) and assignment probabilities were consistent regarding the observer's ability to assess breeding status (see Appendix D.8).

4.4.2 Reduced dataset containing only sexed individuals

In the time-constant model applied to the reduced dataset (Model 6, Table 4.1), estimates were very similar to what was previously obtained (Model 1), but had larger confidence intervals (Appendix D.6). First-year survival probability was very poorly estimated (ϕ_1=0.997 [0,1]). When it was fixed at 0.77 (the value from Model 1), estimates were even more similar (Appendix D.6).

The best time-constant model with sex dependence (Model 6) had 9.48 fewer AICc points than the model without sex dependence (Model 7, Table 4.1). The best model showed no sex-bias in survival. However, there was a sex difference in movement probability, which was irrespective of movement direction (emigration or immigration; on the logit scale: 0.19 [0.02,0.36]). Movement probability was slightly higher for males (e.g. $\delta^{\mathrm{P}}_{\mathrm{io},1}$=0.88 [0.86,0.89] for males and 0.85 [0.83,0.87] for females; Appendix D.6). There also was also an additive sex difference in recruitment probability at age 2 and 3 (on the logit scale: 0.88 [0.27,1.50]). Local recruitment probability was higher for males (r_2=0.31 [0.22,0.42] and r_3=0.92 [0.84,0.96]) than for females (r_2=0.16 [0.10,0.25] and r_3=0.83 [0.72,0.90]).

4.5 Discussion

Because the slender-billed gull is socially monogamous and nomadically breeding, we suggested that the lack of breeding site tenacity and year-to-year territory ownership might induce a limited delay in recruitment age, with females recruiting later than males, but no difference in dispersal according to age or sex. In accordance with these expectations, variability in recruitment age was quite low and males recruited earlier than females. In contrast, we found that temporary emigration was higher in pre-breeders than in breeders and decreased with age. Furthermore, males had a slightly higher tendency to disperse outside the study area than females. These results suggest that other mechanisms than those associated with competition for holding a breeding territory over the years shape between-individual variations in dispersal and recruitment.

4.5.1 Variability in recruitment age

Age at first reproduction is commonly quite variable in long-lived colonial species occupying stable habitats. In these species, few individuals recruit early and recruitment is spread over several age classes (e.g. Lebreton et al. 2003, Hadley et al. 2006, Becker and Bradley 2007, Mills et al. 2008, Aubry et al. 2009, Kim et al. 2011, Desprez et al. 2014). For instance, in kittiwakes or common terns (colonial larids that have about the same size and lifespan as the slender-billed gull), reproduction can begin at age 2, but most recruitment occurs from age 3 to 6 and a few even later (Aubry et al. 2009, Szostek et al. 2014). In the slender-billed gull, recruitment in the natal area was earlier and showed a much narrower spread over age classes (few recruitment occurred at age 2, most at age 3 and a very few at older ages).

In stable habitats, year-to-year colony-site tenacity strengthens the importance of nest-site differences, which imply prospecting, contesting and eventually queuing for good-quality habitats; a competitive process that may expand over several years (Becker and Bradley 2007, van de Pol et al. 2007, Aubry et al. 2009). Nomadic breeders are not constrained by such long-standing competition, which may explain the lower recruitment delays observed in the slender-billed gull. Alternatively, the apparent larger recruitment delays in species in stable habitats might result from the relatively small spatial scale of most studies (one or a few close colonies), whereas we studied recruitment at a regional scale. For instance, in a metapopulation of black-headed gulls, recruitment in the largest colony – probably saturated but of high quality – occurred later (age 2–5) than in smaller colonies – probably less competitive but of lower quality

– (age 2–4; Grosbois 2001). A similar pattern was observed in the great cormorant (*Phalacrocorax carbo*; Hénaux et al. 2007). Accordingly, if one ignores small satellite colonies and focuses only on the largest, saturated colonies where competition for nest sites is stronger, recruitment age is likely to be overestimated.

A decrease in breeding density may thus enhance accessibility to breeding sites, therefore anticipating recruitment (see also e.g. Crespin et al. 2006). Density-dependence is unlikely to operate in the slender-billed gull in our study area. Indeed, the number of breeding pairs on a colony site is usually ca. 100-300 (maximum observed: 722) which is quite low compared to ca. 6000 pairs in Sfax, Tunisia (Sanz-Aguilar et al. 2014). Further, observations in the study area do not suggest that nesting space is limiting in most colony sites. In addition, the absence of year-to-year territory ownership and the low heterogeneity in nest-site quality clearly relax the competition for nest sites, as also suggested by low levels of aggression in this species (Besnard et al. 2006). This is likely to yield low recruitment delays, in accordance with our results. The remaining variability in recruitment age we detected might stem from slight individual differences in behavioural maturation (e.g. gain in competitive and foraging skills), mating and synchronization with the group (Charlesworth 1994, Aubry et al. 2009).

Moreover, temporary emigration of juveniles might conceal some recruitment outside the study area (i.e. natal dispersal; Pradel et al. 1997). In our study, we modelled temporary emigration outside the study area but recruitment only inside the study area. It is, however, likely that actual recruitment covers a wider area (inside and outside the study area). Actual recruitment of slender-billed gulls might thus have occurred at a larger spatial scale so that recruitment might be even less delayed than what our findings indicate. This would be in line with previous findings on the Audouin's gull (*Ichthyaetus audouinii*), another species that is thought to have evolved in unstable habitats. In this species, Oro et al. (2011) showed much more transience in immigrants than in philopatric individuals, but no difference in recruitment rates between them in the largest colony. As in the Audouin's gull, recruitment rates of slender-billed gulls might be the same in the natal or immigration area.

4.5.2 Breeding status- and age-dependence in dispersal

In our models, adult survival was lower than commonly found in similar-sized larids from stable habitats (see *Methods*), which has been interpreted in a previous study as the result of permanent emigration (Doxa et al. 2013). This would indicate that permanent emigration was substantial, providing additional evidence of high dispersal propensity in slender-billed gulls. Unfortunately, juvenile survival estimates were not exploitable because this parameter is hardly distinguishable from juvenile emigration. Yearlings were very likely to be outside the study area, corroborating the fact that immature larids are usually absent from the breeding grounds (e.g. Aubry et al. 2009, Szostek et al. 2014). In addition, and even when excluding yearlings, temporary emigration was lower in breeders than in pre-breeders at the regional scale modelled here (Fig. 4.3). Breeders were much more regionally philopatric than we expected, though they were not philopatric to the colony site and permanent emigration is strongly suspected. Moreover, breeder emigration was higher at age 3 than at age 4 and older (although this was unclear in time-constant models, it was confirmed by time-varying models; Fig. 4.3, Appendix D.5). Even when a habitat is unstable at the local scale, older individuals may benefit from spatial knowledge of potential foraging and breeding zones that do not radically change over the years at the regional scale (e.g. Bradshaw et al. 2004, Wolf et al. 2009); a benefit that should favour a decrease in dispersal propensity with age. This idea is also supported by the clear tendency of slender-billed gulls to use the same wetland complex in the Carmargue over the years (Fig. 4.1), suggesting philopatry benefits at a larger scale than the colony site.

4.5.3 Sex bias in dispersal

In bird species inhabiting stable environments, males usually disperse less than females as breeding habitat predictability offers benefits in holding the same territory over the years (Greenwood and Harvey 1982, Clarke et al. 1997, Lawson Handley and Perrin 2007). In contrast, our results suggest that slender-billed gull males moved in and out the study area slightly more often than did females. Even if the difference between sex was small as expected, the difference – applying to all age classes – was significant and deserves attention.

Interestingly, in slender-billed gull fledglings, the sex ratio at ringing was slightly imbalanced (46% females out of 2392 sexed individuals [χ_1^2=14.32, P<0.001] over the study period, with the same trend in most years: Appendix D.9). As we detected no sex effect on survival, this unbalanced sex ratio should be present in all age classes. The lower availability of females in the population should strengthen competition between males for access to a partner (Jirotkul 1999), thus promoting female choosiness (Berglund 1994), a behaviour that is known to favour male dispersal (Kokko and Rankin 2006). Additionally, higher regional philopatry could offer females a familiarity advantage (Piper 2011) in acquiring feeding experience in the area (e.g. Bradshaw et al. 2004), especially in regards to investment in egg laying (Perrins 1996, Monaghan and Nager 1997, Williams 2005; and see below). Females that need a large amount of energy both for egg production and to succeed in synchronous laying may thus experience higher benefits from philopatry than males.

4.5.4 Sex bias in recruitment

We predicted earlier male recruitment due to the costs for females of egg laying, which would not be (over)compensated by the costs for males of holding a breeding territory over the years. Although rarely documented, sex-biased recruitment has been suggested to be the result of one of the sexes being outnumbered, as the surplus of one sex may strengthen intrasexual competition and thus reduces access to reproduction (Mills 1973, Becker and Bradley 2007). However, in the slender-billed gull, females recruited later than males while they were likely outnumbered by males. Hence competition for mating opportunities may not drive sex-dependence in recruitment in this system. In many birds, including larids, the laying date gets earlier with age and is negatively correlated with breeding success (Forslund and Pärt 1995, Arnold et al. 2004). This may be the consequence of experience-driven improvements in performance, selective disappearance of late-laying individuals and increased reproductive effort with age (Ezard et al. 2007, Bosman et al. 2013). In the slender-billed gull, egg laying is highly synchronous, taking place in a period of less than 15 days (Besnard 2001). Such synchronization is explained by crèching behaviour: late-born chicks are unable to join the crèche when it leaves the colony site and consequently die (Besnard 2001). Young females that lay too late (i.e. are unsynchronized) may thus be prone to delaying recruitment to achieve synchronous laying and avoid having late chicks with no chance of survival. This context of strong asymmetry in reproductive costs suggests that slender-billed gull females might delay recruitment (provided that assortative mating by age do not prevails) to achieve optimal synchronization with older, more experienced individuals.

4.6 Conclusion

Our study invites to revisit recruitment and dispersal paradigms in long-lived species that were mostly elaborated from the study of species incurring territorial costs associated with year-to-year territory maintenance and notably facing competition resulting from density-dependence. Here, we showed that a nomadically breeding bird species with absence of year-to-year territory holding exhibited few differences in dispersal between sexes and had almost no delay and variation in recruitment age. Nonetheless, remaining variations in recruitment age and state-dependent dispersal (here, a delay in female recruitment, a slight male-biased dispersal and increased dispersal with age) suggest the role of other ecological processes such as the sex ratio imbalance, the costs of reproduction and the benefits of regional familiarity.

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5

General discussion

5.1 General remarks and rationale

The main aim of this thesis was to investigate neglected aspects of the decision of where and when to breed in the light of habitat selection processes. I tested hypotheses about patterns of variation in life histories of two species of larids, the black-legged kittiwake and the slender-billed gull, and considered the constraints imposed on habitat selection and the cost-benefit balance involved in individual choices. I interpreted the constraints as essentially concentrated into environmental uncertainty in the breeding habitat and intraspecific competition for breeding positions. These constraints play a part in the acquisition of a mate and a breeding site, that is, necessary requirements for reproduction. These constraints can lead to the choice of a site of the highest possible quality, but not necessarily the highest quality in absolute terms. Constraints are part of the framework within which individuals can attempt to maximize their reproductive success. The strength of these constraints shapes the evolution of habitat selection strategies, which is illustrated by the different life-history patterns characterizing the slender-billed gull and the kittiwake.

In this framework, the benefits of individual decisions concerning where and when to breed are the acquisition of the best sites and mates, i.e. obtaining a breeding position which maximizes fitness. Natural selection should favor behavioral mechanisms which allow individuals to take appropriate decisions ensuring these benefits. Such benefits can last several years when habitat quality is temporally autocorrelated. Site acquisition and retention are favored by competitive advantages brought by familiarity with the habitat. Familiarity confers dominance on a nest site, and allows establishing dear enemy relationships with neighbors. Familiarity also involves knowledge of foraging areas. Individual decisions regarding habitat choice may entail costs; these are the 'dark' side of the coin, resulting from the constraints. Environmental variability may incite individuals to move because habitat quality deteriorates so that the best option is to leave, but dispersal entails costs, and fitness prospects may not be better elsewhere. Further, it is hard for individuals to get the best breeding position when competition requires time-consuming, energetically-demanding, and eventually damaging activities that are of uncertain outcome.

Accordingly, when the breeding habitat is predictable, individuals can disperse, compete, and get the best breeding positions, up to the point at which the outcome of such behaviors is too risky in terms of fitness, as illustrated in the kittiwake (Chapter 2, 3). Indeed, kittiwakes may remain in lower-quality habitats when higher-quality ones are too distant. If local conditions deteriorate, individuals may not manage to get a new breeding position when competition is too strong, or when they stop defending their former site and decide to leave their former habitat without acquiring competitive dominance on a new breeding position at the same time. When the environment is too uncertain, systematic dispersal and a number of other adaptations such as breeding synchrony and crèching may induce new constraints on the decisions of where and when to breed and rend void the constraint of competition for breeding territories, as seen in the slender-billed gull (Chapter 4). Nonetheless, slender-billed gulls may still benefit from knowledge of foraging areas which are probably more predictable than breeding areas, and a substantial part of them may thus exhibit a high level of regional philopatry.

Plate 5.1. 'YO-OBR' (say: "Yellow, Orange, Orange, Blue, Red") and its mate guarding their chick. *Photo credit: Thierry Creux (Ouest France).*

In the three articles included in this dissertation, I highlighted general strategies underlying individual decisions regarding where and when to breed. I suggest that these strategies have evolved under constraints which are specific to my study subjects, but also occur in many taxa. Though these general strategies should be expressed across all individuals, circumstances specific to the individual state (e.g. age, sex, breeding status) make individuals more or less able to face the constraints and bear the associated costs. Individuals are thus more or less able to make decisions that would lead to the highest immediate fitness if constraints where ignored. I attempted to unveil these individual differences and elucidate the consistency of individual decisions with the general patterns. I suggest that apparently sub-optimal choices are still consistent with the principle of fitness maximization in the circumstances specific to each individual.

5.2 Conclusive summary

5.2.1 Breeding habitat selection across spatial scales

Individuals are expected to select the best spots (Fretwell 1972) based on available information on breeding habitat quality (Cody 1985, Clobert et al. 2001, 2009). Individuals should thus occupy the best habitat first ("the ideal free distribution"; Fretwell 1972). Individuals may be particularly prone to use the information on habitat quality provided by reproductive success because it is a sample of fitness realized in a specific breeding habitat (Switzer 1993, Danchin et al. 1998, Doligez et al. 2003). In territorial species, some individuals despotically preempt the highest-quality sites (Fretwell 1972). These individuals are probably the most competitive ones, or simply those that arrive the earliest (Kokko et al. 2006). The order of arrival or the ranking in competitiveness would thus determine the distribution of individuals ("the ideal despotic distribution"; Fretwell 1972). However, habitat selection dilemma may still occur. When competitiveness and timing of arrival do not vary among individuals, which individuals will occupy the best habitats? When habitat quality does not vary, which sites should be chosen? When information is contradictory depending on the spatial scale at which habitat quality is assessed, which information should be relied on?

In Chapter 2, I suggested that the role of dispersal costs (and conversely, of philopatry benefits) has been largely neglected in the literature on habitat selection (see also Stamps et al. 2005, Piper et al. 2011, Burgess et al. 2012), and that the influence of such costs on habitat selection offers great potential for solving habitat selection dilemma. In addition to promoting the identification of the best habitats based on reliable information on habitat quality, natural selection should favor habitat selection strategies minimizing the cost of dispersal. Given that there is generally a positive relationship between the cost of dispersal and dispersal distance (Bonte et al. 2012, Hovestadt et al. 2012), I suggested that individuals may maximize their fitness if they perform a 'sequential proximity search'. According to such strategy, individuals start considering their future breeding position by assessing their own breeding success (i.e. personal information) and deciding whether or not to stay in their own breeding site. This decision can also be made according to breeding success in their close vicinity (i.e. public information). If they decide to leave their own breeding territory, they sequentially expend the surrounding area where they assess habitat quality via public information and decide whether or not to stay there. They do so up to a point in space where they choose a breeding site which is sufficiently close to their previous site and of sufficiently good quality.

I explored spatial scale-dependence in habitat selection in the kittiwake, and I showed that observed patterns are consistent with a strategy of sequential proximity search. When first making the decision to leave their neighborhood, individuals took habitat quality into account only in the neighborhood, and were not influenced by habitat quality at larger scales. For the kittiwake in particular, I suggested that a distance-dependent dispersal cost arises from a tradeoff between defending the currently-owned nest site (to insure an already-acquired breeding position) and competing for a new site farther (to attempt to acquire a higher-quality site). These interpretations were further supported by variation in scale-dependent habitat selection depending on the individual state. Sex, breeding experience, breeding status, own success, and individual identity all modulated habitat selection and notably how far individuals were moving. I interpreted these variations as the result of variations in the ability to bear the distance-dependent cost of dispersal, which should mostly refer to variations in competitive abilities.

To answer the question in title of Chapter 2: grass may appear to be greener on the other side, but one should be satisfied with a lighter grass when the fence is too high. The strategy of sequential proximity search is prone to generate patterns that deviate from the ideal free or despotic distribution (Fretwell 1972). This strategy may thus explain apparent mismatches between habitat preferences and realized fitness that are often detected in empirical studies (see Chalfoun and Schmidt 2012). Moreover, the sequential proximity search hypothesis has the potential for generalization in many species because it relies only on information use and distance-dependence in dispersal costs, which are common in animals (Danchin et al. 2004, Hovestadt et al. 2012).

5.2.2 The decision to breed in a population located at the species range edge

The kittiwake population of the Cap Sizun is located at the edge of the current species distribution in Europe (del Hoyo 1996, Monnat and Cadiou 2004). I showed in Chapter 3 that this population undergoes important fluctuations in fecundity and breeding numbers, and would not be viable in absence of the large immigration rate that I estimated. I depicted the context of a dynamic range, where small, sparse colonies are regularly deserted (see also Monnat and Cadiou 1994). The breeding success in these small colonies is highly vulnerable to predation, which may stem from a very low dilution effect (Foster and Treherne 1981, Wrona and Dixon 1991). Given that kittiwakes disperse to keep track of good-quality habitats on the basis of conspecific reproductive success (Danchin et al. 1998), desertion following severe predation events in nearby colonies (within ca. 200 km around; McCoy et al. 2005) is very likely to explain immigration waves to the Cap Sizun. However, within the study area, we also observed this process of massive dispersal and colonization due to predation (Danchin and Monnat 1992, Cam et al. 2004). It is intriguing that immigrants continue to be attracted to this population and that locals continue to breed there. The insights I provided may help understand how species range limits are maintained, at least at the temporal scale of the monitoring study on kittiwakes.

On the one hand, local adult survival rate in the Cap Sizun was particularly low compared with reported values in other populations located closer to the range core (Frederiksen et al. 2005). I suspected this low apparent survival to result in great part from permanent emigration. This would indicate that the study population would also be quite repulsive compared to other populations located closer to the core. On the other hand, once they established as breeders in the population, the strategy of habitat selection drives some degree of inertia in locals. Dispersal costs that I suppose to shape the evolution of a sequential proximity search (Chapter 2) make individuals prone to stay in a population even if that population is not intrinsically viable. I call this 'inertia' following del Mar Delgado et al. (2011), because individual dispersal responses may not be sufficiently efficient to escape poor environmental conditions experienced by the population. Kittiwakes in the Cap Sizun would thus partly be trapped by their own habitat selection behavior shaped by constrained processes: social information use and competition for breeding sites over the years (Chapter 2). Moreover, while some habitat patches in the population have faced poor conditions leading to desertion over the years, other patches have provided good fitness prospects (Danchin and Monnat 1992, Cam et al. 2004, Aubry et al. 2009). Such a spatiotemporal heterogeneity within the population should maintain a basis to attract newcomers, and for the sequential proximity search to operate and to retain individuals locally.

The decisions to breed in the Cap Sizun regarded at the scale of the population were positively correlated with population productivity and negatively correlated with the number of breeders or nonbreeders (in the year preceding the effective decision). Thus, at this scale, there was no indication of an effect of 'blind' attraction to conspecific abundance (Reed and Dobson 1993, Ward and Schlossberg 2004). However, there was an attraction to good conditions indicated by a positive influence of conspecific success and a negative influence of competition on transitions toward the state 'breeder'. These findings are consistent with the habitat selection strategy described in Chapter 2: *when* to breed in the population is conditioned by the acquisition of a breeding position (i.e. by choices concerning *where* to breed in the population; see also Ens et al. 1995, Frederiksen and Bregnballe 2001). Nonetheless, the aforementioned relationships between transitions toward the status 'breeder' in the population and social information in the previous year were not always supported in all the categories of breeding states considered (i.e. immigrants, first-time breeders, former breeders, and former skippers).

The interpretation of such differences among states is difficult because we cannot exclude the possibility that failure to detect some effects is due to the low sample sizes involved (only 26 observations-years could be used to estimate each partial correlation). If the role of social information is indeed varying between individual categories, this would indicate that the individual state conditions the importance of competition with either breeders or nonbreeders, and the degree of attraction to good-quality habitats.

For example, we only detected a negative effect of the number of present nonbreeders on the immigration rate. This might suggest that though immigrants are involved in a competition with individuals intending to establish as breeders in the population, they essentially compete for secondary breeding sites which are not occupied by breeders, and that they are not attracted by population productivity as a whole. However, they might still be attracted by productive patches within the population, even when the population as a whole has a low productivity because most patches face poor breeding conditions. The analyses conducted in this study at the scale of the population are informative, but not sufficiently to conclude on the latter hypotheses.

5.2.3 Dispersal and recruitment in a nomadically breeding species

After investigating habitat selection in the kittiwake, the slender-billed gull provides an interesting and original case study to expand the perspective on the decisions of where and when to breed. Slender-billed gulls have evolved a life-history strategy which suggests specific adaptations to unstable, ephemeral habitats (Besnard 2001, Besnard et al. 2002). As several bird species occupying bank and islets in rivers and deltas where drought or floods occur frequently, the slender-billed gull is characterized by a very high dispersal propensity and a high between-individual synchrony in breeding activities (e.g. some gulls *Larus* spp., and many terns *Sterna* spp.; McNicholl 1975, Oro et al. 2011).

Plate 5.3. The nesting area in a colony of slender-billed gulls within the few days of chick incubation. *Photo credit: Charlotte Francesiaz.*

Whereas occupying the same location from one year to the next might be beneficial in the kittiwake because habitat quality is sufficiently predictable over the years, the colony sites of slender-billed gulls are almost always deserted from one year to the next (Chapter 4). As a consequence, slender-billed gulls do not face the constraint of competition for holding a territory over the years (which appears has a major driver of breeding decisions in kittiwake). If costs linked with habitat selection occur (e.g. dispersal costs), they are likely to operate through other constraints than competition and at larger scales than the scale of the nesting territory or the scale of the colony site. These other constraints are probably imposed by the crèching strategy of the slender-billed gull (interpreted as an adaptation to within-year habitat instability: Besnard et al. 2002), which implies to achieve highly-synchronous breeding so that chicks will be able to join the crèche.

In the slender-billed gull, I studied recruitment to and dispersal in and out the French Mediterranean coast. I found evidence of a small delay of recruitment age together with a small inter-individual variability in recruitment age. Whereas long-lived birds from relatively “stable” habitats usually show a wide range of recruitment ages (see e.g. in Becker and Bradley 2007; in the kittiwake: Chapter 3), I interpreted particular findings in the slender-billed gull as consistent with the absence of competition for holding a territory over the years. Moreover, I found only a small sex-related bias in dispersal propensity (for a comparison with the kittiwake: see Chapter 2). This can also be explained by the absence of competition for holding a territory over the years, a part usually played by males in birds (Greenwood 1980, Clarke et al. 1997, and see e.g. in the kittiwake: Chapter 2).

Nonetheless, there was a small difference in dispersal propensity between male and female slender-billed gulls (males dispersed more than females). Further, male slender-billed gulls recruited earlier than males. Moreover, dispersal propensity in and out the study area decreased with age. These findings indicated that other constraints than competition for holding a territory over the years were operating in the processes leading to the decisions of where and when to breed in the slender-billed gull. These constraints yield life-history differences between sexes and ages, and have thus to be identified to elucidate the mechanisms that potentially differ between males and females, and between young and old individuals.

Although the slender-billed gull is socially monogamous with biparental care, females lay eggs and thus provide a higher initial investment in reproduction (Monaghan and Nager 1997, Williams 2005). The strength of such constraint in slender-billed gulls is probably exacerbated by the additional constraint of synchronous breeding: females must be ready to lay eggs at the right time, so that chicks do not "miss" the crèche (missing the crèche implying chick death). Further, this cost in females is unlikely to be compensated in males by a cost of competition for territories (that could induce delays of behavioral maturation to acquire competitive skills; Charlesworth 1994, Aubry et al. 2009). Indeed, the competition for nest sites within colony sites is reduced to a few days, over a nesting area where sites weakly differ in quality, and this competition occurs in different colony sites each year. Accordingly, females might benefit from delaying recruitment to acquire skills that would maximize their ability to lay eggs at the right time. These skills might notably include the knowledge of foraging areas. This would also explain why females dispersed slightly less than males. The importance of familiarity with foraging areas may be crucial to maximize fitness, and may also explain the decrease in dispersal with age in both sexes. Moreover, another constraint can be invoked to explain male-biased dispersal: the sex ratio was biased towards males in the study area, implying higher male-male competition for mating (Kokko and Rankin 2006).

My work suggests that competition for holding a good-quality territory over the years is the dominating constraint shaping habitat selection strategies and inducing variation in the decisions of where and when to breed in the kittiwake. This is likely to be the case in many other territorial species from "stable" habitats (Greenwood et al. 1980, Greenwood and Harvey 1982). This idea underlying the interpretations provided in Chapter 2 and 3 in the kittiwake is further supported by the peculiar findings on the slender-billed gull in Chapter 4. Nonetheless, as shown in the slender-billed gull, other constraints should not be neglected. Examples relevant to long-lived, socially monogamous species are: familiarity with feeding areas, density-dependent intrasexual competition, and the higher reproductive investment of females; they may also shape the evolution of mechanisms underlying the decision of where and when to breed.

5.3 Future directions

The study of individual decisions concerning where and when to breed is embedded into the many questions related to habitat selection – a cornerstone in ecological and evolutionary researches (see e.g. the review by Morris, 2003). I believe that this field has still a long, fruitful future ahead. Several perspectives can be identified from my (small) contribution to the field. Hereafter, as a last word I give a few examples of potential future directions, notably for my study subjects.

5.3.1 Sequential proximity search in habitat selection

As stated above, the ubiquity of distance-dependent dispersal costs (Bonte et al. 2012, Hovestadt et al. 2012) and the widespread use of information in habitat selection (Clobert et al. 2001, 2009, 2012) suggest that a strategy of sequential proximity search is likely to have evolved in many taxa. It would be very interesting to conduct theoretical and empirical studies in a variety of species to assess whether my hypothesis can indeed be generalized to other animals. If it is case, this hypothesis might be useful to formalize new predictions on animal distribution patterns, and possibly design a new reference model in habitat selection that could be confronted with ideal distributions (Fretwell 1972). Because I studied scale-dependence in habitat selection from the perspective of *leaving* a previous habitat, it would then be necessary to develop specific predictions concerning the decision to *settle* in a new site.

The issue of settlement in a new site could be studied in the kittiwake to complete the investigation of scale-dependent habitat selection. However, the issue of settling in a new site might be more difficult to handle than the issue of leaving a previous site (e.g. Citta and Lindberg 2007, Kivelä et al. 2014). Indeed, while an individual can only leave one habitat, many options exist for settlement. Here again, a sequence of scale-dependent decisions might solve the dilemma of selecting a habitat among multiple options and with multiple sources of information. For instance, a kittiwake deciding to leave its colony might then select another colony among the remaining ones, then a social group within the colony, then a cliff wall within the social group, then a nest site within the cliff wall. For the empiricist, this would be easier to model than a direct choice between the thousands of nest sites available. It would be necessary to find a way of testing whether individuals directly target a small productive patch, or follow a strategy of sequential search.

Plate 5.2. Long calls by two different pairs of kittiwakes calling in a nest site containing a chick. Are they squatters or owners? *Photo credit: Thierry Creux (Ouest France).*

It would also be useful to consider the fitness consequences of individual choices to assess whether the sequential proximity search is an efficient strategy in terms of realized fitness (see e.g. Aubry et al. 2009). It might be interesting to address whether successful individuals that do not use public information and almost always stay in their nest site or their cliff wall end up paying the cost of their tenacity. They might achieve lower lifetime reproductive success than others when they are confronted with deteriorating conditions, or even achieve the same lifetime reproductive success as those that occupied lower-quality territories and had a higher risk of failure, dispersal, and future nonbreeding. More generally, we could identify individuals which “behave against the current” (see Naves et al. 2006) and assess whether deviating from the general strategy results in a higher probability of breeding failure. It is also tempting to investigate whether there is a link between the individual heterogeneity in dispersal propensity, and survival and reproduction: these two latter traits are known to co-vary among individuals in the study kittiwake population (Cam et al. 2002, 2013). If there is a positive correlation between individual dispersal propensity and reproductive success, this might indicate that the ability to overcome dispersal costs allows individuals to acquire the highest-quality habitats. An additional positive correlation with survival would indicate that frailer individuals are likely to be those that hardly overcome dispersal costs and do not do well in the competition for acquiring good-quality territories.

5.3.2 Breeding decisions in a population varying in space and time

The investigation of the social factors underlying the decision to breed in the Cap Sizun kittiwake population would benefit from a complement at the colony scale. Indeed, the population has been composed of distinct colonies that may provide opposite fitness prospects at the same time (Danchin and Monnat 1992). The colony scale should thus be more appropriate than the scale of the whole population to assess whether immigrants are sufficiently informed to target the highest-quality patches in the population. The integrated population model can be extended to take the colonies into account (McCrea et al. 2010) and estimate colony-specific numbers of immigrants, breeders and nonbreeders, and dispersal between colonies. With this tool, it is possible to address the factors influencing the decisions to leave but also to join a colony, while taking the whole population context into account (and not only the context of departure, as in Chapter 2).

I developed such an integrated "multi-colony" model for the kittiwake in collaboration with Michael Schaub (Appendix E). This model is much more complex than the model described in Chapter 3. Indeed, each of the nine life-history states in the population matrix (Fig. 3.1, Appendix C.2) has to be colony-specific. The number of immigrants and productivity are also colony-specific, and dispersal between colonies has to be included in the model. Further, I defined dispersal rates between colonies as state-specific to address individual differences as done in Chapter 3. Therefore, there are much more parameters to estimate and Bayesian sampling is much slower than for the model in which colonies are not explicitly taken into account (Chapter 3). To accelerate computation time (time to convergence as well as time per iteration), we replaced the individual-based state-space formulation of the multistate capture-recapture submodel by using the multinomial likelihood applied to the m-array summarizing the capture-recapture histories (see Appendix E; Kéry and Schaub 2012). Because development and computation were quite long, I was only able to apply this integrated "multi-colony" model to nine years of the monitoring period, 1989–1997 (a period during which 5 colonies were occupied; one colony was decreasing and went extinct in 1998, while the smallest colony increased and became the largest in 1995).

I obtained preliminary results which partly answer the questions left open at the end of Chapter 3 (see details in Appendix E). First, I obtained new estimates of the annual number of immigrants breeding for the first time in the population by summing up colony-specific estimates. They were more precise, and generally higher than in Chapter 3; 95% credible intervals were all within [189,631] (Appendix E.2). Second, I found evidence of a positive association (from partial correlation) between the number of immigrants and colony productivity and also the number of breeders in the focal colony (in the previous year; Appendix E.3). I retrieved a negative association between the number of immigrants and the number of skippers attending the colony (in the previous year; Appendix E.3). Moreover, I found negative associations in former breeders between the probability of leaving a colony and productivity in that colony and also conspecific abundance in that colony (in the previous year; Appendix E.3). I found positive associations in former breeders and first-time breeders in the probability to join a new colony and colony productivity (in the previous year; Appendix E.3). I did not find associations between social information and the probability of leaving or joining a colony in former skippers (Appendix E.3).

These preliminary results thus suggest that immigrants do use social information available in the year preceding their establishment as breeders. This confirms the hypothesis provided at the end of Chapter 3: some productive patches within the population are driving substantial immigration and thus population maintenance, despite a poor context in the population as a whole. These results also confirm that colony productivity drives departure decisions from the colonies (see Chapter 2), and individual choices among potential colonies of arrival. They show that conspecific abundance in the colonies is another driver of immigrants' attraction and breeders' retention. This point is quite interesting because my dissertation tended to consider such phenomena as negligible in breeding habitat selection by kittiwakes, unlike competition for breeding sites. The picture seems a bit more complex. In the case of local individuals, it should be noted that here (Appendix E) I looked at associations between social information and dispersal, but not the decision to breed (as in Chapter 3). Nonetheless, both models (at the population scale: Chapter 3, and at the colony scale: Appendix E) complete the same story (also depicted in Chapter 2): individuals disperse from low- towards high-quality patches according to social information in order to get a breeding position that will maximize their fitness, but they may be prevented from doing so by competition, and the deterioration of local habitat quality which implies to acquire a new breeding position in another (high-quality) patch.

These integrated “multi-colony” analyses have to be continued and extended to a longer study period to take advantage of the large dataset available, confirm preliminary results, possibly detect other associations, and develop more complete interpretations. The analyses might notably be refined to also address how colony heterogeneity affects transitions toward the state ‘breeder’ (see further discussion in Appendix E.4). We could also model colony-specific apparent survival to address differences among colonies in permanent emigration, because adults share most of their feeding environment in common and are rarely depredated in their breeding habitat. At sea mortality from bycatch in the feeding habitat is unlikely to be colony-specific. Nonetheless, it would be necessary to identify and control for factors that might induce colony-specific mortality if individuals are not distributed independently of their survivorship (see further discussion in Appendix E.4). Moreover, the understanding of factors leading to the decision to breed made by marked individuals would benefit from analyses taking individual factors into account because the individual state is known to influence this decision (see e.g. Cam and Monnat 2000, Desprez et al. 2011). Such analyses might clarify how habitat selection (information use, dispersal, competition) affects the decision of when to breed, and how individual-specific circumstances modulate habitat selection and the decision to breed.

5.3.3 Mechanisms of habitat selection in nomadically breeding species

The biology of nomadically breeding species is poorly known, mostly because it is particularly difficult to monitor individuals that almost always move over wide areas in variable, unknown directions and potentially beyond study boundaries that are affordable to researchers. Habitat selection in these species remains mysterious because it appears to be unpredictable (Erwin et al. 1998, Parejo et al. 2006), as well as the environment within which these species have evolved. In the slender-billed gull, the annual location of colonies is not correlated with previous reproductive success in the marsh zone (Simon et al. *in prep.*). It seems that bird species from unpredictable habitats benefit from a strong reactivity to proximate environmental cues, a quick settlement on colony sites, a short period of attendance at the colony sites, and a very high synchrony in breeding activities among individuals of the same colony (McNicholl 1975). Such features necessarily imply a strong social cohesion, which might be achieved with a high level group adherence over the years (McNicholl 1975). However, group adherence over the years remains to be assessed in nomadically breeding species (as well as in desertion/colonization events in species described as more "philopatric" as the kittiwake).

It would be necessary to rigorously assess whether slender-billed gulls are associated randomly from one year to the next, or form groups that are maintained over the years (Francesiaz et al. *in press*). If we can identify consistent groups, we might then be able to estimate flows of individuals between these groups. This would provide a valuable basis for the understanding of habitat selection mechanisms in nomadic species. For example, rather than selecting a breeding location based on local conspecific reproductive success and local conspecific abundance, nomadic breeders might select the group in which they will breed based on the group success and group size (thus, independently of the locality; see Francesiaz et al. *in press*). However, ecologists are currently lacking appropriate tool to study this issue.

To date, available capture-recapture models for the study of animal movements require defining static sites (or static groups) between which movements are occurring (Thompson et al. 2009). However, due to nomadism, imperfect detection, mortality, and flows of individuals between groups, it may be impossible to differentiate groups by eye. Notably, some groups may amalgamate in some years and split in others years, and some groups may even be temporary absent from the study area (which potentially occurs in the slender-billed gull, see Chapter 4). Such groups should be based on latent probabilities of association between individuals over the years (dependent on resighting in the same site), but not on a priori differences in vital parameters. New tools have to be developed if one wishes to identify latent groups in such a complex context. I began to develop a capture-recapture model in this purpose in a Bayesian framework with Roger Pradel. Such advances in capture-recapture modeling would open an important research path because they will allow taking into account phenomena of group dispersal that induce non-independence among individual capture-recapture histories, and therefore violate one of the assumptions of classical capture-recapture models. These tools might also be of substantial interest for the study of spatiotemporal dynamics of social networks in the wild (Pinter-Wollman et al. 2014), which are increasingly applied to study animal social behavior (Wey et al. 2008, Sih et al. 2009, Kurvers et al. 2014), but currently do not take imperfect detection and mortality into account. For example, these tools might be useful to disentangle individual and collective (informed) decision making in dispersal and fission-fusion of social groups (e.g. Sueur et al. 2011).

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After fifty years of research on habitat selection processes which have led to considerable scientific progress, many issues remain to be addressed in this field. Long-term individual-based data, advanced statistical tools to analyze them, and computing facilities to run analyses are increasingly available. They offer exciting prospects for novel investigations on neglected aspects of the decisions of where and when to breed.

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A

Supporting information to Chapter 1

A.1. Conspecific reproductive success in habitat selection

I performed a census of the literature to find papers that addressed the hypothesis of the use of conspecific reproductive success (i.e. public information) in breeding habitat selection. I found 56 studies that addressed this hypothesis, either through theoretical simulations, empirical analyses, or experimental manipulations. Most of them provided support to the hypothesis, but some did not. The main and usual explanation for such results was the unpredictability of the environment in which mechanisms of habitat selection were supposed to have evolved. Indeed, habitat predictability has been pointed as a major prerequisite to the evolution of the use of public information in breeding habitat selection, notably by the few theoretical studies which investigated this hypothesis.

Further, some studies found evidence of public information use for breeding habitat selection only in particular classes of individuals (for instance defined by sex, age, breeding experience in the study area, breeding status, or individual success) or stage of the dispersal process (i.e. departure, or settlement). Various possible explanations have been provided. They usually referred to biological characteristics of the study system (e.g. territoriality, mating, and features of the breeding sites). Hereafter Table A.1.1 provides the corresponding references. I added the species name and a summary conclusion saying if the studies found some support for public information use (just yes or no). However, I did not detail the class(es) of individuals concerned (see above), and the material and methods (e.g. statistical tools, observational/experimental design, dispersal stage under study, spatial scale of dispersal and information, measure of reproductive success, etc.). I did not intend to provide a detailed review of the hypothesis in this appendix. I invite the reader wishing further information to inspect the references.

I found these publications by searching in the database of Google Scholar (https://scholar.google.fr/). I used different combinations of appropriate keywords such as: "public information", "breeding habitat selection", "social information", "conspecific reproductive success", "habitat copying", "dispersal decisions", "habitat choice", "nest-site selection", "informed dispersal", "information use", etc. I also browsed the references provided in the papers I found. Almost all references gathered in this list and published from 1998 (i.e. after the publication of the seminal papers by Bouliner and Danchin in 1997, Danchin and Wagner in 1997 and Danchin et al. in 1998) explicitly referred to “public information use” (either using this expression or an equivalent term) as a working hypothesis for breeding habitat selection. Papers published before 1998, except Boulinier ad Danchin (1997), did not referred to this hypothesis but provided direct support for such a mechanism of habitat selection. However, conclusions provided by the oldest papers have to be taken more cautiously, notably because of low samples sizes and statistical issues.

Given this bibliographic research, to my knowledge all studies examining the hypothesis of public information use for breeding habitat selection have focused on bird species. However, I do not claim to have conducted a fully exhaustive census. It is likely that I missed a number of papers testing for this hypothesis. Indeed, some authors might have more emphasized another target issue, making their study difficult to emerge from literature searches that are focused on social information use in breeding habitat selection.

It is also worth noting that a non-negligible part of the literature has focused on a quest for evidence of public information gathering during prospection prior to departure and settlement decisions. When I considered that these studies did not provide sufficient support for public information use in breeding habitat selection (i.e. they suggested information gathering but did not related this process to subsequent habitat choice), I excluded them from the list.

Publication				Taxon		Evidence	
Authors	Year	Title	Journal/Book	Species		Type	Ccl
Burger	1982	The Role of Reproductive Success in Colony-Site Selection and Abandonment in Black Skimmers (*Rynchops niger*)	The Auk	*Rynchops niger*	Black skimmer	E	Y
Blancher & Robertson	1985	Site consistency in kingbird breeding performance: implications for site fidelity	J Anim Ecol	*Tyrannus tyrannus*	Eastern kingbird	E	Y
Bollinger & Gavin	1989	The effects of site quality on breeding-site fidelity in Bobolinks	The Auk	*Dolichonyx oryzivorus*	Bobolinks	E	Y
Slagsvold & Lifjeld	1990	Return rates of male pied flycatchers: an experimental study manipulating breeding success	*Population biology of passerine birds*	*Ficedula hypoleuca*	Pied flycatcher	X	Y
Cadiou *et al.*	1993	Population regulation through recruitment, adult fidelity and non breeding in a colonial bird, the Kittiwake *Rissa tridactyla*	Revue d'Ecologie	*Rissa tridactyla*	Kittiwake	E	Y
Boulinier & Danchin	1997	The use of conspecific reproductive success for breeding patch selection in terrestrial migratory species	Evol Ecol	-	-	T	Y
Muller et al.	1997	The effects of conspecific attraction and habitat quality on habitat selection in territorial birds	Am Nat	*Troglodytes aedon*	House wrens	E	Y
Haas	1997	What characteristics of shelterbelts are important to breeding success and return rate of birds?	Am Mid Nat	*Turdus migratori* (1), *Toxostoma rufum* (2)	American robin, brown thrasher	E	N (1) Y (2)
Danchin, Boulinier & Massot	1998	Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality.	Ecology	*Rissa tridactyla*	Kittiwake	E	Y
Erwin et al.	1998	Modeling colony-site dynamics: a case study of gull-billed terns in coastal Virginia	The Auk	*Sterna nilotica*	Gull-billed tern	E	Y
Schjorring, Gregersen & Bregnballe	1999	Prospecting enhances breeding success of first-time breeders in the great cormorant, *Phalacrocorax carbo sinensis*	Anim Behav	*Phalacrocorax carbo sinensis*	Great cormorant	E	Y
Doligez et al.	1999	The use of conspecific reproductive success for breeding habitat selection in a non-colonial, hole-nesting species, the collared flycatcher	J Anim Ecol	*Ficedula albicollis*	Collared flycatcher	E	Y
Brown, Brown & Danchin	2000	Breeding habitat selection in cliff swallows: the effect of conspecific reproductive success on colony choice	J Anim Ecol	*Petrochelidon pyrrhonota*	Cliff swallow	E	Y
Oro & Pradel	2000	Determinants of local recruitment in a growing colony of Audouin's gull	J Anim Ecol	*Ichthyaetus audouinii*	Audouin's gull	E	N

Oro & Ruxton	2001	The formation and growth of seabird colonies: Audouin's gull as a case study	J Anim Ecol	*Ichthyaetus audouinii*	Audouin's gull	E	N
Serrano et al.	2001	Factors affecting breeding dispersal in the facultatively colonial lesser kestrel: individual experience vs. conspecific cues	J Anim Ecol	*Falco naumanni*	Lesser kestrel	E	Y
Frederiksen & Bregnballe	2001	Conspecific reproductive success affects age of recruitment in a great cormorant, Phalacrocorax carbo sinensis, colony	Proc Roy Soc B	*Phalacrocorax carbo sinensis*	Great cormorant	E	Y
Suryan & Irons	2001	Colony and population dynamics of black-legged kittiwakes in a heterogeneous environment	The Auk	*Rissa tridactyla*	Kittiwake	E	Y
Schjorring	2002	The evolution of informed dispersal: inherent versus acquired information	Evol Ecol	-	-	T	Y
Doligez, Danchin & Clobert	2002	Public information and breeding habitat selection in a wild bird population	Science	*Ficedula albicollis*	Collared flycatcher	X	Y
Serrano et al.	2003	Social and individual features affecting natal dispersal in the colonial lesser kestrel	Ecology	*Falco naumanni*	Lesser kestrel	C	N
Serrano & Tella	2003	Dispersal within a spatially structured population of lesser kestrels: the role of spatial isolation and conspecific attraction	J Anim Ecol	*Falco naumanni*	Lesser kestrel	E	N
Martinez Albrain	2003	Modeling temporal and spatial colony-site dynamics in a long-lived seabird	Popul Ecol	*Ichthyaetus audouinii*	Audouin's gull	E	N
Doligez et al.	2003	When to use public information for breeding habitat selection? The role of environmental predictability and density dependence	Anim Behav	-	-	T	Y
Pärt & Doligez	2003	Gathering public information for habitat selection: prospecting birds cue on parental activity	Proc R Soc B	*Ficedula abicollis*	Collared flycatcher	X	Y
Serrano et al.	2004	Dispersal and social attraction affect colony selection and dynamics of lesser kestrels	Ecology	*Falco naumanni*	Lesser kestrel	C	N
Kokko, Harris & Wanless	2004	Competition for breeding sites and site-dependent population regulation in a highly colonial seabird, the common guillemot *Uria aalge*	J Anim Ecol	*Uria aalge*	Common guillemot	C	N
Cam et al.	2004	Assessment of hypotheses about dispersal in a long-lived seabird using multistate capture–recapture models	J Anim Ecol	*Ichthyaetus audouinii*	Audouin's gull	C	N
Safran	2004	Adaptive Site Selection Rules and Variation in Group Size of Barn Swallows: Individual Decisions Predict Population Patterns.	Am Nat	*Hirundo rustica*	Barn swallow	C	N

Dolligez et al.	2004	Availability and use of public information and conspecific density for settlement decisions in the collared flycatcher	J Anim Ecol	*Ficedula abicollis*	Collared flycatcher	C	Y
Weaver & Brown	2005	Colony size, reproductive success, and colony choice in Cave Swallows *Petrochelidon fulva*	Ibis	*Petrochelidon fulva*	Cave swallows	C	N
Ward	2005	Habitat selection by dispersing yellow-headed blackbirds: evidence of prospecting and the use of public information	Oecologica	*Xanthocephalus xanthocephalus*	Yellow-headed blackbirds	C	Y
Sergio & Penteriani	2005	Public information and territory establishment in a loosely colonial raptor	Ecology	*Milvus migrans*	Black kite	C	Y
Kildaw et al.	2005	Formation and growth of new seabird colonies: the significance of habitat quality	Marine Ornithology	*Rissa tridactyla*	Kittiwakes	C	Y
Parejo, Oro & Danchin	2006	Testing habitat copying in breeding habitat selection in a species adapted to variable environments	Ibis	*Larus audouinii*	Audouin's gull	C	N
Pöysä	2006	Public information and conspecific nest parasitism in goldeneyes: targeting safe nests by parasites	Behav Ecol	*Bucephala clangula*	Common goldeneye	C	Y
Naves et al.	2006	Breeding performance, mate fidelity, and nest site fidelity in a long-lived seabird: behaving against the current?	Oikos	*Rissa tridactyla*	Kittiwake	C	Y
Aparicio, Bonal & Munoz	2007	Experimental test on public information use in the colonial Lesser Kestrel	Evol Ecol	*Falco naumanni*	Lesser kestrel	X	Y
Parejo et al.	2007	Blue tits use fledgling quantity and quality as public information in breeding site choice	Ecology	*Cyanistes caeruleus*	Blue tit	X	Y
Sachs et al.	2007	Evolution of coloniality in birds: a test of hypotheses with the red-necked grebe (*Podiceps grisegena*)	The Auk	*Podiceps grisegena*	Red-necked grebes	C	N
Citta & Lindberg	2007	Nest-site selection of passerines: effects of geographic scale and public and personal information	Ecology	Sialia currucoides	Moutain bluebirds	C	Y
Hénaux, Bregnballe & Lebreton	2007	Dispersal and recruitment during population growth in a colonial bird, the great cormorant *Phalacrocorax carbo sinensis*	J Avian Biol	*Phalacrocorax carbo sinensis*	Great cormorant	C	Y
Boulinier et al.	2008	Public information affects breeding dispersal in a colonial bird: kittiwakes cue on neighbours	Biol Lett	*Rissa tridactyla*	Kittiwake	X	Y
Betts et al.	2008	Social information trumps vegetation structure in breeding-site selection by a migrant songbird	Proc Roy Soc B	*Dendroica caerulescens*	Black-throated blue warbler	X	Y
Calabuig et al.	2008	Causes, consequences and mechanisms of breeding dispersal in the colonial lesser kestrel, *Falco naumanni*	Anim Behav	*Falco naumanni*	Lesser kestrel	C	N

Redmond et al.	2009	Public information facilitates habitat selection of a territorial species: the eastern kingbird	Anim Behav	*Tyrannus tyrannus*	Eastern kingbird	C	Y
Aubry, Cam & Monnat	2009	Habitat selection age-specific recruitment and reproductive success in a long-lived seabird	*Modeling Demographic Processes In Marked Populations*	*Rissa tridactyla*	Kittiwake	C	Y
Rioux et al.	2011	Pipping Plovers make decisions regarding dispersal based on personal and public information in a variable coastal ecosystem	*J Field Ornithol*	*Charadrius melodus melodus*	Pipping plover	C	Y
Bled, Royle & Cam	2011	Assessing hypotheses about nesting site occupancy dynamics	Ecology	*Rissa tridactyla*	Kittiwake	C	Y
Pärt et al.	2011	Prospectors combine social and environmental information to improve habitat selection and breeding success in the subsequent year	J Anim Ecol	*Oenanthe oenanthe*	Northern wheatear	C	Y
Mariette & Griffith	2012	Conspecific attraction and nest site selection in a nomadic species, the zebra finch	Oikos	*Taeniopygia guttata*	Zebra finch	C	Y
Hoi et al.	2012	Traditional versus non-traditional nest-site choice: alternative decision strategies for nest-site selection	Oecologica	*Lanius minor*	Lesser grey shrike	C	N
Fernandez-Chacon	2013	When to stay, when to disperse and where to go: survival and dispersal patterns in a spatially structured seabird population	Eco-graphy	*Larus audouinii*	Audouin's gull	C	N
Szostek, Schaub & Becker	2014	Immigrants are attracted by local pre-breeders and recruits in a seabird colony	J Anim Ecol	*Sterna hirundo*	Common tearn	C	N
Kivelä et al.	2014	The past and the present in decision-making: the use of conspecific and heterospecific cues in nest site selection	Ecology	*Ficedula abicollis*	Collared flycatcher	C	Y
Rushing et al.	2015	Habitat features and long-distance dispersal modify the use of social information by a long-distance migratory bird	Ecology	*Setophaga ruticilla*	American redstart	X	N

Type of evidence: empirical (E), experimental (X), theoretical simulations (T); Conclusion ('Ccl') is "yes" (Y) when the results provided some support for public information use in breeding habitat selection (even when it concerned only the departure or settlement phase of dispersal, or not all classes of individuals defined in the study). In the opposite case, the conclusion is "no" (N). When analyses were conducted at the population and the individual level, I referred to the individual level as the most informative for public information use.

B

Supporting information to Chapter 2

B.1. Population history over the study period

B.1.1 History of the kittiwake population

Kittiwakes have been banded in the Cap Sizun since 1979 (Fig. B.1.1). At the beginning of the monitoring program, the study area hosted 4 colonies, which were relatively close to one another (colony 1, 2, 3 and 4, in or near the nature reserve of Goulien; Fig. B.1.1) but only colony 1 was subject to intensive survey and individual monitoring. In 1981 the program was extended to colony 3, and then to colony 2 and colony 4 in 1983 (Fig. B.1.1, B.1.2). A few individuals colonized the Pointe du Raz in 1982, thus establishing colony 5 (Fig. B.1.1, B.1.2) which was included in the program in 1984 and which is still intensively monitored today. While the annual number of nests increased in colony 5 – until it concentrated most of the breeding population –, the other patches were progressively deserted (Fig. B.1.2), and a "new" colony was established between Goulien and the Pointe du Raz (colony 6). There are historical records of presence of kittiwakes in colony 6 before the study started (Guermeur and Monnat 1980). The formerly largest colony (colony 1) went extinct in 1999. A pioneer pair built a complete nest in the Pointe du Van in 2004, thus re-establishing colony 6 (Fig. B.1.1, B.1.2) which was included into the monitoring program. Colony 2 went extinct in 2008, colony 3 and colony 4 contained very few nests in 2012 (17 and 8, respectively) and went extinct in 2013 (Fig. B.1.2). Additional information concerning kittiwake repartition and dynamics in France between 1960 and 2000 (with further details concerning the history of the study population in Brittany) can be found in Guemeur and Monnat (1980), Cadiou (1993) and Monnat and Cadiou (2004).

Table B.1.1 provides the detailed summary of the number of nests, cliffs, social groups and colonies that were active each year in each patch over the study period (1982-2012) in the population. Further, as a complement to the figure showing the breeding population dynamics at the colony scale (Fig. B.1.2), the breeding population dynamics at the social group scale within each colony is given in Fig. B.1.3 and B.1.4.

Table B.1.1. Summary of the annual population structure (in spatial units) across spatial scales over 1982-2012. For each scale the number of spatial units per patch-year is summarized by the range limits (minimum–maximum) and mean ± standard deviation.

Units	Scale			
	Cliff	Social group	Colony	Population
Nests	1–261 30.10 ± 36.50	1–273 66.63 ± 65.42	1–886 207.04 ± 210.10	658–1201 935.03 ± 117.95
Cliffs	–	1–5 2.21 ± 1.09	1–16 6.87 ± 4.00	20–44 31.00 ± 7.18
Social groups	–	–	1–7 3.11 ± 1.73	5–18 14.03 ± 2.76
Colonies	–	–	–	2–5 4.52 ± 0.68

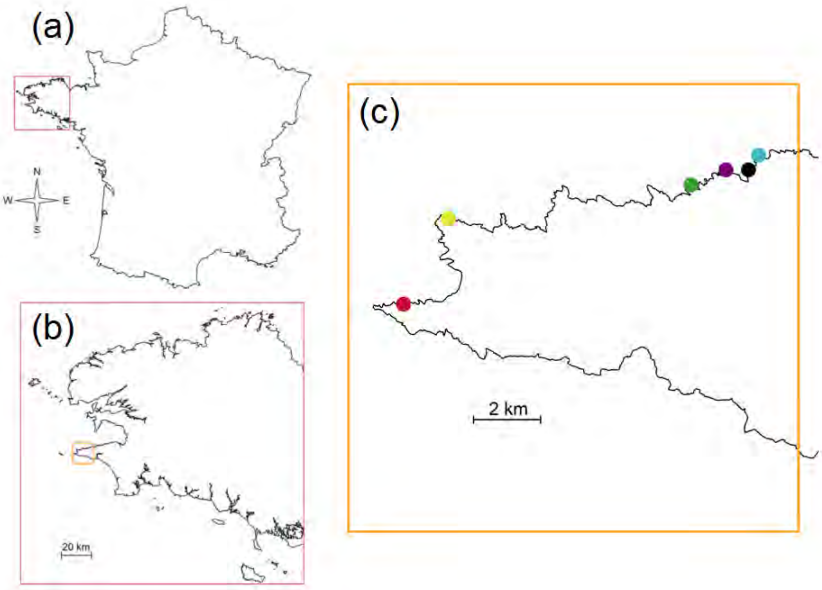

Figure B.1.1. Location of the study area and colony sites. (a) The study population is located in Brittany, northwestern France (red square), (b) in the Cap Sizun (orange square). Dots indicate colony sites (c): colony 1 in green, colony 2 in purple, colony 3 in black, colony 4 in blue, colony 5 in red and colony 6 in yellow.

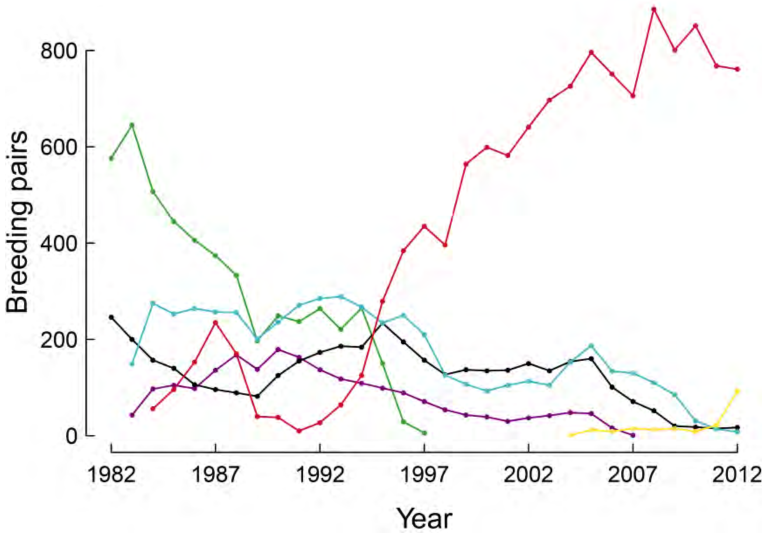

Figure B.1.2. Size of the colonies over 1982-2012. Colony size is expressed in number of breeding pairs, which was approximated by the number of nests that have reached the completion criterion (see *Materials and Methods*). Each time series starts in either 1982 or at the beginning of the monitoring in the given colony. The size is not plotted for colony sites once they have gone extinct. Colony 1 is plotted in green, colony 2 in purple, colony 3 in black, colony 4 in blue, colony 5 in red and colony 6 in yellow.

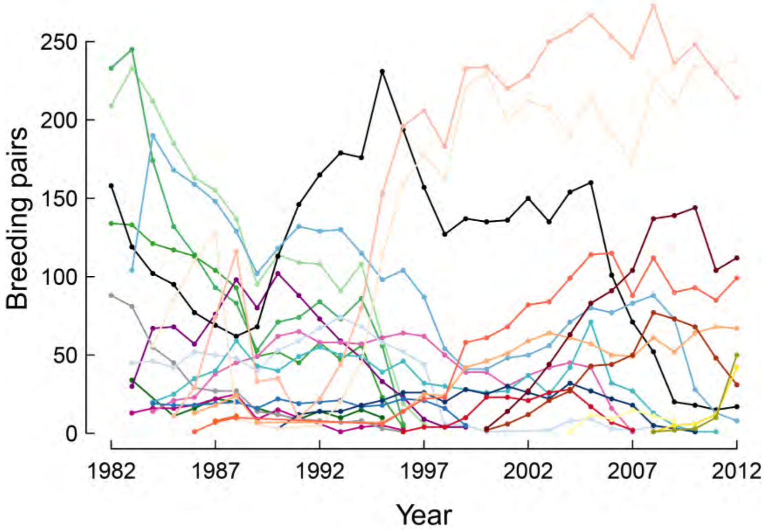

Figure B.1.3. Size of the social groups over 1982-2012. Group size is expressed in number of breeding pairs, which was approximated by the number of nests that have reached the completion criterion (see *Materials and Methods*). Color shades refer to the colonies in which the social group was located, as plotted in Fig. B.1.2: green shades for colony 1, purple shades for colony 2, grey shades for colony 3, blue shades for colony 4, red shades for colony 5 and yellow shades for colony 6. Separate plots for each colony are given in Figure B.1.4.

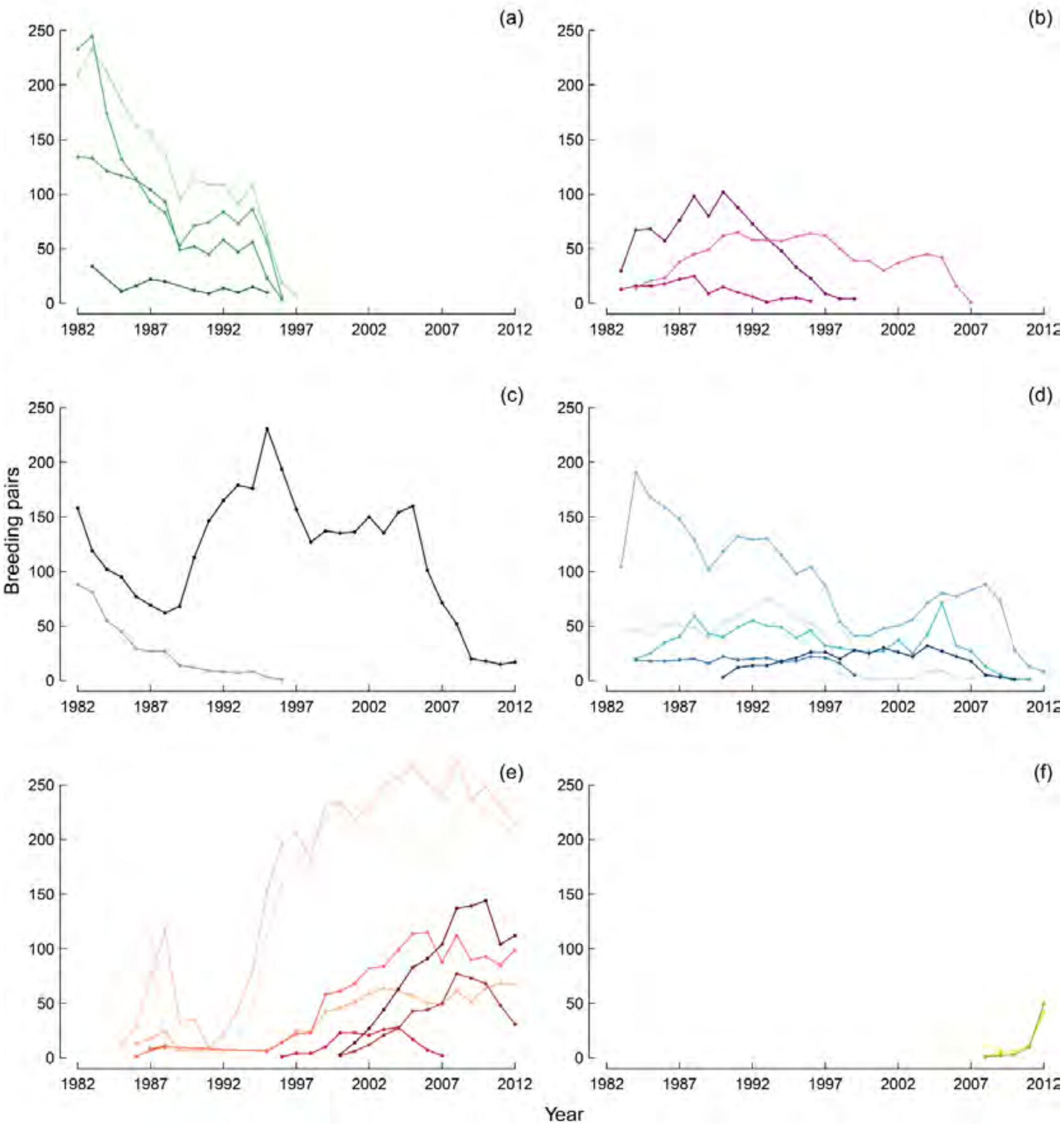

Figure B.1.4. Size of the social groups over 1982-2012 within (a) colony 1, (b) colony 2, (c) colony 3, (d) colony 4, (e) colony 5, (d) colony 6. Group size is expressed in number of breeding pairs, which was approximated by the number of nests that have reached the completion criterion (see *Materials and Methods*).

B.1.2 Literature cited

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B.2 Heterogeneity and predictability in habitat quality

B.2.1 Spatiotemporal heterogeneity of habitat quality

As mentioned in the *Introduction*, one important ecological prerequisite providing evolutionary relevance to public information use is that the environment is heterogeneous with regard to breeding habitat quality (Danchin et al. 1998, Doligez et al. 2003). Such spatiotemporal heterogeneity implies that patch success differs among patches (at a given spatial scale) in space and time, so that the relative quality of patches varies among years (Parejo et al. 2006). Within the largest cliff of the study population, Bled et al. (2011) provided evidence of spatiotemporal variation in nest-site quality (independently of individual characteristics).

Although spatiotemporal patchiness of the habitat has rarely been evaluated in studies referring to the public information use, when this has been done authors have chosen to use two-way analyses of variance (ANOVA) with space (i.e. patches) and time (i.e. years) as explanatory factors and patch success as the response (e.g. Parejo et al. 2006, Aparicio et al. 2007). Others have chosen to use the nest success as the response, which allows introducing an interaction effect between space and time (e.g. Danchin et al. 1998, Doligez et al. 1999). However, these methods might lead to incomplete depiction of the features of spatiotemporal variability that make information use in habitat selection evolutionary relevant (i.e. that the relative quality of patches varies among years).

Indeed, when patch success is the response variable, the ANOVA will allow the detection of consistent spatial effects across years and consistent temporal effects across patches (i.e. process variance). The additional effect of the annual context proper to each patch (which would be captured by an interaction between space and time) is not identifiable because annual patch quality is not repeated and can be measured only once. It is thus confounded into residual variation (i.e. sampling variance) with other factors (e.g. mean individual fecundity in the patch) and measurement error. If the effects of space and time appear to be substantial in the ANOVA, they might not be ecologically relevant in the framework of the evolution of public information use. Indeed, if sampling variance is low compared to process variance, patches would still be consistently ordered according to their quality over time. Such environment should favor the evolution of strict philopatry over other strategies of habitat selection (Doligez et al. 2003). Conversely, even if there is no support for effects of space and time effects in the ANOVA, patch success might still be sufficiently variable in each year and each location to generate heterogeneous conditions; this would create opportunities for public information use in habitat selection to be sufficiently efficient for this mechanism of habitat selection to evolve.

On the other hand, if the response variable of the ANOVA is nest success, the model might then be able to capture an interaction between space and time. However, static and temporally-varying characteristics of the nest site and breeding pair are very likely to influence nest success (e.g. Naves et al. 2006). To our knowledge, these crucial factors have never been included in such analyses to assess spatiotemporal variability in habitat quality (e.g. references above, Brown et al. 2000, Serrano et al. 2004). Further, such down-scaling transfers the issues raised above to the nest-site level.

Consequently, we believe that the use of visual assessment is sufficient to evaluate spatiotemporal heterogeneity of habitat quality. This requires assuming that individuals are distributed in space and time independently of their own characteristics influencing reproductive success (e.g. experience, age). A less restrictive assumption would be that the influence of individual characteristics on local success is sufficiently low that we can ignore the biases this might induce on habitat quality assessed through breeding successes. Hereafter we provide plots of habitat quality (expressed as the proportion of successful nests within a given patch, see *Materials and Methods*) over the 1982-2012 period, at the cliff, social-group and colony scale. We used color gradients to identify colonies and social groups in the different plots and various symbols to identify cliffs.

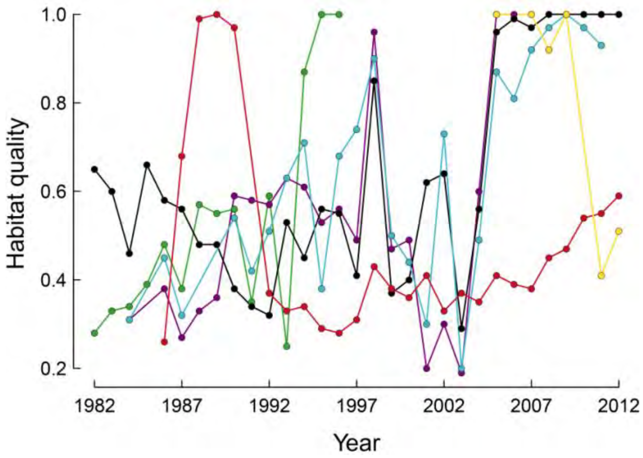

Figure B.2.1. Habitat quality in the colonies over the 1982-2012 period. Colony 1 is in green, colony 2 in purple, colony 3 in black, colony 4 in blue, colony 5 in red and colony 6 in yellow.

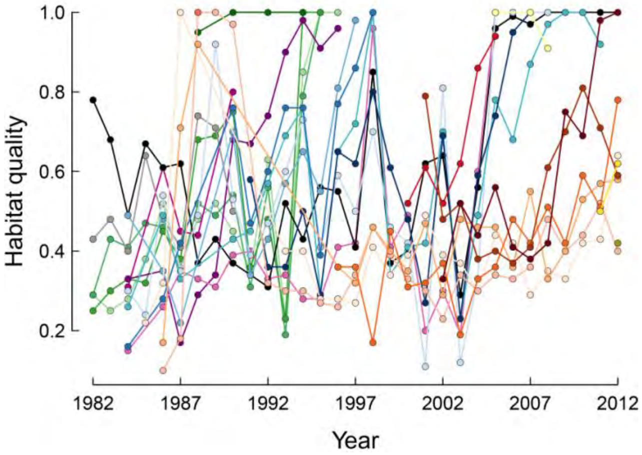

Figure B.2.2. Habitat quality in the social groups over the 1982-2012 period. Gradients of the colors used for colonies in Fig. B.2.1 were used to differentiate social groups within each colony. For clarity, each colony is plotted separately in Fig. B.23 hereafter.

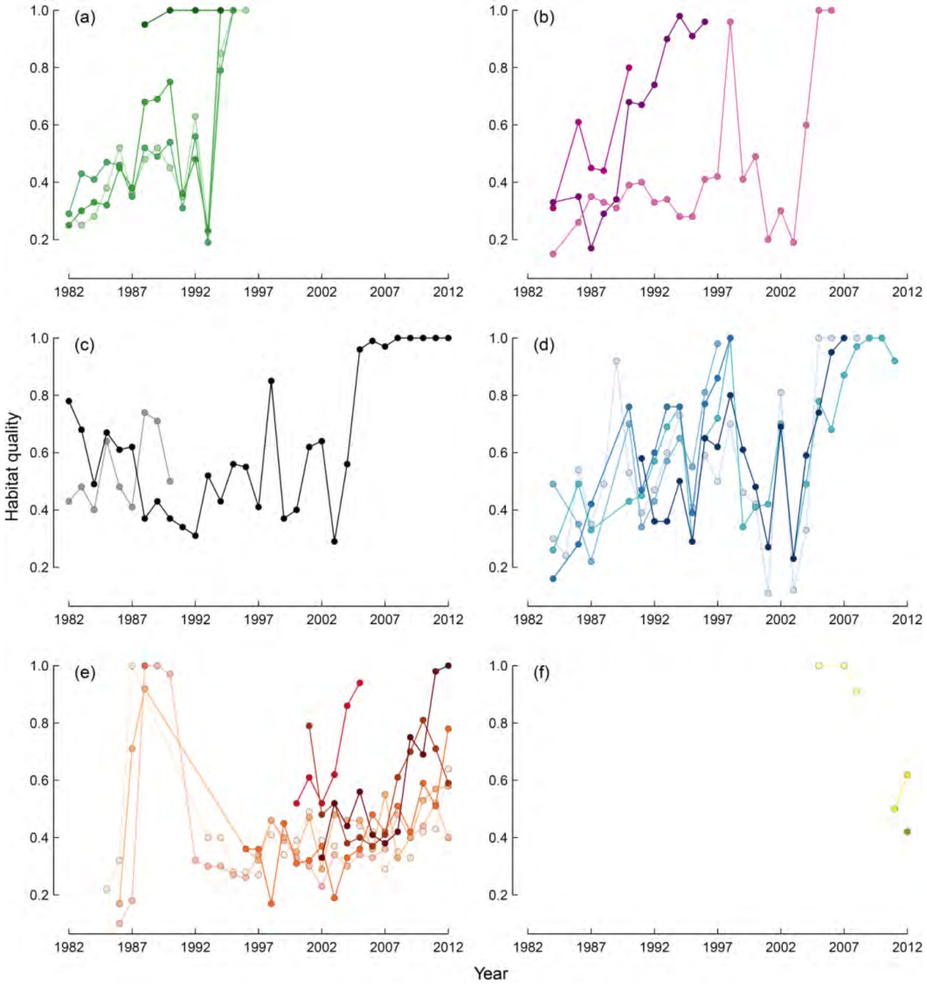

Figure B.2.3. Habitat quality in the social groups over the 1982-2012 period in (a) colony 1, (b) colony 2, (c) colony 3, (d) colony 4, (e) colony 5, (f) colony 6. Gradients of the colors used for colonies in Fig. B.2.1 were used to differentiate social groups within each colony.

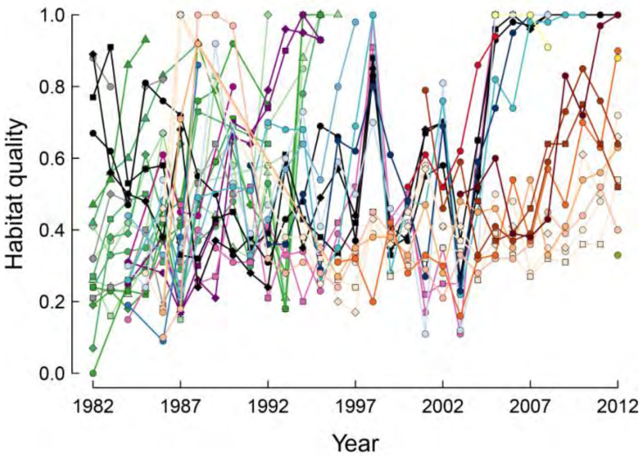

Figure B.2.4. Habitat quality in the cliffs over the 1982-2012 period. Color gradients differentiate colonies and social groups (see Fig. B.2.1, B.2.2). Symbols differentiate cliffs within social groups. For clarity, each colony is plotted separately in Fig. B.2.5.

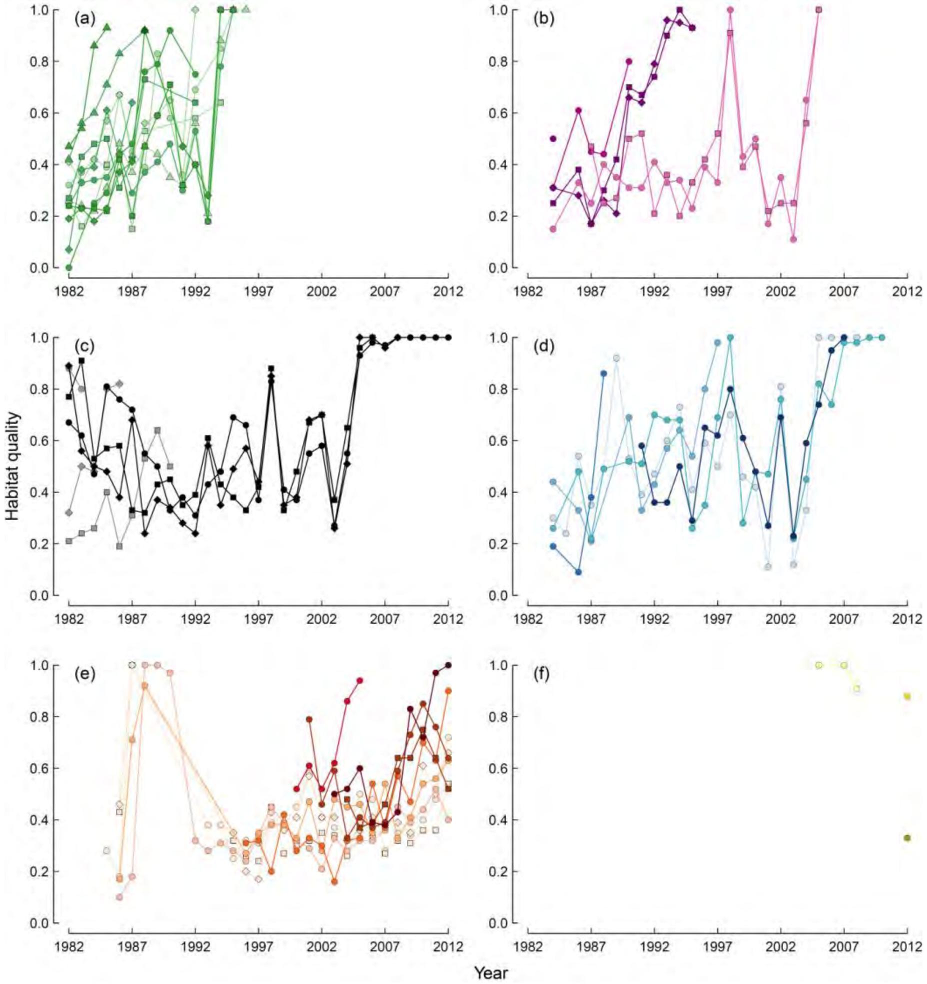

Figure B.2.5. Habitat quality in the cliffs over the 1982-2012 period in (a) colony 1, (b) colony 2, (c) colony 3, (d) colony 4, (e) colony 5, (f) colony 6. Symbols and colors are the same as in Fig. B.2.4.

B.2.2 Temporal autocorrelation of habitat quality

Another evolutionary prerequisite to the use of public information in breeding habitat selection is that habitat quality is partly predictable over time, at least between two breeding occasions, which results in temporal autocorrelation of patch success (Danchin et al. 1998, Doligez et al. 2003). We assessed the predictability of habitat quality in a time-series analysis framework, by inspecting the sample autocorrelation function of local success up to a lag of five years at the cliff, social-group and colony scale.

Autocorrelation estimates are known to be biased down in small samples (under ca. 50 time steps; Box and Jenkins 1976, Huitema and Mckean 1991). Here, we assumed that the same dynamic process potentially leading to temporal predictability of patch success was operating in each patch at a given scale. We thus considered that the autocorrelation function was the same among patches at a given scale. Indeed, we expected roughly similar physical and biological phenomena to influence predictability in habitat quality (*e.g.* geographical characteristics, predation and ectoparasitism; Boulinier and Lemel 1996). At each spatial scale, we therefore used all pairs of local success values distant by t years in the different patches to estimate an overall autocorrelation at lag t. This allowed us to gather all observations from numerous short time series and benefit from larger sample size for accurate estimation.

We handled missing values (due to the data excluded, see *Materials and Methods*) following the approach described by Cryer (1986), which consists in ignoring them by using only complete pairs of values in the time series. In large samples, for a stationary time-series, and under mild conditions (i.e. that the series is a collection of independent and identically distributed realizations of a random variable with finite fourth moment), we can obtain estimates of the standard deviation (that is here, the standard error) for non-autoregressive white noise (WN) or moving average (MA) processes (see Cryer and Chan 2008, Shumway and Stoffer 2011). We can then use these standard errors to get the 95% confidence intervals for non-autoregressive WN and MA processes. If the autocorrelation of our time series fall beyond the 95% confidence limits, we conclude that the process is different from a non-autoregressive process.

The formula of the sample autocorrelation function at lag k ($r(k)$) is the following:

$$r(k) = \frac{\sum_t (x_t - \bar{x})(x_{t+k} - \bar{x})}{\sum_t (x_t - \bar{x})^2}$$

where x_t is the first observation in the pair of values $\{x_t, x_{t+k}\}$ of a time series in a given patch, and x̄ is the average over all time series (i.e. all patches) at a given spatial scale.

For a non-autoregressive WN process, a time-series sample with n non-missing observations, the autocorrelation function at any lag is approximately normally distributed with mean zero and sample standard deviation s:

$$s = \frac{1}{\sqrt{n}}.$$

For a MA process, a time-series sample with n non-missing observations, the autocorrelation function at lag k (r(k) is approximately normally distributed with mean zero and sample standard deviation s:

$$s = \sqrt{\frac{1}{n}(1 + 2 \cdot \sum_{j=1}^{k-1}(r(k)^2)} \; .$$

We considered that autocorrelation estimates were different from WN and MA expectations when they were not included in the 95% confidence interval of WN and MA sample autocorrelation functions. Figure B.2.6 shows plots of habitat quality (i.e. patch success) in year *t* against habitat quality in year *t+1* at the cliff, social-group, and colony scale. Figure B.2.7 shows the autocorrelograms (i.e. graphs of the autocorrelation function, up to lag 5) at the cliff, social-group and colony scale with WN and MA 95% confidence intervals.

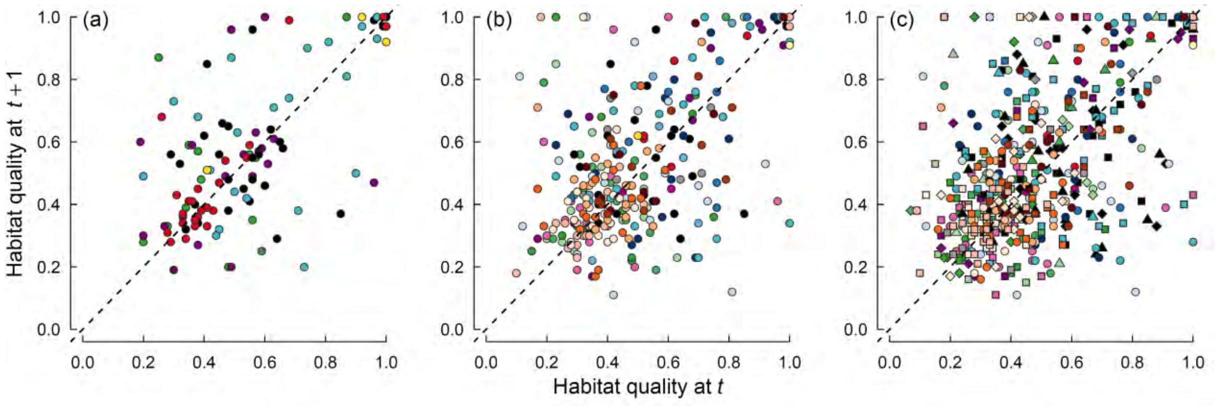

Figure B.2.6. Habitat quality a *t+1* plotted against habitat quality at *t*, at (a) the colony scale, (b) the social-group scale, (c) the cliff scale. The closer the points to the line x=y (dashes), the more predictable habitat quality.

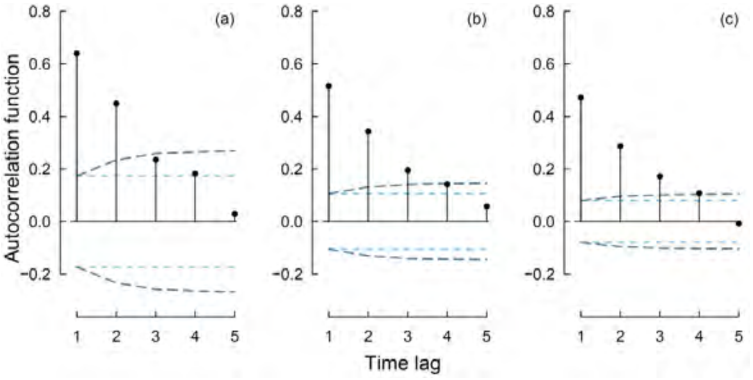

Figure B.2.7. Autocorrelograms of patch success at (a) the colony scale, (b) the social-group scale, (c) the cliff scale**.** Exact values of the autocorrelation function at lag 1 are given in *Results***.** 95% confidence intervals of non-autoregressive processes are given by dashed lines, in light blue for white noise, and in dark blue for moving average. Sample sizes: (a) 128, (b) 344, (c) 608. Complete couples of values (from lag 1 to lag 5): (a) 116, 112, 108, 103, 96, (b) 303, 285, 266, 248, 229, (c) 524, 484, 442, 407, 371.

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B.3 Some model specification and *BUGS* code

B.3.1 Variance-covariance matrix of the individual and year random effects

The variance-covariance matrix Σ_υ of the quadrivariate normal for year and individual random effects takes the following form:

$$\Sigma v = \begin{bmatrix} var(u_v^{(1)}) & cov(u_v^{(1)}, u_v^{(2)}) & cov(u_v^{(1)}, u_v^{(3)}) & cov(u_v^{(1)}, u_v^{(4)}) \\ cov(u_v^{(1)}, u_v^{(2)}) & var(u_v^{(2)}) & cov(u_v^{(2)}, u_v^{(3)}) & cov(u_v^{(2)}, u_v^{(4)}) \\ cov(u_v^{(1)}, u_v^{(3)}) & cov(u_v^{(2)}, u_v^{(3)}) & var(u_v^{(3)}) & cov(u_v^{(3)}, u_v^{(4)}) \\ cov(u_v^{(1)}, u_v^{(4)}) & cov(u_v^{(2)}, u_v^{(4)}) & cov(u_v^{(3)}, u_v^{(4)}) & var(u_v^{(4)}) \end{bmatrix}$$

where *v* is *i* or *t*, $var(u_v^{(j)})$ is the variance of random effect u_υ in model equation of level *j* (see *Materials and Methods* for details), *cov*(*a*,*b*) is the covariance of *a* and *b*. The sign of *cov*(*a*,*b*) indicate if the variation in variables *a* and *b* tends to be in the opposite direction (negative) or the same direction (positive).

We can also reformulate *cov*(*a*,*b*) as a function of the correlation *cor*(*a*,*b*), the magnitude of which indicates the strength of the linear relationship between *a* and *b*:

$$cor(u_v^{(j)}, u_v^{(j+k)}) = \frac{cov(u_v^{(j)}, u_v^{(j+k)})}{\sqrt{var(u_v^{(j)})var(u_v^{(j+k)})}}$$

where $j \in \{1,2,3\}$, $k \in \{2,3,4\}$, and v is i or t.

B.3.2 Additional details on the priors

All prior distributions are represented in Fig. B.3.1 hereafter.

On the horseshoe prior— The horseshoe prior (see *Materials and Methods*) belongs to the class of scale-mixture of normal distributions for model coefficients. Thus, each normal has a different, unknown variance estimated from the data, which is the product of a local (specific to the coefficient) and a global (common to all coefficients) variance parameter. It is obtained by using a standard half-Cauchy to the local variance parameters. We also used a half-Cauchy for the global variance parameter. The Cauchy distribution can be formulated as a scale mixture with an inverse Gamma(0.5,0.5) (see details in model formulation in BUGS code below; Carvalho et al. 2010).

The horseshoe prior offers much better performances than the LASSO (Least Absolute Shrinkage and Selection Operator, Park and Casella 2008), and yields results that are closely similar to what is obtained with full Bayesian model averaging across discrete mixture models (Carvalho et al. 2010). In addition, compared to approaches that are commonly used for variable selection in ecology (e.g. model comparisons via an information criterion such as AIC, BIC or DIC; Burnham et al. 2011, Spiegelhalter et al. 2014, Hooten and Hobbs 2015), the use of shrinkage priors provides a substantial gain in time, computational resources and clarity of analysis. Shrinkage regression involves a unique model for inferences, whereas variable selection may rapidly involve consideration of numerous models, which leads to prohibitively time-consuming analyses when combinations of many variables are considered. Indeed, if the full model contains p parameters and if all possible models are biologically relevant, there would be 2^p models to compare.

On the priors used in the Choleski decomposition — Chen and Dunson (2003) suggested to use a factorization of the 4×4 variance-covariance matrix Σ into a diagonal matrix Λ and lower triangular Γ with a diagonal of 1:

$$\Sigma = \Lambda\Gamma\Gamma'\Lambda$$

$$\text{where } \Lambda = diag(\lambda_1, \ldots, \lambda_4) \text{ and } \Gamma = \begin{matrix} 1 & & & \\ \gamma_{21} & 1 & & \\ \gamma_{31} & \gamma_{32} & 1 & \\ \gamma_{41} & \gamma_{42} & \gamma_{43} & 1 \end{matrix}.$$

This decomposition of the variance-covariance matrix enables investigators to use independent normal distributions instead of directly considering a multivariate normal distribution. In this way, the variance-covariance matrix can be customized to address specific hypotheses. Following Chen and Dunson (2003), we used independent half-normal priors with mean 0 and variance 2.25 for the elements $\lambda_1, \ldots, \lambda_4$ of Λ and independent normal priors with mean 0 and variance 0.25 for the elements γ_{pq}, $2 \le p \le 4, q < p$. These priors give reasonable values (usually <15, see Fig. B.3.1) for the variance of the random effects, and is conservative in the sense that most of the probability mass is put on values <5. These priors thus reflect reasonable doubt concerning large differences between subjects (i.e. here, between years or individuals).

To represent each subject (i.e. here, each year or each individual) random effect, we multiplied a subject deviate picked within a standard normal distribution (i.e. mean 0 and variance 1) by $\Lambda\Gamma$ (see BUGS code below).

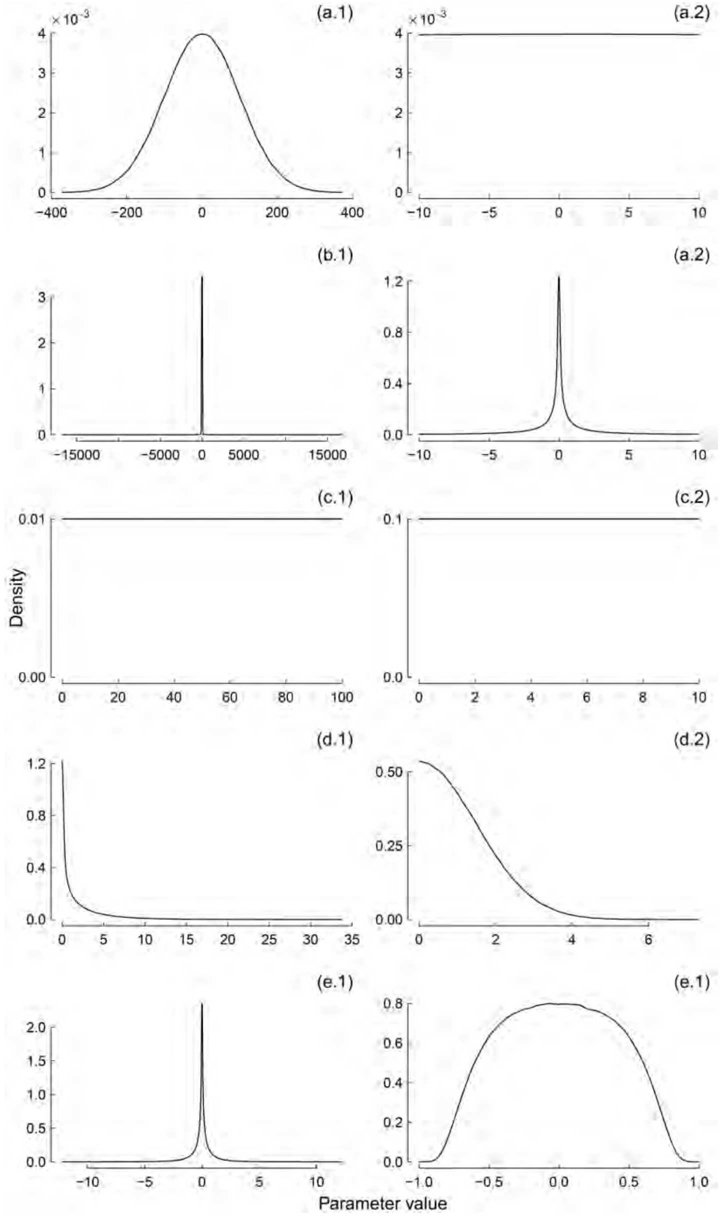

Figure B.3.1. Prior distributions used in the model. (a) Normal prior with mean 0 and variance 10^4 for the intercepts: (a.1) plotted from the 0.01% to 99.99% quantiles, and (a.2) plotted on [-10,10] – a reasonable range on the logit scale. (b) Horseshoe prior used for the fixed effects: (b.1) from the 0.01% to 99.99% quantiles, (b.2) on [-10,10]. (c) Uniform prior used for patch random effects: (c.1) on the range (0,100) for variance, (c.2) on the range (0,10) for standard deviation. (d) Prior used for individual and year random effects (see above): (d.1) for variance, (d.2) for standard deviation. (e.1) Prior used for covariance between individual or year effects. (e.2) Prior used for correlation between individual or year effects. The density of the horseshoe prior tends to infinity near zero. See further details in the BUGS code and *Materials and Methods*.

B.3.3 *BUGS* code

```
Model
{

# Likelihood of the first submodel
 for (i in 1:N1) {
  disp1[i] ~ dbern(P1[i])
  P1[i] <- pt(phi1[i],0,tau.robit,7)
  phi1[i] <- mu1
           + alphaSEX1[SEX1[i]]
          + alphaEXP1[EXP1[i]]
           + alphaRST1[RST1[i]]
           + betaQW1*((QW1[i]-mQW1)/sQW1)
           + intW1[RST1[i]]*((QW1[i]-mQW1)/sQW1)
           + betaQG1*((QG1[i]-mQG1)/sQG1)
           + intG1[RST1[i]]*((QG1[i]-mQG1)/sQG1)
           + betaQC1*((QC1[i]-mQC1)/sQC1)
           + intC1[RST1[i]]*((QC1[i]-mQC1)/sQC1)
           + YEAR[Y1[i],1]
           + SITE[NEST[i]]
           + IND[ID1[i],1]
  # prediction from the model (data replicate)
  pred1[i]  ~ dbern(P1[i])
  # discrepancy measures
  PPC1[i,1] <- ((pred1[i]-P1[i])*(pred1[i]-P1[i]))/(P1[i]*(1-P1[i])) # for replicates
  PPC1[i,2] <- ((disp1[i]-P1[i])*(disp1[i]-P1[i]))/(P1[i]*(1-P1[i])) # for observations
  # true/false positives/negatives
  TFPN1[i]  <- ifelse(disp1[i]==1,
               ifelse(disp1[i]==pred1[i],1,2),
               ifelse(disp1[i]==pred1[i],3,4))
 }

# Likelihood of the second submodel
 for (i in 1:N2) {
  disp2[i] ~ dbern(P2[i])
  P2[i] <- pt(phi2[i],0,tau.robit,7)
  phi2[i] <- mu2
           + betaSEX2[SEX2[i]]
           + betaEXP2[EXP2[i]]
           + betaRST2[RST2[i]]
           + betaQW2*((QW2[i]-mQW2)/sQW2)
           + betaQG2*((QG2[i]-mQG2)/sQG2)
           + betaQC2*((QC2[i]-mQC2)/sQC2)
           + intW2[RST2[i]]*((QW2[i]-mQW2)/sQW2)
           + intG2[RST2[i]]*((QG2[i]-mQG2)/sQG2)
           + intC2[RST2[i]]*((QC2[i]-mQC2)/sQC2)
           + YEAR[Y2[i],2]
           + CLIFF[CLI[i]]
           + IND[ID2[i],2]
  # prediction from the model (data replicates)
  pred2[i]  ~ dbern(P2[i])
  # discrepancy measures
  PPC2[i,1] <- ((pred2[i]-P2[i])*(pred2[i]-P2[i]))/(P2[i]*(1-P2[i])) # for replicates
  PPC2[i,2] <- ((disp2[i]-P2[i])*(disp2[i]-P2[i]))/(P2[i]*(1-P2[i])) # for observations
  # true/false positives/negatives
  TFPN2[i]  <- ifelse(disp2[i]==1,
               ifelse(disp2[i]==pred2[i],1,2),
               ifelse(disp2[i]==pred2[i],3,4))
 }

# Likelihood of the third submodel
 for (i in 1:N3) {
  disp3[i] ~ dbern(P3[i])
  P3[i] <- pt(phi3[i],0,tau.robit,7)
  phi3[i] <- mu3
           + betaSEX3[SEX3[i]]
           + betaEXP3[EXP3[i]]
           + betaRST3[RST3[i]]
           + betaQG3*((QG3[i]-mQG3)/sQG3)
           + betaQC3*((QC3[i]-mQC3)/sQC3)
           + intG3[RST3[i]]*((QG3[i]-mQG3)/sQG3)
           + intC3[RST3[i]]*((QC3[i]-mQC3)/sQC3)
           + YEAR[Y3[i],3]
           + SOCG[GS[i]]
           + IND[ID3[i],3]
  # prediction from the model (data replicates)
  pred3[i]  ~ dbern(P3[i])
  # discrepancy measures
```

```
  PPC3[i,1] <- ((pred3[i]-P3[i])*(pred3[i]-P3[i]))/(P3[i]*(1-P3[i])) # for replicates
  PPC3[i,2] <- ((disp3[i]-P3[i])*(disp3[i]-P3[i]))/(P3[i]*(1-P3[i])) # for observations
  # true/false positives/negatives
  TFPN3[i]  <- ifelse(disp3[i]==1,
               ifelse(disp3[i]==pred3[i],1,2),
               ifelse(disp3[i]==pred3[i],3,4))
 }

# Likelihood of the fourth submodel
 for (i in 1:N4) {
  disp4[i] ~ dbern(P4[i])
  P4[i] <- pt(phi4[i],0,tau.robit,7)
  phi4[i] <- mu4
           + betaSEX4[SEX4[i]]
           + betaEXP4[EXP4[i]]
           + betaRST4[RST4[i]]
           + betaQC4*((QC4[i]-mQC4)/sQC4)
           + intC4[RST4[i]]*((QC4[i]-mQC4)/sQC4)
           + alphaCOL[SE[i]]
           + YEAR[Y4[i],4]
           + IND[ID4[i],4]
  # prediction from the model (data replicates)
  pred4[i]  ~ dbern(P4[i])
  # discrepancy measures
  PPC4[i,1] <- ((pred4[i]-P4[i])*(pred4[i]-P4[i]))/(P4[i]*(1-P4[i])) # for replicates
  PPC4[i,2] <- ((disp4[i]-P4[i])*(disp4[i]-P4[i]))/(P4[i]*(1-P4[i])) # for observations
  # true/false positives/negatives
  TFPN4[i]  <- ifelse(disp4[i]==1,
               ifelse(disp4[i]==pred4[i],1,2),
               ifelse(disp4[i]==pred4[i],3,4))
 }

# Scale parameter for the robit link
 tau.robit <- pow(sigma_res,-2)
 sigma_res <- 1.5485

# Choleski decomposition (with priors) for the year random effects
 for (t in 1:NY){
   for (j in 1:4){
     epsilon.YEAR[t,j] ~ dnorm(0,1)
   }
  YEAR[t,1] <- delta.YEAR[1,1]*epsilon.YEAR[t,1]
  YEAR[t,2] <- delta.YEAR[2,2]*(gamma.YEAR[2,1]*epsilon.YEAR[t,1]
                              + epsilon.YEAR[t,2])
  YEAR[t,3] <- delta.YEAR[3,3]*(gamma.YEAR[3,1]*epsilon.YEAR[t,1]
                              + gamma.YEAR[3,2]*epsilon.YEAR[t,2]
                              + epsilon.YEAR[t,3])
  YEAR[t,4] <- delta.YEAR[4,4]*(gamma.YEAR[4,1]*epsilon.YEAR[t,1]
                              + gamma.YEAR[4,2]*epsilon.YEAR[t,2]
                              + gamma.YEAR[4,3]*epsilon.YEAR[t,3]
                              + epsilon.YEAR[t,4])
 }
 gamma.YEAR[2,1] ~ dnorm(0,4)
 gamma.YEAR[3,1] ~ dnorm(0,4)
 gamma.YEAR[3,2] ~ dnorm(0,4)
 gamma.YEAR[4,1] ~ dnorm(0,4)
 gamma.YEAR[4,2] ~ dnorm(0,4)
 gamma.YEAR[4,3] ~ dnorm(0,4)
 for (j in 1:4){
    delta.YEAR[j,j] ~ dnorm(0,0.45)T(0,)
 }
 D.YEAR <- delta.YEAR%*%gamma.YEAR%*%t(gamma.YEAR)%*%delta.YEAR
 for (j in 1:4) {
   var.YEAR[j] <- D.YEAR[j,j]
   sigma.YEAR[j] <- pow(D.YEAR[j,j],0.5)
 }

    # Covariances
 covar.YEAR[1] <- D.YEAR[2,1]
 covar.YEAR[2] <- D.YEAR[3,1]
 covar.YEAR[3] <- D.YEAR[3,2]
 covar.YEAR[4] <- D.YEAR[4,1]
 covar.YEAR[5] <- D.YEAR[4,2]
 covar.YEAR[6] <- D.YEAR[4,3]

    # Correlations
 rho.YEAR[1] <- D.YEAR[2,1]/pow(D.YEAR[1,1]*D.YEAR[2,2],0.5)
 rho.YEAR[2] <- D.YEAR[3,1]/pow(D.YEAR[1,1]*D.YEAR[3,3],0.5)
 rho.YEAR[3] <- D.YEAR[3,2]/pow(D.YEAR[2,2]*D.YEAR[3,3],0.5)
 rho.YEAR[4] <- D.YEAR[4,1]/pow(D.YEAR[1,1]*D.YEAR[4,4],0.5)
 rho.YEAR[5] <- D.YEAR[4,2]/pow(D.YEAR[2,2]*D.YEAR[4,4],0.5)
 rho.YEAR[6] <- D.YEAR[4,3]/pow(D.YEAR[3,3]*D.YEAR[4,4],0.5)
```

```
# Choleski decomposition (with priors) for the individual random effects
 for (k in 1:NI){
   for (j in 1:4){
     epsilon.IND[k,j] ~ dnorm(0,1)
   }
   IND[k,1] <- delta.IND[1,1]*epsilon.IND[k,1]
   IND[k,2] <- delta.IND[2,2]*(gamma.IND[2,1]*epsilon.IND[k,1]
                             + epsilon.IND[k,2])
   IND[k,3] <- delta.IND[3,3]*(gamma.IND[3,1]*epsilon.IND[k,1]
                             + gamma.IND[3,2]*epsilon.IND[k,2]
                             + epsilon.IND[k,3])
   IND[k,4] <- delta.IND[4,4]*(gamma.IND[4,1]*epsilon.IND[k,1]
                             + gamma.IND[4,2]*epsilon.IND[k,2]
                             + gamma.IND[4,3]*epsilon.IND[k,3]
                             + epsilon.IND[k,4])
 }
 gamma.IND[2,1] ~ dnorm(0,4)
 gamma.IND[3,1] ~ dnorm(0,4)
 gamma.IND[3,2] ~ dnorm(0,4)
 gamma.IND[4,1] ~ dnorm(0,4)
 gamma.IND[4,2] ~ dnorm(0,4)
 gamma.IND[4,3] ~ dnorm(0,4)
 for (n in 1:4){
    delta.IND[j,j] ~ dnorm(0,0.45)T(0,)
 }
 D.IND <- delta.IND%*%gamma.IND%*%t(gamma.IND)%*%delta.IND
 for (j in 1:4) {
 var.IND[j] <- D.IND[j,j]
 sigma.IND[j] <- pow(D.IND[j,j],0.5)
}

    # Covariances
 covar.IND[1] <- D.IND[2,1]
 covar.IND[2] <- D.IND[3,1]
 covar.IND[3] <- D.IND[3,2]
 covar.IND[4] <- D.IND[4,1]
 covar.IND[5] <- D.IND[4,2]
 covar.IND[6] <- D.IND[4,3]

    # Correlations
 rho.IND[1] <- D.IND[2,1]/pow(D.IND[1,1]*D.IND[2,2],0.5)
 rho.IND[2] <- D.IND[3,1]/pow(D.IND[1,1]*D.IND[3,3],0.5)
 rho.IND[3] <- D.IND[3,2]/pow(D.IND[2,2]*D.IND[3,3],0.5)
 rho.IND[4] <- D.IND[4,1]/pow(D.IND[1,1]*D.IND[4,4],0.5)
 rho.IND[5] <- D.IND[4,2]/pow(D.IND[2,2]*D.IND[4,4],0.5)
 rho.IND[6] <- D.IND[4,3]/pow(D.IND[3,3]*D.IND[4,4],0.5)

# Other priors and constraints
for (s in 1:NS1) {
   SITE[s] ~ dnorm(0,SITE.tau)
 }
 SITE.tau <- pow(sigma.SITE,-2)
 sigma.SITE ~ dunif(0,10)
 var.SITE <- pow(sigma.SITE,2)

 for (w in 1:NF2) {
   CLIFF[w] ~ dnorm(0,CLIFF.tau)
 }
 CLIFF.tau <- pow(sigma.CLIFF,-2)
 sigma.CLIFF ~ dunif(0,10)
 var.CLIFF <- pow(sigma.CLIFF,2)

 for (g in 1:NG3) {
   SOCG[g] ~ dnorm(0,SOCG.tau)
 }
 SOCG.tau <- pow(sigma.SOCG,-2)
 sigma.SOCG ~ dunif(0,10)
 var.SOCG <- pow(sigma.SOCG,2)

 mu1 ~ dnorm(0,0.0001)
 mu2 ~ dnorm(0,0.0001)
 mu3 ~ dnorm(0,0.0001)
 mu4 ~ dnorm(0,0.0001)

 betaSEX1[1] <- 0
 betaSEX1[2] <- b[1]
 betaSEX2[1] <- 0
 betaSEX2[2] <- b[2]
 betaSEX3[1] <- 0
 betaSEX3[2] <- b[3]
 betaSEX4[1] <- 0
```

```
betaSEX4[2] <- b[4]

betaEXP1[1] <- 0
betaEXP1[2] <- b[5]
betaEXP2[1] <- 0
betaEXP2[2] <- b[6]
betaEXP3[1] <- 0
betaEXP3[2] <- b[7]
betaEXP4[1] <- 0
betaEXP4[2] <- b[8]

betaQF1 <- b[9]
betaQF2 <- b[10]
mQF1 <- mean(QF1[1:N1])
mQF2 <- mean(QF2[1:N2])
sQF1 <- sd(QF1[1:N1])
sQF2 <- sd(QF2[1:N2])

betaQG1 <- b[11]
betaQG2 <- b[12]
betaQG3 <- b[13]
mQG1 <- mean(QG1[1:N1])
mQG2 <- mean(QG2[1:N2])
mQG3 <- mean(QG3[1:N3])
sQG1 <- sd(QG1[1:N1])
sQG2 <- sd(QG2[1:N2])
sQG3 <- sd(QG3[1:N3])

betaQC1 <- b[14]
betaQC2 <- b[15]
betaQC3 <- b[16]
betaQC4 <- b[17]
mQC1 <- mean(QC1[1:N1])
mQC2 <- mean(QC2[1:N2])
mQC3 <- mean(QC3[1:N3])
mQC4 <- mean(QC4[1:N4])
sQC1 <- sd(QC1[1:N1])
sQC2 <- sd(QC2[1:N2])
sQC3 <- sd(QC3[1:N3])
sQC4 <- sd(QC4[1:N4])

betaRST1[1] <- 0
betaRST1[2] <- b[18]
betaRST1[3] <- b[19]
betaRST2[1] <- 0
betaRST2[2] <- b[20]
betaRST2[3] <- b[21]
betaRST3[1] <- 0
betaRST3[2] <- b[22]
betaRST3[3] <- b[23]
betaRST4[1] <- 0
betaRST4[2] <- b[24]

intW1[1] <- 0
intW1[2] <- b[25]
intW1[3] <- b[26]
intW2[1] <- 0
intW2[2] <- b[31]
intW2[3] <- b[32]

intG1[1] <- 0
intG1[2] <- b[27]
intG1[3] <- b[28]
intG2[1] <- 0
intG2[2] <- b[33]
intG2[3] <- b[34]
intG3[1] <- 0
intG3[2] <- b[37]
intG3[3] <- b[38]

intC1[1] <- 0
intC1[2] <- b[29]
intC1[3] <- b[30]
intC2[1] <- 0
intC2[2] <- b[35]
intC2[3] <- b[36]
intC3[1] <- 0
intC3[2] <- b[39]
intC3[3] <- b[40]
intC4[1] <- 0
intC4[2] <- b[41]
```

```
 alphaCOL[1] <- 0
 for (c in 2:5) {
    alphaCOL[c] <- b[40+c]
 }

# Formulation of the horseshoe prior
 for(i in 1:45) {
    b[i] ~ dnorm(0,prec.b[i])
    prec.b[i] <- 1/(s.b[i]*s.b[i])
    s.b[i] <- global.b*local.b[i]
    local.b[i] ~ dnorm(0,v.b[i])T(0,)
    v.b[i] ~ dgamma(0.5,0.5)
 }
global.b ~ dnorm(0,gamma)T(0,)
gamma ~ dgamma(0.5,0.5)

# Sums for the posterior predictive checks
chisq1[1] <- sum(PPC1[1:N1,1])
chisq1[2] <- sum(PPC1[1:N1,2])
chisq2[1] <- sum(PPC2[1:N2,1])
chisq2[2] <- sum(PPC2[1:N2,2])
chisq3[1] <- sum(PPC3[1:N3,1])
chisq3[2] <- sum(PPC3[1:N3,2])
chisq4[1] <- sum(PPC4[1:N4,1])
chisq4[2] <- sum(PPC4[1:N4,2])

# True/false positives/negatives
for (j in 1:4) {
  TFPN1TOT[j] <- (1/N1)*sum(TFPN1[1:N1]==j)
  TFPN2TOT[j] <- (1/N2)*sum(TFPN2[1:N2]==j)
  TFPN3TOT[j] <- (1/N3)*sum(TFPN3[1:N3]==j)
  TFPN4TOT[j] <- (1/N4)*sum(TFPN4[1:N4]==j)
}
  TFPN1TOT[5] <- (1/sum(disp1[1:N1]==1))*sum(TFPN1[1:N1]==1)
  TFPN1TOT[6] <- (1/sum(disp1[1:N1]==0))*sum(TFPN1[1:N1]==3)
  TFPN2TOT[5] <- (1/sum(disp2[1:N2]==1))*sum(TFPN2[1:N2]==1)
  TFPN2TOT[6] <- (1/sum(disp2[1:N2]==0))*sum(TFPN2[1:N2]==3)
  TFPN3TOT[5] <- (1/sum(disp3[1:N3]==1))*sum(TFPN3[1:N3]==1)
  TFPN3TOT[6] <- (1/sum(disp3[1:N3]==0))*sum(TFPN3[1:N3]==3)
  TFPN4TOT[5] <- (1/sum(disp4[1:N4]==1))*sum(TFPN4[1:N4]==1)
  TFPN4TOT[6] <- (1/sum(disp4[1:N4]==0))*sum(TFPN4[1:N4]==3)

# Proportions of correct predictions
  PCP1 <- TFPN1TOT[1]+TFPN1TOT[3]
  PCP2 <- TFPN2TOT[1]+TFPN2TOT[3]
  PCP3 <- TFPN3TOT[1]+TFPN3TOT[3]
  PCP4 <- TFPN4TOT[1]+TFPN4TOT[3]

# Brier scores
  Brier1 <- (1/N1)*sum((P1[1:N1]-disp1[1:N1])*(P1[1:N1]-disp1[1:N1]))
  Brier2 <- (1/N2)*sum((P2[1:N2]-disp2[1:N2])*(P2[1:N2]-disp2[1:N2]))
  Brier3 <- (1/N3)*sum((P3[1:N3]-disp3[1:N3])*(P3[1:N3]-disp3[1:N3]))
  Brier4 <- (1/N4)*sum((P4[1:N4]-disp4[1:N4])*(P4[1:N4]-disp4[1:N4]))

}
```

B.3.4 Literature cited

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B.4 Summaries of the posterior distributions

B.4.1 Summaries of the parameter estimates

We used the R packages CODA (Plummer et al. 2006) and MCMCglmm (Hadfield 2010) for post-processing of MCMC chains. MCMC chains are composed of pseudorandom-dependent draws from the posterior distribution. A Markov chain is thus always a dependent sequence which is inherently autocorrelated (Lunn et al. 2012, Link and Eaton 2012). In practice, we cannot produce infinite numbers of MCMC samples; we get approximations that are necessarily less precise than would be obtained from independent samples. The error due to imperfect sampling can be summarized by the MCMC standard error (MCSE). This error increases with autocorrelation between successive pseudorandom MCMC samples and decreases with the number of samples (T). MCSE can thus indicate the appropriate decimal place precision: the actual mean is approximately within ±2×MCSE with probability 0.95, within ±2.6×MCSE with probability 0.99, etc. Given that the MCSE of independent samples is asymptotically $\mathrm{SD}/\sqrt{\mathrm{T}}$ (where SD is the posterior standard deviation), we can also approximate the effective sample size, which quantifies the number of independent samples that would contain the same information as the MCMC samples (Lunn et al. 2012).

To summarize parameter estimates, we thus calculated the mean, median, mode, standard deviation, 95% credible intervals of all posterior distributions, and we also calculated the MCSE and effective sample size. In addition, we calculated a measure of sign certainty: the proportion of the posterior samples with the same sign as the mean.

Hereafter we provide summary tables of the posterior distribution of all parameters from each submodel (Table B.4.1 to B.4.7; see *Materials and Methods* for details). All effective sample sizes were >4000. We also provide plots of the posterior densities along with the prior densities of all parameter (Fig. B.4.1 to B.4.7).

Table B.4.1. Posterior estimates of fixed effects for the probability of leaving the nest site.

Parameter		Mean	Median	Mode	SD	95%CI		MCSE	SC
						Lower	Upper		
Intercept	$\mu^{(1)}$	0.498	0.498	0.490	0.111	0.280	0.716	0.001	1.00
Sex (M)	$\alpha_M^{(1)}$	-0.570	-0.569	-0.570	0.060	-0.687	-0.453	0.000	1.00
Experience (E)	$\alpha_E^{(1)}$	-0.581	-0.581	-0.587	0.074	-0.724	-0.434	0.000	1.00
Breeding status (N)	$\alpha_N^{(1)}$	1.821	1.821	1.831	0.115	1.597	2.048	0.000	1.00
Breeding status (S)	$\alpha_S^{(1)}$	-2.139	-2.139	-2.140	0.077	-2.292	-1.990	0.000	1.00
Cliff success	$\beta_W^{(1)}$	-0.315	-0.319	-0.329	0.098	-0.499	-0.121	0.001	1.00
Social group success	$\beta_G^{(1)}$	-0.130	-0.123	0.000	0.105	-0.340	0.053	0.001	0.90
Colony success	$\beta_C^{(1)}$	-0.001	0.000	0.000	0.052	-0.109	0.107	0.000	0.51
Cli. suc. × Ind. suc. (N)	$\gamma_{W,N}^{(1)}$	-0.017	-0.007	0.001	0.160	-0.377	0.310	0.001	0.54
Cli. suc. × Ind. suc. (S)	$\gamma_{W,S}^{(1)}$	0.302	0.310	0.335	0.171	-0.029	0.611	0.001	0.96
Gro. suc. × Ind. suc. (N)	$\gamma_{G,N}^{(1)}$	-0.069	-0.033	0.002	0.186	-0.495	0.279	0.001	0.63
Gro. suc. × Ind. suc. (S)	$\gamma_{G,S}^{(1)}$	0.101	0.070	-0.001	0.168	-0.192	0.474	0.001	0.72
Col. suc. × Ind. suc. (N)	$\gamma_{C,N}^{(1)}$	0.169	0.142	0.002	0.177	-0.121	0.544	0.001	0.84
Col. suc. × Ind. suc. (S)	$\gamma_{C,S}^{(1)}$	0.000	0.000	0.000	0.100	-0.211	0.210	0.000	0.50

Each parameter is followed by the corresponding greek symbol used in Eq. 2 in *Materials and Methods*. The reference category is female (F) for sex, inexperienced (i.e. first-time breeder, I) for experience and unsuccessful breeder (U) for breeding status. × indicate an interaction. Cli., Gro., Col., Suc., Ind. stand for cliff, social group, colony, success, and individual, respectively. SD stands for standard deviation. 95%CI stands for 95% credible interval, Lower for lower bound and Upper for upper bound of the 95%CI. MCSE stands for Markov Chain standard error. SC stands for sign certainty. Given the inaccuracy due to finite MCMC sampling, the actual mean is approximately within ±2×MCSE with probability 0.95, within ±2.6×MCSE with probability 0.99, etc.

Table B.4.2. Posterior estimates of fixed effects for the probability of leaving the cliff conditional on having left the nest site.

Parameter		Mean	Median	Mode	SD	95% CI		MCSE	SC
						Lower	Upper		
Intercept	$\mu^{(2)}$	-0.952	-0.952	-0.936	0.198	-1.342	-0.564	0.001	1.00
Sex (M)	$\alpha_M^{(2)}$	0.075	0.062	0.000	0.097	-0.096	0.283	0.000	0.78
Experience (E)	$\alpha_E^{(2)}$	-0.118	-0.106	0.000	0.118	-0.364	0.083	0.000	0.84
Breeding status (N)	$\alpha_N^{(2)}$	-0.151	-0.130	0.000	0.158	-0.481	0.114	0.000	0.84
Breeding status (S)	$\alpha_S^{(2)}$	-1.073	-1.067	-1.073	0.281	-1.625	-0.526	0.001	1.00
Cliff success	$\beta_W^{(2)}$	-0.971	-0.979	-0.990	0.188	-1.326	-0.595	0.001	1.00
Social group success	$\beta_G^{(2)}$	-0.197	-0.169	-0.001	0.204	-0.629	0.134	0.002	0.84
Colony success	$\beta_C^{(2)}$	-0.081	-0.060	-0.001	0.127	-0.357	0.147	0.001	0.73
Cli. suc. × Ind. suc. (N)	$\gamma_{W,N}^{(2)}$	0.051	0.018	0.001	0.215	-0.369	0.541	0.001	0.58
Cli. suc. × Ind. suc. (S)	$\gamma_{W,S}^{(2)}$	0.313	0.224	0.002	0.388	-0.299	1.161	0.002	0.79
Gro. suc. × Ind. suc. (N)	$\gamma_{G,N}^{(2)}$	-0.040	-0.014	0.002	0.222	-0.537	0.413	0.001	0.57
Gro. suc. × Ind. suc. (S)	$\gamma_{G,S}^{(2)}$	0.362	0.249	0.006	0.461	-0.352	1.382	0.003	0.78
Col. suc. × Ind. suc. (N)	$\gamma_{C,N}^{(2)}$	-0.099	-0.060	0.000	0.194	-0.536	0.252	0.001	0.69
Col. suc. × Ind. suc. (S)	$\gamma_{C,S}^{(2)}$	0.404	0.319	-0.002	0.435	-0.257	1.330	0.002	0.83

Specifications are the same as for Table B.4.1.

Table B.4.3. Posterior estimates of fixed effects for the probability of leaving the social group conditional on having left the cliff.

Parameter		Mean	Median	Mode	SD	95% CI		MCSE	SC
						Lower	Upper		
Intercept	$\mu^{(3)}$	3.280	3.175	2.900	0.952	1.567	5.209	0.012	1.00
Sex (M)	$\alpha_M^{(3)}$	0.679	0.653	0.004	0.458	-0.099	1.556	0.003	0.95
Experience (E)	$\alpha_E^{(3)}$	-0.527	-0.481	-0.004	0.442	-1.410	0.169	0.003	0.90
Breeding status (N)	$\alpha_N^{(3)}$	-0.292	-0.171	0.001	0.432	-1.281	0.382	0.002	0.75
Breeding status (S)	$\alpha_S^{(3)}$	-1.128	-0.862	-0.008	1.171	-3.542	0.466	0.008	0.86
Social group success	$\beta_G^{(3)}$	-3.152	-3.092	-3.011	0.797	-4.782	-1.654	0.009	1.00
Colony success	$\beta_C^{(3)}$	-0.336	-0.174	0.005	0.527	-1.541	0.468	0.005	0.74
Gro. suc. × Ind. suc. (N)	$\gamma_{G,N}^{(3)}$	0.021	0.004	-0.005	0.376	-0.782	0.850	0.001	0.52
Gro. suc. × Ind. suc. (S)	$\gamma_{G,S}^{(3)}$	-0.154	-0.044	0.004	0.630	-1.678	1.062	0.003	0.60
Col. suc. × Ind. suc. (N)	$\gamma_{C,N}^{(3)}$	-0.058	-0.014	0.005	0.383	-0.923	0.724	0.001	0.55
Col. suc. × Ind. suc. (S)	$\gamma_{C,S}^{(3)}$	-0.234	-0.066	-0.010	0.732	-2.051	1.057	0.004	0.62

Specifications are the same as for Table B.4.1.

Table B.4.4. Posterior estimates of fixed effects for the probability of leaving the colony conditional on having left the social group.

Parameter		Mean	Median	Mode	SD	95% CI		MCSE	SC
						Lower	Upper		
Intercept	$\mu^{(4)}$	3.387	3.282	3.031	0.903	1.768	5.189	0.010	1.00
Sex (M)	$\alpha_M^{(4)}$	0.005	0.001	0.003	0.219	-0.459	0.489	0.001	0.51
Experience (E)	$\alpha_E^{(4)}$	-0.090	-0.038	-0.003	0.269	-0.716	0.417	0.001	0.62
Breeding status (N)	$\alpha_N^{(4)}$	0.014	0.000	-0.002	0.372	-0.789	0.819	0.001	0.50
Colony success	$\beta_C^{(4)}$	-1.870	-1.818	-1.708	0.385	-2.643	-1.189	0.003	1.00
Col. suc. × Ind. suc. (N)	$\gamma_{C,N}^{(4)}$	-0.372	-0.195	-0.001	0.559	-1.632	0.451	0.002	0.76
Colony identity (2)	$\alpha_{C2}^{(4)}$	1.172	0.803	0.011	1.301	-0.479	3.908	0.010	0.86
Colony identity (3)	$\alpha_{C3}^{(4)}$	1.756	1.698	0.007	1.148	-0.182	3.856	0.009	0.96
Colony identity (4)	$\alpha_{C4}^{(4)}$	-1.012	-0.950	0.003	0.784	-2.510	0.221	0.007	0.92
Colony identity (5)	$\alpha_{C5}^{(4)}$	-2.098	-2.057	-2.031	0.764	-3.632	-0.628	0.008	1.00

Specifications are the same as for Table B.4.1.

Table B.4.5. Posterior estimates of patch random effects.

Spatial scales	Parameter	Mean	Median	Mode	SD	95% CI		MCSE
						Lower	Upper	
Nest site	SD	0.779	0.779	0.775	0.059	0.663	0.894	0.001
	VAR	0.611	0.607	0.585	0.092	0.433	0.793	0.001
Cliff	SD	0.809	0.796	0.758	0.149	0.535	1.110	0.001
	VAR	0.676	0.633	0.555	0.256	0.255	1.185	0.001
Social group	SD	1.846	1.716	1.499	0.719	0.690	3.265	0.006
	VAR	3.923	2.945	1.765	3.530	0.273	10.164	0.034

The scale of the focal dispersal probability is specified in column 1: of the probability of leaving the nest site, leaving the cliff conditional on having left the nest site, or leaving the social group conditional on having left the cliff. VAR stands for variance. Other specifications are the same as for Table B.4.1.

Table B.4.6. Posterior estimates of individual random effects

Spatial scales	Parameter	Mean	Median	Mode	SD	95% CI		MCSE	SC
						Lower	Upper		
Nest site	SD	0.218	0.223	0.269	0.114	0.000	0.401	0.001	/
	VAR	0.061	0.050	0.001	0.052	0.000	0.160	0.000	/
Cliff	SD	0.634	0.649	0.666	0.192	0.235	1.008	0.002	/
	VAR	0.439	0.421	0.385	0.233	0.000	0.850	0.002	/
Social group	SD	2.918	2.849	2.673	0.724	1.600	4.379	0.008	/
	VAR	9.039	8.114	6.790	4.602	1.972	18.188	0.051	/
Colony	SD	1.091	1.069	1.009	0.557	0.000	2.047	0.005	/
	VAR	1.499	1.143	0.030	1.414	0.000	4.188	0.013	/
Nest site,	COR	-0.015	-0.019	-0.016	0.341	-0.653	0.621	0.003	0.52
Cliff	COV	-0.003	-0.001	0.000	0.049	-0.107	0.099	0.000	0.52
Nest site,	COR	0.201	0.239	0.365	0.324	-0.457	0.762	0.005	0.75
Social group	COV	0.148	0.114	0.002	0.228	-0.272	0.640	0.003	0.75
Nest site,	COR	-0.056	-0.065	-0.060	0.325	-0.659	0.552	0.002	0.57
Colony	COV	-0.016	-0.006	-0.001	0.093	-0.226	0.175	0.001	0.57
Cliff,	COR	0.215	0.232	0.264	0.258	-0.290	0.698	0.003	0.80
Social group	COV	0.421	0.382	0.330	0.513	-0.547	1.477	0.005	0.80
Cliff,	COR	-0.260	-0.296	-0.402	0.291	-0.762	0.319	0.001	0.81
Colony	COV	-0.205	-0.160	-0.003	0.255	-0.766	0.224	0.001	0.81
Social group, Colony	COR	-0.223	-0.248	-0.282	0.273	-0.716	0.318	0.001	0.79
	COV	-0.772	-0.622	-0.021	1.024	-2.970	1.064	0.006	0.79

The first column corresponds either to the scale of the focal dispersal probability for standard deviations (SD) and variances (VAR) (upper panel), or to the two scales of the dispersal probabilities between which covariance (COV) and correlation (COR) of random effects was assessed (bottom panel). Dispersal probability specification: leaving the nest site, leaving the cliff conditional on having left the nest site, leaving the social group conditional on having left the cliff, or leaving the colony conditional on having left the cliff. VAR stands for variance. Sign certainty is not provided for variance and standard deviations, because they are null or positive by definition. Other specifications are the same as for Table B.4.1.

Table B.4.7. Posterior estimates of year random effects

Spatial scales	Parameter	Mean	Median	Mode	SD	95% CI		MCSE	SC
						Lower	Upper		
Nest site	SD	0.441	0.434	0.414	0.071	0.310	0.584	0.000	/
	VAR	0.199	0.188	0.171	0.067	0.090	0.333	0.000	/
Cliff	SD	0.422	0.415	0.403	0.089	0.256	0.602	0.000	/
	VAR	0.186	0.172	0.150	0.079	0.055	0.344	0.000	/
Social group	SD	1.123	1.083	1.033	0.376	0.441	1.884	0.003	/
	VAR	1.401	1.173	0.837	0.971	0.071	3.278	0.008	/
Colony	SD	0.588	0.550	0.480	0.365	0.000	1.242	0.002	/
	VAR	0.479	0.303	0.020	0.574	0.000	1.543	0.003	/
Nest site,	COR	0.578	0.603	0.654	0.158	0.262	0.845	0.001	1.00
Cliff	COV	0.109	0.104	0.094	0.047	0.025	0.205	0.000	1.00
Nest site,	COR	0.257	0.271	0.296	0.232	-0.195	0.688	0.001	0.86
Social group	COV	0.127	0.117	0.090	0.134	-0.130	0.405	0.001	0.86
Nest site,	COR	0.233	0.264	0.325	0.280	-0.325	0.730	0.001	0.80
Colony	COV	0.069	0.051	-0.001	0.094	-0.088	0.275	0.000	0.80
Cliff,	COR	0.506	0.535	0.587	0.192	0.124	0.830	0.001	0.98
Social group	COV	0.246	0.223	0.180	0.151	-0.008	0.558	0.001	0.98
Cliff,	COR	0.222	0.252	0.315	0.288	-0.346	0.732	0.001	0.78
Colony	COV	0.063	0.045	0.002	0.093	-0.092	0.269	0.000	0.78
Social group, Colony	COR	0.083	0.093	0.084	0.308	-0.498	0.659	0.001	0.61
	COV	0.058	0.031	0.001	0.249	-0.444	0.596	0.001	0.61

Specifications are the same as for Table 6.

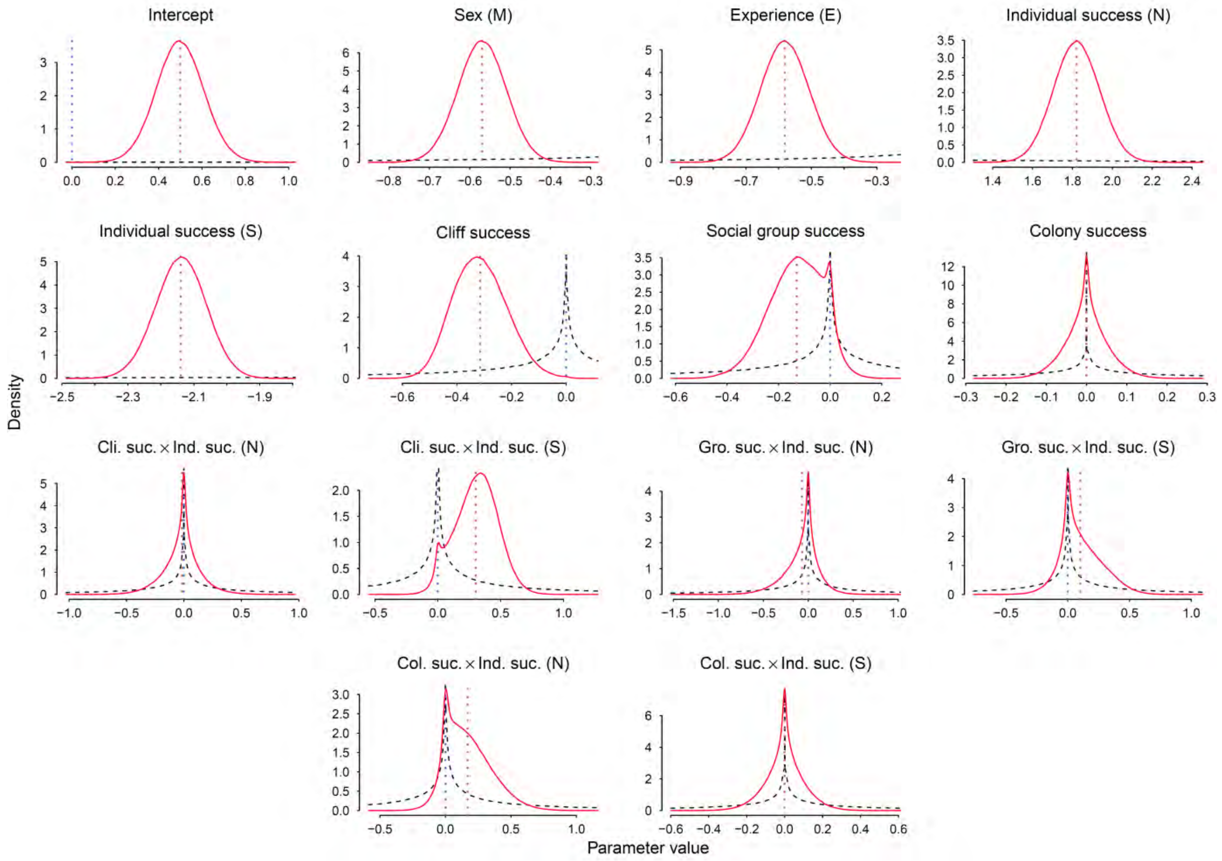

Figure B.4.1. Posterior distributions (red lines) along with prior distributions (dashed grey lines) of fixed effects in the first submodel (see Table B.4.1 for parameter names). Dots indicate posterior mean (in red) and zero (in blue).

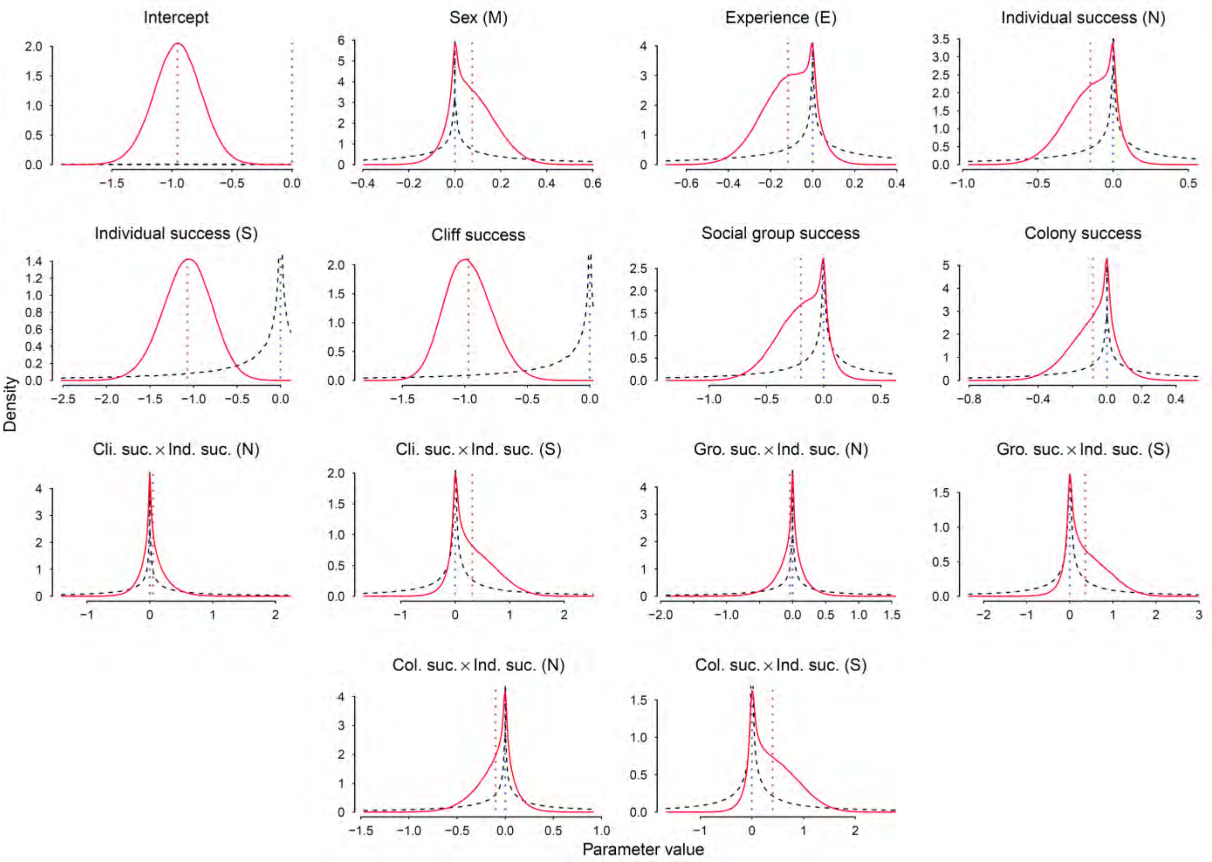

Figure B.4.2. Posterior distributions (red lines) along with prior distributions (dashed grey lines) of fixed effects in the second submodel (see Table B.4.2 for parameter names). Dots indicate posterior mean (in red) and zero (in blue).

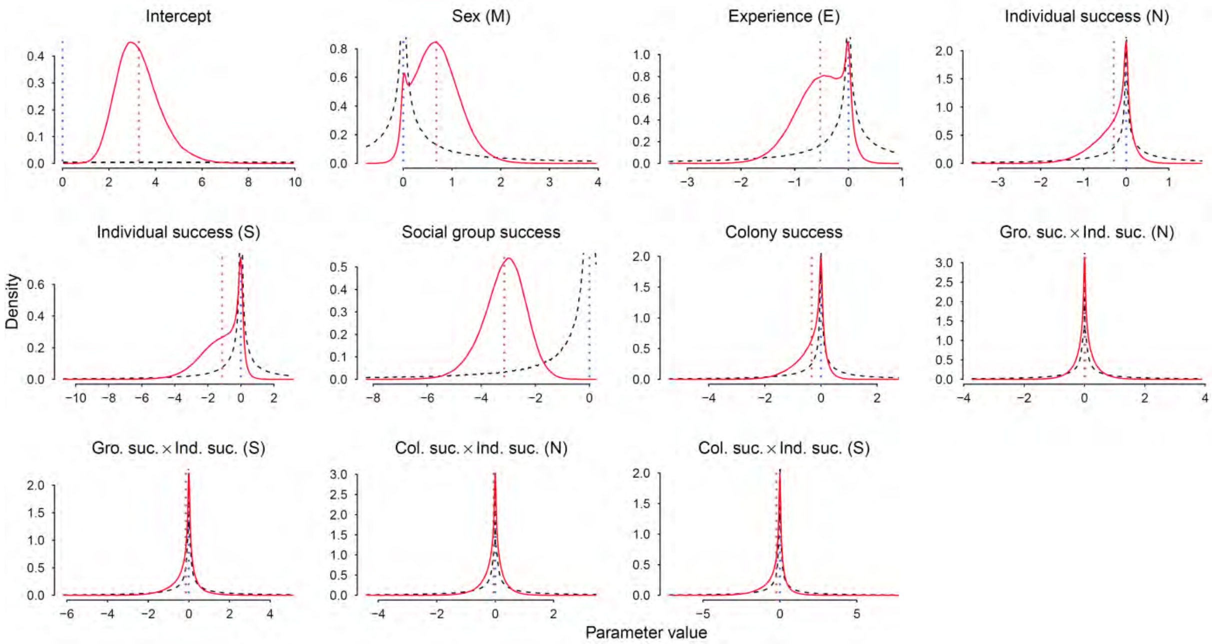

Figure B.4.3. Posterior distributions (red lines) along with prior distributions (dashed grey lines) of fixed effects in the third submodel (see Table B.4.3 for parameter names). Dots indicate posterior mean (in red) and zero (in blue).

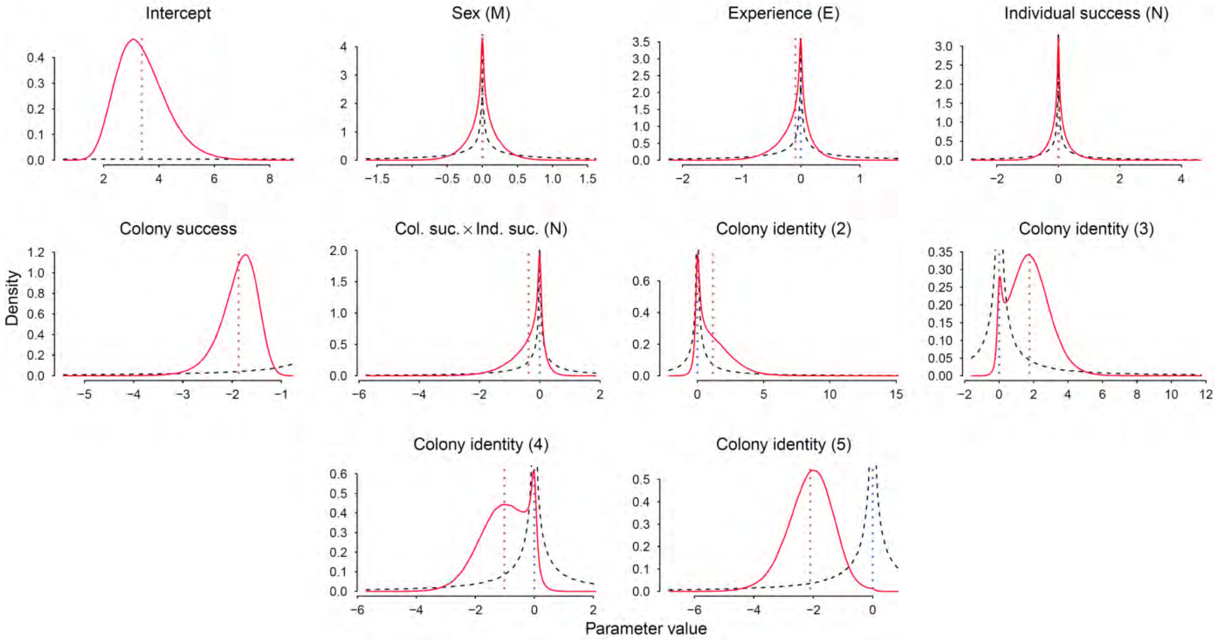

Figure B.4.4. Posterior distributions (red lines) along with prior distributions (dashed grey lines) of fixed effects in the fourth submodel (see Table B.4.4 for parameter names). Dots indicate posterior mean (in red) and zero (in blue).

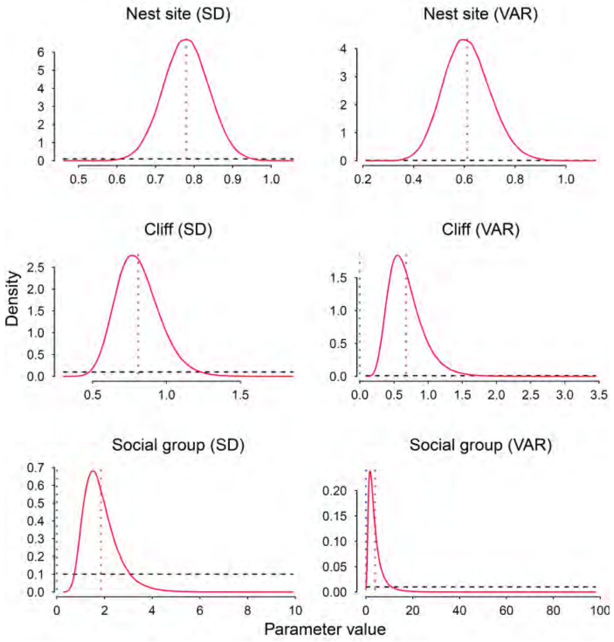

Figure B.4.5. Posterior distributions (red lines) along with prior distributions (dashed grey lines) of patch random effects in the first three submodels (see Table B.4.5 for parameter names). Dots indicate posterior mean (in red) and zero (in blue).

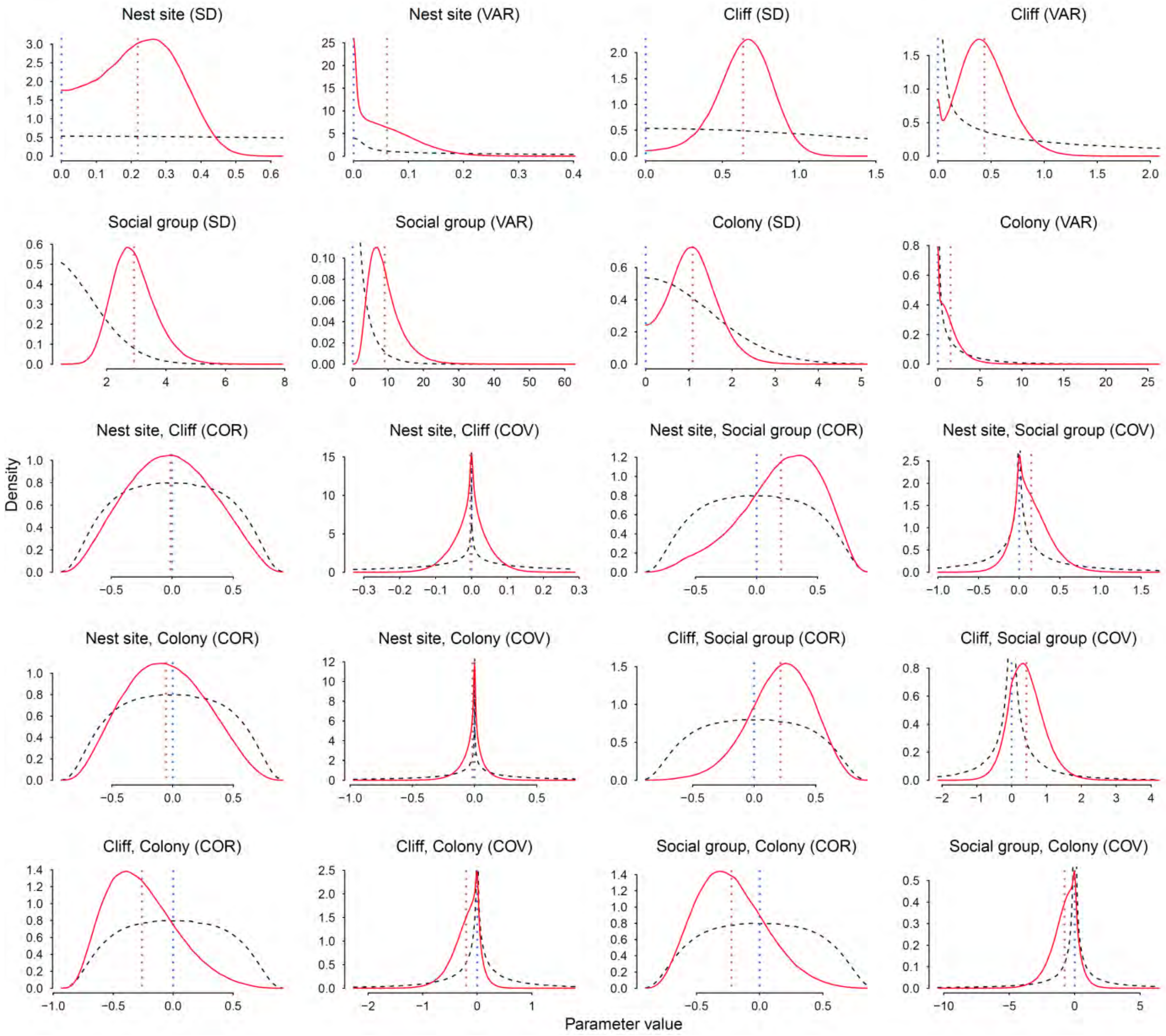

Figure B.4.6. Posterior distributions (red lines) along with prior distributions (dashed grey lines) of individual random effects in the four submodels (see Table B.4.6 for parameter names). Dots indicate posterior mean (in red) and zero (in blue).

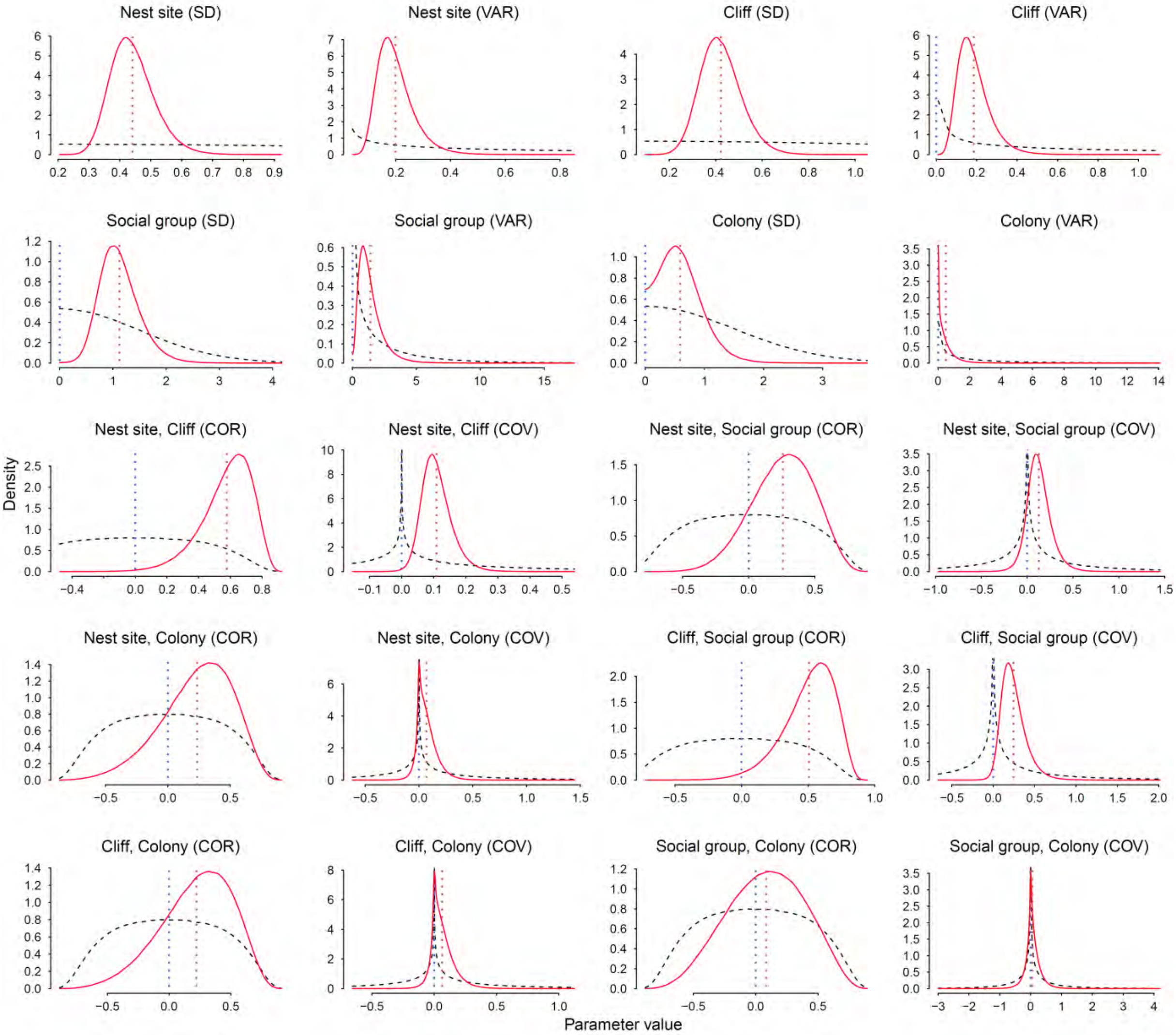

Figure B.4.7. Posterior distributions (red lines) along with prior distributions (dashed grey lines) of year random effects in the four submodels (see Table B.4.7 for parameter names). Dots indicate posterior mean (in red) and zero (in blue).

B.4.2 Graphical summaries of the model

To plot the relationships included in the model (Fig. 2 to 6 of the paper), for each submodel we estimated the posterior distribution of the dispersal probability for each modality of qualitative explanatory variables and 12 points along the range of each continuous variable (patch successes, whose range is [0,1]),. For each continuous variable, we considered the average case regarding the other continuous variable (i.e. they were set to 0, the mean value of standardized variables) and the random effects (i.e. we did not add any particular individual, year, or patch effect). Plots include the 95%CI for the mean relationships. The posterior distributions used to plot the target relationships were derived from the linear combination (following Eq. 2.1 to 2.4 in the paper) of parameters sampled directly within JAGS. We used additional sampling runs with the same number of chains and iterations for adaptive, burnin and monitoring phases as before (see *Materials and Methods*). However, for computing convenience we thinned chains by a rate of 1/8 iterations, yielding 10^5 samples at the end.

Hereafter, we provide additional figures for the relationships with local success that had non-robust effects on dispersal probabilities (Fig. B.4.8 to B.4.11).

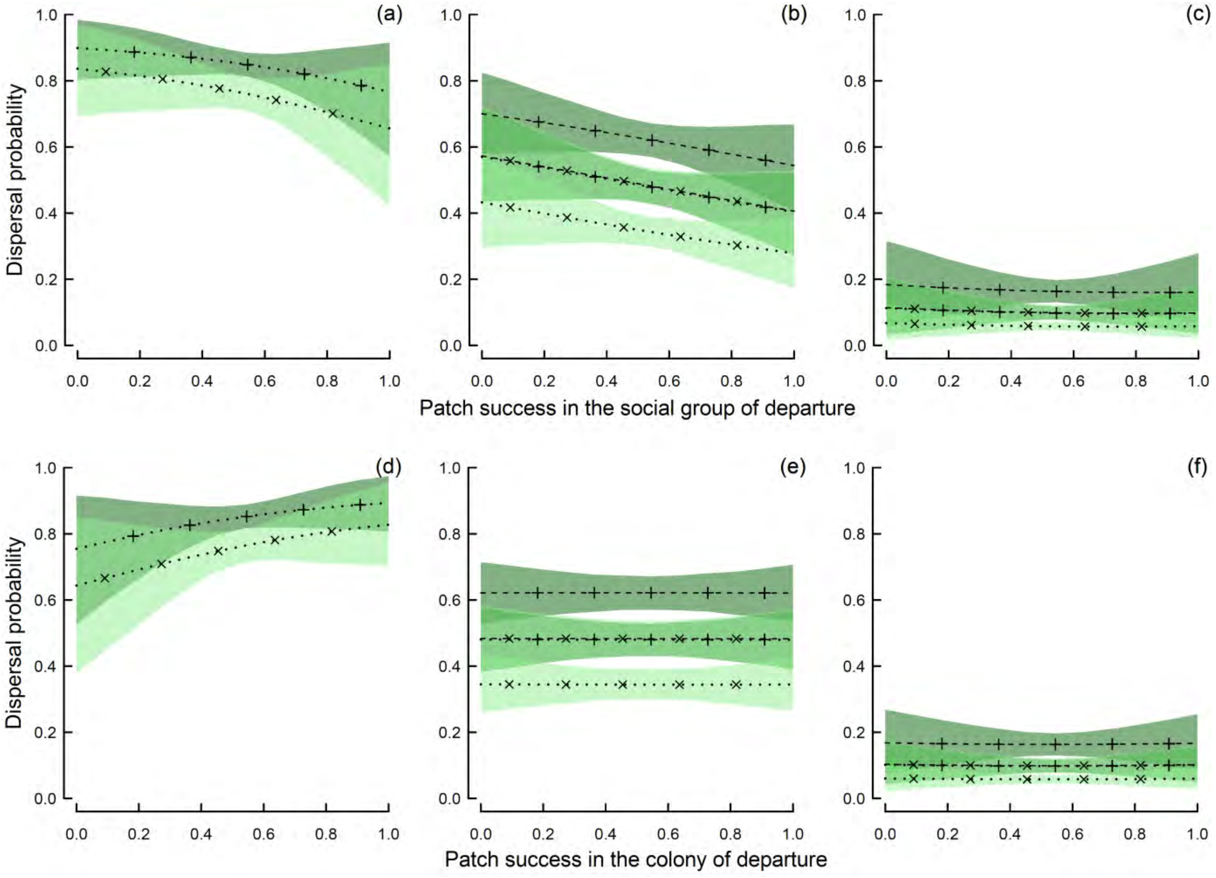

Figure B.4.8. Estimated dispersal probability at the nest-site scale as a function of local success in (a,b,c) the social group of departure and (d,e,f) colony 1: (a,d) nonbreeders, (b,e) unsuccessful breeders, and (c,f) successful breeders. The mean relationship for males: '×', for females: '+', for experienced individuals: dotted lines, and for inexperienced ones: dashed lines. Background transparent bands correspond to 95% credible intervals of the relationships. We considered the average situation regarding the other predictors (i.e. they were set to zero, the mean value of standardized variables and random effects).

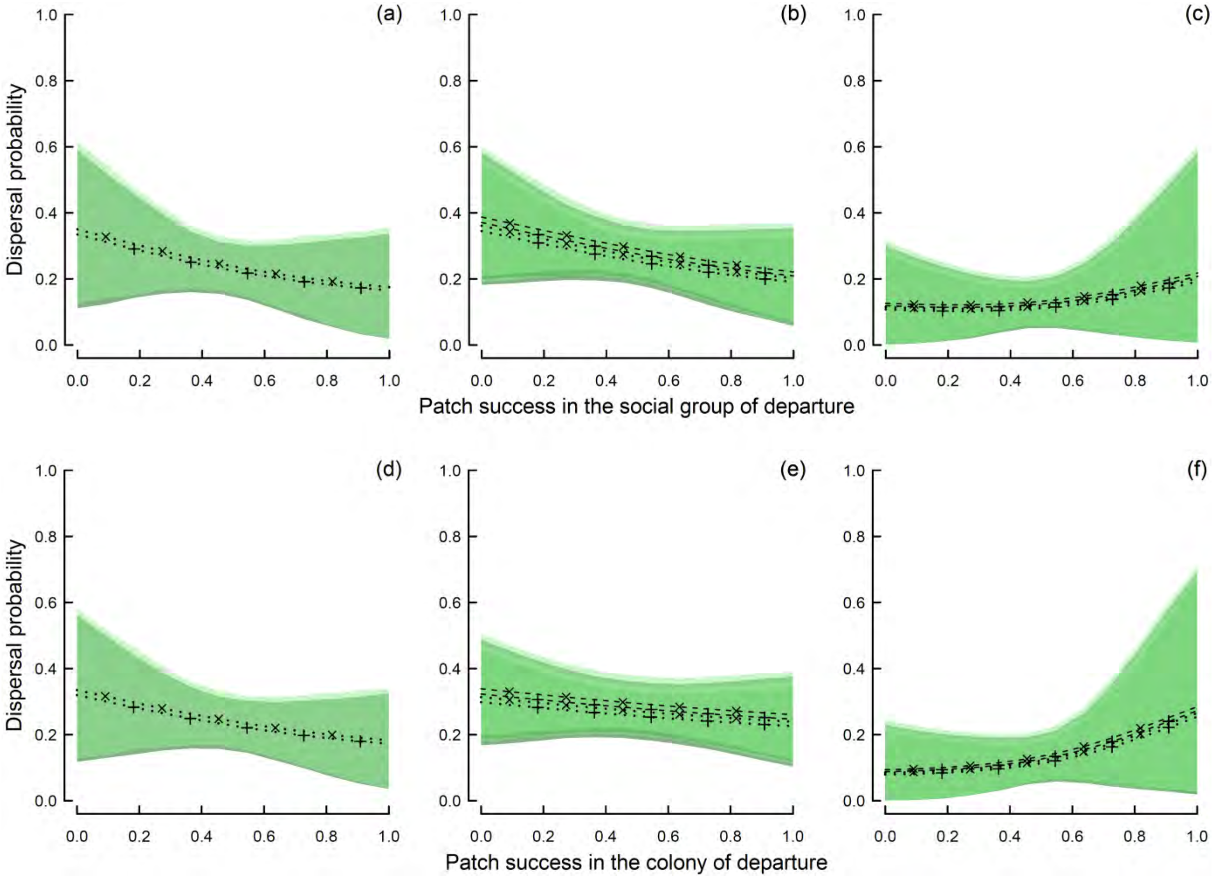

Figure B.4.9. Estimated dispersal probability at the cliff scale as a function of local success in (a,b,c) the social group of departure and (d,e,f) the colony of departure: (a,d) nonbreeders, (b,e) unsuccessful breeders, and (c,f) successful breeders. The mean relationship for males: '×', for females: '+', for experienced individuals: dotted lines, and for inexperienced ones: dashed lines. Background transparent bands correspond to 95% credible intervals of the relationships. We considered the average situation regarding the other predictors (i.e. they were set to zero, the mean value of standardized variables and random effects).

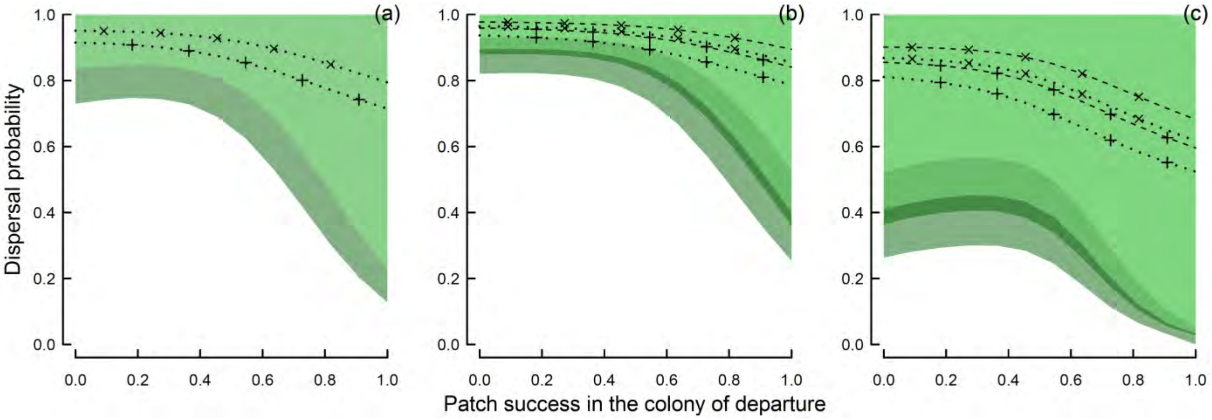

Figure B.4.10. Estimated dispersal probability at the social-group scale as a function of local success in the colony of departure: (a) nonbreeders, (b) unsuccessful breeders, and (c) successful breeders. The mean relationship for males: '×', for females: '+', for experienced individuals: dotted lines, and for inexperienced ones: dashed lines. Background transparent bands correspond to 95% credible intervals of the relationships. We considered the average situation regarding the other predictors (i.e. they were set to zero, the mean value of standardized variables and random effects).

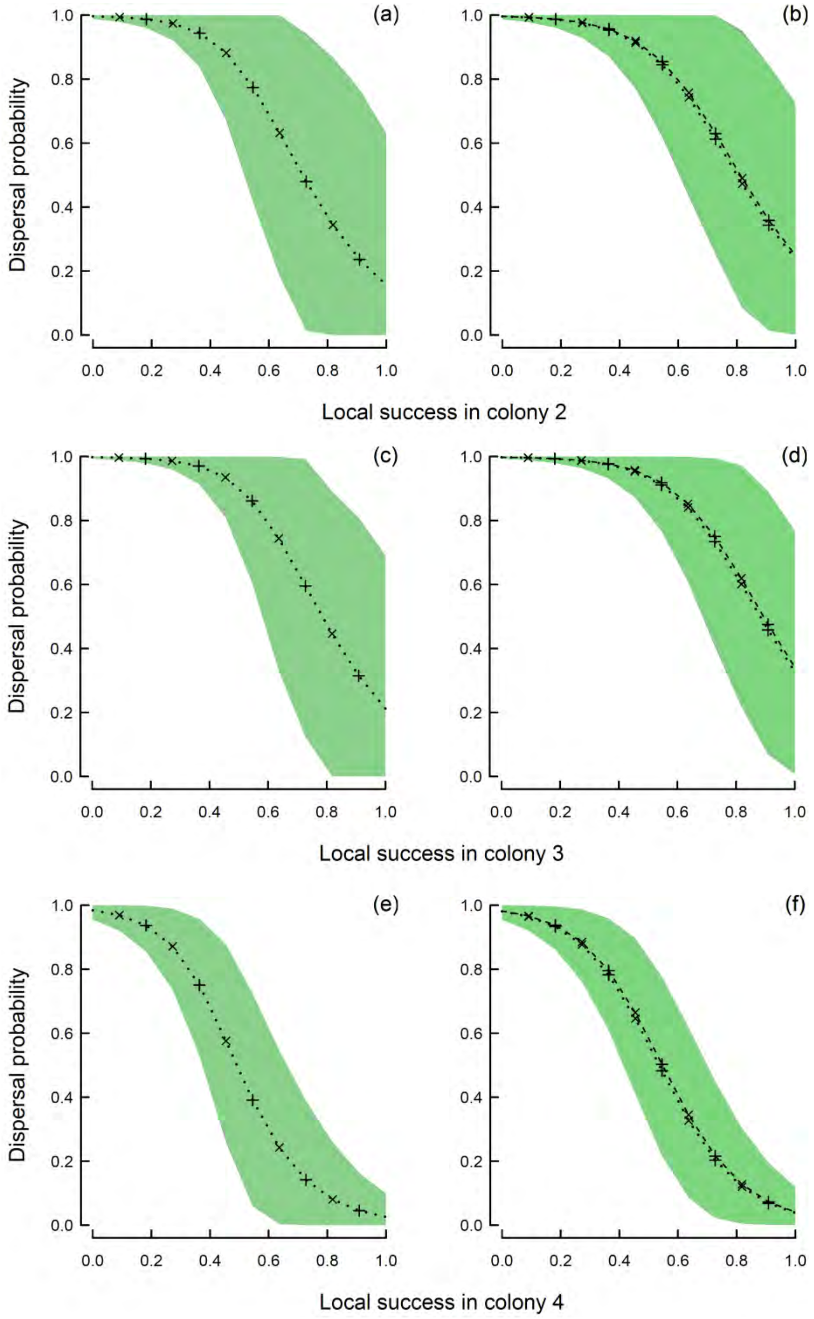

Figure B.4.11. Estimated dispersal probability at the colony scale (conditional on having left the social group) in (a,b) colony 2, (c,d) colony 3, (e,f) colony 4: (a,c,e) nonbreeders, (b,c,f) breeders (mainly unsuccessful). The mean relationship for males: '×', for females: '+', for experienced individuals: dotted lines, and for inexperienced ones: dashed lines. Background transparent bands correspond to 95% credible intervals of the relationships. We considered the average situation regarding the other predictors (i.e. they were set to zero, the mean value of standardized variables and random effects).

B.4.3 Literature cited

Hadfield, J. D. 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. Journal of Statistical Software 33:1–22.

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Lunn, D., C. Jackson, N. Best, A. Thomas, and D. Spiegelhalter. 2012. The BUGS book: A practical introduction to Bayesian analysis. CRC press, New York, USA.

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B.5 Specification and results of the posterior checks

B.5.1 Posterior predictive checks

Data replication (derived from model estimates), other calculations involved in posterior predictive checks (Gelman et al. 1996) and MCMC sampling for parameter estimation were performed simultaneously. Consequently, they involved the same number of chains and the same number of iterations in the burnin and monitoring phases (see *Materials and Methods*). Cross-validation (Green et al. 2009) was impracticable, owing to the huge computation time involved.

The χ^2 discrepancy metric (D_{χ^2}) is the sum of squared Pearson residuals (Gelman et al. 1996); $D_{\chi^2}^{obs}$ quantifies the distance of observed data to the model, and $D_{\chi^2}^{rep}$ quantifies the distance of replicated data to the model (see also model code in Appendix B.3):

$$D_{\chi^2}^{obs} = \sum_{i=1}^{N_j} \sum_{t}^{T_i} \frac{(Z_{it}^{obs} - P_{it}^{(j)})^2}{P_{it}^{(j)}(1 - P_{it}^{(j)})}$$

$$D_{\chi^2}^{rep} = \sum_{i=1}^{N_j} \frac{(Z_{it}^{rep} - P_{it}^{(j)})^2}{P_{it}^{(j)}(1 - P_{it}^{(j)})}$$

where j is the level the submodel (i.e. the spatial scale of study), N_j is the number of individuals involved, T_i is the set of years with observations concerning the individual i, Z is the response (i.e. philopatry: response =0 or dispersal: response=1 at the target spatial scale), P is the model probability that the response is 1; see *Materials and Methods* for details.

The posterior predictive p-value (*PP-value*; Gelman et al. 1996) is the probability that the distance of observed data to the model is greater than the distance of replicated data to the model:

$$PPP\text{-}value = Pr\,(D_{\chi^2}^{rep} > D_{\chi^2}^{obs}).$$

Fig. B.5.1 provides a graphical assessment of the proportion of $D_{\chi^2}^{rep}$ values higher than $D_{\chi^2}^{obs}$ values.

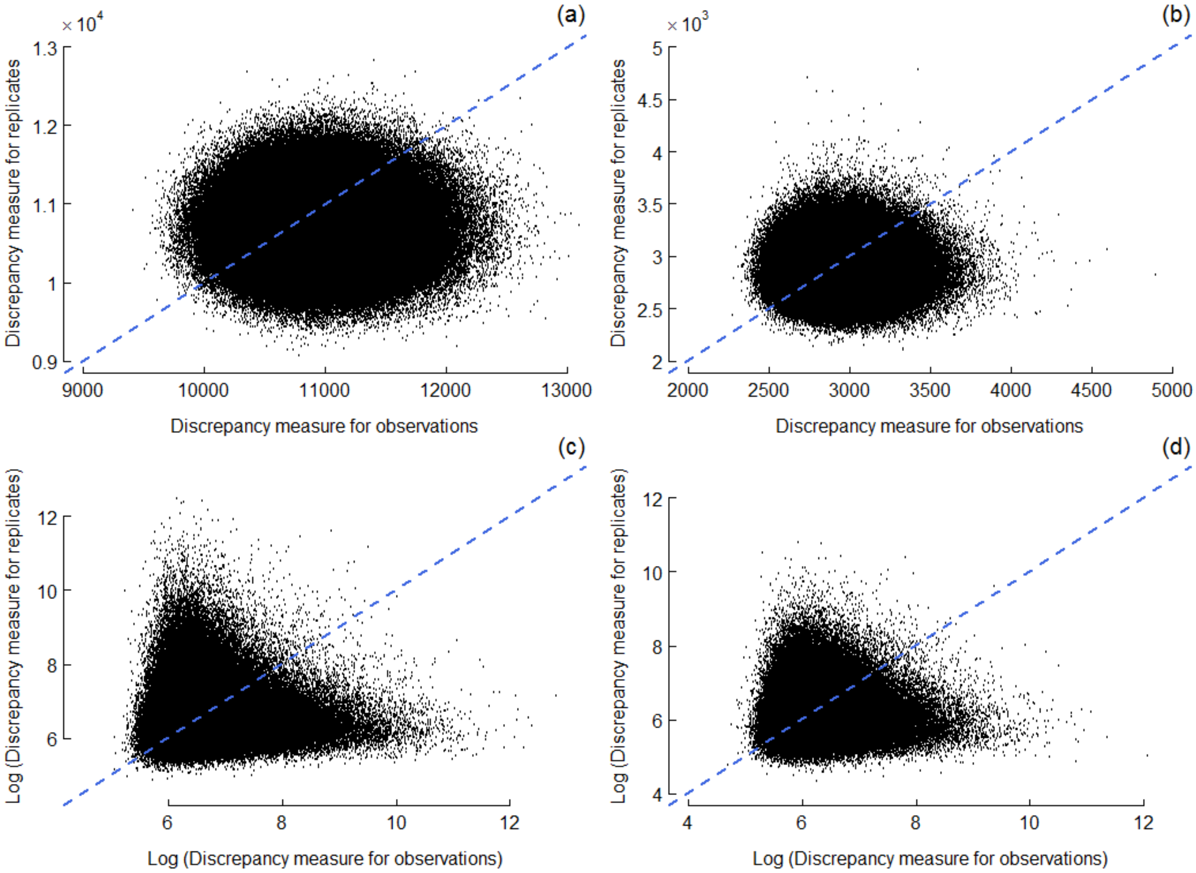

Figure B.5.1. Discrepancy measures for replicates against discrepancy measures for observations in all posterior samples: (a) at the nest-site scale (*PPP-value*=0.35), (b) at the cliff scale (*PPP-value*=0.46), (c) at the social-group scale (*PPP-value*=0.48), (d) at the colony scale (*PPP-value*=0.51). The dashed line is the bisector (x=y).

B.5.2 Accuracy of predictions

For each submodel (i.e. at the nest-site, cliff, social-group, and colony scale), we calculated the proportion of correct predictions over the data replicates used to measure discrepancies (see above). We also calculated the Brier score, i.e. the average distance of expectations (i.e. probability estimates) to observations (philopatry: response =0, or dispersal: response =1). In addition, we used *separation plots* for a deeper visual check of model fit (Greenhill et al. 2011). These plots are made of two panels (Fig. B.5.2): the first is for observations of the event (dispersal: response=1) and the second is for observations of the non-event (philopatry: response=0). Each plot is composed of color bands for probability ranges, arranged in ascending order. Band width is proportional to the number of observations in the data for which the expectation (here, mean probability estimate derived from the model) falls into the corresponding probability range. Such plots allow assessing the separation of events and non-events according to expectations, that is, they allow assessing the predictive performances of the model.

The Brier score at the nest-site and cliff scales was close to 0.13−0.14; it was close to 0.07−0.08 at the social-group and colony scales. At the nest-site and cliff scales ca. 75% of observations were well predicted, with ca. 80% of correct predictions for observations of philopatry but ca. 50% for observations of dispersal (Table B.5.2). At these two scales, separation of observations of philopatry was very strong (almost all dispersal probability estimates were below 0.5 and ca. 70% below 0.2; Fig. B.5.2:1,2), but rather poor for observations of dispersal (only ca. 60% of probability estimates were above 0.5 with few above 0.8; Fig. B.5.2:1,2). At the social-group and colony scales ca. 85% of observations were well predicted, with ca. 80% and 70%, respectively, of correct predictions for observations of philopatry and ca. 90% of correct predictions for observations of dispersal (Table B.5.3, B.5.4). At the two scales, observations of philopatry and dispersal were strongly separated, though separation was better for observations of dispersal (and even more at the colony scale; Fig. B.5.2:3,4).

Table B.5.1. Contingency table for the proportion of true/false positives/negatives in the first submodel: leaving or staying in the nest site.

Observation	Model prediction		Total
	Dispersal	Philopatry	
Dispersal	0.141 ± 0.003 [0.135,0.147]	0.129 ± 0.003 [0.123,0.135]	0.270
Philopatry	0.129 ± 0.004 [0.121,0.136]	0.601 ± 0.004 [0.593,0.608]	0.730
Total	0.270	0.730	

Estimated proportions are given as mean ± standard deviation and followed by 95% credible intervals. Proportion of correct predictions: 0.742±0.005 [0.732,0.752] among all observations, 0.522±0.011 [0.501,0.545] among observations of dispersal (response =1), and 0.823±0.005 [0.813,0.834] among observations of philopatry (response =0). Brier score: 0.129±0.001 [0.126,0.132]. MCMC standard errors were lower than $5 \cdot 10^{-4}$.

Table B.5.2. Contingency table for the proportion of true/false positives/negatives in the second submodel: leaving or staying in the cliff (conditional on leaving the nest site).

Observation	Model prediction		Total
	Dispersal	Philopatry	
Dispersal	0.153 ± 0.007 [0.139,0.165]	0.134 ± 0.007 [0.122,0.148]	0.287
Philopatry	0.134 ± 0.008 [0.118,0.150]	0.579 ± 0.008 [0.563,0.585]	0.713
Total	0.287	0.713	

Estimates are given as mean ± standard deviation and followed by 95% credible intervals. Proportion of correct predictions: 0.731±0.011 [0.708,0.753] among all observations, 0.532±0.023 [0.483,0.574] among observations of dispersal (response =1), and 0.812±0.011 [0.788,0.833] among observations of philopatry (response =0). Brier score: 0.135±0.004 [0.127,0.143]. MCMC standard errors were lower than $5 \cdot 10^{-4}$.

Table B.5.3. Contingency table for the proportion of true/false positives/negatives in the third submodel: leaving or staying in the social-group (conditional on leaving the cliff).

Observation	Model prediction		Total
	Dispersal	Philopatry	
Dispersal	0.575 ± 0.014	0.072 ± 0.014	0.647
	[0.545,0.601]	[0.046,0.101]	
Philopatry	0.072 ± 0.014	0.282 ± 0.014	0.354
	[0.045,0.099]	[0.253,0.308]	
Total	0.647	0.354	

Estimates are given as mean ± standard deviation and followed by 95% credible intervals. Proportion of correct predictions: 0.856±0.025 [0.806,0.903] among all observations, 0.889±0.022 [0.841,0.927] among observations of dispersal (response =1), and 0.797±0.040 [0.717,0.870] among observations of philopatry (response =0). Brier score: 0.072±0.012 [0.049,0.095]. MCMC standard errors were lower than $5 \cdot 10^{-4}$.

Table B.5.4. Contingency table for the proportion of true/false positives/negatives in the fourth submodel: leaving or staying in the colony (conditional on leaving the social group).

Observation	Model prediction		
	Dispersal	Philopatry	Total
Dispersal	0.676 ± 0.015	0.080 ± 0.015	0.647
	[0.646,0.703]	[0.050,0.108]	
Philopatry	0.079 ± 0.014	0.165 ± 0.014	0.354
	[0.050,0.104]	[0.136,0.190]	
Total	0.647	0.354	

Estimates are given as mean ± standard deviation and followed by 95% credible intervals. Proportion of correct predictions: 0.841±0.024 [0.793,0.884] among all observations, 0.895±0.020 [0.854,0.931] among observations of dispersal (response =1), and 0.675±0.057 [0.557,0.779] among observations of philopatry (response =0). Brier score: 0.080±0.010 [0.061,0.097]. MCMC standard errors were lower than $5 \cdot 10^{-4}$.

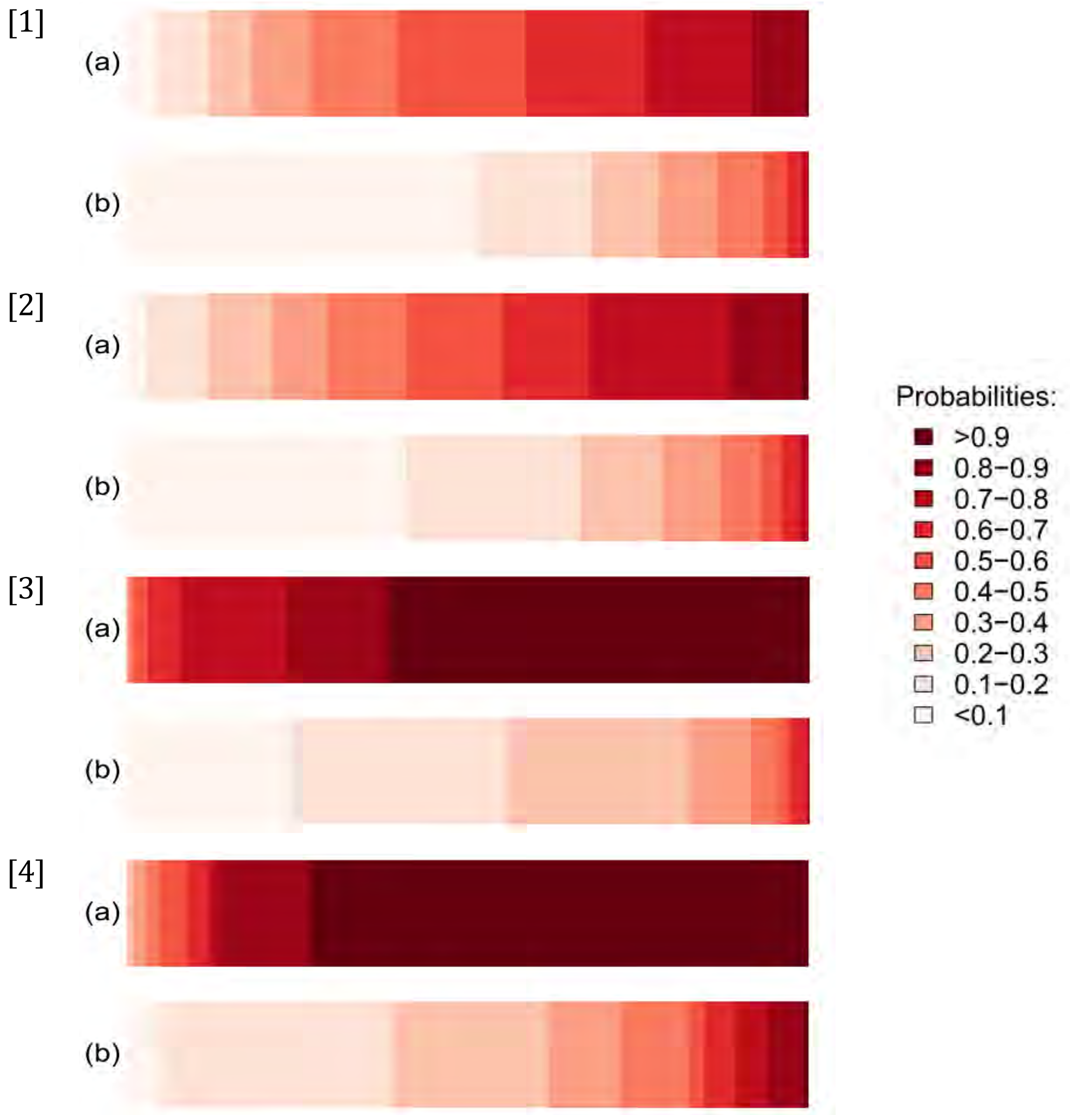

Figure B.5.2. Separation plots for the probability of leaving [1] the nest site, [2] the cliff (conditional on leaving the nest site), [3] the social-group (conditional on leaving the cliff), [4] the colony (conditional on leaving the social group). Panel (a) is for observations of dispersal (response =1; [1] 2888 cases, [2] 829 cases, [3] 536 cases, [4] 405 cases), and panel (b) is for observations of philopatry (response =0; [1] 7814 cases, [2] 2059 cases, [3] 293 cases, [4] 131 cases). Band width and colour indicate the proportion of cases and corresponding probability, respectively. Expectations for all observations (i.e. mean probability estimates) were derived from additional MCMC runs involving the same chain length and number of chains as previously but a thinning rate of 1/16 (to save computer resources) yielding 5×10^4 samples at the end.

B.5.3 Residual analysis

We computed the mean Pearson residual for all observations. The Pearson residual of a given observation is calculated as follows (see *Posterior predictive checks* for notation details):

$$Pres = \frac{(Z_{it}^{obs} - P_{it}^{(j)})^2}{P_{it}^{(j)}(1 - P_{it}^{(j)})}.$$

Expectations (i.e. mean probability estimate) were derived from additional MCMC runs involving chains of the same length and the same number of chains as previously but a thinning rate of 1/16 (to save computer resources) yielding 5×10^4 samples at the end.

Residuals inspection comforted the above conclusions (Fig. B.5.3 to B.5.5). Further, there was no strong difference between males and females (Fig. B.5.6). Experienced individuals had larger residuals than inexperienced ones for observations of dispersal (response =1) at the nest-site scale (Fig. B.5.7a). Philopatric experienced individuals (response =0) had larger residuals than inexperienced ones at the colony scale (Fig. B.5.7d). At each spatial scale successful individuals had clearly larger residuals than unsuccessful ones and nonbreeders when they dispersed, and smaller residuals when they were philopatric (Fig. B.5.8). At the nest site scale, philopatric unsuccessful breeders had larger residuals than successful ones, but lower than nonbreeders (Fig. B.5.8a). At higher scales, philopatric unsuccessful breeders always had larger residuals: this was more pronounced at the colony scale (Fig. B.5.8b,c,d). In addition, at the nest-site scale the size of residuals increased with local success for observations of dispersal, suggesting that many poor predictions concerned successful individuals that dispersed in poor-quality cliffs (Fig. B.5.9a). There was no trend in the residuals for observations of philopatry (Fig. B.5.9). At the cliff scale the size of the residuals increased with local success in the cliff, but for both observations of dispersal (a much better fit unproductive cliffs) and observations of philopatry (a better fit in productive cliffs; Fig. B.5.9b). The same but weaker trend occurred at the social-group and colony scale with local success in the social group and colony (Fig. B.5.9c,d).

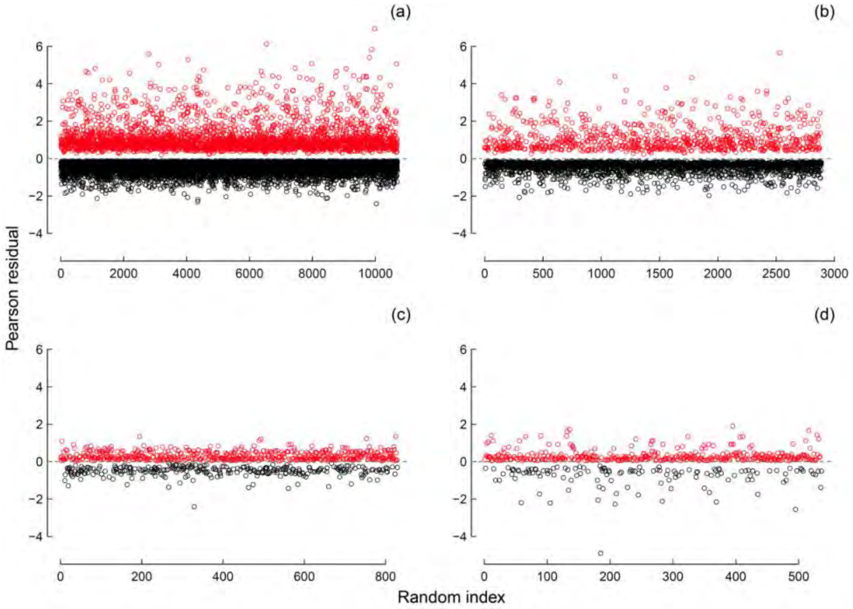

Figure B.5.3. Pearson residuals plotted against a random index for all observations in the four submodels (see *Materials and Methods*): (a) at the nest-site scale, (b) at the cliff scale, (c) at the social-group scale, (d) at the colony scale.

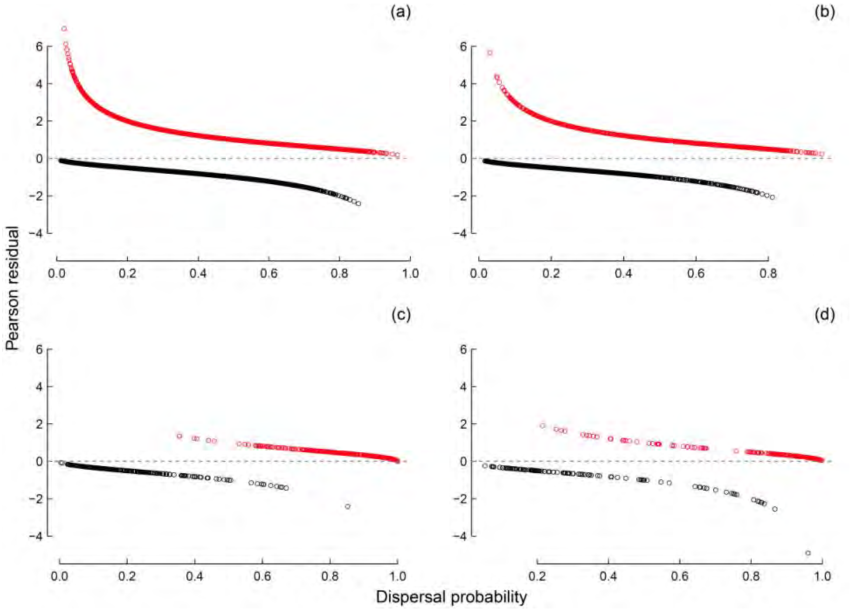

Figure B.5.4. Pearson residuals as a function of dispersal probability estimates, for all observations in the four submodels (see *Materials and Methods*): (a) at the nest-site scale, (b) at the cliff scale, (c) at the social-group scale, (d) at the colony scale.

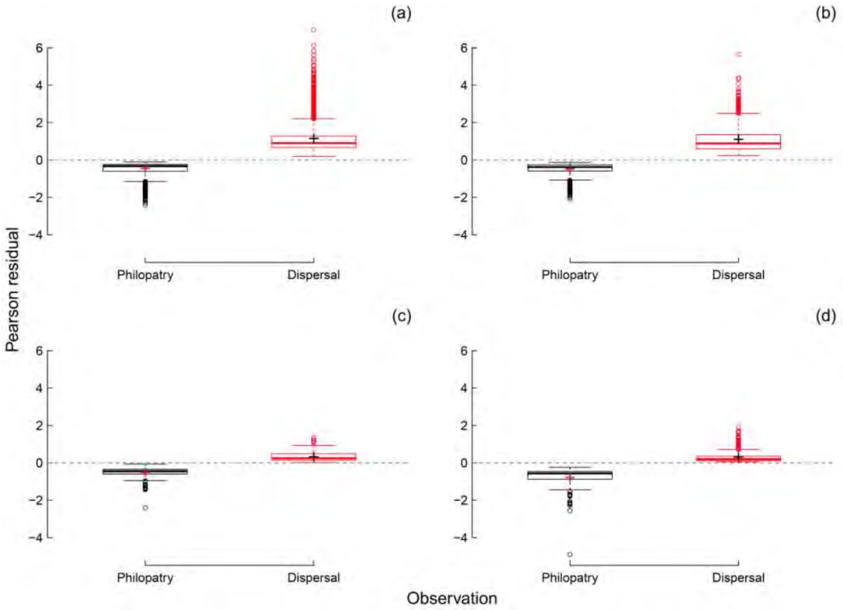

Figure B.5.5. Box plots of Pearson residuals for observations of philopatry (response = 0) and observations of dispersal (response =1), for all observations in the four submodels (see *Materials and Methods*): (a) at the nest-site scale, (b) at the cliff scale, (c) at the social-group scale, (d) at the colony scale.

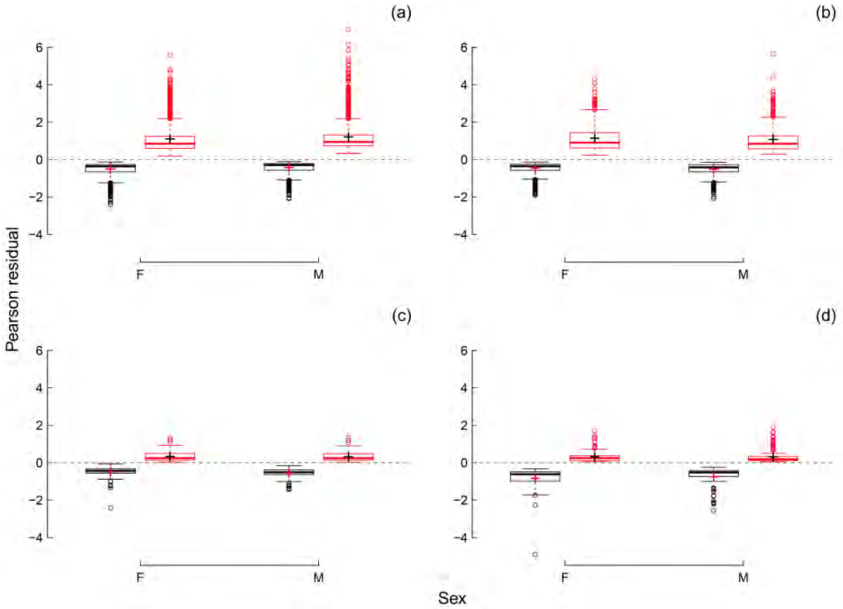

Figure B.5.6. Box plots of Pearson residuals for females (F) and males (M), for all observations in the four submodels (see *Materials and Methods*): (a) at the nest-site scale, (b) at the cliff scale, (c) at the social-group scale, (d) at the colony scale.

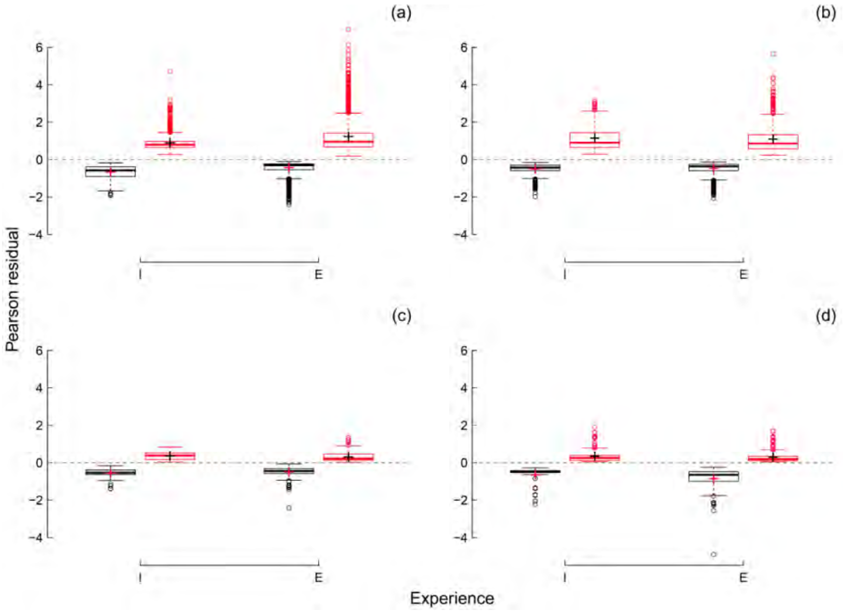

Figure B.5.7. Box plots of Pearson residuals for inexperienced (I) and experienced (E) individuals, for all observations in the four submodels (see *Materials and Methods*): (a) at the nest-site scale, (b) at the cliff scale, (c) at the social-group scale, (d) at the colony scale.

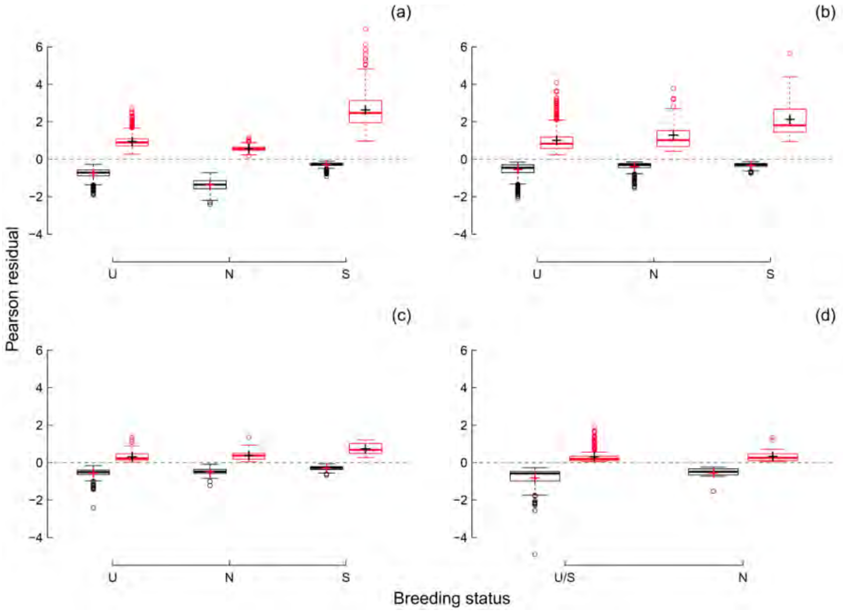

Figure B.5.8. Box plots of Pearson residuals for unsuccessful (U), nonbreeder (N), and successful (S) individuals, for all observations in the four submodels (see *Materials and Methods*): (a) at the nest-site scale, (b) at the cliff scale, (c) at the social-group scale, (d) at the colony scale.

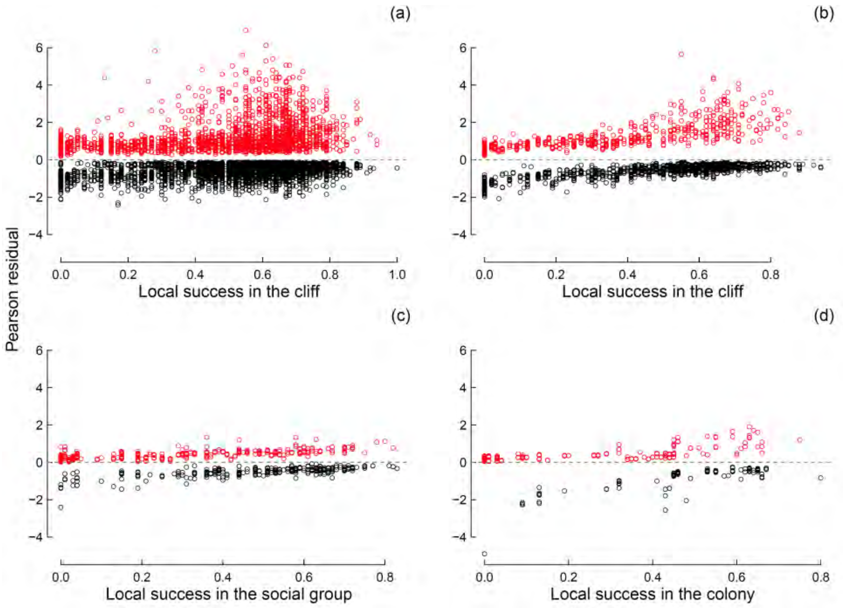

Figure B.5.9. Pearson residuals as a function of dispersal probability estimates, for all observations in the four submodels (see *Materials and Methods*): (a) at the nest-site scale, (b) at the cliff scale, (c) at the social-group scale, (d) at the colony scale.

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B.6 Selective review of opportunity costs of dispersal

B.6.1 Sequential proximity search and distance-dependent costs of dispersal

An important point of the *sequential proximity search* (SPS) hypothesis is that dispersal costs increase with distance. This is a common feature explaining the limitation of dispersal by distance in dispersal kernels (Hovestadt et al. 2012), but the underlying mechanisms depend on species characteristics (Bowler and Benton 2005). Many dispersal costs (reviewed in Bonte et al. 2012) are incremental: they accumulate during the dispersal transfer. This is the case for costs due to energetic expenditure, time spent and risk taken in the movement (e.g. Baker and Rao 2004, Smith and Batzli 2006, Burgess et al. 2012). As stated in the *Discussion* about the kittiwake, these costs are often negligible in highly mobile species such as many large birds that forage everyday farther than they usually move for breeding dispersal. Nonetheless, important distance-dependent dispersal costs may be incurred due to (I) the loss of familiarity and (II) constraints on habitat selection (i.e. 'opportunity costs'; Bonte et al. 2012).

> (I) Breeding habitat familiarity provides multiple benefits of geographical and social knowledge, which is likely to enhance fitness (Greenwood 1980, Beletsky and Orians 1991, Brown et al. 2008, Grabowska-Zhang et al. 2012a, Piper et al. 2011). For instance, benefits may involve efficient locomotion and orientation (Stamps et al. 1995, Able 2000), information on the location of foraging sites (Bradshaw et al. 2004, Wolf et al. 2009) and predation risk (Jacquot and Solomon 1997, Yoder et al. 2004), and success in territorial contests (the 'prior-residence effect'; Kokko et al. 2006). Familiar individuals know each other's behavior and dominance status, which may pacify relationships (the 'dear enemy' hypothesis; Getty 1987, Ydenberg et al. 1988, Eason and Hannon 1994) and promote reciprocity (Getty 1987, St-Pierre et al. 2009), thus favoring territory acquisition (Stamps 1987, Bruinzeel and van de Pol 2004), defensive coalitions against intruders (Getty 1987, Backwell and Jennions 2004), anti-predator behavior (Chivers et al. 1995, Griffiths et al. 2004, Grabowska-Zhang et al. 2012b) or foraging efficiency (Swaney et al. 2001, Griffiths et al. 2004, Aplin et al. 2012). Familiarity may also facilitate mating through the assessment of individual quality (Doutrelant and McGregor 2000, Cheetham et al. 2008). Last, familiarity may promote kinship, which reinforces cooperation benefits (Brown and Brown 1996). All these benefits should decrease with distance to the familiar breeding site because knowledge of the surrounding decreases (e.g. Heinze et al. 1996, van der Jeugd 2001, Péron et al. 2010).

(II) High costs may arise from time and energy requirements linked with activities involved in habitat selection, e.g. gathering public information for dispersal decisions (Danchin et al. 2001), searching a mate in case of divorce or widowhood (Pärt 1994, Jouventin et al. 1999), gaining familiarity in a novel habitat and dominance on a territory (Bruinzeel and van de Pol 2006, Pärt et al. 2011). Due to familiarity benefits and competitive constraints, settlement decisions may result in the despotic preemption of good-quality sites by competitive individuals. Individuals may thereby be forced to nonbreeding, sacrificing breeding occasion(s) waiting for suitable opportunities (the 'queuing' hypothesis; Zack and Stutchbury 1992, Kokko et al. 2001, van de Pol et al. 2007). Because familiarity lowers these constraints on habitat selection, the costs associated with dispersal should increase with distance (e.g. Jakob et al. 2001).

Moreover, the prospecting ability of animals is limited to some point (i.e. the limit of the 'perceptual range'; Lima and Zollner 1996, Delgado et al. 2014). This biological constraint is driven by dispersal costs: the perceptual range is the range within which animals might afford to assess habitat quality without too much affecting their fitness (Delgado et al. 2014). Consequently, there should be a distance beyond which individuals have no knowledge of the environment and thus do not benefit from any familiarity advantage anymore. In the present study we concentrated on a relatively straightforward study case that remains into this species perceptual range. However, particular cases of 'straight' SPS might be observed when the study scale exceeds the perceptual range, and when dispersal is passive (e.g. marine larvae, Elkin and Marshall 2007. In such cases, the sequence of habitat choices would involve a suite of patch encounter events rather than the assessment of all a spatial units composed of several patches. The accumulation of costs with distance would then be driven only by energetic, time and risk costs associated with the transfer movement of dispersal, or maladaptation (Bonte et al. 2012).

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C

Supporting information to Chapter 3

C.1. History and map of the population

C.1.1 History of the kittiwake population

Kittiwakes have been banded in the Cap Sizun since 1979 (Fig. B.1.1). At the beginning of the monitoring program, the study area hosted 4 colonies, which were relatively close to one another (colony 1, 2, 3 and 4, in or near the nature reserve of Goulien; Fig. B.1.1) but only colony 1 was subject to intensive survey and individual monitoring. In 1981 the program was extended to colony 3, and then to colony 2 and colony 4 in 1983 (Fig. B.1.1, B.1.2). A few individuals colonized the Pointe du Raz in 1982, thus establishing colony 5 (Fig. B.1.1, B.1.2) which was included in the program in 1984 and which is still intensively monitored today. The number of nests in colony 5 first increased (1984–1987) then declined towards quasi-extinction (1988–1991) and finally increased to concentrate most of the breeding population. At the same time, the other colonies were progressively deserted (Fig. B.1.2) and a “new” colony was established between Goulien and the Pointe du Raz (colony 6). There are historical records of presence of kittiwakes in colony 6 before the study started (Guermeur and Monnat 1980). The formerly largest colony (colony 1) went extinct in 1999. A pioneer pair built a complete nest in the Pointe du Van in 2004, thus re-establishing colony 6 (Fig. B.1.1, B.1.2) which was included into the monitoring program. Colony 2 went extinct in 2008, colony 3 and colony 4 contained very few nests in 2012 (17 and 8, respectively) and went extinct in 2013 (Fig. B.1.2). Additional information concerning kittiwake repartition and dynamics in France between 1960 and 2000 (with further details concerning the history of the study population in Brittany) can be found in Guemeur and Monnat (1980), Cadiou (1993) and Monnat and Cadiou (2004).

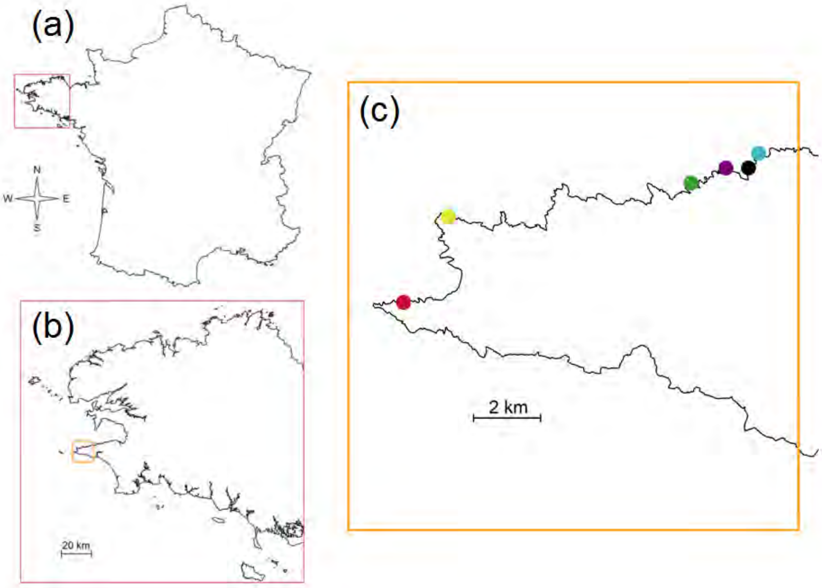

Figure C.1.1. Location of the study area and colony sites. (a) The study population is located in Brittany, northwestern France (red square), (b) in the Cap Sizun (orange square). Dots indicate colony sites (c): colony 1 in green, colony 2 in purple, colony 3 in black, colony 4 in blue, colony 5 in red and colony 6 in yellow.

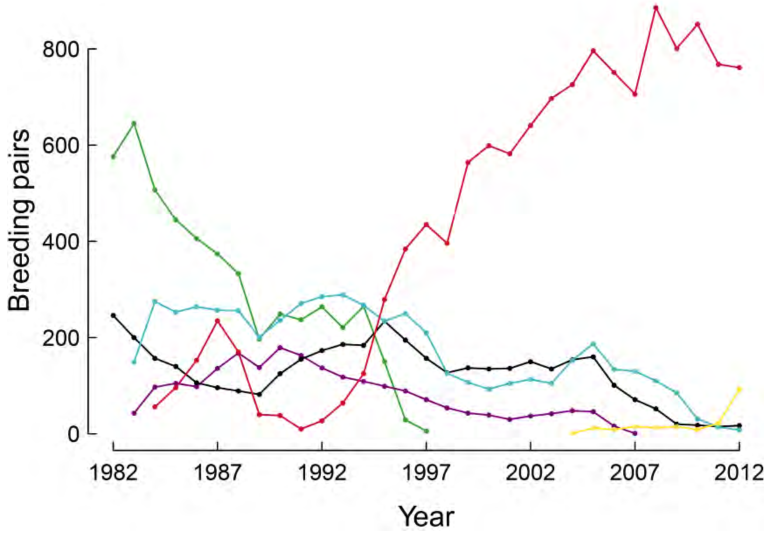

Figure C.1.2. Size of the colonies over 1982-2012. Colony size is expressed in number of breeding pairs, which was approximated by the number of nests that have reached the completion criterion (see *Materials and Methods*). Each time series starts in either 1982 or at the beginning of the monitoring in the given colony. The size is not plotted for colony sites once they have gone extinct. Colony 1 is plotted in green, colony 2 in purple, colony 3 in black, colony 4 in blue, colony 5 in red and colony 6 in yellow.

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C.2. Details on the integrated population model

This appendix provides additional details to the description of the integrated population model (see *Materials and Methods*) and the BUGS code to fit this model in JAGS.

C.2.1 Population matrix and projection equation

The equation below describes changes in the vector of population sizes as a function of the population matrix (deterministic version). The vector of population sizes contains the number of individuals N_i in each life-history state (see *Materials and Methods*). All numbers and demographic rates are time-dependent.

$$\begin{bmatrix} N_Y \\ N_{P2} \\ N_{P3} \\ N_{P4} \\ N_{P5} \\ N_{P6} \\ N_F \\ N_E \\ N_S \end{bmatrix}_t = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & \phi_0\pi_f & \phi_0\pi_e & 0 \\ \phi_0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \phi_2(1\text{-}\rho_3) & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \phi_2(1\text{-}\rho_4) & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \phi_2(1\text{-}\rho_5) & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \phi_2(1\text{-}\rho_6) & 0 & 0 & 0 & 0 \\ 0 & \phi_2\rho_3 & \phi_2\rho_4 & \phi_2\rho_5 & \phi_2\rho_6 & \phi_2 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \phi_2\psi_b & \phi_2\psi_b & \phi_2\psi_s \\ 0 & 0 & 0 & 0 & 0 & 0 & \phi_2(1\text{-}\psi_b) & \phi_2(1\text{-}\psi_b) & \phi_2(1\text{-}\psi_s) \end{bmatrix}_{t-1} \begin{bmatrix} N_Y \\ N_{P2} \\ N_{P3} \\ N_{P4} \\ N_{P5} \\ N_{P6} \\ N_F \\ N_E \\ N_S \end{bmatrix}_{t-1} + \begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ N_I \\ 0 \\ 0 \end{bmatrix}_t$$

where *Y* stands for yearlings, *Pi* stands for prebreeders of age *i* ($2 \le i \le 6$), *F* stands for first-time breeders, *E* stands for experienced breeders, *S* stands for skippers, I stands for immigrants; π_f is the *per capita* productivity of first-time breeders, π_e is the *per capita* productivity of experienced breeders, ϕ_0 is the annual survival rate at age 0 and age 1,

ϕ_2 is the annual survival from age 2, ρ_3 is the recruitment rate at age 3, ..., ρ_6 is the recruitment rate at age 6 (recruitment rate at age 7 is 1), ψ_b is the breeding propensity of former breeders, ψ_s is the breeding propensity of former skippers.

This deterministic version of the matrix population model was extended to include demographic stochasticity. Demographic stochasticity was considered by using binomial and Poisson distributions to describe the link between state-specific numbers in year t+1 and t. Environmental stochasticity is represented by time-dependence in demographic rates and state-specific numbers (they have an index t of year). We thus specified the following relationships:

$N_{Y,t+1} \sim Poisson\ (\phi_{0,t}\, \pi_{f,t}\, N_{F,t} + \phi_{0,t}\, \pi_{e,t}\, N_{E,t})$

$N_{P2,t+1} \sim Binomial\ (\phi_{0,t}\, , Y_t)$

$N_{P3,t+1} \sim Binomial\ (\phi_{2,t}\ (1\text{-}\rho_{3,t}), N_{P2,t})$

$N_{P4,t+1} \sim Binomial\ (\phi_{2,t}\ (1\text{-}\rho_{4,t}), N_{P3,t})$

$N_{P5,t+1} \sim Binomial\ (\phi_{2,t}\ (1\text{-}\rho_{5,t}), N_{P4,t})$

$N_{P6,t+1} \sim Binomial\ (\phi_{2,t}\ (1\text{-}\rho_{6,t}), N_{P5,t})$

$N_{F,t+1} \sim \sum_{i=3}^{6}\left(Binomial\ (\phi_{2,t}\, \rho_{i,t}\, , N_{P(i\text{-}1),t})\right) + Binomial\ (\phi_{2,t}\, , N_{P6,t})$

$N_{E,t+1} \sim Binomial\ (\phi_{2,t}\, \psi_{b,t}\, , N_{F,t}) + Binomial\ (\phi_{2,t}\, \psi_{b,t}\, , N_{E,t}) + Binomial\ (\phi_{2,t}\, \psi_{s,t}\, , N_{S,t})$

$N_{S,t+1} \sim Binomial\ (\phi_{2,t}(1\text{-}\psi_{b,t}), N_{F,t}) + Binomial\ (\phi_{2,t}(1\text{-}\psi_{b,t}), N_{E,t})$

$\qquad + Binomial\ (\phi_{2,t}(1\text{-}\psi_{s,t}), N_{S,t})$.

C.2.2 Likelihood from the count data

The state-space model is composed of a state process model describing the true fluctuations of the breeding population size over time, and an observation model describing the link between the true and the observed size of the breeding population (de Valpine and Hastings 2002). The state process model is described above with the matrix population model. For the observation model we assumed that the observation error was normally distributed on the log scale and constant over time. The count data C_t were thus modeled as follows:

$$\log\left(C_t\right) \sim Normal\left(\log\left(N_{F,t} + N_{E,t}\right), \sigma^2_{obs}\right) .$$

The likelihood for the complete state-space model was composed of the likelihood for the state-process and the observation process (Kéry and Schaub 2012).

C.2.3 Likelihood from the capture-recapture data

To estimate survival, recruitment, and breeding propensities from the capture-resighting histories, we used a multistate capture-recapture model (Lebreton et al. 2009) with a state-space formulation (Gimenez et al. 2007, Kéry and Schaub 2012). We considered a matrix Z with elements $z_{i,t}$, indicating the true state of individual i at time t ($z_{i,t} \in \{1, \ldots, 10\}$). The ten states were ‘fledgling’, ‘yearling’, ‘prebreeder of age 2’, ..., ‘prebreeder of age 6’, ‘breeder’, ‘skipper’ and ‘dead’. We assumed no error in state assignment. Given the state at first observation, we modeled the succession of states over time with a categorical distribution:

$$z_{i,t+1} | z_{i,t} \sim Categorical\left(\Omega_{z_{i,t},1\ldots10,t}\right).$$

where Ω is the state-transition matrix, defined as follows (see above for description of the parameters):

$$\Omega_t = \begin{bmatrix} 0 & \phi_0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1\text{-}\phi_0 \\ 0 & 0 & \phi_1 & 0 & 0 & 0 & 0 & 0 & 0 & 1\text{-}\phi_0 \\ 0 & 0 & 0 & \phi_2(1\text{-}\rho_3) & 0 & 0 & 0 & \phi_2\rho_3 & 0 & 1\text{-}\phi_2 \\ 0 & 0 & 0 & 0 & \phi_2(1\text{-}\rho_4) & 0 & 0 & \phi_2\rho_4 & 0 & 1\text{-}\phi_2 \\ 0 & 0 & 0 & 0 & 0 & \phi_2(1\text{-}\rho_5) & 0 & \phi_2\rho_3 & 0 & 1\text{-}\phi_2 \\ 0 & 0 & 0 & 0 & 0 & 0 & \phi_2(1\text{-}\rho_6) & \phi_2\rho_6 & 0 & 1\text{-}\phi_2 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi_2 & 0 & 1\text{-}\phi_2 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi_2\psi_b & \phi_2\psi_b & 1\text{-}\phi_2 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi_2\psi_s & \phi_2(1\text{-}\psi_s) & 1\text{-}\phi_2 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}_t .$$

There were six observation events: ‘seen as fledgling’ (i.e. at banding), ‘seen as prebreeder’, ‘seen as first-time breeder’, ‘seen as experienced breeder’, ‘seen as skipper’, and ‘not seen’. The observations were provided in the matrix O containing the capture-resighting histories (each element $o_{i,t}$ is the observation event concerning the individual i at time t). The observation process links the true states with the observation events. Given the true state, we modeled the sequences of observations events with a categorical distribution:

$$o_{i,t+1} | o_{i,t} \sim Categorical\left(\Theta_{z_{i,t},1\ldots6,t}\right).$$

where Θ is the observation matrix, defined as follows:

$$\Theta_t=\begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & p_y & 0 & 0 & 0 & 1\text{-}p_y \\ 0 & 0 & p_p & 0 & 0 & 1\text{-}p_p \\ 0 & 0 & p_p & 0 & 0 & 1\text{-}p_p \\ 0 & 0 & p_p & 0 & 0 & 1\text{-}p_p \\ 0 & 0 & p_p & 0 & 0 & 1\text{-}p_p \\ 0 & 0 & p_p & 0 & 0 & 1\text{-}p_p \\ 0 & p_{bs} & 0 & p_{bs} & 0 & 1\text{-}p_{bs} \\ 0 & 0 & 0 & 0 & p_{bs} & 1\text{-}p_{bs} \\ 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}_{\mathrm{t}}$$

where $p_{y,t}$ was the resighting probability of yearlings in year t, $p_{p,t}$ was the resighting probability of prebreeders of age 2 to 6 in year t, and $p_{bs,t}$ was the reencounter probability of breeders and skippers in year t.

All the demographic parameters and resighting probabilities were modeled with random year effects. Thus, any parameter θ_t was modeled as follows:

$$logit\ (\theta_t) \sim Normal\ \left(\bar{\theta}\ ,\sigma_\theta^2\right)$$

where $\bar{\theta}$ is the mean parameter over time on the logit scale, and σ_θ^2 is the temporal variance of the parameter. The use of random time effects results in time-specific parameters that are shrunk towards the mean parameter (Burnham and White 2002). The degree of shrinkage increases when precision decreases, which is a desired property (Kéry and Schaub 2012).

C.2.4 Likelihood from the productivity data

We used three Poisson regressions to extract information on the *per capita* productivity from status-specific counts of fledglings per nest. The first regression refers to the productivity of breeding pairs composed of two first-time breeders. In each year t, $J_{F,t}$ is the total count of fledglings produced by this category of breeding pairs, and $R_{F,t}$ is the count of breeding pairs that raised these fledglings. For this category, the annual productivity was thus modeled as:

$$J_{F,t} \sim Poisson\ (R_{F,t}\, 2\pi_f)\ .$$

The second regression refers to the productivity of breeding pairs composed of two experienced breeders. In each year t, $J_{E,t}$ is the total count of fledglings produced by this category of breeding pairs, and $R_{E,t}$ is the count of breeding pairs that raised these fledglings. For this category, the annual productivity was thus modeled as:

$$J_{E,t} \sim Poisson\ (R_{E,t}\, 2\pi_e)\ .$$

The third regression refers to the productivity of breeding pairs for which the two individuals were of different experience status, or at least one individual was of unknown status. In each year t, $J_{U,t}$ is the total count of fledglings produced by this category of breeding pairs, and $R_{U,t}$ is the count of breeding pairs that raised these fledglings. Because we used *per capita* productivity rates and ignored pair characteristics, we made the assumption that the productivity rate was an average of productivity of inexperienced and experienced breeders weighted by their respective proportion among breeders in the model. For this category of breeding pairs, the annual productivity was thus modeled as:

$$J_{U,t} \sim Poisson\ (R_{U,t}\, 2(\pi_{f,t} \frac{N_{F,t}}{N_{F,t}+N_{E,t}} + \pi_{e,t} \frac{N_{E,t}}{N_{F,t}+N_{E,t}}))\ .$$

We modeled productivity with random year effects, thus we have:

$$log\ (\pi_{f,t}) \sim Normal\ \left(\overline{\pi_f}\ , \sigma^2_{\pi_f}\right)$$

$$log\ (\pi_{e,t}) \sim Normal\ \left(\overline{\pi_e}\ , \sigma^2_{\pi_e}\right)$$

where $\overline{\pi_f}$ is the mean productivity of first-time breeders over time on the log scale, and $\sigma^2_{\pi_f}$ is the temporal variance of this parameter; $\overline{\pi_e}$ is the mean productivity of experienced breeders over time on the log scale, and $\sigma^2_{\pi_e}$ is the temporal variance of this parameter.

C.2.5 Prior distributions

The prior distributions for each parameter are the following:

- Mean survival: $\overline{\phi_0} \sim Uniform\ (0,1)$; $\overline{\phi_2} \sim Uniform\ (0,1)$.
- Temporal variability of survival (priors on the standard deviation, on the logit scale): $\sigma_{\phi_0} \sim Uniform\ (0,10)$; $\sigma_{\phi_2} \sim Uniform\ (0,10)$.
- Mean probability of recruitment: $\overline{\rho_3} \sim Uniform\ (0,1)$; $\overline{\rho_4} \sim Uniform\ (0,1)$; $\overline{\rho_5} \sim Uniform\ (0,1)$; $\overline{\rho_6} \sim Uniform\ (0,1)$.
- Temporal variability of recruitment (priors on the standard deviation, on the logit scale): $\sigma_{\rho_3} \sim Uniform\ (0,10)$; $\sigma_{\rho_4} \sim Uniform\ (0,10)$; $\sigma_{\rho_5} \sim Uniform\ (0,10)$; $\sigma_{\rho_6} \sim Uniform\ (0,10)$.

- Mean breeding propensity: $\overline{\psi_b} \sim Uniform\ (0,1)$; $\overline{\psi_s} \sim Uniform\ (0,1)$.
- Temporal variability of breeding propensity (priors on the standard deviation, on the logit scale): $\sigma_{\psi_b} \sim Uniform\ (0,10)$; $\sigma_{\psi_s} \sim Uniform\ (0,10)$.
- Mean productivity: $\overline{\pi_f} \sim Uniform\ (0,2)$; $\overline{\pi_e} \sim \mathrm{Uniform}(0,2)$.
- Temporal variability of productivity (priors on the standard deviation, on the log scale): $\sigma_{\pi_f} \sim Uniform\ (0,10)$; $\sigma_{\pi_e} \sim Uniform\ (0,10)$.
- Mean resighting probability: $\overline{p_y} \sim Uniform\ (0,1)$; $\overline{p_p} \sim Uniform\ (0,1)$;

  $p_{bs} \sim Uniform\ (0,1)$.
- Temporal variability of resighting probability (priors on the standard deviation, on the logit scale): $\sigma_{p_y} \sim Uniform\ (0,10)$; $\sigma_{p_p} \sim Uniform\ (0,10)$.
- Error of the count data (priors on the precision, i.e. inverse of the variance, on the log scale): $\tau_{obs} \sim Gamma\ (0.001,0.001)$.
- Number of individuals in each state (priors were truncated and rounded to positive integers): $N_{Y,1} \sim Normal\ (506,100)$; $N_{P2,1} \sim Normal\ (361,100)$;

  $N_{P3,1} \sim Normal\ (279,100)$; $N_{P4,1} \sim Normal\ (149,100)$; $N_{P5,1} \sim Normal\ (63,100)$; $N_{P6,1} \sim Normal\ (19,100)$; $N_{F,1} \sim Normal\ (264,100)$; $N_{E,1} \sim Normal\ (1814,100)$;

  $N_{S,1} \sim Normal\ (264,100)$.

  Note that for these normal priors, the mean value was selected according to the stable age distribution (see e.g. Szostek et al. 2014).
- Number of immigrants in each year (prior rounded to integer): $N_{I,t} \sim Uniform\ (-5,1000)$

C.2.6 On the assumption of equal survival in immigrants and natives

Recall that our population integrated model relies on the assumption of equal apparent survival between natives and immigrants once established in the population. This assumption is necessary if immigrants are not individually monitored. If it does not hold, the estimated number of immigrants would be negatively biased in the case of a lower survival of the immigrants than the natives, while it would be positively biased in the case of a higher survival in natives than immigrants.

Several processes might lead to a survival difference between natives and immigrants but we currently have no evidence to give a proper support to one hypothesis or another. We are lacking empirical and theoretical bases to move forwards in the discussion of survival differences between natives and immigrants. This lack of evidence is due to the current impossibility to monitor immigration in highly mobile species with a large geographic range. In the future, electronic devices for individual monitoring might help answering this question (see e.g. Ponchon et al. 2013).

Immigrants might be inferior survivors if they pay a cost of long-distance transfer or maladaptation (Baker and Rao 2004, Burgess et al. 2012, Bonte et al. 2012). Conversely, such dispersal costs could prevent frailer individuals from achieving immigration, which would result in higher survival in immigrants than natives. However, kittiwakes are highly mobile (they winter thousands of kilometers from breeding colonies; Frederiksen et al. 2012), and large effective immigration (as found in our study, see *Results*) should prevent local adaptation in natives (Lenormand 2002). This tends to make the hypothesis of a difference in survival probability due to a survival cost in immigrants fragile.

We could also argue that immigrants might express a dispersal syndrome (Clobert et al. 2012), and therefore would have a higher probability of emigrating permanently than natives. However, heritable components of dispersal propensity would be transmitted to natives by the large effective number of immigrants (Phillips et al. 2008): natives might also exhibit a high dispersal probability. This would be in line with the hypothesis that the low survival in the Cap Sizun population might stem from a high level of permanent emigration (see *Discussion*). Finally, natives might be attracted to more favorable habitats outside the study area while immigrants have been attracted to the study area, which might also translate into lower local survival in natives. Nonetheless, it may be hard to conceive that immigrants once attending the population would not be attracted to the same habitats outside the study area as do locals.

Based on these considerations, survival differences between immigrant and natives appear unlikely.

C.2.7 *BUGS* code

```
model {

# --------------------------
#  PARAMETERS IN THE MODEL
# --------------------------
# phi.0: first and second year survival probability
# phi.2: adult survival probability
# rho.3: probability to start breeding when 3 years old
# rho.4: probability to start breeding when 4 years old
# rho.5: probability to start breeding when 5 years old
# rho.6: probability to start breeding when 6 years old
# probability to start breeding when 7 years old is 1
# psi.b: probability that a breeder at t breeds at t+1
# psi.s: probability that a skipper at t breeds at t+1
# pi.f: productivity of first-time breeders
# pi.e: productivity of experienced breeders
# p.y: recapture probability of yearlings
# p.p: recapture probability of pre-breeders (age > 1)
# p.bs: recapture probability of breeders and skippers (very close to 1)
# ----------------------
#  STATES & OBSERVATIONS
# ----------------------
# States (S):
# 1: fledgling
# 2: yearling
# 3: not yet breeding at age 2 years
# 4: not yet breeding at age 3 years
# 5: not yet breeding at age 4 years
# 6: not yet breeding at age 5 years
# 7: not yet breeding at age 6 years
# 8: first-time breeders
# 9: experienced breeders
# 10: sabbatical individuals
# 11: dead individuals
# Observations (O):
# 1: seen as fledgling (the year of capture)
# 2: seen as prebreeder
# 3: seen as first-time breeder
# 4: seen as experienced breeder
# 5: seen as skipper
# 6: not seen
# ----------------------------------

# ----------------------------
#    PRIORS AND CONSTRAINTS
# ----------------------------

for (t in 1:(n.occasions-1)) {

  logit(phi.0[t]) <- ep.phi.0[t]
  logit(phi.2[t]) <- ep.phi.2[t]
  logit(rho.3[t]) <- ep.rho.3[t]
  logit(rho.4[t]) <- ep.rho.4[t]
  logit(rho.5[t]) <- ep.rho.5[t]
  logit(rho.6[t]) <- ep.rho.6[t]
  logit(psi.b[t]) <- ep.psi.b[t]
  logit(psi.s[t]) <- ep.psi.s[t]
  logit(p.y[t])   <- ep.p.y[t]
  logit(p.p[t])   <- ep.p.p[t]

  ep.phi.0[t] ~ dnorm(mu.phi.0, tau.phi.0)T(-10,10)
  ep.phi.2[t] ~ dnorm(mu.phi.2, tau.phi.2)T(-10,10)
  ep.rho.3[t] ~ dnorm(mu.rho.3, tau.rho.3)T(-10,10)
  ep.rho.4[t] ~ dnorm(mu.rho.4, tau.rho.4)T(-10,10)
  ep.rho.5[t] ~ dnorm(mu.rho.5, tau.rho.5)T(-10,10)
  ep.rho.6[t] ~ dnorm(mu.rho.6, tau.rho.6)T(-10,10)
  ep.psi.b[t] ~ dnorm(mu.psi.b, tau.psi.b)T(-10,10)
  ep.psi.s[t] ~ dnorm(mu.psi.s, tau.psi.s)T(-10,10)
  ep.p.y[t]   ~ dnorm(mu.p.y, tau.p.y)T(-10,10)
  ep.p.p[t]   ~ dnorm(mu.p.p, tau.p.p)T(-10,10)

} #t

mean.phi.0 ~ dunif(0,1)
mu.phi.0 <- log(mean.phi.0 / (1-mean.phi.0))
mean.phi.2 ~ dunif(0,1)
```

```
mu.phi.2 <- log(mean.phi.2 / (1-mean.phi.2))

tau.phi.0 <- pow(sigma.phi.0, -2)
sigma.phi.0 ~ dunif(0,10)
var.phi.0 <- pow(sigma.phi.0, 2)
tau.phi.2 <- pow(sigma.phi.2, -2)
sigma.phi.2 ~ dunif(0,10)
var.phi.2 <- pow(sigma.phi.2, 2)

mean.rho.3 ~ dunif(0,1)
mu.rho.3 <- log(mean.rho.3 / (1-mean.rho.3))
mean.rho.4 ~ dunif(0,1)
mu.rho.4 <- log(mean.rho.4 / (1-mean.rho.4))
mean.rho.5 ~ dunif(0,1)
mu.rho.5 <- log(mean.rho.5 / (1-mean.rho.5))
mean.rho.6 ~ dunif(0,1)
mu.rho.6 <- log(mean.rho.6 / (1-mean.rho.6))

tau.rho.3 <- pow(sigma.rho.3, -2)
sigma.rho.3 ~ dunif(0,10)
var.rho.3 <- pow(sigma.rho.3, 2)
tau.rho.4 <- pow(sigma.rho.4, -2)
sigma.rho.4 ~ dunif(0,10)
var.rho.4 <- pow(sigma.rho.4, 2)
tau.rho.5 <- pow(sigma.rho.5, -2)
sigma.rho.5 ~ dunif(0,10)
var.rho.5 <- pow(sigma.rho.5, 2)
tau.rho.6 <- pow(sigma.rho.6, -2)
sigma.rho.6 ~ dunif(0,10)
var.rho.6 <- pow(sigma.rho.6, 2)

mean.psi.b ~ dunif(0,1)
mu.psi.b <- log(mean.psi.b / (1-mean.psi.b))
mean.psi.s ~ dunif(0,1)
mu.psi.s <- log(mean.psi.s / (1-mean.psi.s))

tau.psi.b <- pow(sigma.psi.b, -2)
sigma.psi.b ~ dunif(0,10)
var.psi.b <- pow(sigma.psi.b, 2)
tau.psi.s <- pow(sigma.psi.s, -2)
sigma.psi.s ~ dunif(0,10)
var.psi.s <- pow(sigma.psi.s, 2)

mean.p.y ~ dunif(0,1)
mu.p.y <- log(mean.p.y / (1-mean.p.y))
mean.p.p ~ dunif(0,1)
mu.p.p <- log(mean.p.p / (1-mean.p.p))

tau.p.y <- pow(sigma.p.y, -2)
sigma.p.y ~ dunif(0,10)
var.p.y <- pow(sigma.p.y, 2)
tau.p.p <- pow(sigma.p.p, -2)
sigma.p.p ~ dunif(0,10)
var.p.p <- pow(sigma.p.p, 2)

p.bs ~ dunif(0,1)
p.bs <- p.bs

for (t in 1:n.occasions){

  log(pi.f[t]) <- ep.pi.f[t]
  log(pi.e[t]) <- ep.pi.e[t]

  ep.pi.f[t] ~ dnorm(mu.pi.f, tau.pi.f)T(-10,10)
  ep.pi.e[t] ~ dnorm(mu.pi.e, tau.pi.e)T(-10,10)

  nrNI[t] ~ dunif(-5,1000)
  NI[t]  <- round(nrNI[t])

} #t

mean.pi.f ~ dunif(0, 2)
mu.pi.f <- log(mean.pi.f)

mean.pi.e ~ dunif(0, 2)
mu.pi.e <- log(mean.pi.e)

tau.pi.f <- pow(sigma.pi.f, -2)
sigma.pi.f ~ dunif(0,10)
var.pi.f <- pow(sigma.pi.f, 2)

tau.pi.e <- pow(sigma.pi.e, -2)
```

```
sigma.pi.e ~ dunif(0,10)
var.pi.e <- pow(sigma.pi.e, 2)

nrNY  ~ dnorm(506,0.01)T(0,)
nrNP2 ~ dnorm(361,0.01)T(0,)
nrNP3 ~ dnorm(279,0.01)T(0,)
nrNP4 ~ dnorm(149,0.01)T(0,)
nrNP5 ~ dnorm(63,0.01)T(0,)
nrNP6 ~ dnorm(19,0.01)T(0,)
nrNF  ~ dnorm(264,0.01)T(0,)
nrNE  ~ dnorm(1814,0.01)T(0,)
nrNS  ~ dnorm(264,0.01)T(0,)

NY[1]  <- round(nrNY)
NP2[1] <- round(nrNP2)
NP3[1] <- round(nrNP3)
NP4[1] <- round(nrNP4)
NP5[1] <- round(nrNP5)
NP6[1] <- round(nrNP6)
NF[1]  <- round(nrNF)
NE[1]  <- round(nrNE)
NS[1]  <- round(nrNS)
NB[1]  <- NF[1]+NE[1]

tau.obs    ~ dgamma(0.001, 0.001)
var.obs   <- 1/tau.obs
sigma.obs <- pow(var.obs,0.5)

# -----------------------------------------------------
#   LIKELIHOOD OF THE STATE-SPACE MODEL FOR COUNT DATA
# -----------------------------------------------------

    ## State process

for (t in 1:(n.occasions-1)) {

    NY[t+1] ~ dpois(mu1[t])
    mu1[t] <- NF[t] * pi.f[t] * phi.0[t] + NE[t] * pi.e[t] * phi.0[t]

    NP2[t+1] ~ dbin(mu2[t], NY[t])
    mu2[t] <- phi.0[t]

    NP3[t+1] ~ dbin(mu3[t], NP2[t])
    mu3[t] <- phi.2[t] * (1-rho.3[t])

    NP4[t+1] ~ dbin(mu4[t], NP3[t])
    mu4[t] <- phi.2[t] * (1-rho.4[t])

    NP5[t+1] ~ dbin(mu5[t], NP4[t])
    mu5[t] <- phi.2[t] * (1-rho.5[t])

    NP6[t+1] ~ dbin(mu6[t], NP5[t])
    mu6[t] <- phi.2[t] * (1-rho.6[t])

    NF3[t+1] ~ dbin(mu7[t], NP2[t])
    mu7[t] <- phi.2[t] * rho.3[t]

    NF4[t+1] ~ dbin(mu8[t], NP3[t])
    mu8[t] <- phi.2[t] * rho.4[t]

    NF5[t+1] ~ dbin(mu9[t], NP4[t])
    mu9[t] <- phi.2[t] * rho.5[t]

    NF6[t+1] ~ dbin(mu10[t], NP5[t])
    mu10[t] <- phi.2[t] * rho.6[t]

    NF7[t+1] ~ dbin(mu11[t], NP6[t])
    mu11[t] <- phi.2[t]
    # Note: IM[t] is given in another loop (that covers all time steps)

    NEF[t+1] ~ dbin(mu12[t], NF[t])
    mu12[t] <- phi.2[t] * psi.b[t]

    NEE[t+1] ~ dbin(mu13[t], NE[t])
    mu13[t] <- phi.2[t] * psi.b[t]

    NES[t+1] ~ dbin(mu14[t], NS[t])
    mu14[t] <- phi.2[t] * psi.s[t]

    NSF[t+1] ~ dbin(mu15[t], NF[t])
    mu15[t] <- phi.2[t] * (1-psi.b[t])
```

```
    NSE[t+1] ~ dbin(mu16[t], NE[t])
    mu16[t] <- phi.2[t] * (1-psi.b[t])

    NSS[t+1] ~ dbin(mu17[t], NS[t])
    mu17[t] <- phi.2[t] * (1-psi.s[t])

   } #t

## Observation process

for (t in 2:n.occasions) {

    NF[t] <- NF3[t] + NF4[t] + NF5[t] + NF6[t] + NF7[t] + NI[t]
    NE[t] <- NEF[t] + NEE[t] + NES[t]
    NS[t] <- NSF[t] + NSE[t] + NSS[t]
    NB[t] <- NF[t]  + NE[t]            # total breeding population size

} #t


 for (t in 1:n.occasions) {

    lNB[t] <- log(NB[t])
    C[t]    ~ dnorm(lNB[t], tau.obs)

}

#---------------------------------------------------------
#  LIKELIHOOD FOR PRODUCTIVITY DATA: POISSON REGRESSIONS
#---------------------------------------------------------

for (t in 1:n.occasions) {

  JF[t] ~ dpois(mu.f[t])
  log(mu.f[t]) <- log(RF[t]) + log(pi.f[t]*2)

  JB[t] ~ dpois(rho.b[t])
  log(mu.b[t]) <- log(RB[t]) + log(pi.e[t]*2)

  JU[t] ~ dpois(rho.u[t])
  log(mu.u[t]) <- log(RU[t])+log(2*(pi.f[t]*prop[t]+pi.e[t]*(1-prop[t])))

  prop[t] <- NF[t]/NB[t]

    } #t

# --------------------------------------------------------
#   LIKELIHOOD OF THE MULTISTATE CAPTURE-RECAPTURE MODEL
# --------------------------------------------------------

## Define state-transition and observation matrices

  # Define probabilities of state Z(t+1) given Z(t)

for (t in 1:(n.occasions-1)){

  ps[1,t,1]  <- 0
  ps[1,t,2]  <- phi.0[t]
  ps[1,t,3]  <- 0
  ps[1,t,4]  <- 0
  ps[1,t,5]  <- 0
  ps[1,t,6]  <- 0
  ps[1,t,7]  <- 0
  ps[1,t,8]  <- 0
  ps[1,t,9]  <- 0
  ps[1,t,10] <- 0
  ps[1,t,11] <- 1-phi.0[t]

  ps[2,t,1]  <- 0
  ps[2,t,2]  <- 0
  ps[2,t,3]  <- phi.0[t]
  ps[2,t,4]  <- 0
  ps[2,t,5]  <- 0
  ps[2,t,6]  <- 0
  ps[2,t,7]  <- 0
  ps[2,t,8]  <- 0
  ps[2,t,9]  <- 0
  ps[2,t,10] <- 0
  ps[2,t,11] <- 1-phi.0[t]

  ps[3,t,1]  <- 0
```

```
        ps[3,t,2]  <- 0
        ps[3,t,3]  <- 0
        ps[3,t,4]  <- phi.2[t] * (1-rho.3[t])
        ps[3,t,5]  <- 0
        ps[3,t,6]  <- 0
        ps[3,t,7]  <- 0
        ps[3,t,8]  <- phi.2[t] * rho.3[t]
        ps[3,t,9]  <- 0
        ps[3,t,10] <- 0
        ps[3,t,11] <- 1-phi.2[t]

        ps[4,t,1]  <- 0
        ps[4,t,2]  <- 0
        ps[4,t,3]  <- 0
        ps[4,t,4]  <- 0
        ps[4,t,5]  <- phi.2[t] * (1-rho.4[t])
        ps[4,t,6]  <- 0
        ps[4,t,7]  <- 0
        ps[4,t,8]  <- phi.2[t] * rho.4[t]
        ps[4,t,9]  <- 0
        ps[4,t,10] <- 0
        ps[4,t,11] <- 1-phi.2[t]

        ps[5,t,1]  <- 0
        ps[5,t,2]  <- 0
        ps[5,t,3]  <- 0
        ps[5,t,4]  <- 0
        ps[5,t,5]  <- 0
        ps[5,t,6]  <- phi.2[t] * (1-rho.5[t])
        ps[5,t,7]  <- 0
        ps[5,t,8]  <- phi.2[t] * rho.5[t]
        ps[5,t,9]  <- 0
        ps[5,t,10] <- 0
        ps[5,t,11] <- 1-phi.2[t]

        ps[6,t,1]  <- 0
        ps[6,t,2]  <- 0
        ps[6,t,3]  <- 0
        ps[6,t,4]  <- 0
        ps[6,t,5]  <- 0
        ps[6,t,6]  <- 0
        ps[6,t,7]  <- phi.2[t] * (1-rho.6[t])
        ps[6,t,8]  <- phi.2[t] * rho.6[t]
        ps[6,t,9]  <- 0
        ps[6,t,10] <- 0
        ps[6,t,11] <- 1-phi.2[t]

        ps[7,t,1]  <- 0
        ps[7,t,2]  <- 0
        ps[7,t,3]  <- 0
        ps[7,t,4]  <- 0
        ps[7,t,5]  <- 0
        ps[7,t,6]  <- 0
        ps[7,t,7]  <- 0
        ps[7,t,8]  <- phi.2[t]
        ps[7,t,9]  <- 0
        ps[7,t,10] <- 0
        ps[7,t,11] <- 1-phi.2[t]

        ps[8,t,1]  <- 0
        ps[8,t,2]  <- 0
        ps[8,t,3]  <- 0
        ps[8,t,4]  <- 0
        ps[8,t,5]  <- 0
        ps[8,t,6]  <- 0
        ps[8,t,7]  <- 0
        ps[8,t,8]  <- 0
        ps[8,t,9]  <- phi.2[t] * psi.b[t]
        ps[8,t,10] <- phi.2[t] * (1-psi.b[t])
        ps[8,t,11] <- 1-phi.2[t]

        ps[9,t,1]  <- 0
        ps[9,t,2]  <- 0
        ps[9,t,3]  <- 0
        ps[9,t,4]  <- 0
        ps[9,t,5]  <- 0
        ps[9,t,6]  <- 0
        ps[9,t,7]  <- 0
        ps[9,t,8]  <- 0
        ps[9,t,9]  <- phi.2[t] * psi.b[t]
        ps[9,t,10] <- phi.2[t] * (1-psi.b[t])
        ps[9,t,11] <- 1-phi.2[t]
```

```
    ps[10,t,1]  <- 0
    ps[10,t,2]  <- 0
    ps[10,t,3]  <- 0
    ps[10,t,4]  <- 0
    ps[10,t,5]  <- 0
    ps[10,t,6]  <- 0
    ps[10,t,7]  <- 0
    ps[10,t,8]  <- 0
    ps[10,t,9]  <- phi.2[t] * psi.s[t]
    ps[10,t,10] <- phi.2[t] * (1-psi.s[t])
    ps[10,t,11] <- 1-phi.2[t]

    ps[11,t,1]  <- 0
    ps[11,t,2]  <- 0
    ps[11,t,3]  <- 0
    ps[11,t,4]  <- 0
    ps[11,t,5]  <- 0
    ps[11,t,6]  <- 0
    ps[11,t,7]  <- 0
    ps[11,t,8]  <- 0
    ps[11,t,9]  <- 0
    ps[11,t,10] <- 0
    ps[11,t,11] <- 1


    # Define probabilities of O(t) given Z(t)

    po[1,t,1]  <- 1
    po[1,t,2]  <- 0
    po[1,t,3]  <- 0
    po[1,t,4]  <- 0
    po[1,t,5]  <- 0
    po[1,t,6]  <- 0

    po[2,t,1]  <- 0
    po[2,t,2]  <- p.y[t]
    po[2,t,3]  <- 0
    po[2,t,4]  <- 0
    po[2,t,5]  <- 0
    po[2,t,6]  <- 1-p.y[t]

    po[3,t,1]  <- 0
    po[3,t,2]  <- p.p[t]
    po[3,t,3]  <- 0
    po[3,t,4]  <- 0
    po[3,t,5]  <- 0
    po[3,t,6]  <- 1-p.p[t]

    po[4,t,1]  <- 0
    po[4,t,2]  <- p.p[t]
    po[4,t,3]  <- 0
    po[4,t,4]  <- 0
    po[4,t,5]  <- 0
    po[4,t,6]  <- 1-p.p[t]

    po[5,t,1]  <- 0
    po[5,t,2]  <- p.p[t]
    po[5,t,3]  <- 0
    po[5,t,4]  <- 0
    po[5,t,5]  <- 0
    po[5,t,6]  <- 1-p.p[t]

    po[6,t,1]  <- 0
    po[6,t,2]  <- p.p[t]
    po[6,t,3]  <- 0
    po[6,t,4]  <- 0
    po[6,t,5]  <- 0
    po[6,t,6]  <- 1-p.p[t]

    po[7,t,1]  <- 0
    po[7,t,2]  <- p.p[t]
    po[7,t,3]  <- 0
    po[7,t,4]  <- 0
    po[7,t,5]  <- 0
    po[7,t,6]  <- 1-p.p[t]

    po[8,t,1]  <- 0
    po[8,t,2]  <- 0
    po[8,t,3]  <- p.bs
    po[8,t,4]  <- 0
    po[8,t,5]  <- 0
```

```
    po[8,t,6]  <- 1-p.bs

    po[9,t,1]  <- 0
    po[9,t,2]  <- 0
    po[9,t,3]  <- 0
    po[9,t,4]  <- p.bs
    po[9,t,5]  <- 0
    po[9,t,6]  <- 1-p.bs

    po[10,t,1]  <- 0
    po[10,t,2]  <- 0
    po[10,t,3]  <- 0
    po[10,t,4]  <- 0
    po[10,t,5]  <- p.bs
    po[10,t,6]  <- 1-p.bs

    po[11,t,1]  <- 0
    po[11,t,2]  <- 0
    po[11,t,3]  <- 0
    po[11,t,4]  <- 0
    po[11,t,5]  <- 0
    po[11,t,6]  <- 1

  } #t

  # Likelihood

  for (i in 1:nind){

    # Define latent state at first capture in the histories
    z[i,f[i]] <- rs[i]
     # the vector f contains the year of first capture for each individual
     # the vector rs contains the state at first capture for each individual

    for (t in (f[i]+1):n.occasions){

      # State process: draw z(t) given z(t-1)
      z[i,t] ~ dcat(ps[z[i,t-1],t-1,])

      # Observation process: draw o(t) given z(t)
      o[i,t] ~ dcat(po[z[i,t],t-1,])

      } #t

   } #i

  } #model
```

C.2.8 Literature cited

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C.3. Summaries of the posterior distributions

C.3.1 Foreword of the section

This appendix contains summaries for the following demographic parameters: local survival, local recruitment, breeding propensity, productivity (Fig. C.3.1 to C.3.4). Second, we give summaries for resighting probabilities (Fig. C.3.5) and observation error for count data. Due to the huge number of parameters involved, we provide only a graphical summary for time-specific parameters (with posterior means and 95% credible intervals in each year). When time variation was specified with random effects (see Appendix C.2), we provide temporal means and standard deviations (along with 95%CI between brackets) as a note to the figure. Third, we provide large figures to facilitate the visual assessment of the number of individuals in each life-history state (Fig. C.3.6). We used the R packages CODA (Plummer et al. 2006) and MCMCglmm (Hadfield 2010) for post-processing of the MCMC chains.

We also give some details on the Brooks-Gelman-Rubin diagnostic $\widehat{R}$, the Monte Carlo standard error (MCSE), and the effective sample size (ESS). In brief, $\widehat{R}$ is a measure of convergence of the MCMC chains (Brooks and Gelman 1998); the closer to one, the better. In practice, one considers that convergence is achieved when $\widehat{R}<1.1$. MCSE is a measure of the error due to imperfect sampling, because MCMC chains are dependent sequences of pseudo-random draws (Lunn et al. 2012). This error increases with autocorrelation between MCMC samples and decreases with the number of samples. MCSE thus indicates the appropriate decimal place precision: the actual mean is approximately within ±2×MCSE around the posterior mean with probability 0.95, within ±2.6×MCSE with probability 0.99, etc. The ESS quantifies the number of independent samples that would contain the same information as the dependent MCMC samples (Lunn et al. 2012). According to Raftery and Lewis (1992), ESS=4000 is sufficient for well-behaved posterior distributions to provide the 2.5% quantiles within ±0.005 with probability 0.95 (i.e. reported 95% credible intervals then have posterior probability within [0.94,0.96]).

C.3.2 Demographic parameters

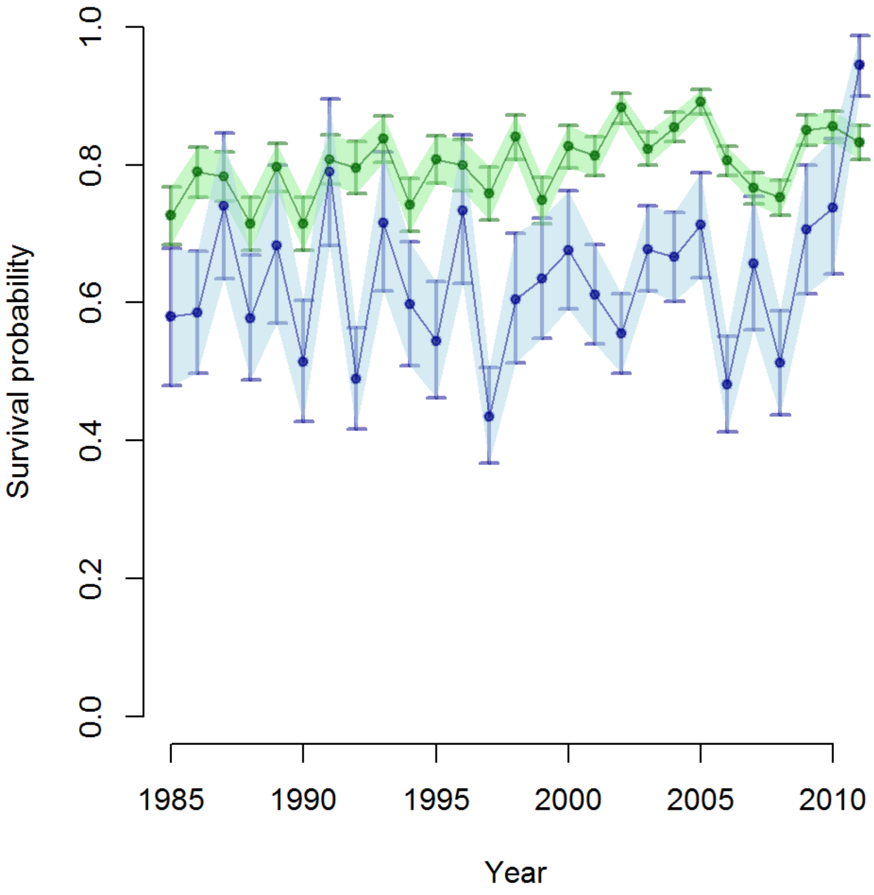

Figure C.3.1. Estimates of kittiwake apparent survival probabilities over 1985–2011 in the Cap Sizun population. Annual survival between age 0 and age 2 is in blue. Annual survival between from age 2 is in green. Points indicate posterior means. Color backgrounds and segments indicate 95%CI. The mean annual survival at age 0 and age 1 ($\overline{\phi_0}$) was 0.649 [0.587,0.710], temporal standard deviation on the logit scale (σ_{ϕ_0}) was 0.688 [0.435,0.975]. The mean annual survival from age 2 ($\overline{\phi_2}$) was 0.805 [0.783,0.827], temporal standard deviation on the logit scale (σ_{ϕ_2}) was 0.347 [0.247,0.459]. All $\widehat{R}$ < 1.002, all MCSE ≤ 0.001, all ESS > 7547.

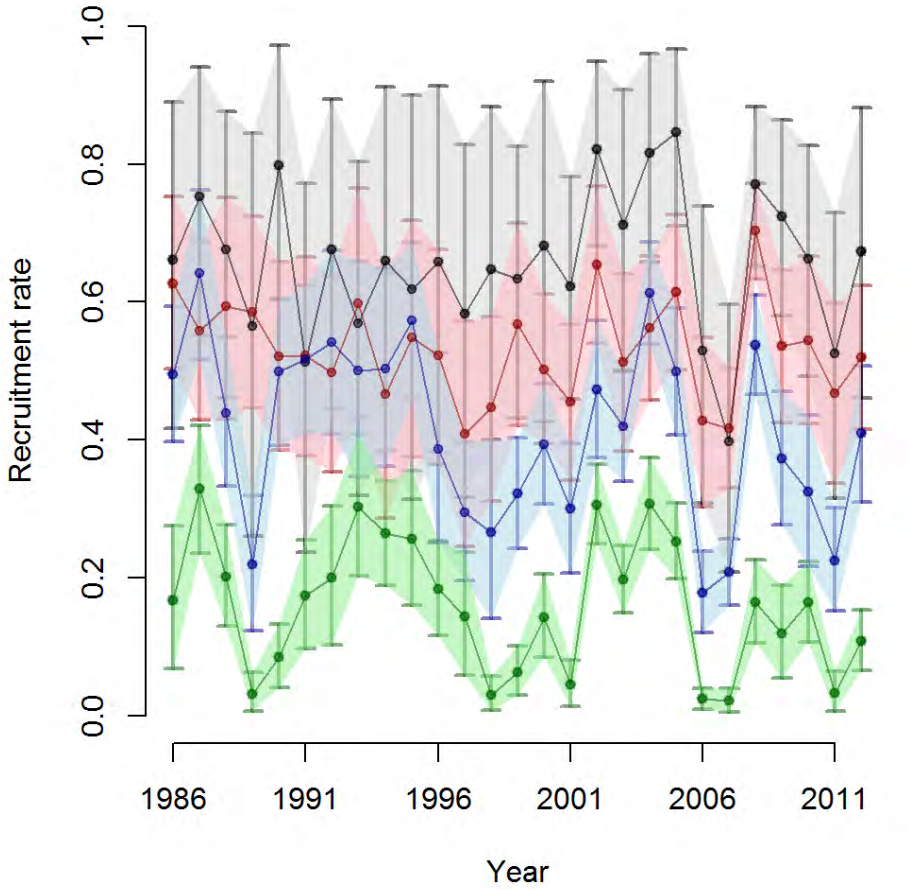

Figure C.3.2. Estimates of kittiwake local recruitment probability over 1986–2012 in the Cap Sizun population. Recruitment at age 3 is in green, recruitment at age 4 is in blue, recruitment at age 5 is in red, recruitment at age 6 is in grey; recruitment rate at age 7 is 1. Color backgrounds and segments indicate 95%CI. The mean recruitment rate at age 3 was $\bar{\rho}_3$ = 0.128 [0.082,0.179], with temporal standard deviation (on the logit scale) σ_{ρ_3} = 1.107 [0.765,1.484]. The mean recruitment rate at age 3 was $\bar{\rho}_4$ = 0.406 [0.342,0.471], with temporal standard deviation σ_{ρ_4} = 0.659 [0.457,0.883]. The mean recruitment rate at age 3 was $\bar{\rho}_5$ = 0.534 [0.479,0.586], with temporal standard deviation σ_{ρ_5} = 0.429 [0.243,0.632]. The mean recruitment rate at age 3 was $\bar{\rho}_6$ = 0.674 [0.583,0.764], with temporal standard deviation σ_{ρ_6} = 0.780 [0.377,0.1.229]. All $\widehat{R}$ < 1.002, all MCSE ≤ 0.001, all ESS > 13003.

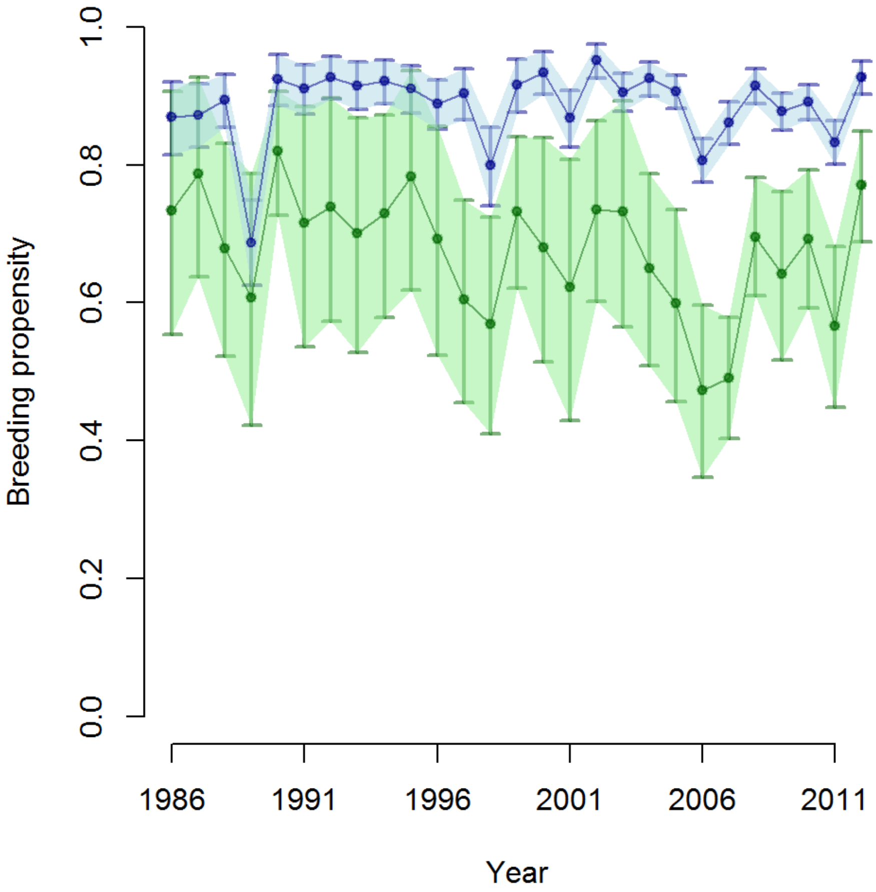

Figure C.3.3. Estimates of kittiwake breeding probability over 1986–2012 in the Cap Sizun population. Breeding propensity of former breeders is in blue. Breeding propensity of former skippers is in green. Points indicate posterior means. Color backgrounds and segments indicate 95%CI. The mean breeding propensity of former breeder ($\overline{\psi_b}$) was 0.895 [0.874,0.915], temporal standard deviation on the logit scale (σ_{ψ_b}) was 0.530 [0.366,0.714]. The mean annual survival between from age 2 ($\overline{\psi_s}$) was 0.685 [0.624,0.747], temporal standard deviation on the logit scale (σ_{ψ_s}) was 0.570 [0.325,0.846]. All $\widehat{R} < 1.002$, all MCSE ≤ 0.001, all ESS > 9218.

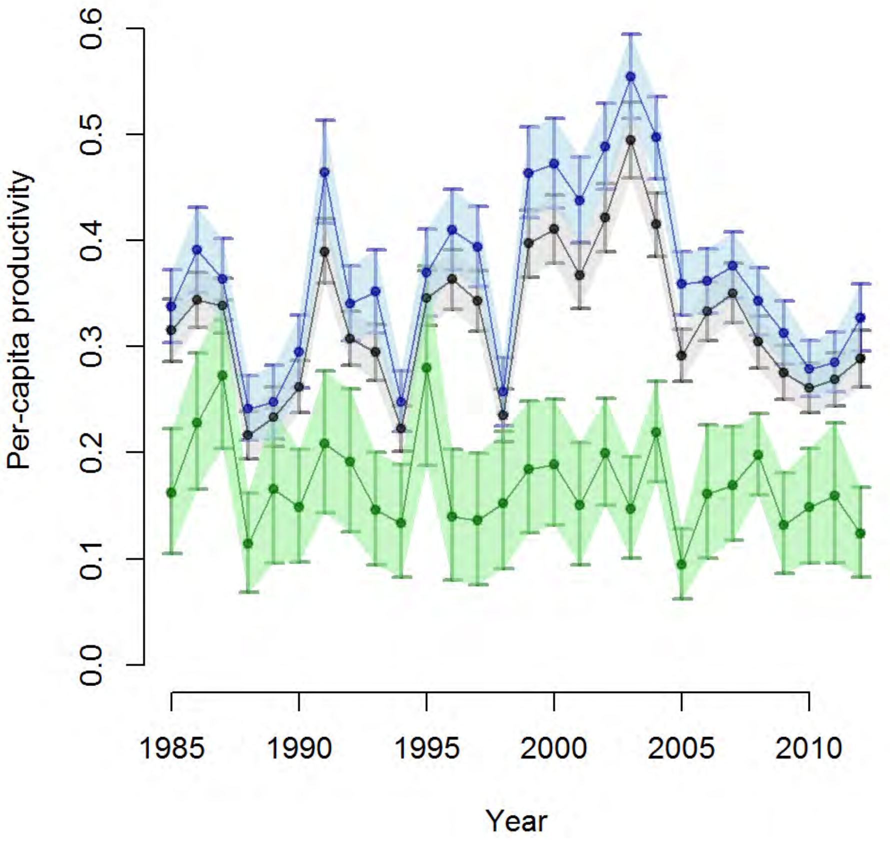

Figure C.3.4. Estimates of kittiwake *per capita* fledgling productivity rates over 1986–2012 in the Cap Sizun population. The productivity of pairs formed by two former breeders is in blue. The productivity of pairs formed by two first-time breeders is in green. The productivity of pairs form by two breeders of different breeding experience, or at least one breeder of unknown status is in grey. This latter productivity was assumed to be an average of productivity of inexperienced and experienced pairs weighted by their respective proportion among breeders. Points indicate posterior means. Color backgrounds and segments indicate 95%CI. The mean productivity of first-time breeders ($\overline{\pi_f}$) was 0.163 [0.139,0.187], temporal standard deviation on the log scale (σ_{π_f}) was 0.322 [0.201,0.457]. The mean annual survival between from age 2 ($\overline{\pi_e}$) was 0.358 [0.325,0.393], temporal standard deviation on the log scale (σ_{π_e}) was 0.246 [0.178,0.320]. All $\widehat{R} < 1.002$, all MCSE < 0.001, all ESS > 14557.

C.3.3 Resighting probabilities and observation errors on count data

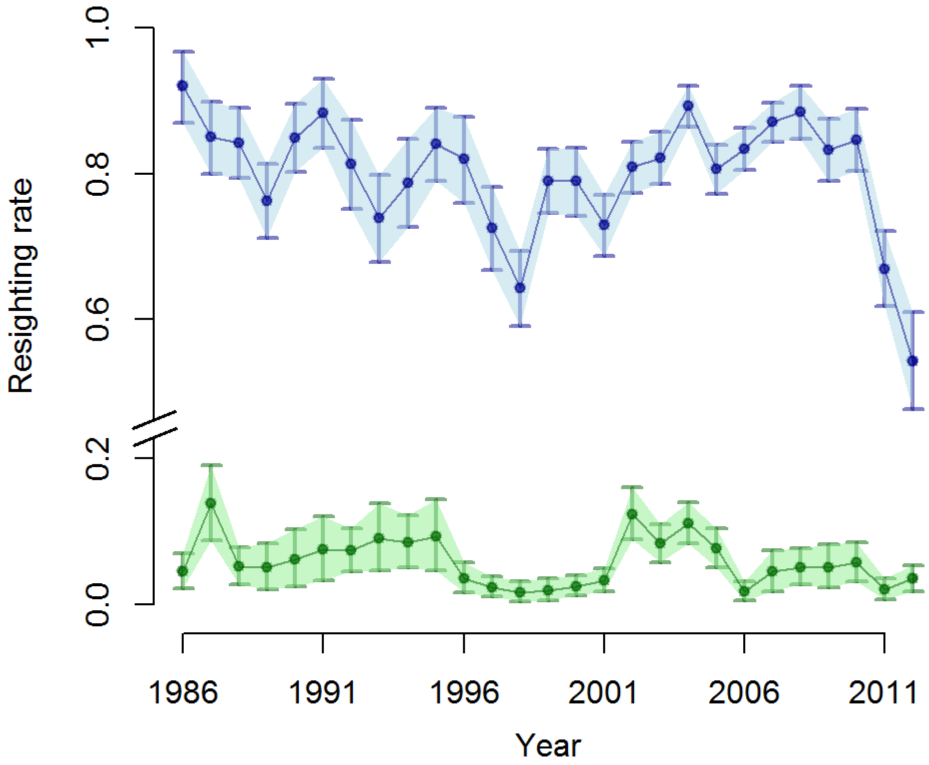

Figure C.3.5. Estimates of kittiwake resighting probability over 1986–2011 in the Cap Sizun population, for yearlings (green) and prebreeders (blue). Points indicate posterior means. Color backgrounds and segments indicate 95%CI. The mean resighting probability of yearlings ($\bar{p}_y$) was 0.050 [0.036,0.065], temporal standard deviation on the logit scale (σ_{p_y}) was 0.810 [0.775,0.844]. The mean resighting probability of prebreeders ($\bar{p}_p$) was 0.805 [0.783,0.827], temporal standard deviation on the logit scale (σ_{p_p}) was 0.556 [0.386,0.745]. All $\hat{R} < 1.001$, all MCSE ≤ 0.0005, all ESS > 15295.

Resighting probability of breeders and skippers (p_{bs} – not shown in Figure C.3.5) was 0.998 [0.997,0.999] ($\hat{R} < 1.0001$, MCSE < 0.0001, ESS = 348976).

Observation error for count data on the log scale (σ_{obs}) was 0.051 [0.016,0.097] ($\hat{R} = 1.017$, MCSE < 0.001, ESS = 1282).

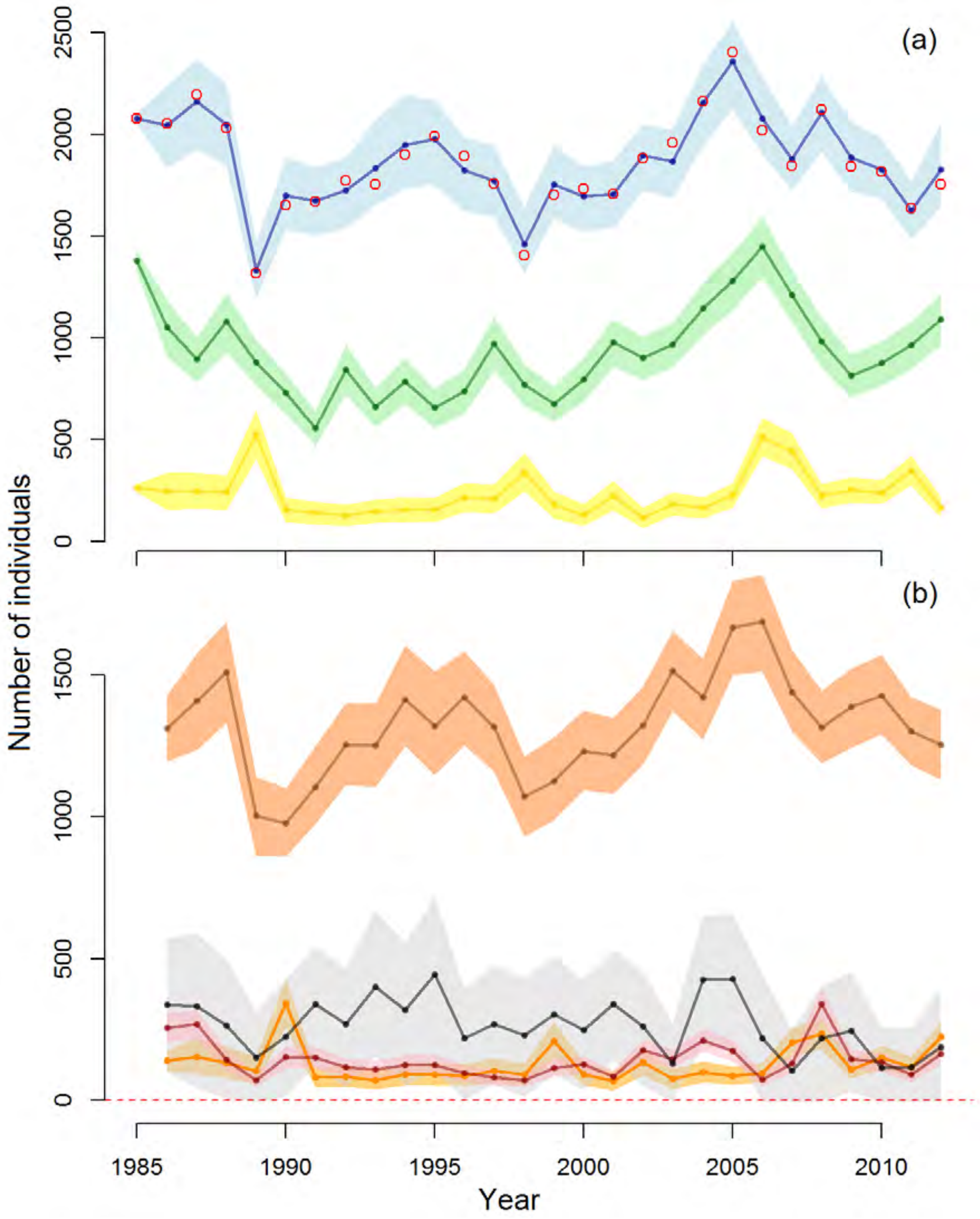

Figure C.3.6. Dynamics of the kittiwake population at Cap Sizun over 1985–2012. (a) Numbers of yearlings and prebreeders (yellow), skippers (green), and breeders (blue) along with count data (red circles). (b) Number of individuals from different origins among breeders: immigrants of the year (grey), local first-time breeders (pink), former skippers (orange), former breeders (brown). Points indicate posterior means and color backgrounds indicate 95% credible intervals.

C.3.4 Literature cited

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C.4. Posterior checks

C.4.1 Foreword of the section

Data replication (i.e. predictions derived from posterior samples of the model), and other calculations involved in posterior checks were performed aside from the main MCMC sampling to save computer resources. We used the same number of iterations in the burnin and monitoring phase as for estimation of parameters (see *Materials and Methods*) but we used only 10 chains, yielding a total of 7×10^5 samples at the end. Hereafter we describe methods to get discrepancy measures and posterior-predictive p-values for the submodels for count data and productivity data. Then we explain how to get proportions of correct predictions for the capture-recapture data.

C.4.2 Posterior checks for the submodels for count and productivity data

Methods— Following Gelman et al. (1996), we used the χ^2 discrepancy metric to assess the overall goodness of fit. The χ^2 discrepancy metric (D_{χ^2}) is the sum of squared Pearson residuals; $D_{\chi^2}^{\mathrm{obs}}$ quantifies the distance of observed data to the model, and $D_{\chi^2}^{\mathrm{rep}}$ quantifies the distance of replicated data to the model:

$$D_{\chi^2}^{obs} = \sum_{i=1}^{n} \frac{(y_i^{obs} - E(y_i|\theta))^2}{Var(y_i|\theta)}$$

$$D_{\chi^2}^{rep} = \sum_{i=1}^{n} \frac{(y_i^{rep} - E(y_i|\theta))^2}{Var(y_i|\theta)}$$

where *n* is the number of observations, *y* designates the response variable, y_i^{obs} is the *i*th observation, y_i^{rep} is the prediction (replicate) for the *i*th observation, θ is the parameter vector (i.e. the model), *E* is the expectation (i.e. $E(y_i/\theta)$ is the model expectation for y_i) and *Var* is the variance (i.e. $Var(y_i/\theta)$ is the variance of the response variable according to the model).

The piece of code to get data replicates and discrepancy measures for the submodels for count data and productivity data is given below (this code can be easily embedded into the original code given in Appendix C.2):

```
## This piece of code has to be added to the main code (see Appendix C.2)
for (t in 1:n.occasion) {
## Calculations for posterior predictive checks for count data:
      # data replicates
       pred.C[t] ~ dnorm(lNB[t],tau.obs)

    # discrepancy measures
      # distances from replicates to the model
       D.C[t,1] <- ((pred.C[t]-lNB[t])*(pred.C[t]-lNB[t]))/var.obs
      # distances from observations to the model
       D.C[t,2] <- ((C[t]-lNB[t])*(C[t]-lNB[t]))/var.obs

## Calculations for posterior predictive checks for productivity data:
       # data replicates
      pred.JF[t] ~ dpois(mu.f[t])
      pred.JB[t] ~ dpois(mu.b[t])
      pred.JU[t] ~ dpois(mu.u[t])

    # discrepancy measures
      # distances from replicates to the model
       D.JF[t,1] <- ((pred.JF[t]-mu.f[t])*(pred.JF[t]-mu.f[t]))/mu.f[t]
       D.JB[t,1] <- ((pred.JB[t]-mu.b[t])*(pred.JB[t]-mu.b[t]))/mu.b[t]
       D.JU[t,1] <- ((pred.JU[t]-mu.u[t])*(pred.JU[t]-mu.u[t]))/mu.u[t]
      # distances from observations to the model
       D.JF[t,2] <- ((JF[t]-mu.f[t])*(JF[t]-mu.f[t]))/mu.f[t]
       D.JB[t,2] <- ((JB[t]-mu.b[t])*(JB[t]-mu.b[t]))/mu.b[t]
       D.JU[t,2] <- ((JU[t]-mu.u[t])*(JU[t]-mu.u[t]))/mu.u[t]

  } #t

         # overall PPC
       sumchi2[1,1] <- sum(D.C[,1])
       sumchi2[2,1] <- sum(D.C[,2])
       sumchi2[1,2] <- sum(D.JF[,1])
       sumchi2[2,2] <- sum(D.JF[,2])
       sumchi2[1,3] <- sum(D.JB[,1])
       sumchi2[2,3] <- sum(D.JB[,2])
       sumchi2[1,4] <- sum(D.JU[,1])
       sumchi2[2,4] <- sum(D.JU[,2])
```

The posterior predictive p-value (*PPP-value*; Gelman et al. 1996) is the probability that the distance of observed data to the model is greater than the distance of replicated data to the model (a value close to 0.5 suggests a model with a good fit, whereas a value close to 0 or 1 indicates substantial lack of fit):

$$PPP\text{-}value = \Pr\,(D_{\chi^2}^{rep} > D_{\chi^2}^{obs}).$$

We computed *PPP-values* over all years and for each year, in the state-space model for count data and the Poisson regressions for productivity data. Cross-validation (Green et al. 2009) was impracticable because of the huge computation time involved.

Results— Fig. C.4.1 provides a graphical assessment of the amount of $D_{\chi^2}^{rep}$ values higher than $D_{\chi^2}^{obs}$ values (both summed over all years in the data) for the state-space model and the three Poisson regressions, with corresponding *PPP-values*. Table C.4.1 provides the *PPP-values* in each year. Further, we provide posterior predictive distributions (i.e. distribution of replicates) for each response in each year, plotted against the observation (Fig. C.4.2 to C.4.5).

Most *PPP-values* were close to 0.5 and away from 0 and 1, and none indicated a substantial lack of fit. Observed values were always clearly within the distribution of predicted values and usually at the median.

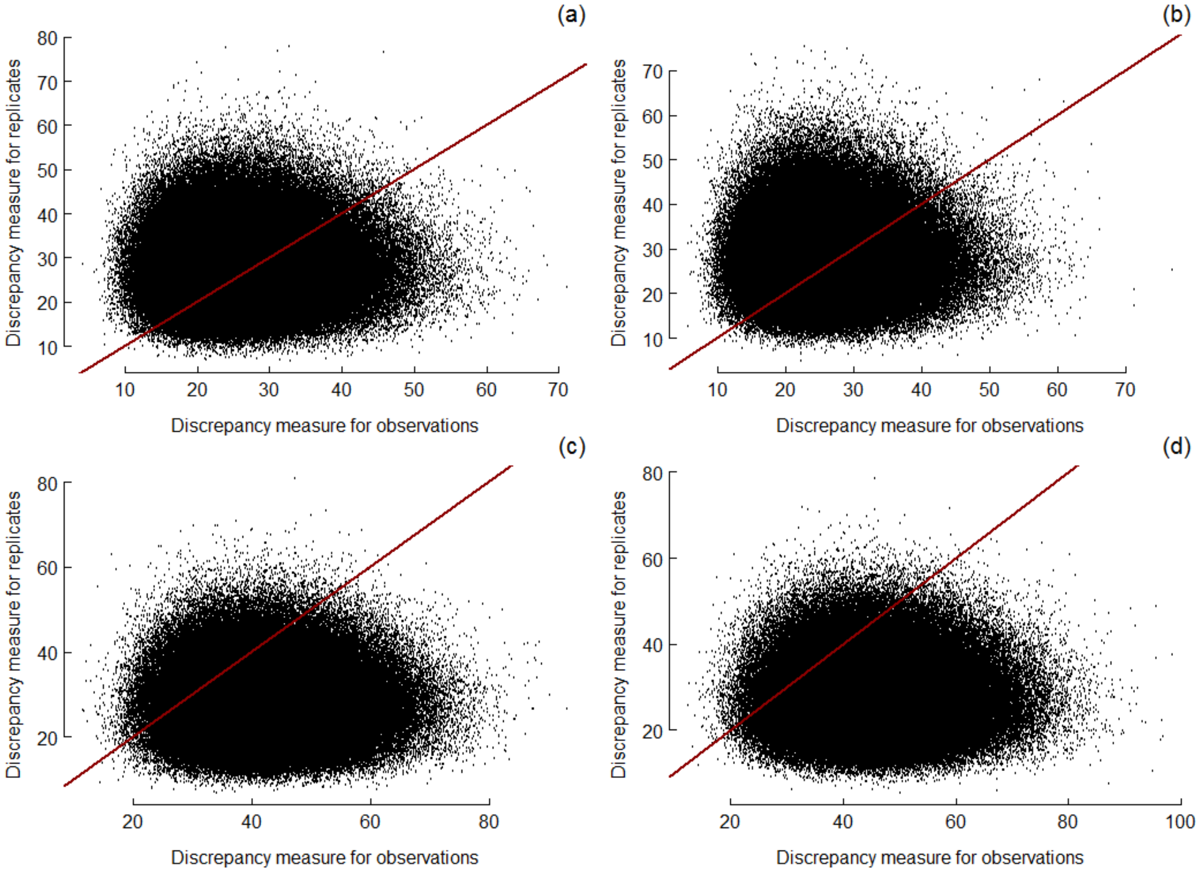

Figure C.4.1. Discrepancy measures for replicates against discrepancy measures for observations summed over all years in all posterior samples. Panel (a) is for count data: *PPP-value* = 0.55. Panel (b) is for fledgling productivity of pairs formed by two first-time breeders: *PPP-value* = 0.55. Panel (c) is for fledgling productivity of pairs formed by two experienced breeders: *PPP-value* = 0.11. Panel (d) is for fledgling productivity of pairs formed by two breeders of different experience, or at least one breeder of unknown experience: *PPP-value* = 0.08. In red is the x=y line. The relatively low values *PPP-values* in (c) and (d) − although not indicative of a lack of fit − seem to stem from one or two years in particular, for which the fit was less satisfying than in the other years (see Table C.4.1, Fig. C.4.4, C.4.5).

Table C.4.1. Posterior predictive p-values associated with χ^2 discrepancies for the different data: breeding population counts, and fledgling productivity of (F) pairs formed by two first-time breeders, (E) pairs formed by two experienced breeders, (U) pairs formed by two breeders of different experience or at least one breeder of unknown experience.

Year	Data			
	Counts	Fledgling productivity		
		F	E	U
1985	0.90	0.53	0.34	0.45
1986	0.52	0.47	0.62	0.54
1987	0.50	0.36	0.59	0.55
1988	0.53	0.46	0.46	0.37
1989	0.52	0.48	0.51	0.38
1990	0.48	0.55	0.46	0.45
1991	0.52	0.49	0.59	0.53
1992	0.48	0.53	0.54	0.52
1993	0.43	0.51	0.22	0.32
1994	0.47	0.38	0.31	0.50
1995	0.51	0.38	0.04	0.11
1996	0.45	0.39	0.47	0.45
1997	0.53	0.54	0.37	0.45
1998	0.45	0.45	0.33	0.23
1999	0.48	0.52	0.58	0.52
2000	0.50	0.50	0.29	0.25
2001	0.54	0.50	0.56	0.52
2002	0.55	0.50	0.57	0.51
2003	0.38	0.49	0.49	0.35
2004	0.53	0.38	0.28	0.29
2005	0.52	0.38	0.40	0.37
2006	0.50	0.45	0.15	0.08
2007	0.55	0.52	0.53	0.56
2008	0.54	0.45	0.41	0.34
2009	0.52	0.55	0.33	0.20
2010	0.57	0.52	0.53	0.60
2011	0.55	0.56	0.56	0.61
2012	0.45	0.52	0.36	0.28

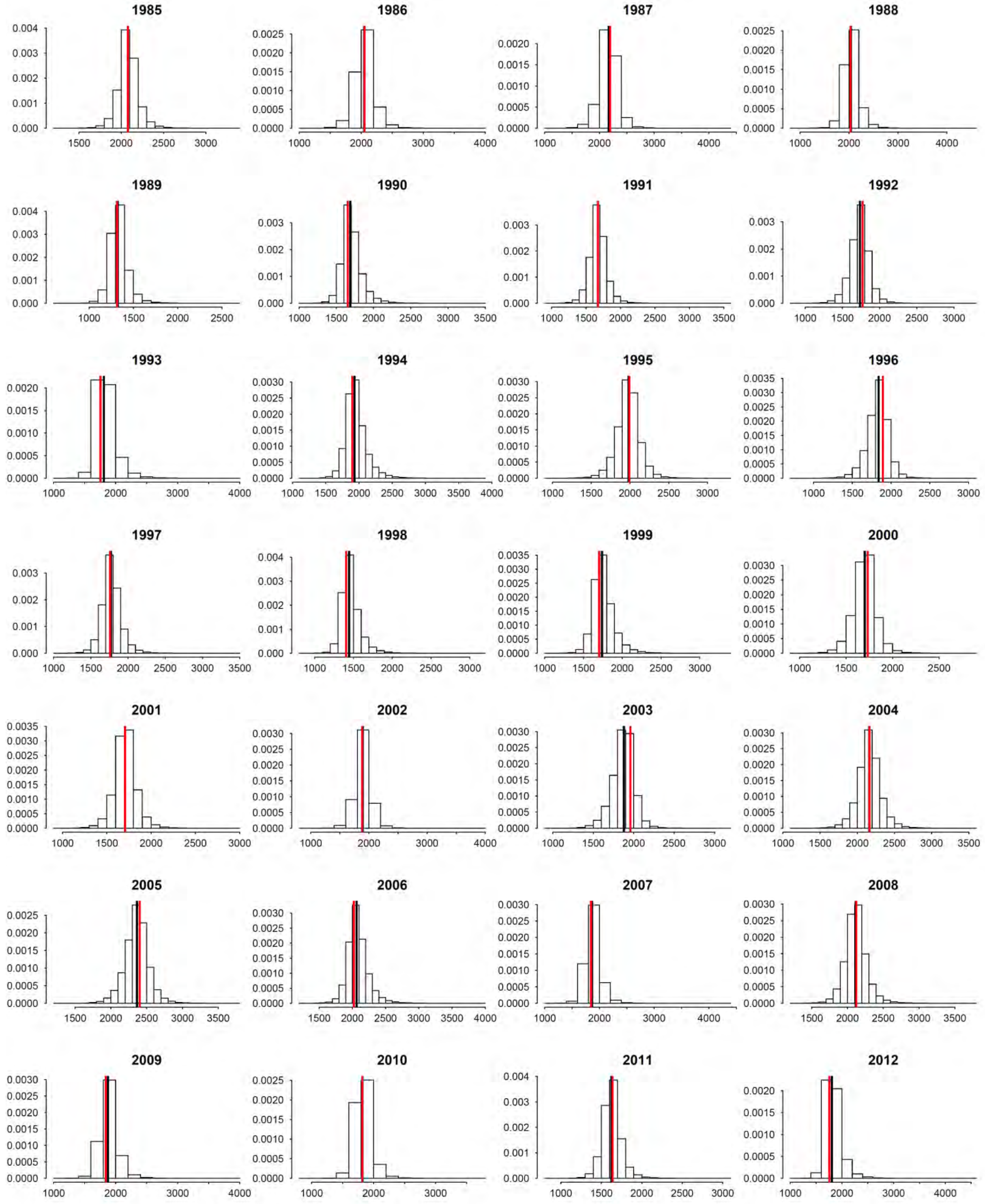

Figure C.4.2. Posterior predictive distribution of the breeding population count in each year over the study period. In abscissa of the histogram is the value, in ordinate is the density. The red line indicates the observed value, the bold black line indicates the median.

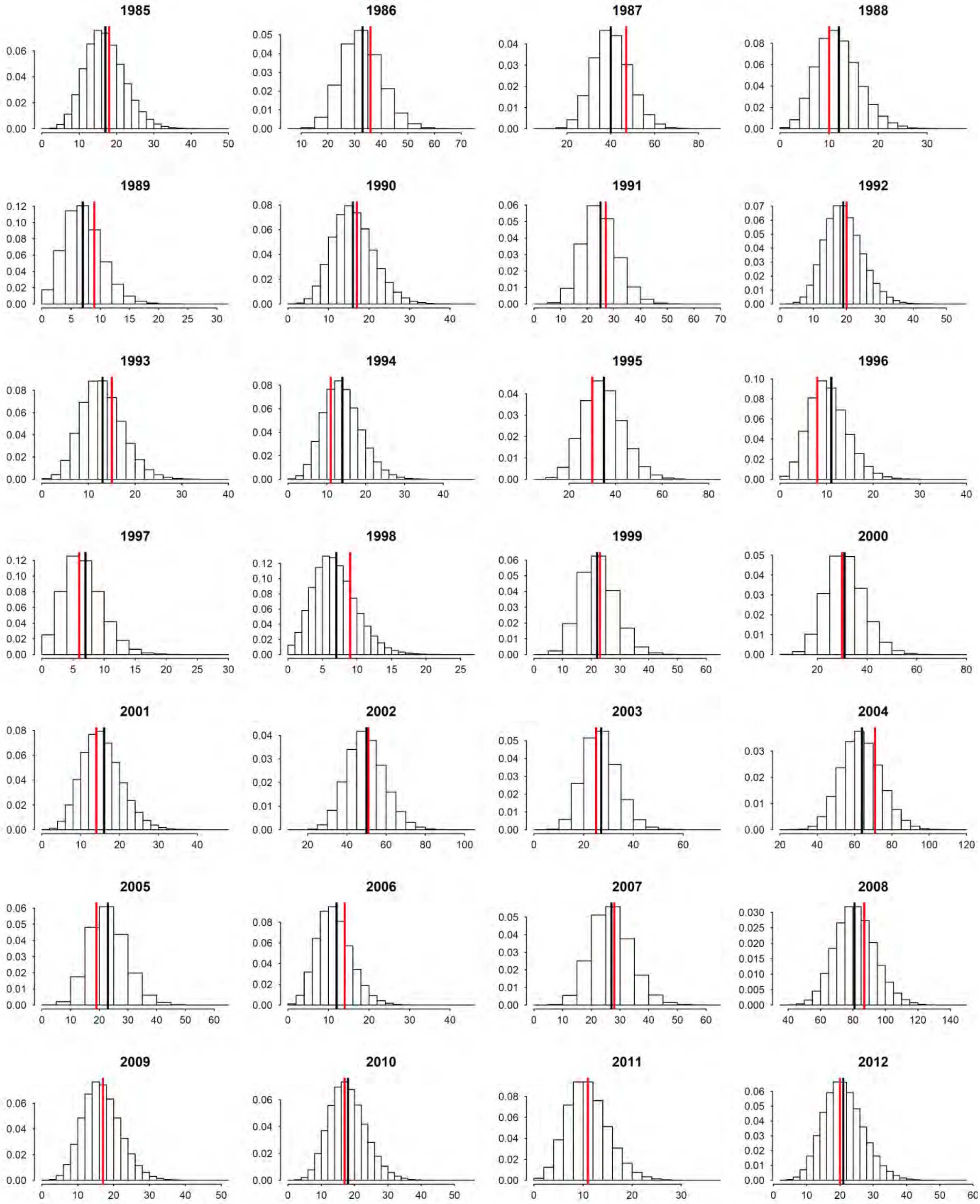

Figure C.4.3. Posterior predictive distribution of the fledgling count from breeding pairs composed of two first-time breeders in each year over the study period. In abscissa of the histogram is the value, in ordinate is the density. The red line indicates the observed value, the bold black line indicates the median.

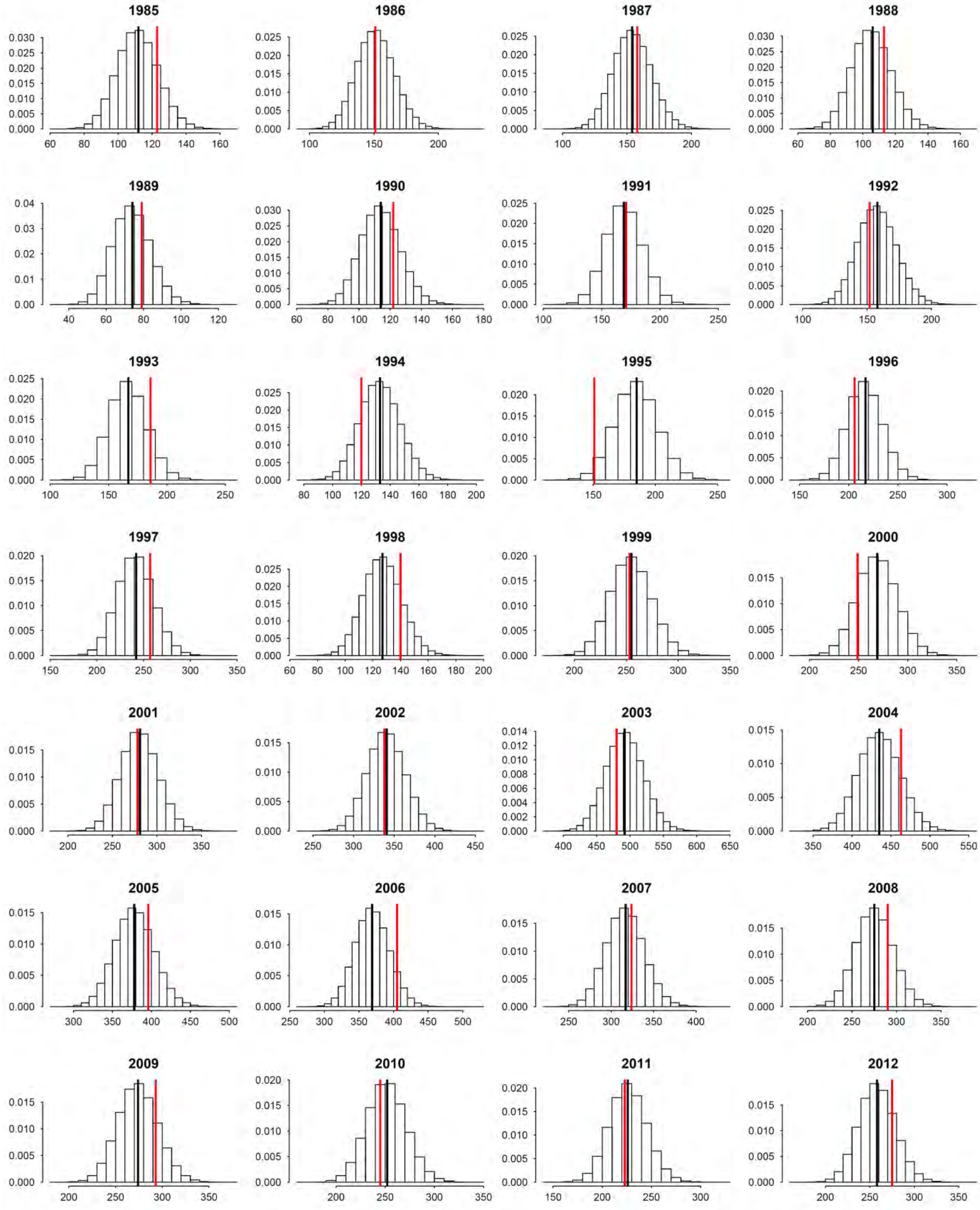

Figure C.4.4. Posterior predictive distribution of the fledgling count from breeding pairs composed of two experienced breeders in each year over the study period. In abscissa of the histogram is the value, in ordinate is the density. The red line indicates the observed value, the bold black line indicates the median.

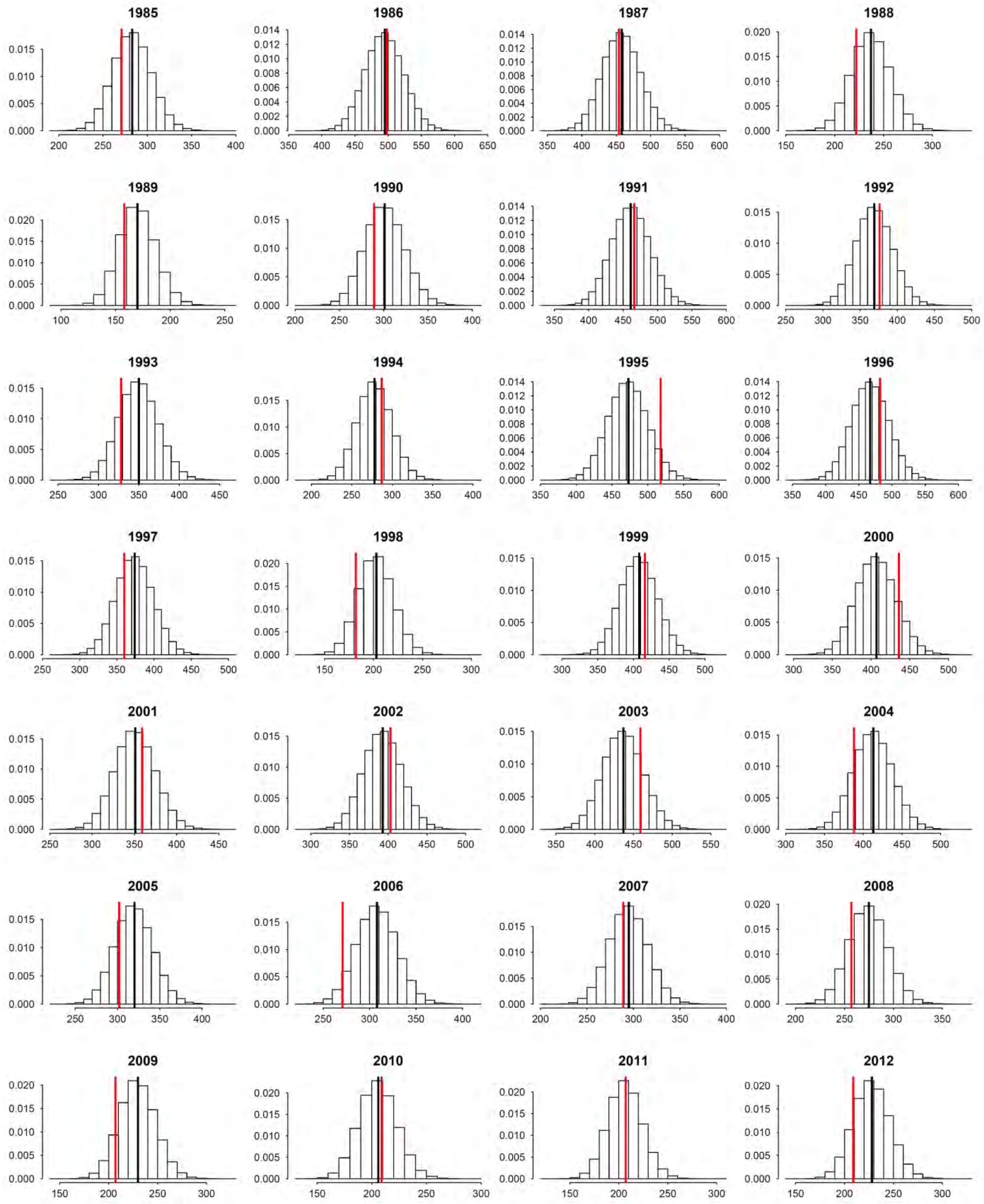

Figure C.4.5. Posterior predictive distribution of the fledgling count from breeding pairs composed of either two breeders of different experience, or at least one breeder of unknown experience, in each year over the study period. In abscissa of the histogram is the value, in ordinate is the density. The red line indicates the observed value, the bold black line indicates the median.

C.4.3 Proportion of correct predictions for the capture-recapture data

For each observation in every capture-recapture history, we computed the proportion of correct predictions (see Greenhill et al. 2011). For this purpose, we predicted the observation from the categorical distribution used to model the observation (see Appendix C.2) parameterized by resighting probabilities given the true state (both inferred from the model). Then, we calculated the number of predictions that matched the corresponding observation event in the data. The corresponding piece of *BUGS* code is given below.

```
## This piece of code has to be added to the main code (see Appendix C.2)

for (i in 1:nind){

  for (t in (f[i]+1):n.occasions){

    # data replicates
    pred.o[i,t] ~ dcat(po[z[i,t],t-1,])

    # save information: correct predictions = 1, incorrect prediction = 0
    CP[i,t] <- ifelse(pred.o[i,t]==o[i,t],1,0)

  } #t

} #i

for (t in 1:n.occasions) {

  # Proportion of correct prediction in each year
  PCP.t[t] <- sum(CP[,t])/nii[t]
    # the nii contains the number of individuals for which there may be a
    # resighting event (i.e. individuals in the data after first capture)

} #t

# Proportion of correct prediction over all years
PCP <- sum(CP)/sum(recap[2:n.occasions])
```

The proportion of correct predictions was 0.977 [0.976,0.978] (posterior mean and 95%CI) over all years. Among years, this proportion varied from 0.921 [0.901,0.935] to 0.990 [0.989,0.993]. In this study, individual states are observed without error and detection is almost perfect for all observations from first-breeding in the population, and very low for yearlings. As a consequence a real doubt on the true individual state only exists for the few individuals that have never recruited, from their last resighting to the last possible age of first breeding. Indeed, they might be dead or alive in the prebreeder state at the focal age. The capture-recapture model used in this study can hardly contradict the capture-recapture data used in this study.

C.4.4 Literature cited

Green, M. J., G. F. Medley, and W. J. Browne. 2009. Use of posterior predictive assessments to evaluate model fit in multilevel logistic regression. Veterinary Research 40:30–10.

Greenhill, B., M. D. Ward, and A. Sacks. 2011. The separation plot: a new visual method for evaluating the fit of binary models. American Journal of Political Science 55:991–1002.

Gelman, A., X.-L. Meng, and H. Stern. 1996. Posterior predictive assessment of model fitness via realized discrepancies. Statistica Sinica 6:733–760.

C.5. Specification and results of the derived analyses

Several explanations provided in this appendix refer to parameters defined in Appendix C.2 (details of the integrated population model).

C.5.1 Growth rate of the breeding population

The annual breeding population growth rate in year t (λ_t) is defined as follows:

$$\lambda_t = \frac{N_{F,t} + N_{E,t}}{N_{F,t-1} + N_{E,t-1}} = \frac{N_{B,t}}{N_{B,t-1}}$$

where $N_{B,t}$ is the number of breeders in year t.

If we consider a geometric growth of the population with a constant (average) growth rate ($\bar{\lambda}$) from the starting number of breeders in 1985, then we have:

$$N_{B,t} = N_{B,1985}\,\bar{\lambda}^t$$

with $t \in \{1986,...,2012\}$.

Using a log-transformation, we have:

$$log(N_{B,t}) = log(N_{B,1985}) + t\,log(\bar{\lambda})\,.$$

Thus, the slope of an ordinary least squares regression line of log($N_{B,t}$) ($t \in \{1985,...,2012\}$) against t will be log($\bar{\lambda}$), and the intercept will be log($N_{B,1985}$). The exponential slope of the regression line is thus $\bar{\lambda}$.

Accordingly, we performed an ordinary least squares regression of $N_{B,t}$ against t in each posterior sample to get a posterior distribution of $\bar{\lambda}$. Results are given in the main text of the paper.

C.5.2 Population projections without the pulse of immigrants

Population projections without the pulse of immigrants were performed following the projection equation (see Appendix C.2) but without adding the number of immigrants to the number of first-time breeders each year. The equation was thus written as follows:

$$\begin{bmatrix} N_Y \\ N_{P2} \\ N_{P3} \\ N_{P4} \\ N_{P5} \\ N_{P6} \\ N_F \\ N_E \\ N_S \end{bmatrix}_t = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & \phi_0\pi_\mathrm{f} & \phi_0\pi_\mathrm{e} & 0 \\ \phi_0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \phi_2(1\text{-}\rho_3) & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \phi_2(1\text{-}\rho_4) & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \phi_2(1\text{-}\rho_5) & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \phi_2(1\text{-}\rho_6) & 0 & 0 & 0 & 0 \\ 0 & \phi_2\rho_3 & \phi_2\rho_4 & \phi_2\rho_5 & \phi_2\rho_6 & \phi_2 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \phi_2\psi_\mathrm{b} & \phi_2\psi_\mathrm{b} & \phi_2\psi_\mathrm{s} \\ 0 & 0 & 0 & 0 & 0 & 0 & \phi_2(1\text{-}\psi_\mathrm{b}) & \phi_2(1\text{-}\psi_\mathrm{b}) & \phi_2(1\text{-}\psi_\mathrm{s}) \end{bmatrix}_{t-1} \begin{bmatrix} N_Y \\ N_{P2} \\ N_{P3} \\ N_{P4} \\ N_{P5} \\ N_{P6} \\ N_F \\ N_E \\ N_S \end{bmatrix}_{t-1} .$$

For the population projection, we started from the initial vector of state-specific population sizes and used time-specific demographic parameters estimated with each posterior sample. We followed the same method to calculate the average breeding population growth rate over 1985-2012. Results are given in the main text of the paper.

C.5.3 Calculation details and posterior distributions of derived parameters

The formula used to calculate the annual growth rate between year t-1 and year t (also given at the beginning of this appendix) was:

$$\lambda_t = \frac{N_{F,t} + N_{E,t}}{N_{F,t-1} + N_{E,t-1}} .$$

We defined the integrative recruitment rate as the proportion of first-time breeders among individuals that have never bred before within all age classes that could recruit individuals in the current year t (age 3, ..., 6). In other words, it is the number of local first-time breeders in the current year t (i.e. first-time breeders minus immigrants) divided by the number of prebreeders of age 3, ..., 6 plus the number of local first-time breeders. The formula used to calculate the integrative recruitment rate ρ_{all} was thus:

$$\rho_{all} = \frac{N_{F,t} - N_{I,t}}{N_{P3,t} + N_{P4,t} + N_{P5,t} + N_{P6,t} + N_{F,t} - N_{I,t}} \ .$$

We defined the annual immigration rate (ω_t) as the proportion of immigrants among breeders in the current year *t*:

$$\omega_t = \frac{N_{I,t}}{N_{F,t} + N_{E,t}} \ .$$

We defined the number of present nonbreeders as the number prebreeders (age 2, ..., 6) plus the number of skippers present in the area. Thus, we added the number of skippers to the number of prebreeders multiplied by the resighting rate of prebreeders in the current year. We did not corrected the number of skippers by their resighting rate because it was virtually equal to 1. The formula used to calculate the number of nonbreeders $N_{PN,t}$ was thus:

$$N_{PN,t} = p_p(N_{P3,t} + N_{P4,t} + N_{P5,t} + N_{P6,t}) + N_{PN,t} \ .$$

We defined the population per-capita productivity rate Π_t as the *per nest* average of the productivity of first-time breeders and experienced breeders weighted by their respective proportion in the population:

$$\Pi_t = 2\left(\pi_{f,t} \frac{N_{F,t}}{N_{F,t} + N_{E,t}} + \pi_{e,t} \frac{N_{E,t}}{N_{F,t} + N_{E,t}} \right) \ .$$

Graphical summaries of the time-specific growth rates, integrative recruitment rates, the immigration rates, and the number of nonbreeders present (Fig C.5.1, C.5.2, C.5.3, C.5.4, respectively) are provided below.

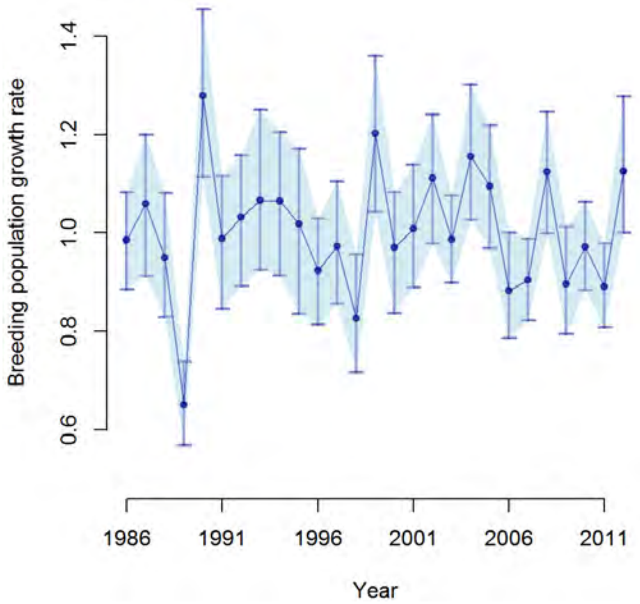

Figure C.5.1. Estimates of kittiwake annual breeding population growth rates over 1986–2012 in the Cap Sizun population. Color backgrounds and segments indicate 95%CI.

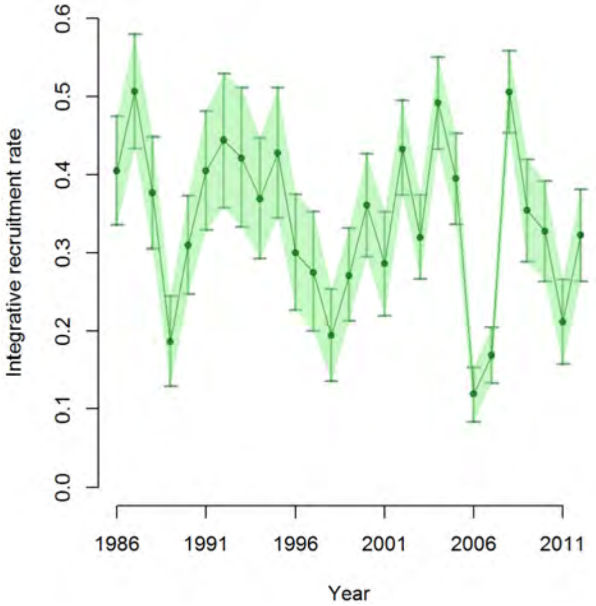

Figure C.5.2. Estimates of kittiwake integrative recruitment rates over 1986–2012 in the Cap Sizun population. Color backgrounds and segments indicate 95%CI.

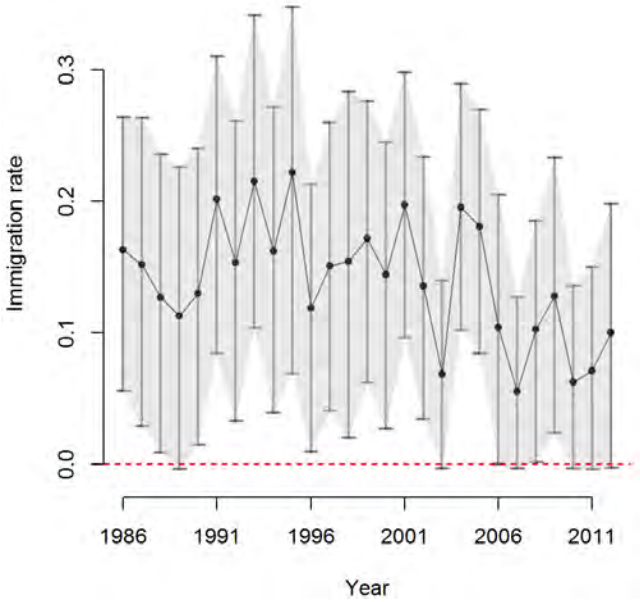

Figure C.5.3. Estimates of kittiwake immigration rates over 1986–2012 in the Cap Sizun population. Grey backgrounds and segments indicate 95%CI.

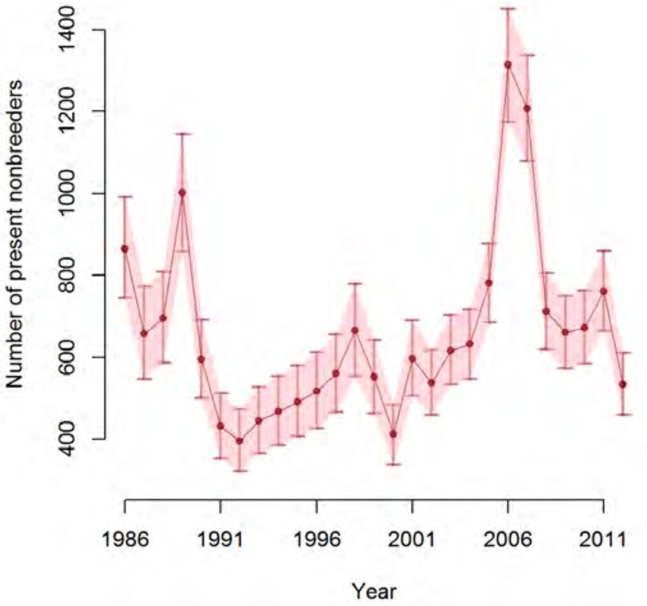

Figure C.5.4. Estimates of kittiwake numbers of present nonbreeders over 1986–2012 in the Cap Sizun population. Color backgrounds and segments indicate 95%CI.

C.5.4 Partial correlation analyses

Additional details on the method— Partial correlation measures the correlation between two random variables, with the effect of a set of control random variables removed. More precisely, a partial correlation between variables X and Y while controlling for *n* variables Z_1, ..., Z_n is the correlation between the residuals of two linear regressions: (i) a regression with X as the response and Z_1, ..., Z_n as the explanatory variables, and (ii) a regression with Y as the response and Z_1, ..., Z_n as the explanatory variables.

Accordingly, to calculate each partial correlation between two focal variables derived from by the model inference, we computed (in each posterior sample): (i) one ordinary least squares (OLS) regression between the first focal variable and a set of control variable, (ii) one OLS regression between the second focal variable and the same set of control variable. Then we calculated the correlation between the residuals of the two latter regressions. We also computed an OLS regression between the residuals of the two latter regressions to add the partial regression line on the partial residual plot (see e.g. Fig. 1, 2 in the article).

Additional details on the results— Hereafter we provide partial regression plots for partial correlation which had a 95%CI that included zero (that were not provided in the main text). Fig. C.5.5 is for partial correlations in the purpose of examining contributions to the breeding population growth rate, and Fig. C.5.6 is for partial correlations in the purpose of examining individual breeding motivations. We also provide partial regression plots for partial correlation between the number of immigrants (instead of the immigration rate) in year *t* and either population productivity at *t-1*, the number of breeders at *t-1*, or the number of nonbreeders present at *t-1* (Fig. C.5.7).

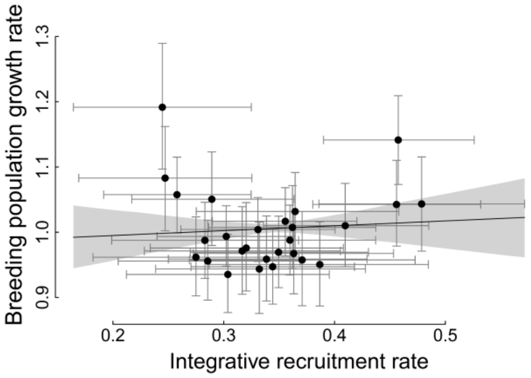

Figure C.5.5. Partial residual plot for the partial correlation between the growth rate and integrative recruitment rate (while controlling for the effect of adult survival, productivity, and breeding propensities). The partial correlation was 0.082 [-0.197,0.356] (posterior mean [95%CI]). Residuals were centered around the variable mean to rescale variation within the original range. Points indicate posterior means and segments indicate 95% credible intervals. The solid line is the posterior mean of the corresponding OLS regression line, along with the 95% credible interval in grey background.

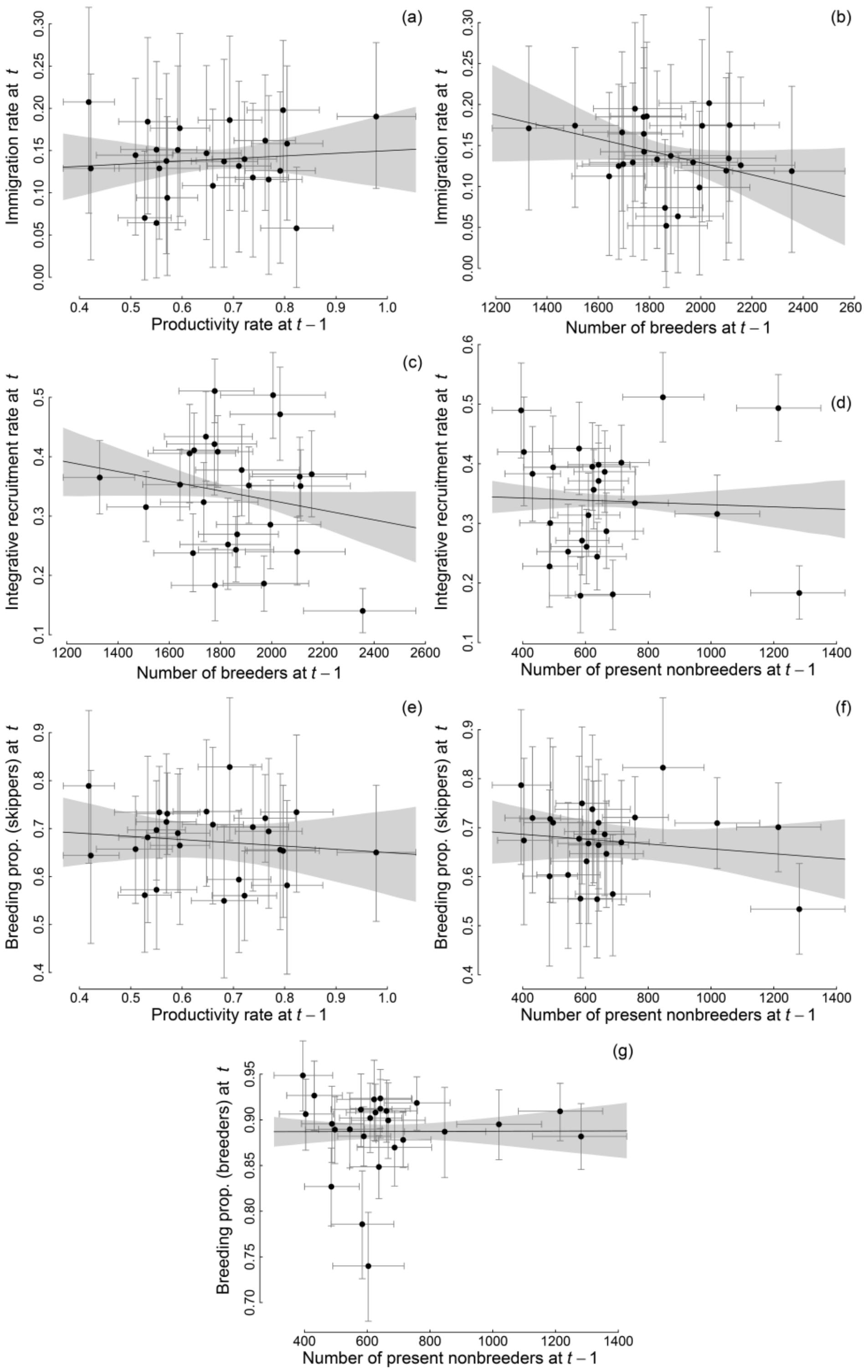

Figure C.5.6. Partial residual plots for the relationship between social information and breeding decisions. Immigration rate (at *t*) against (a) productivity (at *t-1*), and (b) number of breeders (at *t-1*). Integrative recruitment rate (*t*) against (c) number of breeders (*t-1*), and (d) number of nonbreeders present (*t-1*). Breeding propensity of former breeders (*t*) against (e) productivity (*t-1*), and (f) number of nonbreeders present (*t-1*). (g) Breeding propensity of former skippers (*t*) against the number of nonbreeders present at (*t-1*). See further details in *Materials and Methods*, and partial correlation values in *Results*. Specifications are the same as for Fig. C.5.5.

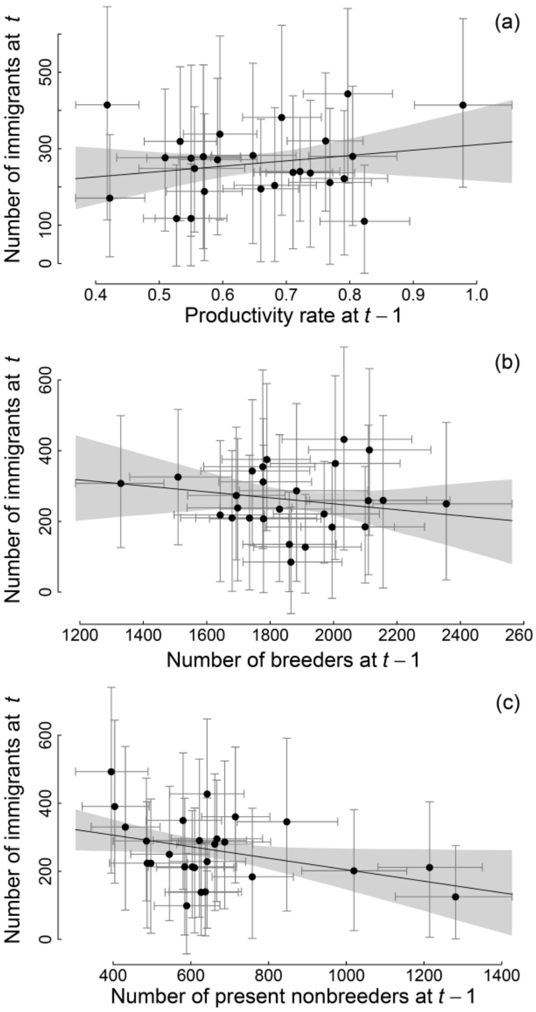

Figure C.5.7. Partial residual plots of the relationships between the number of immigrants in year *t* and (a) productivity at *t-1*, (b) number of breeders at *t-1*, (c) number of nonbreeders present at *t-1.* The partial correlation was (a) 0.148 [-0.125,0.413], (b) -0.140 [-0.407, 0.135], and (c) -0.278 [-0.525,0.014]. See further details in *Materials and Methods*, and partial correlation values in *Results*. Specifications are the same as for Fig. C.5.5.

C.5.5 Predictability in social information

Temporal autocorrelation in social information— We calculated the temporal autocorrelation in social information: population productivity, and number of breeders and number of nonbreeders present. Population productivity was calculated as the average productivity of inexperienced and experienced breeders weighted by their respective proportion among breeders (see Appendix C.2 for calculation details and Appendix C.3 for a graphical summary of this productivity rate over time). More precisely, we calculated the sample autocorrelation function (the correlation of a random variable with itself at different points in time; Cryer and Chan 2008, Schumway and Stoffer 2011) at lag 1 year in each posterior sample. The formula of the sample autocorrelation function at lag k ($r(k)$) is the following (results are given in the article):

$$r(k) \; = \frac{\sum_t (x_t - \bar{x})(x_{t+k} - \bar{x})}{\sum_t (x_t - \bar{x})^2}$$

where x_t is the value observed in the time series of a random variable in year t, and $\bar{x}$ is the average over the time series.

First, autocorrelation estimates are known to be biased down for short times series (under approximately 50 times steps; Box and Jenkins 1976, Huitema and Mckean 1991). Because they were calculated on time-series lasting only 27 years, the autocorrelation values we reported are very likely to lower than the true autocorrelation. Second, these autocorrelation values should be compared to the confidence interval of the sample autocorrelation function (here at lag 1) for non-autoregressive processes. The usual reference for non-autoregressive processes is a simple white noise or moving average, for which the autocorrelation function at lag 1 in a large series is approximately normally distributed with mean 0 an standard deviation $s_{r(1)}$:

$$s_{r(1)} = \frac{1}{\sqrt{n}}$$

where n is the number of observations in the time series.

For a series of 27 observations, the 95% credible interval would thus be approximately $2/\sqrt{27}$ = 0.38, which falls below the reported mean posterior values for autocorrelations at lag 1 (see *Results*), but above the lower limit of the 95%CIs for population productivity and number of breeders. This 95%CI for a non-autoregressive is valid for large time series, but the reported autocorrelation values are biased down in small series as ours. Thus our results suggest that there is some autocorrelation, but our time series are too short for a proper assessment.

Correlation among social information from one year to the next— The number of breeders in year t was predictive of the number of former breeders among breeders in year *t+1*: the mean correlation derived from posterior samples was 0.747, and 95%CI was [0.646,0.841]. The number of nonbreeders in year t was predictive of the number of local first-time breeders in year *t+1*: correlation was 0.735 [0.646,0.821]. The number of nonbreeders in year t was predictive of the number of former skippers among breeders in year *t+1*: correlation was 0.494 [0.381,0.602].

C.5.6 Literature cited

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D

Supporting information to Chapter 4

D.1. Population dynamics in the study area

To characterize the population dynamics, we calculated breeding-site turnover rates over the study period (1998-2010) at the scale of the colony site (i.e. colony-site turnover rate, see below). We also present annual breeding population sizes and breeding success at the scale of the study area and over the study period (Fig. D.1.1).

D.1.1 Colony-site turnover rate

Following Erwin et al. (1981), the annual colony-site turnover rate *T* is defined as:

$$T = \frac{1}{2}\left(\frac{S_1}{N_1} + \frac{S_2}{N_2}\right)$$

where N_1 is the total number of sites occupied at first census (i.e. the sum of the number of sites occupied in the first year of each pair of successive years in the study period), S_1 is the number of sites occupied only at first census (i.e. the sum of the number of sites occupied *only* in the first year of each pair of successive years), N_2 is the total number of sites occupied at second census (i.e. as N_1 but for the *second year* of each pair of successive years), S_2 is the number of sites occupied only at second census (i.e. as S_1 but for the *second year* of each pair of successive years). This measure gives the proportion of breeding sites that are abandoned from one year to the next. Its complement (1-*T*) gives the proportion of breeding sites that are still occupied from one year to the next.

From 1998 to 2010, in ascending year order, the study area comprised 4 colonies, then 4, 7, 5, 4, 2, 3, 3, 4, 6, 3, 10 and finally 5 colonies. The number of reoccupied colony sites was 2 in 1999, then 1, 1, 1, 1, 0, 1, 1, 1, 0, 0, and finally 1 in 2010. Accordingly, one may proceed as follow to derive the turnover rate across years:

N_1 = 4+4+7+5+4+2+3+3+4+6+3+10 = 55,

N_2 = 4+7+5+4+2+3+3+4+6+3+10+5 = 56,

S_1 = (4-2)+(4-1)+(7-1)+(5-1)+(4-0)+(2-1)+(3-1)+(3-1)+(4-1)+(6-0)+(3-0)+(10-1) = 45,

S_2 = (4-2)+(7-1)+(5-1)+(4-1)+(2-0)+(3-1)+(3-1)+(4-1)+(6-1)+(3-1)+(10-1)+(5-1) = 46.

To calculate S_1 and S_2, the short way is simply to subtract the sum of reoccupied sites in each pair of successive years (2+1+1+1+1+0+1+1+1+0+0+1=10) to N_1 and N_2, respectively.

Thus, T = 0.82 over all the study period. In each year from 1999 to 2010, the colony-site turnover rate was respectively 0.50, 0.80, 0.83, 0.78, 0.63, 1.00, 0.67, 0.71, 0.79, 1.00, 1.00, 0.85 (mean = 0.80 ± sd = 0.16).

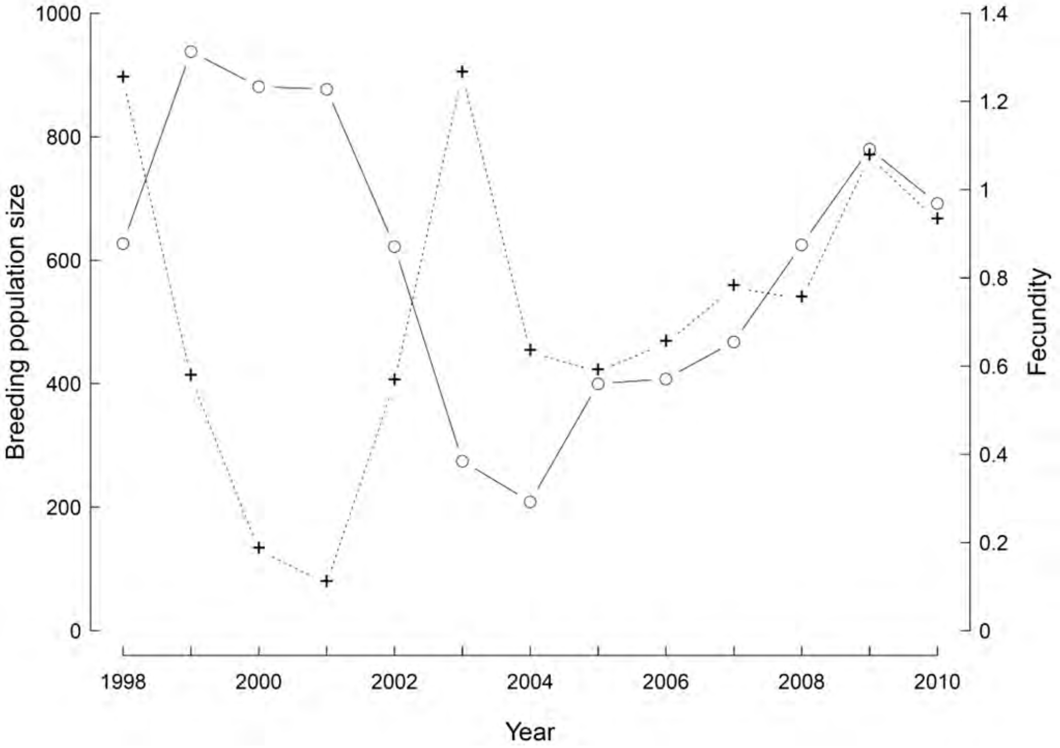

Figure D.1.1. Breeding population size and breeding success of slender-billed gulls in France between 1998 and 2010. Annual breeding population sizes (open circles) were approximated by nest counts at the peak of laying activity. Annual fecundity rates (plus signs) were estimated as the number of chicks in the crèche (just before fledging) divided by the number of nests counted in the colony at the peak of laying.

D.1.2 Literature cited

Erwin, R. M., J. Galli, and J. Burger. 1981. Colony site dynamics and habitat use in Atlantic coast seabirds. The Auk 98:550–561.

D.2. Details on the multievent models

D.2.1 Foreword of the section

To complement the information given in *Methods*, hereafter are given the matrix patterns of state and event transitions for the multievent capture-recapture models (Pradel 2005) developed in this paper. These matrices were used in E-SURGE (Choquet et al. 2009) as a general specification for the structure of all models considered in the capture-recapture analyses of our study (summarized graphically in Fig. 4.2). Statistical and software details can be found in E-SURGE manual (Choquet and Nogue 2011). In these matrices, rows correspond to the previous states (or transitory states) and columns correspond to the next states (or transitory states). Each element of the matrices contains the probability to be in the corresponding next state (given by the column) for an individual that was in the corresponding previous state (given by the row). Transitions that cannot occur have a probability of 0, obligate transitions (or stagnations) have a probability of 1.

Here are abbreviations of the individual states: PI for "pre-breeder inside the study area", PO for "pre-breeder outside the study area", BI for "breeder inside the study area", BO for "breeder outside the study area", D for "dead". The five possible observation events are coded as follow: 0 for "not seen", 1 for "certain pre-breeder", 2 for "uncertain breeder", 3 for "possible breeder", 4 for "certain breeder" (see Table D.2.1 hereafter).

D.2.2 Initial state

At the initial state (capture) all individuals are pre-fledging chicks. Hence the probability to be in state PI is 1. No individual can be dead at that point. The matrix pattern is thus:

$$\begin{array}{cccc} \text{PI} & \text{PO} & \text{BI} & \text{BO} \\ \hline \multicolumn{1}{|c}{1} & 0 & 0 & \multicolumn{1}{c|}{0} \\ \hline \end{array}$$

D.2.3 State transitions

Survival— The first transition step is local survival, the corresponding parameter is denoted by ϕ. SPI, SPO, SBI and SBO are transitory states for alive individuals before the next transition step. The matrix pattern is thus:

$$
\begin{array}{c|ccccc|}
 & \mathrm{SPI} & \mathrm{SPO} & \mathrm{SBI} & \mathrm{SBO} & \mathrm{D} \\
\hline
\mathrm{PI} & \phi & 0 & 0 & 0 & 1-\phi \\
\mathrm{PO} & 0 & \phi & 0 & 0 & 1-\phi \\
\mathrm{BI} & 0 & 0 & \phi & 0 & 1-\phi \\
\mathrm{BO} & 0 & 0 & 0 & \phi & 1-\phi \\
\mathrm{D} & 0 & 0 & 0 & 0 & 1 \\
\hline
\end{array}
$$

Movement— The second transition step is movement, the corresponding parameter is denoted by δ. MPI, MPO, MBI and MBO are transitory states for alive individuals that moved/stay inside or outside the population before the next transition step. However, at that point pre-breeder remain pre-breeders and breeders remain breeders. Their breeding status does not change, but they can move. The matrix pattern is thus (for the sake of simplicity, we specify the sense of the movement using straightforward subscripts after δ, see below and also Fig. 4.2):

$$
\begin{array}{c|ccccc|}
 & \mathrm{MPI} & \mathrm{MPO} & \mathrm{MBI} & \mathrm{MBO} & \mathrm{D} \\
\hline
\mathrm{SPI} & 1-\delta_{\mathrm{io}} & \delta_{\mathrm{io}} & 0 & 0 & 0 \\
\mathrm{SPO} & \delta_{\mathrm{oi}} & 1-\delta_{\mathrm{oi}} & 0 & 0 & 0 \\
\mathrm{SBI} & 0 & 0 & 1-\delta_{\mathrm{io}} & \delta_{\mathrm{io}} & 0 \\
\mathrm{SBO} & 0 & 0 & \delta_{\mathrm{oi}} & 1-\delta_{\mathrm{oi}} & 0 \\
\mathrm{D} & 0 & 0 & 0 & 0 & 1 \\
\hline
\end{array}
$$

Recruitment— The last transition step is local recruitment, the corresponding parameter is denoted by r. Only pre-breeders inside the population can recruit (those that remained or moved to the study area at the preceding step). Thus only those in the transitory state MPI have a recruitment probability, and the matrix pattern is as follows:

$$
\begin{array}{c|ccccc|}
 & \mathrm{PI} & \mathrm{PO} & \mathrm{BI} & \mathrm{BO} & \mathrm{D} \\
\hline
\mathrm{MPI} & 1-r & 0 & r & 0 & 0 \\
\mathrm{MPO} & 0 & 1 & 0 & 0 & 0 \\
\mathrm{MBI} & 0 & 0 & 1 & 0 & 0 \\
\mathrm{MBO} & 0 & 0 & 0 & 1 & 0 \\
\mathrm{D} & 0 & 0 & 0 & 0 & 1 \\
\hline
\end{array}
$$

D.2.4 Observation events

Detection— The first step of observation events is detection (i.e. resightment, denoted by p). An individual is detectable only if it is present in the study area, and dead individuals are not detectable. Individuals may be not encountered (NE), encountered as they were pre-breeders (EP) or breeders (EB). The matrix pattern is thus as follow:

$$\begin{array}{c|ccc|}
 & \mathrm{NE} & \mathrm{EP} & \mathrm{EB} \\
\hline
\mathrm{PI} & 1-p & p & 0 \\
\mathrm{PO} & 1 & 0 & 0 \\
\mathrm{BI} & 1-p & 0 & p \\
\mathrm{BO} & 1 & 0 & 0 \\
\mathrm{D} & 1 & 0 & 0 \\
\hline
\end{array}$$

Assignment— The second step of observation events is assignment (i.e. the evaluation of the breeding status by the observer, with a probability to be assigned to one of the four categories of observations denoted α). Every alive individual is assigned to one of the observational classes (Table D.2.1), or not observed if it was not resighted. Pre-breeder individuals cannot be identified as "certain breeder". Conversely, breeder individuals cannot be identified as "certain pre-breeder". Note that transitions (i.e. matrix elements) expressed as the complement of parameters of sum of parameters (e.g. 1 - $\alpha_{\mathrm{c}}^{\mathrm{P}}$ - $\alpha_{\mathrm{p}}^{\mathrm{P}}$) are not estimated. When some constraints might be implemented in the model, it is important to carefully choose which transition is expressed as the complement of the others in order to be able to fix certain parameters to constrained values before estimation. This is only possible for parameters which are not expressed as a complement of others. Here, the matrix pattern used was as follows (see parameter constraints below; we specify the assignment probabilities using straightforward subscripts after α, see also Fig. 4.2):

$$\begin{array}{c|ccccc|}
 & 0 & 1 & 2 & 3 & 4 \\
\hline
\mathrm{NE} & 1 & 0 & 0 & 0 & 0 \\
\mathrm{EP} & 0 & \alpha_{\mathrm{c}}^{\mathrm{P}} & 1-\alpha_{\mathrm{c}}^{\mathrm{P}}-\alpha_{\mathrm{p}}^{\mathrm{P}} & \alpha_{\mathrm{p}}^{\mathrm{P}} & 0 \\
\mathrm{EB} & 0 & 0 & \alpha_{\mathrm{u}}^{\mathrm{B}} & \alpha_{\mathrm{p}}^{\mathrm{B}} & 1-\alpha_{\mathrm{u}}^{\mathrm{B}}-\alpha_{\mathrm{p}}^{\mathrm{B}} \\
\hline
\end{array}$$

D.2.5 Impossible transitions

When age was included as a covariate in our models, several parameters were not estimable or had to be constrained to fixed values. Given the biology of the slender-billed gull some transitions were impossible at certain ages, or at least never observed on the field and thus considered as impossible in our capture-recapture analyses.

Survival was not constrained to a fixed value. Pre-breeder immigration ($\delta_{\mathrm{oi}}^{\mathrm{P}}$) was impossible at age 1 because all the individuals were born and marked inside the study area ($\delta_{\mathrm{oi},1}^{\mathrm{P}} = NA$). Recruitment at age 1 was not allowed, and thus constrained to 0 ($r_1 = 0$). Breeder emigration ($\delta_{\mathrm{io}}^{\mathrm{B}}$) was impossible before age 3 because individuals can become breeders (i.e. they recruit) only at age 2 and only in the study area, it was thus constrained to 0 ($\delta_{\mathrm{io},\leq 2}^{\mathrm{B}} = NA$). For the same reasons, breeder immigration ($\delta_{\mathrm{oi}}^{\mathrm{B}}$) was impossible before age 4 ($\delta_{\mathrm{oi},\leq 3}^{\mathrm{B}} = NA$). Here the initial state was capture at ringing, thus encounter probability at the initial state was 1 for every individual ($p_0 = 1$). For the same reason, at initial state individuals could only be observed as "certain pre-breeder" and thus assigned to the corresponding category ($\alpha_{\mathrm{c},0}^{\mathrm{P}} = 1$). After that, pre-breeders could not be observed as "certain pre-breeder" anymore, the corresponding assignment probability was thus constrained to 0 for all the following age classes ($\alpha_{\mathrm{c},\geq 1}^{\mathrm{P}} = 0$).

Table D.2.1. Behavioural observations for each observation event

Observation event	Behaviour
1: "certain pre-breeder"	Pre-fledging chick (at capture)
2: "uncertain breeder"	No specific behaviour Courtship Resting Feeding Hurt or ill
3: "possible breeder"	Accompanying a chick Begging another adult Begged by a chick Feeding another adult Fed by another adult Manipulating nest material Copulating
4: "certain breeder"	Incubating Feeding a chick Replacing its mate on the nest

D.2.6 Literature cited

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D.3. Analyses of goodness of fit

D.3.1 Details on the results

We could not use the goodness-of-fit (GOF) test designed for Jolly Move and variants multi-event models because states did not correspond to events (Pradel et al. 2005). We grouped the observable events to obtain binary capture histories with observed and unobserved individuals. To test the GOF to our data we used the Cormack-Jolly-Seber model (software U-CARE v2.3.2, Choquet et al. 2009; Pradel et al. 2005). This step allows to compare our data with the assumptions supported by the Cormack-Jolly Seber model. All tests were highly significant (Global test: χ^2_{62}=1543.35, P<0.001; TEST2CT indicated trap-happiness: N(0,1) signed statistic =-7.02, χ^2_{10}=128.09, P<0.001; TEST 3.SR for transience: χ^2_{11}=738.76, P<0.001).

Because the transience effect was very likely to be due to a lower (local) survival at the early life of birds (Pradel et al. 1995; Schmidt et al. 2002; Choquet et al. 2009), we thus removed first encounters from the dataset to perform the GOF test once again. The tests were still significant (Global test: χ^2_{38}=130.58, P<0.001; TEST2CT indicated trap-happiness: N(0,1) signed statistic =-5.13, χ^2_{9}=35.74, P<0.001; TEST 3.SR for transience: χ^2_{10}=65.43, P<0.001). We then removed the second encounters from the dataset (thus the first and second encounters were removed). The GOF test was just below the 5% level of significance and did not indicated transience anymore but was still indicating "trap-happiness" (Global test: χ^2_{29}=44.04, P=0.036. TEST2CT indicated trap-happiness:

N(0,1) signed statistic =-3.29, χ^2_7=19.60, P=0.007; TEST 3.SR for transience : χ^2_9=12.23, P=0.20).

By putting an age effect on survival and through age-dependent emigration, we explicitly accounted for transience caused by the lower local survival at the early life of birds (Pradel et al. 1995; Schmidt et al. 2002; Choquet et al. 2009). The trap-happiness was likely to be due to the high mobility of slender-billed gulls which we expected to cause much temporal emigration in the study population. Other possible explanations were unlikely because they suppose that capture sites are the same from one year to another, or that capture methods and/or devices induce trap-dependence (Pradel et al. 2005; Choquet et al. 2009; Pradel and Sanz-Aguilar 2012). This was not the case for our population: locations of the colonies change every year, birds are caught only once with all the crèche of chicks before fledgling and resightings are carried out from a floating blind which does not disturb the birds (Doxa *et al.* 2013). By modelling temporal emigration with a 'ghost site' (see *Materials and Methods*) our model explicitly handled this phenomenon.

Since most of these departure from modelling hypotheses highlighted by the GOF tests were explicitly handled by the structure of our model, we did not use an overdispersion factor (i.e. variance inflation factor or *c-hat*) to correct the estimated (co)variances and deviance (Pradel et al. 2005; Choquet et al. 2009).

D.3.2 Literature cited

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D.4. Complete summary of model selection

D.4.1 Foreword of the section

Hereafter are provided the two complete summary of models involved in the selection with the complete dataset containing all individuals, and the reduced dataset containing only sexed individuals, see *Materials and Methods* (Table D.4.1, D.4.2).

Table D.4.1. Summary of capture-recapture models for slender-billed gulls regional demography on the French Mediterranean coast, using a first set of data containing all the individuals marked as chicks (sexed and unsexed; see notes below).

Mo.	St.	Model formulation					K	Deviance	AICc	ΔAICc (within steps)	wAICc (within steps)	ΔAICc (among steps)	wAICc (among steps)
		Survival	Movement	Recruitment	Encounter	Assignment							
12	II	a(1,2:12).t	f.[a(1,2,3,4:12)+a(1:12).t]	a(1,2,3,4:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	78	12927.17	13085.32	0.00	0.99	0.00	0.99
13	II	a(1,2:12).t	f.[a(1,2,3,4:12)+a(1:12).t]	a(1,2,3,4:12)+a(2:3).t	Fe+Ne	Fe.[f.to]+Ne.[f.to]	88	12916.97	13095.70	10.38	0.01	10.38	0.01
14	II	a(1,2:12).t	f.[a(1,2,3,4:12)+a(1:12).t]	a(1,2,3,4:12)+a(2:12).t	Fe+Ne	Fe.[f.to]+Ne.[f.to]	88	12918.93	13097.66	12.35	0.00	12.35	0.00
15	II	a(1,2:12).t	f.[a(1,2,3,4:12)+a(1:12).t]	a(1)+a(2).t+a(3,4:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	88	12919.46	13098.19	12.88	0.00	12.88	0.00
16	II	a(1,2:12).t	f.[a(1,2,3,4:12)+a(1:12).t]	a(1,2,3)+a(4:12).t	Fe+Ne	Fe.[f.to]+Ne.[f.to]	86	12925.52	13100.13	14.81	0.00	14.81	0.00
17	II	a(1,2:12).t	f.[a(1,2,3,4:12)+a(1:12).t]	a(1)+a(2,3,4:12)+a(3:12).t	Fe+Ne	Fe.[f.to]+Ne.[f.to]	87	12923.67	13100.34	15.02	0.00	15.02	0.00
18	II	a(1,2:12).t	f.[a(1,2,3,4:12)+a(1:12).t]	a(1)+a(2,3).t+a(4:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	97	12908.57	13105.86	20.54	0.00	20.54	0.00
19	II	a(1,2:12).t	f.[a(1,2,3,4:12)+a(2:12).t]	a(1,2,3,4:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	77	12950.76	13106.86	21.54	0.00	21.54	0.00
20	II	a(1,2:12).t	f.[a(1,2,3,4:12)+a(3:12).t]	a(1,2,3,4:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	75	12961.78	13113.76	28.44	0.00	28.44	0.00
21	II	a(1,2:12).t	f.[a(1,2,3,4:12)+a(1:12).t]	a(1)+a(2,3,4:12).t	Fe+Ne	Fe.[f.to]+Ne.[f.to]	105	12906.97	13120.87	35.55	0.00	35.55	0.00
22	II	a(1,2:12).t	f.[a(1,2,3,4:12)+a(1:12).t]	a(1)+a(2)+a(3,4:12).t	Fe+Ne	Fe.[f.to]+Ne.[f.to]	95	12934.14	13127.33	42.01	0.00	42.01	0.00
23	II	a(1,2:12).t	f.a(1,2,3,4:12).t	a(1,2,3,4:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	127	12870.13	13129.84	44.52	0.00	44.52	0.00
24	II	a(1,2:12).t	f.[a(1,2)+a(3,4:12).t]	a(1,2,3,4:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	99	12930.90	13132.36	47.04	0.00	47.04	0.00
25	II	a(1,2:12).t	f.[a(1)+a(2,3,4:12).t]	a(1,2,3,4:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	118	12892.13	13133.84	48.52	0.00	48.52	0.00
26	II	a(1,2:12).t	f.[a(1,2,3,4:12)+a(1:3).t]	a(1,2,3,4:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	70	13025.19	13166.91	81.60	0.00	81.60	0.00
27	II	a(1,2:12).t	f.[a(1).t+a(2,3,4:12)]	a(1,2,3,4:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	50	13066.13	13167.02	81.70	0.00	81.70	0.00
28	II	a(1,2:12).t	f.[a(1,2,3,4:12)+a(1:2).t]	a(1,2,3,4:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	61	13045.22	13171.54	86.22	0.00	86.22	0.00
29	II	a(1,2:12).t	f.[a(1,2).t+a(3,4:12)]	a(1,2,3,4:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	69	13041.45	13181.13	95.82	0.00	95.82	0.00
30	II	a(1,2:12).t	f.[a(1,2,3).t+a(4:12)]	a(1,2,3,4:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	96	12993.06	13188.31	102.99	0.00	102.99	0.00
31	II	a(1,2:12).t	f.a(1,2,3,4:12)	a(1,2,3,4:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	40	13108.96	13189.53	104.21	0.00	104.21	0.00
32	II	a(1).t+a(2:12)	f.a(1,2,3,4:12)	a(1,2,3,4:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	30	13157.58	13217.90	132.58	0.00	132.58	0.00
33	II	a(1,2:12)+t	f.a(1,2,3,4:12)	a(1,2,3,4:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	30	13172.82	13233.14	147.83	0.00	147.83	0.00
34	II	a(1)+a(2:12).t	f.a(1,2,3,4:12)	a(1,2,3,4:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	29	13261.46	13319.77	234.45	0.00	234.45	0.00
1	I	a(1,2:12)	f.a(1,2,3,4:12)	a(1,2,3,4:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	19	13346.72	13384.85	0.00	0.23	299.53	0.00
2	I	a(1,2:12)	f.a(1,2,3,4:12)	a(1,2,3,4,5:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	20	13346.03	13386.17	1.32	0.12	300.85	0.00
3	I	a(1,2:12)	f.a(1,2,3,4:12)	a(1,2,3,4:12)	Fe+Ne.f	Fe.[f.to]+Ne.[f.to]	20	13346.13	13386.27	1.43	0.11	300.96	0.00
4	I	a(1:2,3:12)	f.a(1,2,3,4:12)	a(1,2,3,4:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	19	13348.50	13386.63	1.78	0.10	301.32	0.00

5	I	a(1,2,3:12)	f.a(1,2,3,4:12)	a(1,2,3,4:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	20	13346.69	13386.84	1.99	0.09	301.52	0.00
35	I	a(1:2,3:12)	f.a(1,2,3,4:12)	a(1,2,3,4:12)	Fe+Ne.f	Fe.[f.to]+Ne.[f.to]	20	13347.41	13387.56	2.71	0.06	302.24	0.00
36	I	a(1,2,3:12)	f.a(1,2,3,4:12)	a(1,2,3,4:12)	Fe+Ne.f	Fe.[f.to]+Ne.[f.to]	21	13345.84	13388.00	3.15	0.05	302.69	0.00
37	I	a(1,2,3:12)	f.a(1,2,3,4:12)	a(1,2,3,4,5:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	21	13345.95	13388.10	3.26	0.05	302.79	0.00
38	I	a(1:2,3:12)	f.a(1,2,3,4:12)	a(1,2,3,4,5:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	20	13348.00	13388.15	3.30	0.05	302.83	0.00
39	I	a(1,2:12)	f.a(1,2,3,4:12)	a(1,2,3,4,5,6:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	21	13346.03	13388.18	3.34	0.04	302.87	0.00
40	I	a(1,2,3,4:12)	f.a(1,2,3,4:12)	a(1,2,3,4:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	21	13346.77	13388.93	4.08	0.03	303.62	0.00
41	I	a(1:2,3:12)	f.a(1,2,3,4:12)	a(1,2,3,4,5,6:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	21	13347.78	13389.94	5.09	0.02	304.62	0.00
42	I	a(1,2,3:12)	f.a(1,2,3,4:12)	a(1,2,3,4,5,6:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	22	13345.94	13390.12	5.27	0.02	304.80	0.00
43	I	a(1,2,3,4:12)	f.a(1,2,3,4:12)	a(1,2,3,4:12)	Fe+Ne.f	Fe.[f.to]+Ne.[f.to]	22	13346.06	13390.24	5.39	0.02	304.92	0.00
44	I	a(1,2,3,4:12)	f.a(1,2,3,4:12)	a(1,2,3,4,5:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	22	13346.10	13390.27	5.42	0.02	304.95	0.00
45	I	a(1,2,3,4:12)	f.a(1,2,3,4:12)	a(1,2,3,4,5,6:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	23	13346.02	13392.21	7.36	0.01	306.90	0.00
46	I	a(1,2:12)	f.a(1,2,3,4:12)	a(1,2,3:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	18	13391.05	13427.17	42.32	0.00	341.85	0.00
47	I	a(1,2,3:12)	f.a(1,2,3,4:12)	a(1,2,3:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	19	13391.05	13429.18	44.33	0.00	343.86	0.00
48	I	a(1:2,3:12)	f.a(1,2,3,4:12)	a(1,2,3:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	18	13393.08	13429.19	44.34	0.00	343.88	0.00
49	I	a(1,2,3,4:12)	f.a(1,2,3,4:12)	a(1,2,3:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	20	13391.15	13431.30	46.45	0.00	345.98	0.00
50	I	a(1,2,3,4:12)	f.a(1,2,3:12)	a(1,2,3,4,5:12)	Fe+Ne.f	Fe.[f.to]+Ne.[f.to]	20	13391.92	13432.07	47.22	0.00	346.75	0.00
51	I	a(1,2:12)	f.a(1,2,3:12)	a(1,2,3,4,5:12)	Fe+Ne.f	Fe.[f.to]+Ne.[f.to]	18	13402.35	13438.47	53.62	0.00	353.15	0.00
52	I	a(1,2,3:12)	f.a(1,2,3:12)	a(1,2,3,4,5:12)	Fe+Ne.f	Fe.[f.to]+Ne.[f.to]	19	13402.10	13440.23	55.38	0.00	354.91	0.00
53	I	a(1:2,3:12)	f.a(1,2,3:12)	a(1,2,3,4,5:12)	Fe+Ne.f	Fe.[f.to]+Ne.[f.to]	18	13404.37	13440.49	55.64	0.00	355.17	0.00
54	I	a(1,2:12)	f.a(1,2,3,4:12)	a(1,2:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	17	13435.46	13469.56	84.71	0.00	384.24	0.00
55	I	a(1:2,3:12)	f.a(1,2,3,4:12)	a(1,2:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	17	13436.91	13471.02	86.17	0.00	385.70	0.00
56	I	a(1,2,3:12)	f.a(1,2,3,4:12)	a(1,2:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	18	13435.23	13471.35	86.50	0.00	386.03	0.00
57	I	a(1,2,3,4:12)	f.a(1,2,3,4:12)	a(1,2:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	19	13435.49	13473.62	88.77	0.00	388.30	0.00
58	I	a(1,2,3:12)	f.a(1,2,3:12)	a(1,2,3,4,5:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	18	13441.08	13477.20	92.35	0.00	391.88	0.00
59	I	a(1,2:12)	f.a(1,2,3:12)	a(1,2,3,4,5:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	17	13443.95	13478.06	93.21	0.00	392.74	0.00
60	I	a(1,2,3,4:12)	f.a(1,2,3:12)	a(1,2,3,4,5:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	19	13440.07	13478.20	93.35	0.00	392.88	0.00
61	I	a(1,2,3:12)	f.a(1,2,3:12)	a(1,2,3,4,5,6:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	19	13440.38	13478.51	93.66	0.00	393.19	0.00
62	I	a(1,2:12)	f.a(1,2,3:12)	a(1,2,3,4,5,6:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	18	13443.21	13479.33	94.48	0.00	394.01	0.00
63	I	a(1,2,3,4:12)	f.a(1,2,3:12)	a(1,2,3,4,5,6:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	20	13439.24	13479.39	94.54	0.00	394.07	0.00
64	I	a(1,2,3:12)	f.a(1,2,3:12)	a(1,2,3:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	16	13447.68	13479.77	94.92	0.00	394.46	0.00
65	I	a(1,2:12)	f.a(1,2,3:12)	a(1,2,3:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	15	13450.49	13480.57	95.72	0.00	395.26	0.00

66	I	a(1,2,3,4:12)	f.a(1,2,3:12)	a(1,2,3:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	17	13446.51	13480.61	95.76	0.00	395.30	0.00
67	I	a(1,2,3:12)	f.a(1,2,3:12)	a(1,2,3,4:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	17	13447.60	13481.71	96.86	0.00	396.39	0.00
68	I	a(1,2,3,4:12)	f.a(1,2,3:12)	a(1,2,3,4:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	18	13446.26	13482.38	97.53	0.00	397.06	0.00
69	I	a(1,2:12)	f.a(1,2,3:12)	a(1,2,3,4:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	16	13450.43	13482.53	97.68	0.00	397.21	0.00
70	I	a(1:2,3:12)	f.a(1,2,3:12)	a(1,2,3,4,5:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	17	13450.16	13484.26	99.41	0.00	398.95	0.00
71	I	a(1:2,3:12)	f.a(1,2,3:12)	a(1,2,3,4,5,6:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	18	13449.53	13485.65	100.80	0.00	400.34	0.00
72	I	a(1:2,3:12)	f.a(1,2,3:12)	a(1,2,3:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	15	13456.69	13486.77	101.92	0.00	401.46	0.00
73	I	a(1:2,3:12)	f.a(1,2,3:12)	a(1,2,3,4:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	16	13456.68	13488.78	103.93	0.00	403.46	0.00
74	I	a(1,2,3:12)	f.a(1,2:12)	a(1,2,3,4,5:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	16	13475.80	13507.90	123.05	0.00	422.58	0.00
75	I	a(1,2,3:12)	f.a(1,2:12)	a(1,2,3,4,5:12)	Fe+Ne.f	Fe.[f.to]+Ne.[f.to]	17	13474.64	13508.74	123.90	0.00	423.43	0.00
76	I	a(1,2,3:12)	f.a(1,2:12)	a(1,2,3,4,5,6:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	17	13474.90	13509.01	124.16	0.00	423.69	0.00
77	I	a(1,2,3,4:12)	f.a(1,2:12)	a(1,2,3,4,5:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	17	13475.05	13509.15	124.30	0.00	423.84	0.00
78	I	a(1,2,3,4:12)	f.a(1,2:12)	a(1,2,3,4,5:12)	Fe+Ne.f	Fe.[f.to]+Ne.[f.to]	18	13473.30	13509.42	124.57	0.00	424.10	0.00
79	II	a(1,2:12).t	f.[a(1,2,3)+a(4:12).t]	a(1,2,3,4:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	73	13361.64	13509.52	424.21	0.00	424.21	0.00
80	I	a(1,2,3:12)	f.a(1,2:12)	a(1,2,3:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	14	13482.02	13510.09	125.24	0.00	424.78	0.00
81	I	a(1,2,3,4:12)	f.a(1,2:12)	a(1,2,3,4,5,6:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	18	13474.21	13510.33	125.48	0.00	425.01	0.00
82	I	a(1,2:12)	f.a(1,2:12)	a(1,2,3,4,5:12)	Fe+Ne.f	Fe.[f.to]+Ne.[f.to]	16	13478.72	13510.81	125.96	0.00	425.49	0.00
83	I	a(1,2:12)	f.a(1,2:12)	a(1,2,3,4,5:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	15	13480.91	13510.99	126.14	0.00	425.68	0.00
84	I	a(1,2,3,4:12)	f.a(1,2:12)	a(1,2,3:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	15	13481.41	13511.49	126.64	0.00	426.17	0.00
85	I	a(1,2:12)	f.a(1,2:12)	a(1,2,3,4,5,6:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	16	13479.81	13511.91	127.06	0.00	426.59	0.00
86	I	a(1,2,3:12)	f.a(1,2:12)	a(1,2,3,4:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	15	13482.02	13512.10	127.25	0.00	426.78	0.00
87	I	a(1,2:12)	f.a(1,2:12)	a(1,2,3,4,5,6,7:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	17	13478.54	13512.65	127.80	0.00	427.33	0.00
88	I	a(1,2:12)	f.a(1,2:12)	a(1,2,3:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	13	13486.75	13512.81	127.96	0.00	427.49	0.00
89	I	a(1,2,3,4:12)	f.a(1,2:12)	a(1,2,3,4:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	16	13481.37	13513.46	128.61	0.00	428.14	0.00
90	I	a(1,2:12)	f.a(1,2:12)	a(1,2,3,4:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	14	13486.48	13514.56	129.71	0.00	429.24	0.00
91	I	a(1:2,3:12)	f.a(1,2:12)	a(1,2,3,4,5:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	15	13491.12	13521.21	136.36	0.00	435.89	0.00
92	I	a(1:2,3:12)	f.a(1,2:12)	a(1,2,3,4,5,6:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	16	13490.35	13522.44	137.60	0.00	437.13	0.00
93	I	a(1:2,3:12)	f.a(1,2:12)	a(1,2,3,4,5:12)	Fe+Ne.f	Fe.[f.to]+Ne.[f.to]	16	13490.68	13522.78	137.93	0.00	437.46	0.00
94	I	a(1:2,3:12)	f.a(1,2:12)	a(1,2,3:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	13	13497.54	13523.60	138.76	0.00	438.29	0.00
95	I	a(1:2,3:12)	f.a(1,2:12)	a(1,2,3,4:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	14	13497.34	13525.41	140.56	0.00	440.09	0.00
96	I	a(1,2,3,4:12)	f.a(1,2,3:12)	a(1,2:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	16	13495.82	13527.92	143.07	0.00	442.60	0.00
97	I	a(1,2,3:12)	f.a(1,2,3:12)	a(1,2:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	15	13502.19	13532.27	147.42	0.00	446.96	0.00

98	I	a(1,2:12)	f.a(1,2,3:12)	a(1,2:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	14	13505.42	13533.49	148.64	0.00	448.17	0.00
99	I	a(1:2,3:12)	f.a(1,2,3:12)	a(1,2:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	14	13508.96	13537.03	152.18	0.00	451.71	0.00
100	I	a(1,2,3:12)	f.a(1,2:12)	a(1,2:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	13	13541.94	13568.00	183.16	0.00	482.69	0.00
101	I	a(1,2:12)	f.a(1,2:12)	a(1,2:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	12	13544.48	13568.53	183.68	0.00	483.21	0.00
102	I	a(1,2,3,4:12)	f.a(1,2:12)	a(1,2:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	14	13541.67	13569.74	184.90	0.00	484.43	0.00
103	I	a(1:2,3:12)	f.a(1,2:12)	a(1,2:12)	Fe+Ne	Fe.[f.to]+Ne.[f.to]	12	13559.64	13583.70	198.85	0.00	498.38	0.00

Mo. is model numbering, which follows numbering in Table 4.1. St. is the step of model selection (see Appendix D.6 for details). In step I we ran 73 models to select the best model structure and pattern of variation with age. In step II we ran 21 models to select the best pattern of variation with time. For the sake of simplicity, we used the GEPAT phrases from E-SURGE to indicate model formulation (see precise explanations in E-SURGE Manual, Choquet and Nogue 2011). "a" designates age classes, f stands for "from" and to for "to" (i.e. establishes dependency to the previous or next state or event), "t" is time (here in years). "." is for multiplicative effects and "+" for additive effects, within parenthesises are specified how classes are divided (by a comma) or combined (by a colon). For instance, "a(x,y)+a(x:y).t" specifies different intercept for the age classes x and y, but a similar (i.e. additive) effect of time among age classes (i.e. each year, the parameter for each age classes is affected in the same way, though there is a constant difference between age classes). "Fe" is used here to abbreviate "firste" which, in GEPAT phrases, indicates first event. "Ne" is used here to abbreviate "nexte" which, in GEPAT phrases, indicates all events following the first one. As exposed before, some parameters are not estimable because the corresponding transition does not exist, or constrained to a given value : they are included in model formulation and then set to a fixed value (e.g. recruitment at age 1 is fixed at 0, i.e. a(1) according to GEPAT phrase formulation). K is the number of parameters. Deviance is $-2 \times \log(likelihood)$. AIC, the Akaike Information Criteria is $Deviance + 2K$. AICc, the corrected AIC, is $AIC + 2K(K+1)/(n-K-1)$, where n is the effective sample size. ΔAICc the difference in AICc, wAICc is the AICc weights. Both are given with respect to all models tested ("among steps") or only the models in the corresponding step ("within steps"). Extended explanations on the models and selection procedure are given in *Materials & Methods*.

Table D.4.2. Summary of capture-recapture models for slender-billed gulls regional demography on the French Mediterranean coast, using a second set of data containing only the sexed individuals marked as chicks (see note below).

Mo.	St.	Model formulation			K	Deviance	AICc	ΔAICc (within steps)	wAICc (within steps)	ΔAICc (among steps)	wAICc (among steps)
		Survival	Movement	Recruitment							
104	VI	a(1,2:12).t	f.[a(1,2,3,4:12)+a(1:12).t]+ g(1,2)	a(1,2,3,4:12)+a(2:3).g(2,1)	80	11446.37	11609.25	0.00	1.00	0.00	0.99
105	V	a(1,2:12).t	f.[a(1,2,3,4:12)+a(1:12).t]	a(1,2,3,4:12)	78	11459.34	11618.08	0.00	1.00	8.83	0.01
7	IV	a(1,2:12)	f.a(1,2,3,4:12)+g(1,2)	a(1,2,3,4:12)+a(2:3).g(2,1)	21	11802.88	11845.09	0.00	0.39	235.84	0.00
8	IV	a(1,2:12)	f.a(1,2,3,4:12)+g(1,2)	a(1)+a(2,3).g(1,2)+a(4:12)	22	11802.52	11846.74	1.66	0.17	237.49	0.00
9	IV	a(1,2:12)	f.a(1,2,3,4:12)+g(1,2)	a(1)+a(2,3,4:12)+a(2 :12).g(2,1)	21	11805.45	11847.65	2.57	0.11	238.40	0.00
10	IV	a(1,2:12)	f.a(1,2,3,4:12)+g(1,2)	a(1)+a(2,3,4:12).g(1,2)	23	11801.89	11848.13	3.05	0.08	238.89	0.00
11	IV	a(1,2:12)	f.a(1,2,3,4:12)+g(1,2)	a(1,2)+a(3).g(1,2)+a(4 :12)	21	11806.50	11848.70	3.61	0.06	239.45	0.00
106	IV	a(1,2:12)	f.a(1,2,3,4:12)+g(1,2)	a(1)+a(2).g(1,2)+a(3,4:12)	21	11806.55	11848.75	3.67	0.06	239.50	0.00
107	IV	a(1,2:12)	f.a(1,2,3,4:12)+g(1,2)	a(1)+a(2)+a(3,4:12).g(1,2)	22	11805.86	11850.09	5.00	0.03	240.84	0.00
108	IV	a(1,2:12)	f.a(1,2,3,4:12)+g(1,2)	a(1,2,3,4:12)	20	11811.64	11851.83	6.74	0.01	242.58	0.00
109	IV	a(1,2:12)	f.a(1,2,3,4:12)+g(1,2)	a(1,2,3,4:12)+a(3 :12).g(2,1)	21	11809.82	11852.03	6.94	0.01	242.78	0.00
110	IV	a(1,2:12)	f.[a(1,2,3,4:12)]+a(1:3).g(1,2)	a(1,2,3,4:12)	20	11811.94	11852.13	7.04	0.01	242.88	0.00
111	IV	a(1,2:12)	f.a(1,2,3,4:12)+ a(1:2).g(1,2)	a(1,2,3,4:12)	20	11812.64	11852.82	7.74	0.01	243.57	0.00
112	IV	a(1,2:12)	f.[a(1,2,3,4 :12)+a(2:4).g(1,2)]	a(1,2,3,4:12)	27	11798.67	11853.00	7.92	0.01	243.75	0.00
113	IV	a(1,2:12)	f.a(1,2,3,4:12)+g(1,2)	a(1) + a(2,3) + a(4:12).g(1,2)	21	11811.13	11853.34	8.25	0.01	244.09	0.00
114	IV	a(1,2:12)	f.[a(1,2,3,4:12)+a(3:4).g(1,2)]	a(1,2,3,4:12)	27	11799.28	11853.61	8.52	0.01	244.36	0.00
115	IV	a(1,2:12)	f.[a(1).g(1,2)+ a(2,3,4 :12)]	a(1,2,3,4:12)	20	11814.15	11854.34	9.25	0.00	245.09	0.00
116	IV	a(1,2:12)	f.a(1,2,3,4:12)+a(1).g(1,2)	a(1,2,3,4:12)	20	11814.15	11854.34	9.25	0.00	245.09	0.00
117	IV	a(1,2:12)	f.a(1,2,3,4:12)+a(2:3).g(1,2)	a(1,2,3,4:12)	20	11814.35	11854.53	9.45	0.00	245.29	0.00
6	III	a(1,2:12)	f.a(1,2,3,4:12)	a(1,2,3,4:12)	19	11816.41	11854.57	0.00	1.00	245.32	0.00
118	IV	a(1,2:12)	f.a(1,2,3,4:12)+g(2).g(1,2)	a(1,2,3,4:12)	20	11815.03	11855.21	10.13	0.00	245.96	0.00
119	IV	a(1,2:12)+g(1,2)	f.a(1,2,3,4:12)	a(1,2,3,4:12)	20	11815.26	11855.44	10.35	0.00	246.19	0.00
120	IV	a(1)+a(2:12).g(1,2)	f.a(1,2,3,4:12)	a(1,2,3,4:12)	20	11815.26	11855.44	10.35	0.00	246.19	0.00
121	IV	a(1,2:12)	f.a(1,2,3,4:12)+a(3).g(1,2)	a(1,2,3,4:12)	20	11815.44	11855.63	10.54	0.00	246.38	0.00
122	IV	a(1,2:12)	f.a(1,2,3,4:12)+a(4:12).g(1,2)	a(1,2,3,4:12)	20	11816.06	11856.24	11.16	0.00	246.99	0.00
123	IV	a(1).g(1,2)+a(2:12)	f.a(1,2,3,4:12)	a(1,2,3,4:12)	20	11816.18	11856.37	11.28	0.00	247.12	0.00

124	IV	a(1,2:12)	f.[a(1,2).g(1,2)+a(3,4 :12)]	a(1,2,3,4:12)	22	11812.44	11856.67	11.58	0.00	247.42	0.00
125	IV	a(1,2:12)	f.a(1,2,3,4 :12)+a(2:4).g(1,2)	a(1,2,3,4:12)	21	11814.66	11856.87	11.78	0.00	247.62	0.00
126	IV	a(1,2:12)	f.[a(1)+a(2).g(1,2)+a(3,4 :12)]	a(1,2,3,4:12)	21	11814.88	11857.08	11.99	0.00	247.83	0.00
127	IV	a(1,2:12).g(1,2)	f.a(1,2,3,4:12)	a(1,2,3,4:12)	21	11815.26	11857.46	12.37	0.00	248.21	0.00
128	IV	a(1,2:12)	f.a(1,2,3,4 :12)+a(3:4).g(1,2)	a(1,2,3,4:12)	21	11815.74	11857.94	12.85	0.00	248.69	0.00
129	IV	a(1,2:12)	f.[a(1,2,3,4 :12)+a(2:3).g(1,2)]	a(1,2,3,4:12)	22	11814.34	11858.56	13.48	0.00	249.31	0.00
130	IV	a(1,2:12)	f.[a(1,2)+a(3).g(1,2)+a(4:12)]	a(1,2,3,4:12)	22	11815.10	11859.32	14.24	0.00	250.07	0.00
131	IV	a(1,2:12)	f.[a(1,2,3)+a(4 :12).g(1,2)]	a(1,2,3,4:12)	23	11814.29	11860.53	15.44	0.00	251.28	0.00
132	IV	a(1,2:12)	f.[a(1,2,3).g(1,2)+a(4 :12)]	a(1,2,3,4:12)	25	11811.32	11861.61	16.52	0.00	252.36	0.00
133	IV	a(1,2:12)	f.[a(1)+a(2,3).g(1,2)+a(4:12)]	a(1,2,3,4:12)	24	11813.76	11862.02	16.94	0.00	252.77	0.00
134	IV	a(1,2:12)	f.[a(1,2)+a(3,4:12).g(1,2)]	a(1,2,3,4:12)	26	11812.98	11865.29	20.21	0.00	256.04	0.00
135	IV	a(1,2:12)	f.a(1,2,3,4 :12).g(1,2)	a(1,2,3,4:12)	29	11809.22	11867.60	22.51	0.00	258.35	0.00
136	IV	a(1,2:12)	f.[a(1)+a(2,3,4:12).g(1,2)]	a(1,2,3,4:12)	28	11811.65	11868.01	22.92	0.00	258.76	0.00
137	IV	a(1,2:12)	f.[a(1,2,3,4 :12)+a(1:2).g(1,2)]	a(1,2,3,4:12)	20	11862.43	11902.62	57.53	0.00	293.37	0.00
138	IV	a(1,2:12)	f.[a(1,2,3,4 :12)+a(1:3).g(1,2)]	a(1,2,3,4:12)	20	12192.80	12232.99	387.90	0.00	623.74	0.00
139	IV	a(1,2:12)	f.[a(1,2,3,4 :12)+g(1,2)]	a(1,2,3,4:12)	22	12600.02	12644.24	799.16	0.00	1034.99	0.00

Specifications are the same as for Table D.4.1. In subset III we only ran one model with the same structure as selected in subset I of model selection using the dataset containing all the individuals (sexed and unsexed, Table 4.1). In subset IV, 39 models were compared by adding sex as a covariate with the different demographic parameters. In subset V we only ran one model containing time-variation with the same structure as selected in subset II of model selection using the dataset containing all the individuals (Table 4.1). In subset VI we only ran one model containing time-variation and sex, by adding sex as a covariate in the same way as the best model selected in subset IV. GEPAT phrase for encounter step was "firste+nexte" in all models. GEPAT phrase for assignment was "firste.[f.to]+nexte.[f.to]" for all models. "g" (i.e. groups) designate sex classes (males and females).

D.4.2 Literature cited

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D.5. Time-varying models

D.5.1 Methods

At each step of model selection we also selected time-varying models to check whether temporal variations revealed major differences that would have questioned results from time-constant models. After having first selected the best time-constant structure of age-dependency with the complete data set (step I), we started from this best age-dependency structure and selected the best time-varying model (step II). Then, using the reduced dataset containing only sexed individuals, we fitted the time-constant model structure previously selected (step III) and started from this model to select sex effects (step IV). We finished by fitting the time-varying structure previously selected (step V) and added sex effects as just selected (step VI). The complete list of models involved is given in Table D.4.1 and D.4.2.

In step II, we first selected the best structure of temporal variation on survival, then on movements and finally on recruitment. In each step, we compared all possible models that were biologically relevant. Moreover, we noted that detection probability was overestimated at this step (see 'Results' hereafter). We thus ran a model in which detection was fixed at the value obtained with the best time-constant model to inspect the consequences on other estimations.

D.5.2 Results

Note: Tables are given after the list of references.

Complete dataset containing all individuals— The best time-constant model (Model 1, Table 4.1, Table D.4.1) had around 300 AICc points more than the best time-varying model (Model 12, Table D.4.1). Time-variation on movements accounted for around 100 AICc points in this decrease. In Model 12, there was temporal variation on survival and movements but not on recruitment. Time-dependence was multiplicative for survival and additive between age classes but not between states for movements (Table D.4.1).

Juvenile survival was greatly affected by time-dependence. The annual estimates varied between 0.27 [0.15,0.43] and 0.94 [0,1] but confidence intervals were large, especially around high values (Fig. D.5.1, Table D.5.1) and when reproductive success was low the preceding year (Fig. D.5.1). Adult survival showed much smaller fluctuations and remained always higher than 0.70 (Fig. D.5.1).

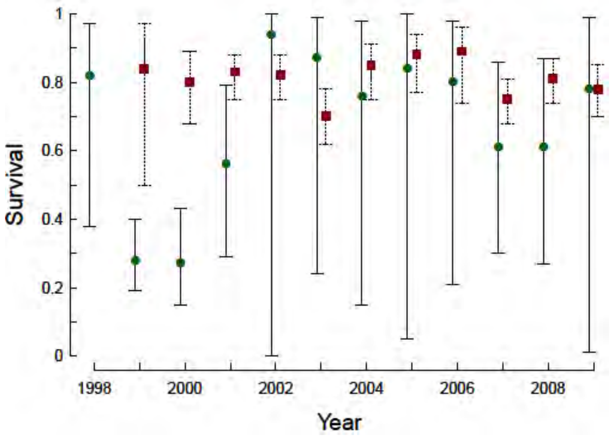

Figure D.5.1. Age-dependent survival rates of slender-billed gulls over 1998-2010. Estimates for the first year of life are plotted with circles, estimates for older individuals are plotted with squares. Segments indicate 95% confidence intervals. Estimates are derived from the best time-dependent model using the complete dataset (Model 12, Table D.4.1).

Estimations for breeders movements were difficult or impossible in many years (Fig. D.5.2, Table D.5.1). Detection was overestimated in the best time-varying model (p=0.94 [0.91,0.96]; Model 12, Table D.4.1). However, we observed coherent compensations between survival and movements: survival and immigration probabilities increased whereas emigration probabilities decreased when detection was fixed (Table D.5.2) at 0.86 (estimate from Model 1). This warned us on biases, but the variations themselves were not questioned.

Reduced dataset containing only sexed individuals— The time-varying model without sex-dependence (Model 105, Table D.5.3, Table D.4.1) had 236.49 AICc points less than the time-constant model without sex-dependence (Model 6, Table 4.1, Table D.4.1). Adding sex-dependence offered an even better fit (Model 104, Table D.5.4, Table D.4.2) with 8.83 AICc points less.

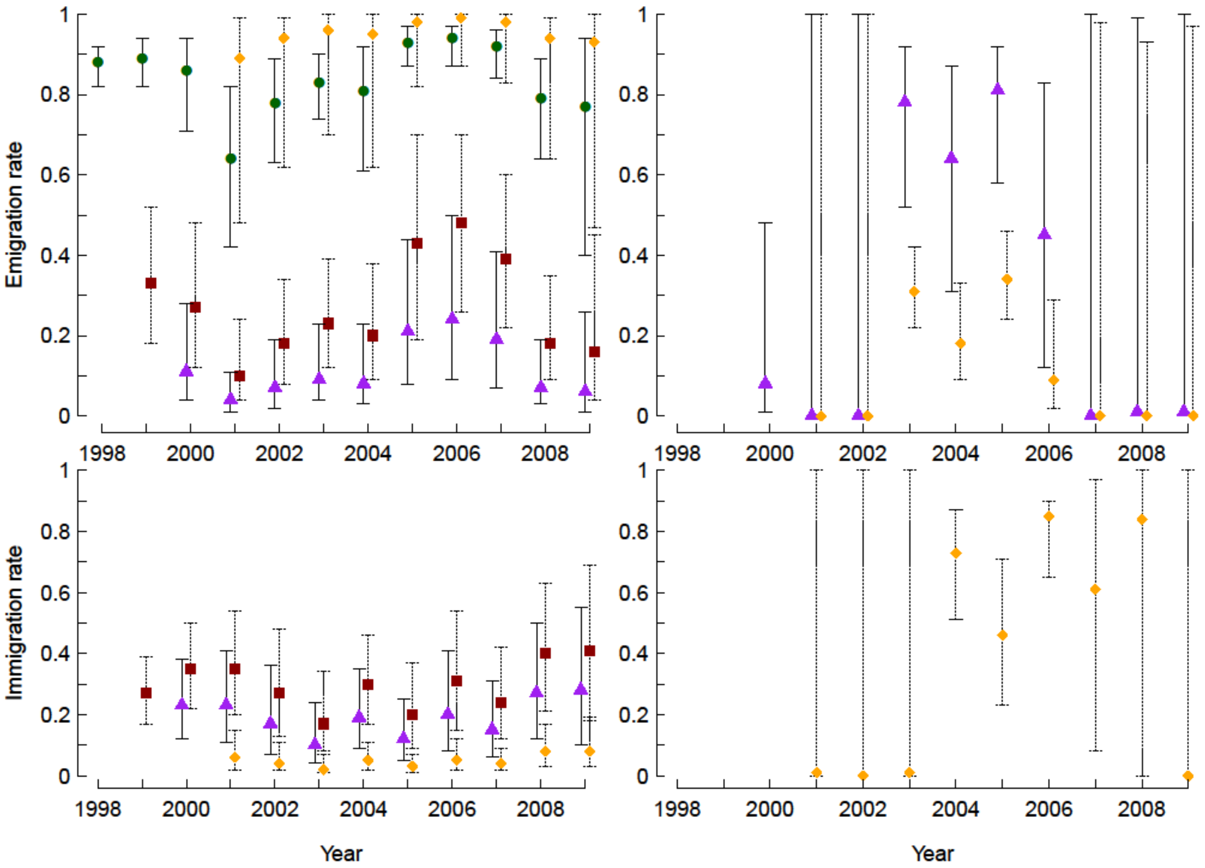

Figure D.5.2. Annual age-dependent movement rates of slender-billed gulls over 1998-2010. Movement rates are the probabilities to change location from one breeding season to the next, conditional on survival. Four types of movements were considered: emigration outside the study area (a) in pre-breeders and (b) in breeders, and immigration to the study area (c) in pre-breeders and (d) in breeders. Movements are plotted with circles at 1, with squares at 2, with triangles at 3 and with diamonds at 4 and older. Segments indicate the 95% confidence intervals. Estimates were obtained with the best time-varying model using the complete dataset (Model 12, Table D.5.1).

D.5.3 Discussion

Juvenile survival was much more variable than adult survival, which is usual in long-lived species due to evolutionary canalization and lower juvenile ability to face adverse conditions (Pardo et al. 2013). It might also have arisen from a difference in temporal variability of permanent emigration (Balkız et al. 2010; Sanz-Aguilar et al. 2014). However, the large confidence intervals make these changes difficult to comment. More data would be needed to get proper estimates.

In species from stable habitats, colony-site philopatry should be associated with less temporal variations in dispersal (Burger 1982; McNicholl 1975; Erwin et al. 1981). Here survival and movements varied strongly between years. This seems to contrast with the results of models without time-variations that suggest that breeders showed high regional philopatry. In fact, our results suggest that breeder emigration was null in most years but relatively high in some years followed by high immigration back. Such temporal changes in dispersal rates are particularly likely given the arbitrariness of our study boundaries, the mobility of slender-billed gulls and the instability and patchy distribution of potential breeding locations. Necessarily, locations of any new colony within or without the study area are, to some extent, apparently stochastic. Nonetheless, such strong variability also makes sense given that dispersal is highly context-dependent and might be partly triggered by temporally varying factors (or related cues) influencing habitat quality (e.g. food abundance, presence of predators; Clobert et al. 2001; Bowler and Benton 2005). Investigating how candidate variables correlate with local survival and movements would help understanding these temporal variations.

D.5.4 Literature cited

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Table D.5.1. Estimates of transition parameters obtained with the best model using the complete dataset (containing sexed and unsexed individuals) with temporal variation (Model 12, Table D.4.1). This model was selected to define the best pattern of variation with time for the capture-recapture data of the slender-billed gull on the French Mediterranean coast.

Transition step	Parameter	Estimates											
		1998 1999	1999 2000	2000 2001	2001 2002	2002 2003	2003 2004	2004 2005	2005 2006	2006 2007	2007 2008	2008 2009	2009 2010
Survival	ϕ_1	0.82 (0.38,0.97)	0.28 (0.19,0.40)	0.27 (0.15,0.43)	0.56 (0.29,0.79)	0.94 (0.00,1.00)	0.87 (0.24,0.99)	0.76 (0.15,0.98)	0.84 (0.05,1.00)	0.80 (0.21,0.98)	0.61 (0.30,0.86)	0.61 (0.27,0.87)	0.78 (0.01,0.99)
	$\phi_{\geq 2}$	–	0.84 (0.50,0.97)	0.80 (0.68,0.89)	0.83 (0.75,0.88)	0.82 (0.75,0.88)	0.70 (0.62,0.78)	0.85 (0.75,0.91)	0.88 (0.77,0.94)	0.89 (0.74,0.96)	0.75 (0.68,0.81)	0.81 (0.74,0.87)	0.78 (0.70,0.85)
Movement	$\delta^{\mathrm{P}}_{\mathrm{io},1}$	0.88 (0.82,0.92)	0.89 (0.82,0.94)	0.86 (0.71,0.94)	0.64 (0.42,0.82)	0.78 (0.63,0.89)	0.83 (0.74,0.90)	0.81 (0.61,0.92)	0.93 (0.87,0.97)	0.94 (0.87,0.97)	0.92 (0.84,0.96)	0.79 (0.64,0.89)	0.77 (0.40,0.94)
	$\delta^{\mathrm{P}}_{\mathrm{oi},2}$	–	0.27 (0.17,0.39)	0.35 (0.22,0.50)	0.35 (0.20,0.54)	0.27 (0.13,0.48)	0.17 (0.08,0.34)	0.30 (0.17,0.46)	0.20 (0.09,0.37)	0.31 (0.15,0.54)	0.24 (0.12,0.42)	0.40 (0.21,0.63)	0.41 (0.18,0.69)
	$\delta^{\mathrm{P}}_{\mathrm{io},2}$	–	0.33 (0.18,0.52)	0.27 (0.12,0.48)	0.10 (0.04,0.24)	0.18 (0.08,0.34)	0.23 (0.12,0.39)	0.20 (0.09,0.38)	0.43 (0.19,0.70)	0.48 (0.26,0.70)	0.39 (0.22,0.60)	0.18 (0.09,0.35)	0.16 (0.04,0.45)
	$\delta^{\mathrm{P}}_{\mathrm{oi},3}$	–	–	0.23 (0.12,0.38)	0.23 (0.11,0.41)	0.17 (0.07,0.36)	0.10 (0.04,0.24)	0.19 (0.09,0.35)	0.12 (0.05,0.25)	0.20 (0.08,0.41)	0.15 (0.06,0.31)	0.27 (0.12,0.50)	0.28 (0.10,0.55)
	$\delta^{\mathrm{P}}_{\mathrm{io},3}$	–	–	0.11 (0.04,0.28)	0.04 (0.01,0.11)	0.07 (0.02,0.19)	0.09 (0.04,0.23)	0.08 (0.03,0.23)	0.21 (0.08,0.44)	0.24 (0.09,0.50)	0.19 (0.07,0.41)	0.07 (0.03,0.19)	0.06 (0.01,0.26)
	$\delta^{\mathrm{B}}_{\mathrm{io},3}$	–	–	0.08 (0.01,0.48)	0.00 (0.00,1.00)	0.00 (0.00,1.00)	0.78 (0.52,0.92)	0.64 (0.31,0.87)	0.81 (0.58,0.92)	0.45 (0.12,0.83)	0.00 (0.00,1.00)	0.01 (0.00,0.99)	0.01 (0.00,1.00)
	$\delta^{\mathrm{P}}_{\mathrm{oi},\geq 4}$	–	–	–	0.06 (0.02,0.15)	0.04 (0.02,0.11)	0.02 (0.01,0.07)	0.05 (0.02,0.11)	0.03 (0.01,0.07)	0.05 (0.02,0.12)	0.04 (0.02,0.09)	0.08 (0.03,0.17)	0.08 (0.03,0.19)
	$\delta^{\mathrm{P}}_{\mathrm{io},\geq 4}$	–	–	–	0.89 (0.48,0.99)	0.94 (0.62,0.99)	0.96 (0.70,1.00)	0.95 (0.62,1.00)	0.98 (0.82,1.00)	0.99 (0.87,1.00)	0.98 (0.83,1.00)	0.94 (0.64,0.99)	0.93 (0.47,1.00)
	$\delta^{\mathrm{B}}_{\mathrm{oi},\geq 4}$	–	–	–	0.01 (0.00,1.00)	0.00 (0.00,1.00)	0.01 (0.00,1.00)	0.73 (0.51,0.87)	0.46 (0.23,0.71)	0.85 (0.65,0.90)	0.61 (0.08,0.97)	0.84 (0.00,1.00)	0.00 (0.00,1.00)
	$\delta^{\mathrm{B}}_{\mathrm{io},\geq 4}$	–	–	–	0.00 (0.00,1.00)	0.00 (0.00,1.00)	0.31 (0.22,0.42)	0.18 (0.09,0.33)	0.34 (0.24,0.46)	0.09 (0.02,0.29)	0.00 (0.00,0.98)	0.00 (0.00,0.93)	0.00 (0.00,0.97)
Recruitment	r_2	0.32 (0.24,0.40)											
	r_3	0.87 (0.79,0.92)											

	$r_{\geq 4}$	0.32 (0.20,0.48)
Detection	p	0.94 (0.91,0.96)
Assignment	$\alpha_{\mathrm{u}}^{\mathrm{B}}$	0.45 (0.43,0.48)
	$\alpha_{\mathrm{p}}^{\mathrm{P}}$	0.06 (0.04,0.10)
	$\alpha_{\mathrm{p}}^{\mathrm{B}}$	0.13 (0.11,0.15)

Parameter super- and subscripts indicate what class of individuals the probability applies on. When absent, this means that the parameter of interest do not vary among individuals according to the expected super- or subscript (e.g. age, breeding state, location, event). ϕ_i is survival at age i. $\delta_{\mathrm{io},i}^{\mathrm{S}}$ is the probability that surviving individuals move from inside to outside the study area (i.e. emigration) for individuals at age i in breeding state S (*i.e.* either PB for "pre-breeder" or B for "breeder"). $\delta_{\mathrm{oi},i}^{\mathrm{S}}$ is the probability that surviving individuals move from outside to inside the study area (i.e. immigration) for individuals at age i in breeding state S. Obviously, the probability to stay inside the study area is 1-$\delta_{\mathrm{io},i}^{\mathrm{S}}$, and the probability to stay outside is 1-$\delta_{\mathrm{oi},i}^{\mathrm{S}}$. r_i is the probability that surviving pre-breeders that moved to or stayed inside the study area recruit into the breeding part of the population in the current breeding season. p is the detection (i.e. encounter) probability. α_j^{S} is the probability for an individual in breeding state S to be assigned to the observational category j (*i.e.* either u for "uncertain breeder" or p for "possible breeder" or c for "certain breeder"). Pre-breeders are never observed as "certain pre-breeder" after capture and never observed as "certain breeder", thus $\alpha_{\mathrm{u}}^{\mathrm{P}} = 1 - \alpha_{\mathrm{p}}^{\mathrm{P}}$. Breeders can be assigned to one of the three observational categories mentioned above, thus $\alpha_{\mathrm{c}}^{\mathrm{B}} = 1 - \alpha_{\mathrm{u}}^{\mathrm{B}} - \alpha_{\mathrm{p}}^{\mathrm{B}}$. Estimates are given with the lower and upper boundaries of the 95% confidence interval between parentheses. Further details on the model are given in the manuscript and previous supplementary material. All capture-recapture histories started at birth, therefore for several parameters that were both age- and time-dependent there was no estimation in the very first years. Indeed, there were no individuals in the corresponding age classes yet. Large confidence intervals covering all the [0,1] probability space (or almost) clearly indicate a lack of data for precise inference. In this model, this is particularly symptomatic of the inference on breeders' movements at advanced ages. Indeed, at several occasions very few individuals were available in the corresponding classes.

Table D.5.2. Parameter estimates from the time-varying model with fixed detection.

Transition step	Parameter	Estimates											
		1998 1999	1999 2000	2000 2001	2001 2002	2002 2003	2003 2004	2004 2005	2005 2006	2006 2007	2007 2008	2008 2009	2009 2010
Survival	ϕ_1	1.00	0.45	0.58	0.46	1.00	0.83	0.93	0.45	0.98	0.36	0.43	0.53
		(0.99,1.00)	(0.24,0.68)	(0.17,0.91)	(0.12,0.85)	(0.99,1.00)	(0.35,0.98)	(0.7,0.99)	(0.21,0.72)	(0.00,1.00)	(0.25,0.49)	(0.02,0.97)	(0.00,1.00)
	$\phi_{\geq 2}$		0.72	0.78	0.85	0.82	0.71	0.84	0.96	0.93	0.76	0.87	0.87
			(0.44,0.89)	(0.68,0.85)	(0.77,0.91)	(0.75,0.88)	(0.62,0.8)	(0.74,0.91)	(0.12,1.00)	(0.35,1.00)	(0.69,0.83)	(0.39,0.99)	(0.58,0.97)
Movement	$\delta^{\mathrm{P}}_{\mathrm{io},1}$	0.90	0.93	0.94	0.53	0.79	0.81	0.84	0.82	0.94	0.85	0.67	0.63
		(0.87,0.92)	(0.86,0.97)	(0.82,0.98)	(0.14,0.89)	(0.70,0.86)	(0.70,0.88)	(0.63,0.94)	(0.46,0.96)	(0.89,0.97)	(0.74,0.92)	(0.09,0.98)	(0.00,1.00)
	$\delta^{\mathrm{P}}_{\mathrm{oi},2}$		0.26	0.23	0.15	0.47	0.14	0.35	0.02	0.61	0.21	0.74	0.62
			(0.18,0.37)	(0.12,0.40)	(0.05,0.36)	(0.02,0.98)	(0.06,0.27)	(0.20,0.55)	(0.00,0.65)	(0.16,0.92)	(0.13,0.33)	(0.36,0.94)	(0.00,1.00)
	$\delta^{\mathrm{P}}_{\mathrm{io},2}$		0.11	0.18	0.19	0.00	0.24	0.17	0.00	1.00	0.26	0.40	0.21
			(0.00,0.87)	(0.02,0.68)	(0.01,0.82)	(0.00,0.00)	(0.04,0.70)	(0.05,0.43)	(0.00,0.01)	(0.99,1.00)	(0.04,0.72)	(0.09,0.81)	(0.06,0.54)
	$\delta^{\mathrm{P}}_{\mathrm{oi},3}$			0.21	0.07	0.00	0.00	0.17	0.12	0.24	0.83	0.17	0.86
				(0.12,0.34)	(0.02,0.2)	(0.00,0.00)	(0.00,0.00)	(0.08,0.34)	(0.05,0.29)	(0.09,0.51)	(0.00,1.00)	(0.08,0.33)	(0.00,1.00)
	$\delta^{\mathrm{P}}_{\mathrm{io},3}$			0.00	0.00	0.00	0.14	0.00	0.27	0.40	0.00	0.08	0.01
				(0.00,0.00)	(0.00,0.00)	(0.00,0.00)	(0.00,0.84)	(0.00,0.00)	(0.12,0.51)	(0.04,0.92)	(0.00,0.03)	(0.00,0.96)	(0.00,0.07)
	$\delta^{\mathrm{B}}_{\mathrm{io},3}$			0.16	0.00	0.00	0.32	0.00	0.83	0.03	0.91	0.01	0.08
				(0.03,0.50)	(0.00,0.00)	(0.00,0.01)	(0.03,0.88)	(0.00,0.01)	(0.52,0.96)	(0.00,0.26)	(0.00,1.00)	(0.00,0.99)	(0.00,0.99)
	$\delta^{\mathrm{P}}_{\mathrm{oi},\geq 4}$				0.07	0.03	0.02	0.01	0.02	0.03	0.02	0.06	0.04
					(0.03,0.17)	(0.01,0.08)	(0.01,0.07)	(0.00,0.06)	(0.01,0.07)	(0.01,0.08)	(0.00,0.05)	(0.02,0.14)	(0.02,0.10)
	$\delta^{\mathrm{P}}_{\mathrm{io},\geq 4}$				1.00	0.85	1.00	0.76	0.68	1.00	0.99	1.00	0.70
					(1.00,1.00)	(0.29,0.99)	(0.97,1.00)	(0.21,0.97)	(0.09,0.98)	(0.99,1.00)	(0.00,1.00)	(0.94,1.00)	(0.22,0.95)
	$\delta^{\mathrm{B}}_{\mathrm{oi},\geq 4}$				0.00	0.00	0.00	0.71	0.09	0.73	0.00	0.18	0.00
					(0.00,0.00)	(0.00,0.00)	(0.00,0.01)	(0.41,0.89)	(0.00,0.93)	(0.19,0.97)	(0.00,1.00)	(0.01,0.83)	(0.00,1.00)
	$\delta^{\mathrm{B}}_{\mathrm{io},\geq 4}$				0.00	0.00	0.29	0.08	0.31	0.05	0.00	0.06	0.06
					(0.00,0.00)	(0.00,0.00)	(0.18,0.42)	(0.02,0.31)	(0.16,0.53)	(0.00,0.82)	(0.00,0.00)	(0.00,0.90)	(0.00,0.77)
Recruitment	r_2	0.28 (0.21,0.36)											
	r_3	0.85 (0.77,0.9)											
	$r_{\geq 4}$	0.24 (0.13,0.4)											

Detection	p	0.86 (0.86,0.86)
Assignment	$\alpha_{\mathrm{u}}^{\mathrm{B}}$	0.45 (0.42,0.47)
	$\alpha_{\mathrm{p}}^{\mathrm{P}}$	0.07 (0.05,0.11)
	$\alpha_{\mathrm{p}}^{\mathrm{B}}$	0.12 (0.11,0.14)

Specifications are the same as for Table Table D.5.1. Detection probability was fixed at 0.86 and the model was fitted with the structure of the best time-varying model (Model 12, Table D.4.1).

Table D.5.3. Estimates of transition parameters obtained with the best model using only sexed individuals, with temporal variation but without sex-dependent variations (Model 105, Table D.4.2). This model has the same structure as the model that was selected to define the best pattern of variation with time for the capture-recapture data of the slender-billed gull on the French Mediterranean coast (Model 12, Table D.4.1).

Transition step	Parameter	Estimates											
		1998 1999	1999 2000	2000 2001	2001 2002	2002 2003	2003 2004	2004 2005	2005 2006	2006 2007	2007 2008	2008 2009	2009 2010
Survival	ϕ_1	1.00 (1.00,1.00)	0.67 (0.49,0.82)	0.25 (0.16,0.38)	0.48 (0.31,0.66)	0.73 (0.45,0.90)	0.70 (0.52,0.84)	1.00 (1.00,1.00)	1.00 (1.00,1.00)	0.69 (0.42,0.87)	0.53 (0.35,0.70)	0.54 (0.33,0.74)	0.64 (0.03,0.99)
	$\phi_{\geq 2}$	–	0.92 (0.51,0.99)	0.78 (0.67,0.85)	0.82 (0.75,0.88)	0.81 (0.74,0.87)	0.69 (0.60,0.76)	0.85 (0.75,0.91)	0.88 (0.76,0.95)	0.93 (0.12,1.00)	0.75 (0.68,0.82)	0.81 (0.74,0.87)	0.79 (0.65,0.88)
Movement	$\delta_{\mathrm{io},1}^{\mathrm{P}}$	0.84 (0.80,0.87)	0.88 (0.81,0.93)	0.81 (0.66,0.90)	0.58 (0.38,0.75)	0.72 (0.58,0.83)	0.79 (0.71,0.86)	0.67 (0.42,0.85)	0.90 (0.74,0.97)	0.93 (0.87,0.96)	0.90 (0.82,0.95)	0.74 (0.61,0.84)	0.72 (0.30,0.94)
	$\delta_{\mathrm{oi},2}^{\mathrm{P}}$	–	0.36 (0.28,0.45)	0.43 (0.32,0.55)	0.41 (0.27,0.57)	0.36 (0.21,0.54)	0.26 (0.14,0.43)	0.39 (0.27,0.51)	0.29 (0.17,0.46)	0.44 (0.27,0.63)	0.32 (0.20,0.47)	0.51 (0.33,0.69)	0.54 (0.29,0.77)
	$\delta_{\mathrm{io},2}^{\mathrm{P}}$	–	0.37 (0.23,0.54)	0.26 (0.12,0.46)	0.10 (0.04,0.23)	0.17 (0.08,0.32)	0.24 (0.13,0.39)	0.14 (0.05,0.32)	0.42 (0.18,0.71)	0.52 (0.30,0.73)	0.42 (0.25,0.62)	0.19 (0.09,0.34)	0.17 (0.04,0.54)
	$\delta_{\mathrm{oi},3}^{\mathrm{P}}$	–	–	0.34 (0.23,0.48)	0.32 (0.20,0.48)	0.28 (0.15,0.46)	0.20 (0.10,0.37)	0.30 (0.19,0.45)	0.22 (0.12,0.36)	0.35 (0.20,0.55)	0.25 (0.13,0.41)	0.42 (0.24,0.62)	0.44 (0.21,0.70)
	$\delta_{\mathrm{io},3}^{\mathrm{P}}$	–	–	0.12 (0.05,0.27)	0.04 (0.01,0.12)	0.07 (0.03,0.19)	0.11 (0.04,0.25)	0.06 (0.02,0.19)	0.22 (0.08,0.47)	0.29 (0.12,0.56)	0.22 (0.09,0.45)	0.08 (0.03,0.21)	0.07 (0.01,0.34)
	$\delta_{\mathrm{io},3}^{\mathrm{B}}$	–	–	0.00	0.00	0.02	0.77	0.66	0.80	0.56	0.00	0.00	0.11

				(0.00,0.00)	(0.00,0.00)	(0.00,1.00)	(0.49,0.92)	(0.34,0.88)	(0.57,0.92)	(0.06,0.96)	(0.00,1.00)	(0.00,0.00)	(0.00,0.96)
	$\delta^{\mathrm{P}}_{\mathrm{oi},\geq 4}$	–	–	–	0.09 (0.04,0.18)	0.07 (0.03,0.15)	0.05 (0.02,0.11)	0.08 (0.04,0.15)	0.05 (0.02,0.11)	0.10 (0.05,0.19)	0.06 (0.03,0.12)	0.12 (0.06,0.23)	0.13 (0.06,0.29)
	$\delta^{\mathrm{P}}_{\mathrm{io},\geq 4}$	–	–	–	0.86 (0.51,0.97)	0.92 (0.65,0.99)	0.95 (0.74,0.99)	0.90 (0.54,0.99)	0.98 (0.83,1.00)	0.98 (0.90,1.00)	0.98 (0.86,1.00)	0.93 (0.67,0.99)	0.92 (0.45,0.99)
	$\delta^{\mathrm{B}}_{\mathrm{oi},\geq 4}$	–	–	–	0.01 (0.00,0.96)	0.01 (0.00,0.96)	0.00 (0.00,0.56)	0.76 (0.52,0.90)	0.52 (0.27,0.76)	0.87 (0.41,0.99)	0.51 (0.01,0.99)	0.50 (0.00,1.00)	0.00 (0.00,0.10)
	$\delta^{\mathrm{B}}_{\mathrm{io},\geq 4}$	–	–	–	0.00 (0.00,0.00)	0.00 (0.00,0.99)	0.29 (0.20,0.41)	0.20 (0.11,0.34)	0.34 (0.23,0.46)	0.14 (0.01,0.66)	0.00 (0.00,1.00)	0.00 (0.00,0.00)	0.02 (0.00,0.80)
Recruitment	r_2	0.33 (0.25,0.42)											
	r_3	0.86 (0.78,0.92)											
	$r_{\geq 4}$	0.31 (0.18,0.47)											
Detection	p	0.94 (0.91,0.96)											
Assignment	$\alpha^{\mathrm{B}}_{\mathrm{u}}$	0.45 (0.42,0.48)											
	$\alpha^{\mathrm{P}}_{\mathrm{p}}$	0.06 (0.04,0.10)											
	$\alpha^{\mathrm{B}}_{\mathrm{p}}$	0.13 (0.11,0.15)											

Specifications are the same as for Table Table D.5.1.

Table D.5.4. Estimates of transition parameters obtained with the best model using only sexed individuals, with temporal and sex-related variation (Model 104, Table D.4.2). This model has the same structure as the model that was selected to define the best pattern of variation with time (Model 12, Table D.4.1) and the same structure of variation with sex as the model was selected to define the best pattern of variation with sex (Model 105, Table D.4.2) for the capture-recapture data of the slender-billed gull on the French Mediterranean coast.

Transition step	Sex	Parameter	Estimates											
			1998 1999	1999 2000	2000 2001	2001 2002	2002 2003	2003 2004	2004 2005	2005 2006	2006 2007	2007 2008	2008 2009	2009 2010
Survival	Both	ϕ_1	1.00 (1.00,1.00)	0.68 (0.49,0.83)	0.26 (0.16,0.39)	0.49 (0.31,0.67)	0.73 (0.45,0.90)	0.70 (0.51,0.84)	1.00 (1.00,1.00)	1.00 (1.00,1.00)	0.67 (0.42,0.85)	0.51 (0.35,0.67)	0.52 (0.33,0.71)	0.68 (0.01,1.00)
		$\phi_{\geq 2}$		0.94	0.78	0.82	0.81	0.69	0.84	0.88	0.90	0.75	0.82	0.81

			–	(0.40,1.00)	(0.67,0.86)	(0.75,0.88)	(0.74,0.87)	(0.60,0.76)	(0.75,0.91)	(0.77,0.95)	(0.80,0.96)	(0.68,0.82)	(0.74,0.87)	(0.50,0.95)
Movement	Males	$\delta_{\mathrm{io},1}^{\mathrm{P}}$	0.85 (0.81,0.88)	0.89 (0.82,0.93)	0.83 (0.69,0.92)	0.60 (0.40,0.77)	0.73 (0.60,0.84)	0.81 (0.72,0.87)	0.67 (0.43,0.85)	0.91 (0.76,0.97)	0.93 (0.87,0.97)	0.90 (0.83,0.95)	0.75 (0.62,0.85)	0.76 (0.22,0.97)
		$\delta_{\mathrm{oi},2}^{\mathrm{P}}$	–	0.37 (0.28,0.47)	0.45 (0.33,0.57)	0.43 (0.28,0.59)	0.37 (0.21,0.57)	0.28 (0.15,0.45)	0.41 (0.29,0.54)	0.31 (0.17,0.48)	0.47 (0.30,0.65)	0.35 (0.23,0.50)	0.55 (0.37,0.72)	0.57 (0.31,0.79)
		$\delta_{\mathrm{io},2}^{\mathrm{P}}$	–	0.41 (0.25,0.58)	0.29 (0.14,0.51)	0.11 (0.04,0.26)	0.19 (0.09,0.35)	0.26 (0.14,0.43)	0.15 (0.06,0.33)	0.45 (0.20,0.72)	0.54 (0.32,0.75)	0.44 (0.26,0.65)	0.20 (0.10,0.37)	0.21 (0.03,0.72)
		$\delta_{\mathrm{oi},3}^{\mathrm{P}}$	–	–	0.35 (0.24,0.49)	0.33 (0.20,0.50)	0.29 (0.15,0.48)	0.21 (0.10,0.38)	0.32 (0.19,0.47)	0.23 (0.13,0.38)	0.38 (0.22,0.57)	0.27 (0.15,0.44)	0.45 (0.27,0.64)	0.47 (0.23,0.72)
		$\delta_{\mathrm{io},3}^{\mathrm{P}}$	–	–	0.13 (0.05,0.31)	0.05 (0.01,0.14)	0.08 (0.03,0.21)	0.12 (0.04,0.27)	0.06 (0.02,0.19)	0.23 (0.09,0.49)	0.31 (0.12,0.59)	0.23 (0.09,0.47)	0.09 (0.03,0.22)	0.09 (0.01,0.51)
		$\delta_{\mathrm{io},3}^{\mathrm{B}}$	–	–	0.00 (0,0)	0.00 (0,0)	0.03 (0,0.98)	0.76 (0.47,0.92)	0.66 (0.32,0.89)	0.80 (0.56,0.93)	0.47 (0.15,0.82)	0.00 (0,0.02)	0.00 (0,0)	0.26 (0,0.96)
		$\delta_{\mathrm{oi},\geq 4}^{\mathrm{P}}$	–	–	–	0.09 (0.04,0.18)	0.07 (0.03,0.15)	0.05 (0.02,0.11)	0.08 (0.04,0.16)	0.05 (0.02,0.12)	0.10 (0.05,0.19)	0.06 (0.03,0.13)	0.14 (0.07,0.24)	0.15 (0.06,0.30)
		$\delta_{\mathrm{io},\geq 4}^{\mathrm{P}}$	–	–	–	0.87 (0.54,0.98)	0.93 (0.66,0.99)	0.95 (0.75,0.99)	0.90 (0.55,0.99)	0.98 (0.84,1.00)	0.98 (0.91,1.00)	0.98 (0.86,1.00)	0.93 (0.69,0.99)	0.93 (0.35,1.00)
		$\delta_{\mathrm{oi},\geq 4}^{\mathrm{B}}$	–	–	–	0.04 (0.00,1.00)	0.03 (0.00,1.00)	0.00 (0.00,0.00)	0.77 (0.54,0.91)	0.54 (0.29,0.77)	0.90 (0.71,0.97)	0.69 (0.31,0.92)	1.00 (0.10,1.00)	0.00 (0.00,0.87)
		$\delta_{\mathrm{io},\geq 4}^{\mathrm{B}}$	–	–	–	0.00 (0,0)	0.00 (0,0.9)	0.31 (0.21,0.43)	0.21 (0.11,0.36)	0.36 (0.25,0.48)	0.11 (0.04,0.26)	0.00 (0,0)	0.00 (0,0)	0.05 (0,0.87)
	Females	$\delta_{\mathrm{io},1}^{\mathrm{P}}$	0.82 (0.77,0.86)	0.87 (0.79,0.92)	0.80 (0.64,0.90)	0.56 (0.36,0.74)	0.70 (0.55,0.81)	0.77 (0.68,0.85)	0.63 (0.39,0.82)	0.89 (0.73,0.96)	0.92 (0.85,0.96)	0.89 (0.80,0.94)	0.71 (0.57,0.82)	0.72 (0.19,0.97)
		$\delta_{\mathrm{oi},2}^{\mathrm{P}}$	–	0.33 (0.25,0.42)	0.40 (0.29,0.53)	0.38 (0.24,0.55)	0.33 (0.18,0.52)	0.24 (0.13,0.41)	0.36 (0.25,0.49)	0.27 (0.15,0.44)	0.43 (0.27,0.61)	0.31 (0.20,0.45)	0.50 (0.33,0.67)	0.52 (0.28,0.76)
		$\delta_{\mathrm{io},2}^{\mathrm{P}}$	–	0.36 (0.22,0.54)	0.26 (0.12,0.46)	0.10 (0.04,0.23)	0.16 (0.08,0.31)	0.23 (0.12,0.38)	0.13 (0.05,0.29)	0.40 (0.18,0.68)	0.50 (0.28,0.72)	0.40 (0.22,0.60)	0.17 (0.08,0.33)	0.18 (0.02,0.68)
		$\delta_{\mathrm{oi},3}^{\mathrm{P}}$	–	–	0.31 (0.20,0.44)	0.29 (0.17,0.45)	0.25 (0.13,0.43)	0.18 (0.08,0.34)	0.28 (0.17,0.42)	0.20 (0.11,0.34)	0.33 (0.19,0.52)	0.23 (0.13,0.39)	0.41 (0.24,0.59)	0.42 (0.20,0.68)
		$\delta_{\mathrm{io},3}^{\mathrm{P}}$	–	–	0.11 (0.04,0.27)	0.04 (0.01,0.12)	0.07 (0.02,0.18)	0.10 (0.04,0.24)	0.05 (0.01,0.17)	0.20 (0.08,0.44)	0.27 (0.10,0.54)	0.20 (0.07,0.43)	0.07 (0.03,0.19)	0.07 (0.01,0.46)
		$\delta_{\mathrm{io},3}^{\mathrm{B}}$	–	–	0.00	0.00	0.02	0.73	0.61	0.77	0.43	0.00	0.00	0.23

					(0,0)	(0,0)	(0,0.98)	(0.42,0.91)	(0.28,0.87)	(0.51,0.91)	(0.13,0.79)	(0,0.01)	(0,0)	(0,0.96)
		$\delta^{\mathrm{P}}_{\mathrm{oi},\geq 4}$	–	–	–	0.07 (0.03,0.16)	0.06 (0.03,0.13)	0.04 (0.02,0.09)	0.07 (0.03,0.14)	0.05 (0.02,0.10)	0.09 (0.04,0.16)	0.05 (0.03,0.11)	0.12 (0.06,0.21)	0.12 (0.05,0.26)
		$\delta^{\mathrm{P}}_{\mathrm{io},\geq 4}$	–	–	–	0.85 (0.49,0.97)	0.91 (0.62,0.99)	0.94 (0.71,0.99)	0.89 (0.51,0.98)	0.97 (0.81,1.00)	0.98 (0.89,1.00)	0.97 (0.84,1.00)	0.92 (0.64,0.99)	0.92 (0.31,1.00)
		$\delta^{\mathrm{B}}_{\mathrm{oi},\geq 4}$	–	–	–	0.03 (0.00,1.00)	0.02 (0.00,1.00)	0.00 (0.00,0.00)	0.74 (0.49,0.89)	0.49 (0.25,0.74)	0.89 (0.68,0.97)	0.65 (0.27,0.90)	1.00 (0.08,1.00)	0.00 (0.00,0.85)
		$\delta^{\mathrm{B}}_{\mathrm{io},\geq 4}$	–	–	–	0.00 (0,0)	0.00 (0,0.89)	0.27 (0.18,0.39)	0.18 (0.09,0.32)	0.31 (0.21,0.44)	0.09 (0.03,0.22)	0.00 (0,0)	0.00 (0,0)	0.04 (0,0.84)
Recruitment	Males	r_2	0.39 (0.30,0.50)											
		r_3	0.90 (0.82,0.95)											
	Females	r_2	0.23 (0.15,0.34)											
		r_3	0.81 (0.70,0.88)											
	Both	$r_{\geq 4}$	0.31 (0.19,0.47)											
Detection	Both	p	0.94 (0.91,0.96)											
Assignment	Both	$\alpha^{\mathrm{B}}_{\mathrm{u}}$	0.45 (0.42,0.48)											
		$\alpha^{\mathrm{P}}_{\mathrm{p}}$	0.07 (0.04,0.10)											
		$\alpha^{\mathrm{B}}_{\mathrm{p}}$	0.13 (0.11,0.15)											

Specifications are the same as for Table Table D.5.1.

D.6 Parameter estimates from time-constant models

Table D.6.1. Estimates of transition parameters obtained (i) with the best model using the complete dataset (including unsexed and sexed individuals) without temporal variation (Model 1, Table 4.1, Table D.4.1), (ii) with the same model using only sexed individuals (Model 6, Table 4.1, Table D.4.2), and (iii) with the best model using only sexed individuals with sex-related variations and without temporal variation (Model 7, Table 4.1, Table D.4.2).

Transition step	Parameter	Estimates			
		(i) Model 1	(ii) Model 6	(iii) Model 7	
				Males	Females
Survival	ϕ_1	0.77 (0.30,0.96)	1.00 (0.00,1.00)	1.00 (1.00,1.00)	
	$\phi_{\geq 2}$	0.83 (0.79,0.86)	0.82 (0.79,0.85)	0.82 (0.80,0.85)	
Movement	$\delta^{\mathrm{P}}_{\mathrm{io},1}$	0.87 (0.80,0.92)	0.87 (0.84,0.89)	0.88 (0.86,0.89)	0.85 (0.83,0.87)
	$\delta^{\mathrm{P}}_{\mathrm{oi},2}$	0.25 (0.14,0.41)	0.27 (0.23,0.31)	0.29 (0.25,0.32)	0.25 (0.22,0.28)
	$\delta^{\mathrm{P}}_{\mathrm{io},2}$	0.20 (0.12,0.30)	0.16 (0.09,0.28)	0.18 (0.10,0.30)	0.15 (0.08,0.26)
	$\delta^{\mathrm{P}}_{\mathrm{oi},3}$	0.13 (0.06,0.27)	0.17 (0.13,0.22)	0.18 (0.14,0.22)	0.15 (0.12,0.19)
	$\delta^{\mathrm{P}}_{\mathrm{io},3}$	0.07 (0.02,0.20)	0.07 (0.02,0.20)	0.07 (0.02,0.21)	0.06 (0.02,0.18)
	$\delta^{\mathrm{B}}_{\mathrm{io},3}$	0.05 (0.00,0.57)	0.00 (0.00,0.00)	0.00 (0.00,0.00)	0.00 (0.00,0.00)
	$\delta^{\mathrm{P}}_{\mathrm{oi},\geq 4}$	0.03 (0.01,0.07)	0.04 (0.03,0.06)	0.05 (0.03,0.07)	0.04 (0.03,0.06)
	$\delta^{\mathrm{P}}_{\mathrm{io},\geq 4}$	0.95 (0.36,1.00)	0.95 (0.38,1.00)	0.94 (0.62,0.99)	0.92 (0.57,0.99)
	$\delta^{\mathrm{B}}_{\mathrm{oi},\geq 4}$	0.19 (0.03,0.61)	0.25 (0.04,0.72)	0.30 (0.07,0.69)	0.26 (0.06,0.65)
	$\delta^{\mathrm{B}}_{\mathrm{io},\geq 4}$	0.05 (0.02,0.11)	0.04 (0.02,0.10)	0.05 (0.02,0.10)	0.04 (0.02,0.08)
Recruitment	r_2	0.24 (0.18,0.32)	0.24 (0.18,0.33)	0.31 (0.22,0.42)	0.16 (0.10,0.25)
	r_3	0.89 (0.81,0.96)	0.89 (0.80,0.94)	0.92 (0.84,0.96)	0.83 (0.72,0.90)
	$r_{\geq 4}$	0.24 (0.13,0.41)	0.25 (0.13,0.43)	0.24 (0.13,0.41)	
Detection	p	0.86 (0.83,0.88)	0.86 (0.83,0.88)	0.86 (0.83,0.88)	

Assignment	$\alpha_{\mathrm{u}}^{\mathrm{B}}$	0.45 (0.42,0.48)	0.45 (0.42,0.48)	0.45 (0.42,0.47)
	$\alpha_{\mathrm{p}}^{\mathrm{P}}$	0.08 (0.06,0.11)	0.08 (0.06,0.11)	0.08 (0.06,0.11)
	$\alpha_{\mathrm{p}}^{\mathrm{B}}$	0.12 (0.10,0.14)	0.12 (0.11,0.14)	0.12 (0.11,0.14)

Parameter super- and subscripts indicate what class of individuals the probability applies on. When absent, this means that the parameter of interest do not vary among individuals according to the expected super- or subscript (e.g. age, breeding state, location, event). ϕ_i is survival at age i. $\delta_{\mathrm{io},i}^{\mathrm{S}}$ is the probability that surviving individuals move from inside to outside the study area (i.e. emigration) for individuals at age i in breeding state S (*i.e.* either PB for "pre-breeder" or B for "breeder"). $\delta_{\mathrm{oi},i}^{\mathrm{S}}$ is the probability that surviving individuals move from outside to inside the study area (i.e. immigration) for individuals at age i in breeding state S. Obviously, the probability to stay inside the study area is 1-$\delta_{\mathrm{io},i}^{\mathrm{S}}$, and the probability to stay outside is 1-$\delta_{\mathrm{oi},i}^{\mathrm{S}}$. r_i is the probability that surviving pre-breeders that moved to or stayed inside the study area recruit into the breeding part of the population in the current breeding season. p is the detection (i.e. encounter) probability. α_j^{S} is the probability for an individual in breeding state S to be assigned to the observational category j (*i.e.* either u for "uncertain breeder" or p for "possible breeder" or c for "certain breeder"). Pre-breeders are never observed as "certain pre-breeder" after capture and never observed as "certain breeder", thus $\alpha_{\mathrm{u}}^{\mathrm{P}} = 1 - \alpha_{\mathrm{p}}^{\mathrm{P}}$. Breeders can be assigned to one of the three observational categories mentioned above, thus $\alpha_{\mathrm{c}}^{\mathrm{B}} = 1 - \alpha_{\mathrm{u}}^{\mathrm{B}} - \alpha_{\mathrm{p}}^{\mathrm{B}}$. Estimates are given with the lower and upper boundaries of the 95% confidence interval between parentheses. Further details on the model are given in the manuscript and previous supplementary material.

Table D.6.2. Parameter estimates from time-constant models with fixed values.

Transition step	Parameter	Estimates			
		(i) Model 1B	(ii) Model 1C	(iii) Model 7B	
				Males	Females
Survival	ϕ_1	0.50	0.95 (0.95,0.95)	0.77	
	$\phi_{\geq 2}$	0.83 (0.79,0.86)	0.83 (0.79,0.87)	0.82 (0.79,0.85)	
Movement	$\delta^{\mathrm{P}}_{\mathrm{io},1}$	0.81 (0.78,0.83)	0.90 (0.88,0.91)	0.84 (0.82,0.86)	0.81 (0.78,0.84)
	$\delta^{\mathrm{P}}_{\mathrm{oi},2}$	0.41 (0.37,0.45)	0.19 (0.17,0.22)	0.39 (0.34,0.43)	0.34 (0.30,0.38)
	$\delta^{\mathrm{P}}_{\mathrm{io},2}$	0.20 (0.12,0.31)	0.19 (0.12,0.30)	0.18 (0.10,0.31)	0.15 (0.08,0.27)
	$\delta^{\mathrm{P}}_{\mathrm{oi},3}$	0.28 (0.21,0.35)	0.10 (0.08,0.12)	0.27 (0.22,0.34)	0.23 (0.18,0.29)
	$\delta^{\mathrm{P}}_{\mathrm{io},3}$	0.06 (0.02,0.20)	0.07 (0.02,0.20)	0.07 (0.02,0.21)	0.06 (0.02,0.18)
	$\delta^{\mathrm{B}}_{\mathrm{io},3}$	0.06 (0.00,0.61)	0.05 (0.00,0.54)	0.00 (0.00,0.00)	0.00 (0.00,0.00)
	$\delta^{\mathrm{P}}_{\mathrm{oi},\geq 4}$	0.07 (0.05,0.11)	0.02 (0.01,0.03)	0.08 (0.05,0.12)	0.06 (0.04,0.10)
	$\delta^{\mathrm{P}}_{\mathrm{io},\geq 4}$	0.93 (0.59,0.99)	0.96 (0.18,1.00)	0.93 (0.65,0.99)	0.92 (0.60,0.99)
	$\delta^{\mathrm{B}}_{\mathrm{oi},\geq 4}$	0.18 (0.02,0.67)	0.18 (0.03,0.61)	0.30 (0.07,0.71)	0.26 (0.06,0.66)
	$\delta^{\mathrm{B}}_{\mathrm{io},\geq 4}$	0.05 (0.02,0.11)	0.05 (0.02,0.11)	0.05 (0.02,0.10)	0.04 (0.02,0.08)
Recruitment	r_2	0.24 (0.18,0.32)	0.24 (0.18,0.32)	0.31 (0.23,0.42)	0.16 (0.09,0.25)
	r_3	0.90 (0.81,0.95)	0.89 (0.81,0.94)	0.93 (0.85,0.96)	0.84 (0.72,0.91)
	$r_{\geq 4}$	0.25 (0.13,0.41)	0.24 (0.12,0.42)	0.25 (0.13,0.42)	
Detection	p	0.86 (0.83,0.88)	0.85 (0.83,0.88)	0.86 (0.83,0.88)	
Assignment	$\alpha^{\mathrm{B}}_{\mathrm{u}}$	0.45 (0.42,0.48)	0.45 (0.42,0.48)	0.45 (0.42,0.47)	
	$\alpha^{\mathrm{P}}_{\mathrm{p}}$	0.08 (0.06,0.11)	0.08 (0.06,0.11)	0.08 (0.06,0.11)	
	$\alpha^{\mathrm{B}}_{\mathrm{p}}$	0.12 (0.10,0.14)	0.12 (0.10,0.14)	0.12 (0.11,0.14)	

Specifications are the same as for Table Table D.6.1. (i) Model 1B had juvenile survival fixed at 0.5, (ii) Model 1C had juvenile survival fixed at 0.95. Except these fixed values, both were fitted with the structure of the best time-constant model (Model 1, Table 4.1, Table D.4.1) and using the complete dataset. (iii) Model 7B had juvenile survival fixed at 0.77 (estimate from Model 1) and was fitted with the structure of the best time-constant model with sex-dependence (Model 7, Table 4.1, Table D.4.2) using the reduced dataset containing only sexed individuals.

D.7. Life-history probabilities from time-constant models

D.7.1 Foreword of the section

In order to provide a better understanding of life-history differences according to age, sex and breeding status, we calculated some specific life-history probabilities offering relevant views on dispersal and recruitment. Indeed, in our models the emigration and immigration probabilities at time *t* are conditional on survival between *t-1* and *t*, and the local recruitment probability is conditional on being inside the population at time *t* after movement (i.e. having stayed or come back to the study area at time *t*). We thus computed at all possible ages for both sex and for each sex separately: (i) the probabilities for alive pre-breeders to be inside or outside the study area, (ii) the probabilities to recruit in the birth area for any alive pre-breeder, (iii) the probabilities to be alive and recruit in the birth area for any (pre-breeder) individual, and (iv) the probabilities for alive breeders to be inside or outside the study area. To do so, we used the maximum-likelihood estimates of survival, movement and recruitment parameters from the best time-constant model fitted with the complete dataset (Model 1, Table 4.1, Table D.6.1), and the best time-constant but sex-dependent model fitted with the reduced dataset (Model 7, Table 4.1, Table D.6.1).

Note: results are provided in tables and figures after the list of references.

D.7.2 Probability of being inside or outside the study area for alive pre-breeders

At any age i the probability for alive individuals (noted A_i) to be inside the study area ($Pr(I_i|A_i)$) is the complement of their probability to be outside the study area: $Pr(O_0|A_i) = 1 - Pr(I_i|A_i)$. At birth (i.e. capture for ringing; age 0), the probability to be inside the study area ($Pr(I_0)$) is 1 and the probability to be outside the study area is:

$$Pr(O_0) = 1 - Pr(I_0) = 0 .$$

After that, and for pre-breeders (noted P), at age i, the probability to be inside the study area is a function of the previous probabilities of localisation, emigration probability ($\delta^{\mathrm{P}}_{\mathrm{io},i}$) and immigration probability ($\delta^{\mathrm{P}}_{\mathrm{oi},i}$) which are conditional on being alive (A_i):

$$Pr(I_i|P,A_i) = Pr(I_{i-1}|P,A_i) \cdot \left(1 - \delta^P_{io,i}\right) + \ Pr(O_{i-1}|P,A_i) \cdot \delta^P_{oi,i} \ ,$$

$$Pr(O_i|P,A_i) = Pr(I_{i-1}|P,A_i) \cdot \delta^P_{io,i} + \ Pr(O_{i-1}|P,A_i) \cdot \left(1 - \delta^P_{oi,i}\right) = 1 - Pr(I_i|P,A_i) \ .$$

The complete formulas rapidly becomes very long and complex when age increases. In order to gain time and avoid the potential formulating errors it is prone to produce, we used a calculation loop over possible ages in ascendant order (results are provided in Table D.7.1, Fig. 4.3c and D.7.1a). This "for" loop was coded with R 3.1.2 as follows:

```
## Compute localisation probabilities for alive pre-breeders at different ages ##
# define the sex classes for the parameters
sexes <- c('all','males','females')

# define the age classes for the parameters
ages <- c(1:3,'4+')

# em.AP[i] is pre-breeder emigration probability at age class i
# estimates are from Model 1 (first row, both sexes)
# and Model 12 (second row: males, third row: females)
em.AP <- rbind(c(0.87,0.2,0.07,0.95),c(0.88,0.18,0.07,0.94),c(0.85,0.15,0.06,0.92))
colnames(em.AP) <- ages
rownames(em.AP) <- sexes

# im.AP[i] is pre-breeder immigration probability at age class i
# estimates are from Model 1 (first row, both sexes)
# and Model 12 (second row: males, third row: females)
im.AP <- rbind(c(0,0.25,0.13,0.03),c(0,0.29,0.18,0.05),c(0,0.25,0.15,0.04))
colnames(im.AP) <- ages
rownames(im.AP) <- sexes

# pI.AP[i] is the probability to be inside the area at age i-1 for alive pre-breeders
# first row: both sexes, second row: males, third row: females
pI.AP <- matrix(nrow=3,ncol=11)
colnames(pI.AP) <- 0:10                     # we'll compute pI.P[i] from age 1 to 10
rownames(pI.AP) <- sexes

# and pO.AP[i] the probability to be outside the area at age i for alive pre-breeders
pO.AP <- matrix(nrow=3,ncol=11)
colnames(pO.AP) <- 0:10                       # we'll compute pO.P[i] from age 1 to 10
rownames(pO.AP) <- sexes

# compute pI.AP and pO.AP using the for loop over ages
for (s in 1:3) {         # for the three sex classes
  pI.AP[s,1] <- 1          # at capture (i.e. birth, age 0) all individuals are inside
the area
  pO.AP[s,1] <- 0
  for (i in 2:11) {      # for age 1 to age 10
    if (i<=5) {
       pI.AP[s,i] <- pI.AP[s,i-1]*(1-em.AP[s,i-1]) + pO.AP[s,i-1]*im.AP[s,i-1]
       pO.AP[s,i] <- pI.AP[s,i-1]*em.AP[s,i-1] + pO.AP[s,i-1]*(1-im.AP[s,i-1])
    }
    if (i>5) {
       pI.AP[s,i] <- pI.AP[s,i-1]*(1-em.AP[s,4]) + pO.AP[s,i-1]*im.AP[s,4]
       pO.AP[s,i] <- pI.AP[s,i-1]*em.AP[s,4] + pO.AP[s,i-1]*(1-im.AP[s,4])
    }
  }
}

print(round(pI.AP,2))
print(round(pO.AP,2))
```

D.7.3 Annual probability of recruiting in the birth area for any alive pre-breeder

In our models, the local recruitment probability at age *i* (r_i) is conditional on being alive (A_i) and present in the study area (see *Methods*, Appendix D.2, Fig. 4.2 and Table D.7.2a hereafter). Therefore, at any age *i* ≥ 2 the probability to recruit in the birth area for any alive (pre-breeder) individual ($Pr(R_i|P, A_i)$) is a function of the probability to be inside the study area:

$$Pr(R_i|P, A_i) = Pr(I_i|P, A_i) \cdot r_i \, .$$

We thus computed probabilities of recruiting in the birth area for any alive pre-breeder considering the probabilities $Pr(I_i|P, A_i)$ computed as exposed above (results are provided in Table D.7.2, Fig. D.7.2b), using a "for" loop coded with R 3.1.2 as follows:

```
## Compute probabilities of recruiting in the birth area for any alive pre-breeder ##
# the following code uses R variables defined in the R code exposed in previous
section: sexes, ages and pI.AP

# r[i] is local recruitment probability at age class i
# estimates are from Model 1 (first row, both sexes) and Model 12 (second row: males,
third row: females)
r <- rbind(c(0,0.24,0.89,0.24),c(0,0.31,0.92,0.24),c(0,0.16,0.83,0.24))
colnames(r) <- ages
rownames(r) <- sexes

# pRA[i] is the probability to recruit at age i for any pre-breeder (first row: both
sexes, second row: males, third row: females)
pRA <- matrix(nrow=3,ncol=10)
colnames(pRA) <- 1:10              # we'll compute pRA[i] from age 1 to 10
rownames(pRA) <- sexes

# compute pRA using the for loop over ages
for (s in 1:3) {         # for the three sex classes
  for (i in 1:10) {      # for age 1 to age 10
    if (i<4) {
       pRA[s,i] <- pI.AP[s,i+1]*r[s,i]
    }
    if (i>=4) {
       pRA[s,i] <- pI.AP[s,i+1]*r[s,4]
    }
  }
}
print(round(pRA,2))
print(round(pRA,2))
```

D.7.4 Probability to be alive and recruit in the birth area for any (pre-breeder) individual

At any age *i*, the probability for any individual in the dataset to be alive ($Pr(A_i)$) is the product of age-dependent survival probabilities (ϕ_i) until age *i*:

$$Pr(A_i) = Pr(A_{i-1}) * \phi_i = \prod_{k=1}^{i} \phi_i \,.$$

Following the same reasoning as above, at any age $i \geq 2$ the probability to recruit in the birth area for any individual that had not recruited yet (i.e. any pre-breeder actually alive or not; $Pr(R_i|P)$) is a function of the probability to be alive and the probability to recruit in the birth area for any alive individual:

$$Pr(R_i|P) = Pr(R_i|P, A_i) \cdot Pr(A_i) \,.$$

Again, we used a "for" loop to compute these probabilities (results are provided in Table D.7.3, Fig. D.7.2c), coded with R 3.1.2 as follows:

```
## Compute probabilities of recruiting in the birth area for any pre-breeder (alive or
not) ##
# the following code uses R variables defined in the R code exposed in previous
section: sexes, ages and pRA
# define survival probabilities
phi <- rbind(c(0.77,0.83),c(1,0.82),c(1,0.82))
colnames(phi) <- c(1,'2+')
rownames(phi) <- c(sexes)

# pA[i] is the probability to be alive at age i for any individual
pA <- matrix(nrow=3,ncol=10)
colnames(pA) <- 1:10                # we'll compute pA[i] from age 1 to 10
rownames(pA) <- sexes

# pR[i] is the probability to recruit at age i for any pre-breeder (alive or not)
(first row: both sexes, second row: males, third row: females)
pR <- matrix(nrow=3,ncol=10)
colnames(pR) <- 1:10                # we'll compute pR[i] from age 1 to 10
rownames(pR) <- sexes

# compute pRA using the for loop over ages
for (s in 1:3) {         # for the three sex classes
  for (i in 1:10) {      # for age 1 to age 10
    if (i==1) {
       pA[s,i] <- phi[s,1]
    }
    else {
       pA[s,i] <- pA[s,i-1]*phi[s,2]
    }
       pR[s,i] <- pRA[s,i]*pA[s,i]
  }
}
print(round(pA,2))
print(round(pA,2))
```

D.7.5 Annual probability of being inside or outside the study area for alive breeders

At recruitment, because it occurs only locally, the probability to be inside the study area is 1 and the probability to be outside is 0. After that, at age $i \geq 2$ the probability for breeders (noted B) to be inside the study area is a function of the previous probabilities of localisation, emigration probability ($\delta^{\mathrm{B}}_{\mathrm{io},i}$) and immigration probability ($\delta^{\mathrm{B}}_{\mathrm{oi},i}$):

$$Pr(I_i|B,A_i) = Pr(I_{i-1}|B,A_i)\cdot\left(1-\delta^{P}_{io,i}\right) + Pr(O_{i-1}|B,A_i)\cdot\delta^{P}_{oi,i}\ ,$$

$$\mathrm{Pr}(\mathrm{O}_i|\mathrm{B},\mathrm{A}_i) = \mathrm{Pr}(\mathrm{I}_{i-1}|\mathrm{B},\mathrm{A}_i)\cdot\delta^{\mathrm{P}}_{\mathrm{io},i} + \mathrm{Pr}(\mathrm{O}_{i-1}|\mathrm{B},\mathrm{A}_i)\cdot\left(1-\delta^{\mathrm{P}}_{\mathrm{oi},i}\right) = 1-\mathrm{Pr}(\mathrm{I}_i|\mathrm{B},\mathrm{A}_i)\ .$$

Accordingly, because individuals may recruit at different ages, $Pr(I_i|B,A_i)$ et $Pr(O_i|B,A_i)$ will depend on age at first reproduction. However because emigration and immigration probabilities do not change from 4 years old, the probabilities for alive breeders to be inside or outside the study area will be same at any age *j+k* (where *j* is the age at recruitment and *k* is the number of years after first reproduction).

Again, we used a "for" loop to compute these probabilities (results are provided in Table D.7.4, Fig 3c and S4b), coded with R 3.1.2 as follows:

```
## Compute localisation probabilities for alive breeders at different ages ##

# define the sex classes for the parameters
sexes <- c('all','males','females')

# define the age classes for the parameters
ages.B <- c(3,'4+')
# define age classes for first breeding
agesFB <- c(2,'3+')
# because emigration and immigration are the same after 3 years old, we define only two
# classes for age at first breeding (indeed, the probability to inside or outside will
be the
# same for individuals that first reproduce at 3, 4 and older.

# em.BA[i] is breeder emigration probability at age class i
# estimates are from Model 1 (first row, both sexes)
# and Model 12 (second row: males, third row: females)
em.BA <- rbind(c(0.05,0.05),c(0,0.05),c(0,0.04))
colnames(em.BA) <- ages.B
rownames(em.BA) <- sexes

# im.BA[i] is pre-breeder immigration probability at age class i
# estimates are from Model 1 (first row, both sexes)
# and Model 12 (second row: males, third row: females)
im.BA <- cbind(c(NA,NA,NA),c(0.19,0.30,0.26))
colnames(im.BA) <- ages.B
rownames(im.BA) <- sexes

# pI.BA[[j]][i], for alive breeders that recruited at age k (age class j),
# is the probability to be inside the area at age k+i-1
# first row: both sexes, second row: males, third row: females
pI.BA <- list(matrix(nrow=3,ncol=24),matrix(nrow=3,ncol=24))
names(pI.BA) <- agesFB
colnames(pI.BA[[1]]) <- 2:25                 # we'll compute pI.BA[i] from age k+1 to
k+23
colnames(pI.BA[[2]]) <- paste(c('k',rep('k+',23)),c('',1:23),sep='')
rownames(pI.BA[[1]]) <- rownames(pI.BA[[2]]) <- sexes

# and pO.BA[[j]][i], for alive breeders that recruited at age k (age class j),
```

```
# is the probability to be outside the area at age k+i-1
pO.BA <- list(matrix(nrow=3,ncol=24),matrix(nrow=3,ncol=24))
names(pO.BA) <- agesFB
colnames(pO.BA[[1]]) <- 2:25                   # we'll compute pO.B[i] from age k+1 to
k+23
colnames(pO.BA[[2]]) <- paste(c('k',rep('k+',23)),c('',1:23),sep='')
rownames(pO.BA[[1]]) <- rownames(pO.BA[[2]]) <- sexes

# compute pI.B and pO.B using the for loop over ages
# first element of the lists are probabilities for individuals that recruited at age
k=2
# second element are probabilities for individuals that recruited at age k>2
for (s in 1:3) {
  for (j in 1:2) {
    pI.BA[[j]][s,1] <- 1
    pO.BA[[j]][s,1] <- 0
    pI.BA[[j]][s,2] <- pI.BA[[j]][s,1]*(1-em.BA[s,j])
    pO.BA[[j]][s,2] <- pI.BA[[j]][s,1]*em.BA[s,j]
    for (i in 3:24) {
        pI.BA[[j]][s,i]   <-   pI.BA[[j]][s,i-1]*(1-em.BA[s,2])   +   pO.BA[[j]][s,i-
1]*im.BA[s,2]
        pO.BA[[j]][s,i]   <-   pI.BA[[j]][s,i-1]*em.BA[s,2]   +   pO.BA[[j]][s,i-1]*(1-
im.BA[s,2])
    }
  }
}
rd.pI.BA <- rd.pO.BA <- list()
rd.pI.BA[[1]] <- round(pI.BA[[1]],2)
rd.pI.BA[[2]] <- round(pI.BA[[2]],2)
rd.pO.BA[[1]] <- round(pO.BA[[1]],2)
rd.pO.BA[[2]] <- round(pO.BA[[2]],2)
print(rd.pI.BA)
print(rd.pO.BA)
```

D.7.6 Literature cited

R Development Core Team (2011) R: A Language and Environment for Statistical Computing. Vienna, Austria : the R Foundation for Statistical Computing. http://www.R-project.org/

Table D.7.1. Annual probability of being inside the study area (I) for alive (A) pre-breeders (P) at any age *i* ($\mathbf{Pr}(\mathbf{I}_i|\mathbf{A}_i,\mathbf{P})$).

Sex	Age					
	0	1	2	3	4	≥ 5
All	1	0.13	0.32	0.39	0.04	0.03
Males	1	0.12	0.35	0.45	0.05	0.05
Females	1	0.15	0.34	0.42	0.06	0.04

Calculations were based on estimates from Model 1 (Table 1, Table D.4.1, Table D.6.1) for both sexes together, and estimates from Model 7 (Table 1, Table D.4.2, Table D.6.1) for males and females separately.

Table D.7.2. Annual probability of recruiting (R) in the birth area for alive (A) pre-breeders (P) at any age *i* ($\mathbf{Pr}(\mathbf{R}_i|\mathbf{P},\mathbf{A}_\mathrm{i})$).

Sex	Age			
	1	2	3	≥4
All	0	0.08	0.34	0.01
Males	0	0.11	0.41	0.01
Females	0	0.05	0.35	0.01

Specifications are the same as for Table D.7.1.

Table D.7.3. Annual probability to be alive and recruit (R) in the birth area for any (pre-breeder, P) individual in the dataset at any age *i* ($\mathbf{Pr}(\mathbf{R}_i|\mathbf{P})$).

Sex	Age					
	1	2	3	4	5	≥6
All	0	0.05	0.18	0.00	0.00	0.00
Males	0	0.09	0.28	0.01	0.01	0.00
Females	0	0.04	0.23	0.01	0.00	0.00

Specifications are the same as for Table D.7.1.

Table D.7.4. Annual probability of being inside the study area (I) for alive (A) breeders (B) that recruited at age *k*, at any age *i* ($\mathbf{Pr}(\mathbf{I}_i|\mathbf{A}_i,\mathbf{B})$).

Sex	*k*	Age										
		k+1	k+2	k+3	k+4	k+5	k+6	k+7	k+8	k+9	≥(k+10) ≤(k+15)	≥k+16
All	≥2	0.95	0.91	0.88	0.86	0.84	0.83	0.82	0.82	0.81	0.80	0.79
Males	2	1.00	0.95	0.92	0.90	0.88	0.87	0.87	0.86	0.86	0.86	0.86
	≥3	0.95	0.92	0.90	0.88	0.87		0.86				
Females	2	1.00	0.96	0.93	0.91	0.90	0.89	0.88	0.88	0.87	0.87	0.87
	≥3	0.96	0.93	0.91	0.90	0.89	0.88		0.87			

Specifications are the same as for Table D.7.1. Here the age-dependent probabilities depend on the recruitment age (*k*).

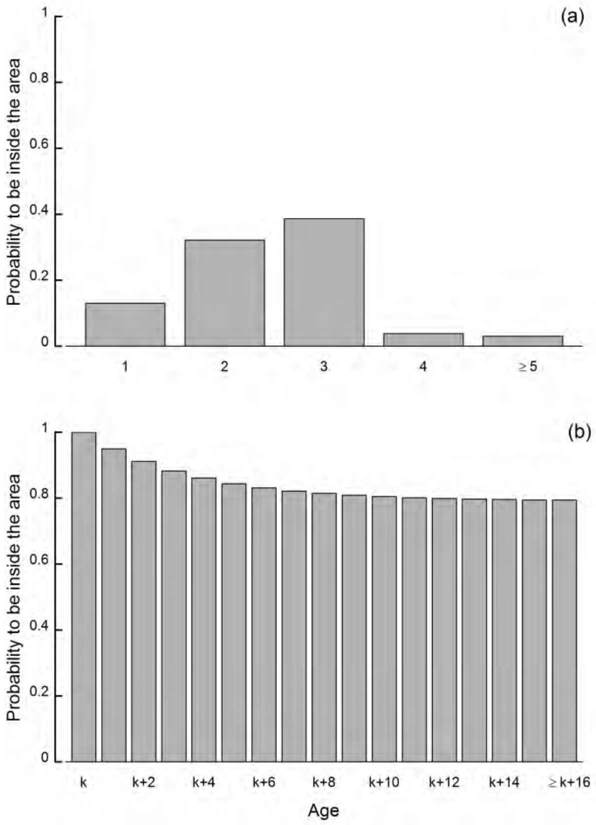

Figure D.7.1. Age-dependent annual probability of being inside the study area (a) for alive pre-breeders, and (b) for alive breeders that recruited at age *k*. Values were derived from Model 1 (see details in Table D.7.1, D.7.2).

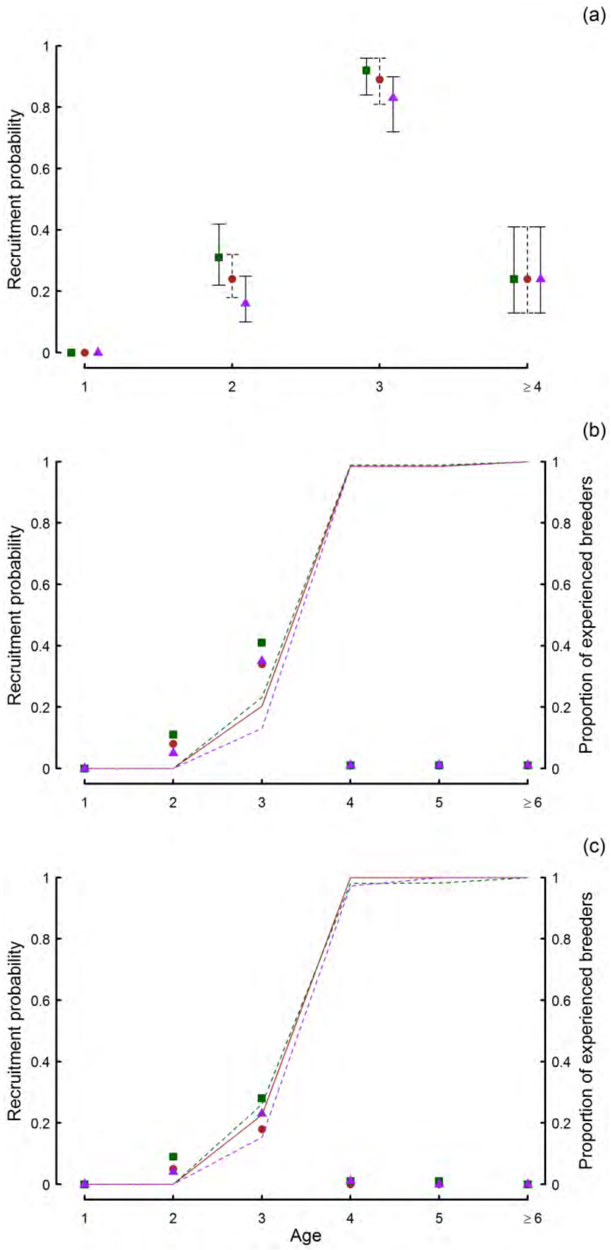

Figure D.7.2. Age-dependent recruitment probability (a) for alive pre-breeders inside the study area, (b) for alive breeders (inside or outside the area), (c) for any (pre-breeder) individual (alive or not). Values for both sexes together (circles) were derived from Model 1; male (squares) and female (triangles) values were derived from Model 7 (see Table D.6.1). In (b) and (c), lines indicate the proportion of experienced breeder among breeders in each age class (i.e. the probability that a breeder in the considered age class has recruited previously – is not a first-time breeder).

D.8 State assignment probabilities

D.8.1 Results and discussion

In the best time-constant model with the complete dataset (Model 1, Table 4.1, Table D.4.1), the probability of pre-breeders of being assigned to the observational category "possible breeder" was 0.08 (95%CI = [0.06,0.11]). Thus, their probability of being assigned to the category "uncertain breeder" was 0.92. The probability of breeders (either nesting or sabbatical breeders) of being assigned to "uncertain breeder" was 0.45 (95%CI = [0.42,0.48]), and their probability of being assigned to "possible breeder" was 0.12 (95%CI = [0.10,0.14]). Thus, their probability of being assigned to "certain breeder" was 0.43.

Behavioural clues are rarely completely sure but are often the only option to asses an individual's state (Pradel 2009). We faced two problems in the reproductive status evaluation in our recruitment study. First, individuals might attempt to breed but not be seen performing activities that can only relate to breeding (*e.g.* incubating eggs, feeding chicks). Second, once recruited individuals might skip breeding attempts. Multievent models allowed us to take uncertainty in assignment into account and make use of available information without taking arbitrary decisions concerning observational assessments (Pradel 2005, 2009).

Individuals in the pre-breeder state were mostly assigned to the category "uncertain breeder" and rarely to the category "possible breeder". This indicates that sometimes they express behaviours associated with breeding but this could also reflect observational errors (Genovart et al. 2012). Individuals in the breeder state were equally assigned to the categories "uncertain breeder" and "certain breeder" and sometimes to the category "possible breeder". Breeders assigned to "uncertain breeder" and "possible breeder" could be either individuals that skipped a breeding attempt but were present at the study colonies, or individuals that failed early in the season and for which being certain they attempted to breed was difficult. These results comfort our modelling choices. They show that arbitrary decisions on status assignment would have yielded spurious results and misleading conclusions.

D.8.2 Literature cited

Genovart, M., R. Pradel, and D. Oro. 2012. Exploiting uncertain ecological fieldwork data with multi-event capture–recapture modelling: an example with bird sex assignment. Journal of Animal Ecology 81:970-977.

Pradel, R. 2005. Multievent: an extension of multistate capture-recapture models to uncertain states. Biometrics 61:442–447.

Pradel, R. 2009. The stakes of capture–recapture models with state uncertainty. Pages 791–795 *in* D. L. Thomson, E. G. Cooch, and M. J. Conroy, editors. Modeling Demographic Processes In Marked Populations. Springer, Boston, USA.

D.9. Sex ratio bias

In the following table are given the number of females and males among sexed fledglings in each year and over all the study period, the corresponding sex ratio and the proportion of females with chi squared statistics of a test of equal proportions.

Table D.9.1. Sex ratio bias among fledglings in each cohort and over all the study period.

Year	**Number of females**	**Number of males**	**Sex ratio (males/females)**	**Proportion of females**	χ^2_1	***P***
1998	163	223	1.37	0.42	9.02	0.003
1999	127	109	0.86	0.54	1.22	0.269
2000	69	85	1.23	0.45	1.46	0.227
2001	39	49	1.26	0.44	0.92	0.337
2002	50	59	1.18	0.46	0.59	0.444
2003	125	157	1.26	0.44	3.41	0.065
2004	4	6	1.50	0.40	0.10	0.752
2005	8	8	1.00	0.50	0.00	1.000
2006	98	121	1.28	0.45	2.21	0.137
2007	90	115	1.27	0.44	2.81	0.094
2008	171	185	1.08	0.48	0.47	0.491
2009	38	39	1.03	0.49	0.00	1.000
2010	121	133	1.10	0.48	0.48	0.490
ALL	1103	1289	1.17	0.46	14.32	< 0.001

E

Supporting information to Chapter 5

E.1 Introduction of the appendix

In this appendix, I detail the model, analyses and results evoked in section 5.3.2 (of the *General Discussion*). This model is an extended version of the integrated population model for the Cap Sizun kittiwake population presented in Chapter 3 and Appendix C. This new model is an integrated "multi-colony" model in which each colony is now explicitly modeled. There is no equivalent in the ecological literature: to date, no study has been published in which a metapopulation model was used to simultaneously estimate the number of immigrants (and classes containing unmarked individuals that cannot be counted such as nonbreeders) in several subpopulations, together with dispersal rates between these subpopulations. I used the estimates from this model to address hypotheses on habitat selection developed in *Introduction* of Chapter 3 (i.e. the use of social information in the choice of a breeding habitat).

The results presented here are preliminary results concerning a shorter period (1989–1997) than the study period in Chapter 3 (1985–2012). I addressed hypotheses of social information use in breeding habitat selection in:

- immigrants, i.e. individuals born outside the Cap Sizun who choose their colony of first reproduction in the Cap Sizun in the current year *t*,
- first-time breeders, i.e. individuals born in the Cap Sizun who choose their colony of first reproduction in the Cap Sizun at *t*,
- former first-time breeders, i.e. individuals that bred for the first-time in the Cap Sizun at *t-1* and choose to stay in their previous colony or go to another colony at *t*,
- former experienced breeders, i.e. individuals that bred at *t-1* and were already established as breeders in the population before that, and stay in their previous colony or go to another colony at *t*,
- former attached skippers, i.e. experienced individuals that were skippers at *t-1* and mostly attended the same colony at that time (sometimes starting to build an incomplete nest there, and regularly attending the same nest site), and stay in their previous colony or go to another colony at *t*,
- former floating skippers, i.e. experienced individuals that skipped the reproduction at *t* and could not be considered as attached to one specific colony.

Hereafter, I provide details on the model and inference (Appendix E.2), the posterior distributions (Appendix E.3), derived analysis addressing social information use (with results and some discussion; Appendix E.4), and the *BUGS* code of the Bayesian analysis (Appendix E.5).

E.2 Details on the multi-colony model

E.2.1 Description of the model

The integrated multi-colony model (hereafter named 'IMM') is an extension of the integrated population model (hereafter named 'IPM') presented in Chapter 3. Accordingly, much of its content is similar to the content of the IPM and has already been described in Chapter 3 and Appendix D. I already summarized most of the refinements specific to the IMM (Chapter 5: section 5.3.2, Appendix E.1). Along this section (Appendix E.2), I foremost expose details of the specificities of the IMM. In 1989–1997 (study period used to get preliminary results with the IMM), there were 5 colonies in the population.

The datasets (capture-recapture data, population count data, and productivity data) are the same as used in Chapter 3 with the IPM, expect that here they are now colony-specific. Each observation event in individual capture-recapture histories is now coded so that it informs on whether the individual was resighted or not, (and if it was resighted:) the individual state (yearling, pre-breeder of age 2, …, prebreeder of age 6, first-time breeder, experienced breeder, skipper) and the individual location (i.e. the colony where the individual was born for pre-breeders, and the colony attended by the individual for breeders and skippers). Note the exception of floating skippers for which a specific colony of attendance is not assigned, and prebreeders for which we keep track of the birth colony but for which a specific colony of attendance is not assigned. Moreover, the number of breeding individuals is now counted in each colony. Productivity of pairs formed by (i) first-time breeders, (ii) experienced breeders, and (iii) one first-time breeder and one experienced breeder, or at least one individual of unknown experience, is now assessed in each colony.

The matrix metapopulation model at the core of the IMM is an extension of the matrix population model at the core of the IPM (see Chapter 3). Each of the nine life-history states defined in Chapter 3 is divided into five *substates* corresponding to the five possible locations (i.e. the five colonies). There is also an additional state for floating skippers.

Flows of individuals between colonies are represented by dispersal rates. Each dispersal rate $\delta_K^{i,j}$ was modeled as depending on the colony of departure (*i*), the colony of arrival (*j*), and the individual state (*K*). I did not considered dispersal for pre-breeders because they were not assigned to a particular colony of attendance (and were not always resighted). I considered natal dispersal, i.e. dispersal of individuals at recruitment (for their first breeding attempt). For each natal dispersal rate, the colony of departure was the colony of birth. Further, I considered different dispersal rates for former first-time breeders, former experienced breeders, former attached skippers, and former floating skippers. Because floating skippers have no colony of departure, their dispersal rates depended only on the colony of arrival. Conditional on transition toward the state ‘skipper’, individuals can become ‘attached skipper’ or ‘floating skipper’ according to the probability α of ‘being attached’. Experience-dependent *per capita* productivity rates were also modeled as colony-specific.

As in the population projection model described for the IPM in Chapter 3, in the metapopulation projection model for the IMM the number of individuals in each substate in year $t+1$ is a function of the number of individuals in all substates in year t and demographic rates in year t (describing transitions between states and movement between colonies, that is, transition between substates). Moreover, each colony has its own pulse of immigrants added to local first-time breeders in that colony in each year.

All other specifications of the matrix projection model are the same as for the projection model for the IPM (Chapter 3): I used Poisson and Binomial distributions to account for demographic stochasticity, all demographic rates were modeled as time-dependent, the annual survival rate is the same at age 0 and age 1, the annual survival rate is the same from age 2, recruitment occurs from age 3 to age 7, survival is the same for individuals born inside and outside the population. Further, recruitment rates, breeding rates, and survival rates were not modeled as colony-specific.

E.2.2 Likelihood of the model

As for the IPM (Chapter 3), the likelihood of the IMM is the product of three likelihoods of three models for the three datasets.

The likelihood from the count data was formulated as that of a multisite state-space model (Hinrichsen and Holmes 2009). The state-process was defined by the metapopulation projection model in which fluctuations in colony-specific number of breeders are described (see section E.2.1 above, and section E.2.3 below). I assumed a log-normal distribution for the counts, with a constant error over time that was not colony-specific.

The likelihood from productivity data was formulated as that of three Poisson regressions per colony (3×5 regressions) of the total number of fledglings produced as a function of the number of nests, and the *per capita* productivity involved (i.e. twice the *per nest* productivity; see section E.2.3 below). For each colony, one regression was for pairs of first-time (inexperienced) breeders, one for pairs of experienced breeders, and another for pairs of individuals of unknown or different levels of experience. For the latter, because I used *per capita* productivity rates and ignored pair characteristics, I made the assumption that the productivity rate was an average of productivity of inexperienced and experienced breeders weighted by their respective proportion among breeders in the focal colony (inferred in the model).

The likelihood from capture-resighting histories was formulated as that of a multistate capture-recapture model. More specifically, I used a multinomial state-space formulation (Kéry and Schaub 2012, see section E.2.3 below), which is different from the state-space formulation used in the integrated population model described in Chapter 3. For such a formulation, the capture-resighting histories are summarized into an 'm-array' (Williams et al. 2002). The m-array is a matrix in which rows refer to release occasions (here, an "artificial" release after resighting), and columns refer to resighting occasions, with one row and column for each true individual state (i.e. each substate referring to the breeding state and location, as described above). Each element of this array is the number of individuals resighted in the state and at the occasion of the corresponding column that were previously released in the state and at the occasion of the corresponding row. An additional column refers to individuals that were never resighted, and each element of this column is the number of individuals that were released in the state and at the occasion given by the corresponding row. I assumed different time-varying resighting rates for yearlings and prebreeders (not colony-specific), equal constant resighting rate for breeders and skippers (not colony-specific), and no error in state assignment at resighting (Cam et al. 2002).

The expected values of the elements of the m-array can be calculated according to the model parameters (i.e. probabilities of detection, survival, transition between breeding states, and dispersal; see section E.2.1 above) and the number of released individuals. Each row of the observed m-array follows a multinomial distribution with index equal to the number of released individuals in the focal state and at the focal occasion, and the vector of probabilities as a function of the model parameters.

E.2.3 Formulation details

Most of the formulation of the IMM is similar to the formulation of the IPM detailed in Appendix C.2.

***Metapopulation matrix and projection equation*—** The projection equation describes changes in the vector V_t of the number of individuals in each substate of the population (i.e. in each state in each colony), as a function of the metapopulation matrix $\mathrm{M}_{t\text{-}1}$ parameterized by demographic rates describing transitions between states from year *t-1* to year *t*, the same vector V_{t-1} in the previous year *t-1*, and a vector W_t for the pulse of immigrants into first-time breeders in year *t*. The deterministic version of this equation is as follows:

$$V_t = M_{t-1}V_{t-1} + W_t \quad .$$

The vector of population sizes contains the number of individuals N_K^i in each life-history state *K* and each colony *i*. All numbers and demographic rates are time-dependent. In total, 9×5+1=46 substates are defined (9 nine states in each colony plus one state for floating skippers). The size of the matrix *M* is thus 46 by 46. This matrix is so large that it cannot be represented here. For a pedagogical purpose, hereafter is given the matrix written in full for the hypothetical case with only two colonies. The reader will thus easily understand how the matrix for five colonies can be written:

$$\begin{bmatrix}
0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi_0\pi_f^1 & \phi_0\pi_e^1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\phi_0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & \phi_2(1\text{-}\rho_3) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & \phi_2(1\text{-}\rho_4) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & \phi_2(1\text{-}\rho_5) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & \phi_2(1\text{-}\rho_6) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & \phi_2\rho_3\delta_P^{1,1} & \phi_2\rho_4\delta_P^{1,1} & \phi_2\rho_5\delta_P^{1,1} & \phi_2\rho_6\delta_P^{1,1} & \phi_2\delta_P^{1,1} & 0 & 0 & 0 & 0 & \phi_2\rho_3\delta_P^{2,1} & \phi_2\rho_4\delta_P^{2,1} & \phi_2\rho_5\delta_P^{2,1} & \phi_2\rho_6\delta_P^{2,1} & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & \phi_2\psi_b\delta_F^{1,1} & \phi_2\psi_b\delta_E^{1,1} & \phi_2\psi_s\delta_S^{1,1} & 0 & 0 & 0 & 0 & 0 & 0 & \phi_2\psi_b\delta_F^{2,1} & \phi_2\psi_b\delta_E^{2,1} & \phi_2\psi_s\delta_S^{2,1} & \phi_2\psi_s\delta_S^{\emptyset,1} \\
0 & 0 & 0 & 0 & 0 & 0 & \phi_2(1\text{-}\psi_b)\alpha\delta_F^{1,1} & \phi_2(1\text{-}\psi_b)\alpha\delta_E^{1,1} & \phi_2(1\text{-}\psi_s)\alpha\delta_S^{1,1} & 0 & 0 & 0 & 0 & 0 & 0 & \phi_2(1\text{-}\psi_b)\alpha\delta_F^{2,1} & \phi_2(1\text{-}\psi_b)\alpha\delta_E^{2,1} & \phi_2(1\text{-}\psi_s)\alpha\delta_S^{2,1} & \phi_2(1\text{-}\psi_s)\alpha\delta_S^{\emptyset,1} \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi_0\pi_f^2 & \phi_0\pi_e^2 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi_0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi_2(1\text{-}\rho_3)(1\text{-}\delta_1^2) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi_2(1\text{-}\rho_4) & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi_2(1\text{-}\rho_5) & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \phi_2(1\text{-}\rho_6) & 0 & 0 & 0 & 0 & 0 \\
0 & \phi_2\rho_3\delta_P^{1,2} & \phi_2\rho_4\delta_P^{1,2} & \phi_2\rho_5\delta_P^{1,2} & \phi_2\rho_6\delta_P^{1,2} & \phi_2\delta_P^{1,2} & 0 & 0 & 0 & 0 & \phi_2\rho_3\delta_P^{2,2} & \phi_2\rho_4\delta_P^{2,2} & \phi_2\rho_5\delta_P^{2,2} & \phi_2\rho_6\delta_P^{2,2} & \phi_2\delta_P^{2,2} & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & \phi_2\psi_b\delta_F^{1,2} & \phi_2\psi_b\delta_E^{1,2} & \phi_2\psi_s\delta_S^{1,2} & 0 & 0 & 0 & 0 & 0 & 0 & \phi_2\psi_b\delta_F^{2,2} & \phi_2\psi_b\delta_E^{2,2} & \phi_2\psi_s\delta_S^{2,2} & \phi_2\psi_s\delta_S^{\emptyset,2} \\
0 & 0 & 0 & 0 & 0 & 0 & \phi_2(1\text{-}\psi_b)\alpha\delta_F^{1,2} & \phi_2(1\text{-}\psi_b)\alpha\delta_E^{1,2} & \phi_2(1\text{-}\psi_s)\alpha\delta_S^{1,2} & 0 & 0 & 0 & 0 & 0 & 0 & \phi_2(1\text{-}\psi_b)\alpha\delta_F^{2,2} & \phi_2(1\text{-}\psi_b)\alpha\delta_E^{2,2} & \phi_2(1\text{-}\psi_s)\alpha\delta_S^{2,2} & \phi_2(1\text{-}\psi_s)\alpha\delta_S^{\emptyset,2} \\
0 & 0 & 0 & 0 & 0 & 0 & \phi_2(1\text{-}\psi_b)(1\text{-}\alpha) & \phi_2(1\text{-}\psi_b)(1\text{-}\alpha) & \phi_2(1\text{-}\psi_s)(1\text{-}\alpha) & 0 & 0 & 0 & 0 & 0 & 0 & \phi_2(1\text{-}\psi_b)(1\text{-}\alpha) & \phi_2(1\text{-}\psi_b)(1\text{-}\alpha) & \phi_2(1\text{-}\psi_s)(1\text{-}\alpha) & \phi_2(1\text{-}\psi_s)(1\text{-}\alpha)
\end{bmatrix}_t ,$$

where π_f^i is the *per capita* productivity of first-time breeders in colony i (in this two-colony example, $i \in \{1,2\}$; in the multi-colony model for the kittiwake in the Cap Sizun over 1989–1997, $i \in \{1,2,\dots,5\}$), π_e^i is the *per capita* productivity of experienced breeders in colony i, ϕ_0 is the annual survival rate at age 0 and age 1, ϕ_2 is the annual survival from age 2, ρ_3 is the recruitment rate at age 3, ..., ρ_6 is the recruitment rate at age 6 (recruitment rate at age 7 is 1), ψ_b is the breeding propensity of former breeders, ψ_s is the breeding propensity of former skippers, $\delta_K^{i,j}$ is the dispersal rate from colony i towards colony j of individuals in state K (i is $\emptyset$ for floating skippers; K is P for prebreeders, F for first-time breeders, E for experienced breeders, and S for skippers) and $\delta_K^{i,i}$ is the probability of not dispersing.

To save space, the probability of not dispersing was named $\delta_K^{i,i}$. However, it is the complement of the probability of leaving the colony, that is, 1 minus the sum of all the probabilities of dispersing towards another colony:

$$\delta_K^{i,i} = 1 - \sum_{\substack{j=1 \\ j \neq i}}^{L} \delta_K^{i,j}$$

where L is the number of colonies in the population.

To complete the projection equation: V_t is a column vector, but to save space it is here given as a row vector (again, in the case of two colonies):

$$[N_Y^1\ N_{P2}^1\ N_{P3}^1\ N_{P4}^1\ N_{P5}^1\ N_{P6}^1\ N_F^1\ N_E^1\ N_S^1\ N_Y^1\ N_{P2}^1\ N_{P3}^1\ N_{P4}^1\ N_{P5}^1\ N_{P6}^1\ N_F^1\ N_E^1\ N_S^1\ N_S^{\emptyset}]_{\mathrm{t}};$$

W_t is a column vector, but to save space it is here given as a row vector (again, in the case of two colonies):

$$[0\ 0\ 0\ 0\ 0\ 0\ N_I^1\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ 0\ N_I^2\ 0\ 0\ 0]_{\mathrm{t}};$$

N_K^i is the number of individuals in state K in the colony i (or no specific colony: $\emptyset$), Y stands for yearlings, Pj stands for prebreeders of age j ($2 \leq j \leq 6$), F stands for first-time breeders, E stands for experienced breeders, S stands for skippers, I stands for immigrants.

As for the IPM (Chapter 3, Appendix C.2.1), demographic stochasticity was considered by using binomial and Poisson distributions to describe the link between state-specific numbers in each colony in year t+1 and t, and environmental stochasticity was represented by time-dependence in demographic rates and state-specific numbers.

Likelihood from count data— Likelihood from count data was formulated as a state-space model, similarly to the integrated population model described in Chapter 3 (see Appendix C.2.2) but for five different colonies. The state process is described above. We assumed that the observation error was the same for all colonies. The count data C_t in the population integrated model are now C_t^i (i.e. annual counts in each colony i), but the error remains σ_{obs}^2 (it does not take an index for colony; see Appendix C.2.2 for details).

Likelihood from capture-recapture data— As exposed above (section E.2.2), we used a multinomial formulation for the likelihood from capture-recapture data. Capture-recapture data summarized in the m-array were thus modeled as follows:

$$A^i_{K,t} \sim Multinomial\ (X^i_{K,t}, H^i_{K,t})$$

where $A^i_{K,t}$is the row of the m-array (i.e. a vector) referring to individuals released at occasion t in state K in colony i, $X^i_{K,t}$ is the vector of corresponding probabilities (i.e. expected frequencies of individuals resighted in each state, in each colony and at each occasion given release at occasion t in state K in colony i), $H^i_{K,t}$ is the number of individuals released at occasion t in state K in colony i.

The expected frequencies of individuals in each element of each rows of the m-array was calculated from the state-transition matrix (see Appendix C.2.3) extended for five-colonies (as we did for the population matrix, see above) and state-specific resighting probabilities (that were not colony-dependent). Due to its complexity, this method developed by Michael Schaub is not explained here. However, this calculation is provided in the S-PLUS language in the *BUGS* code (section E.5).

Likelihood from productivity data**—** We used Poisson regression to estimate the *per-capita* productivities from counts of fledglings per nest, similarly to the integrated population model described in Chapter 3 (see Appendix C.2.4) but in the five colonies. Accordingly, the counts of fledglings ($J_{F,t}$,$J_{E,t}$,$J_{U,t}$), the counts of corresponding number of breeders ($R_{F,t}$, $R_{E,t}$, $R_{U,t}$), the *per-capita* productivities of first-time breeders ($\pi_{f,t}$) and experienced breeders ($\pi_{e,t}$), the mean productivities and temporal variances on the log scale ($\overline{\pi_f}$, $\sigma^2_{\pi_f}$, $\overline{\pi_e}$, $\sigma^2_{\pi_e}$; see Appendix C.2.4) all now take an index for colony (e.g. $J^1_{F,t}$ is the number of fledglings produced by pairs formed by two first-time breeders in colony 1).

E.2.4 Inference and prior distributions

Inference was conducted by analyzing the joint likelihood of the integrated population model in the Bayesian framework (Kéry and Schaub 2012). We specified vague prior distributions with reasonable bounds for all parameters. These priors were the same as those used for the integrated population model described in Chapter 3 (see Appendix C.2.5 for details); they were declined in each colony for colony-specific parameters. The probability for skippers of being attached (α) was modeled with random time effects (e.g. as did for survival probabilities). For dispersal rates, we did not formulated temporal variation with random effects; we only specified a different rate at each time step and used the uniform distribution on [0,1] as the prior. Priors for the initial number of individuals in each substate of the population (i.e. in each state and each colony) can be found in the *BUGS* code (section E.5). We used the uniform distribution over [-5,750] as the prior for the number of immigrants in each colony. The inclusion of negative values enables to test whether there is immigration at all (Schaub and Fletcher 2015).

We performed Markov Chain Monte Carlo (MCMC) simulation with software JAGS 3.4.0 (Plummer 2003; see model code in Appendix C.2) run from R (R Core Team 2016) with the *rjags* package (Plummer 2015). We used a particular method to save time because time per iteration and time to convergence were long. First, we ran 10 chains with 20000 iterations per chain. We saved the last state (i.e. the last posterior sample of the model parameters) of one of six chains that had converged within the 20000 iterations (for this particular chain, convergence was reached at ca. 10000 iterations). We then ran 12 chains starting from this last state but from different seeds of the random-number generator. Therefore, these 12 chains targeted the posterior distribution from the first iteration. We discarded the first 1000 iterations and used the subsequent 35000 iterations for posterior exploration (4.2×10^5 samples). Chains were not thinned to keep all information they contained (Link and Eaton 2012). Convergence was assessed using the Brooks-Gelman-Rubin diagnostic $\widehat{R}$ (Brooks and Gelman 1998) and was satisfactory (all $\widehat{R}<1.04$).

E.2.5 Literature cited

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E.3 Posterior distributions

The number of parameters in the IMM is huge, and values of the many dispersal rates would make little sense for the reader. Therefore, it would not be reasonable to summarize all posterior distributions here. Further, posterior distributions of demographic rates that were not colony-specific were very similar to those reported for the IPM in Chapter 3 and Appendix C.3. However, the purpose of this appendix is mostly to provide estimates of colony-specific numbers of immigrants, and results with keys to understand preliminary results of habitat selection analysis evoked in Chapter 5.

Hereafter are provided graphical summaries of the estimates of colony-specific numbers of individuals in different states that are attached to a specific colony: breeders (Fig. E.3.1), immigrants (Fig. E.3.2), and attached sabbaticals (Fig. E.3.3). Graphical summaries of the estimates of numbers of immigrants and breeders (including immigrants) in the population as a whole (i.e. summed up over all colonies) are provided in Fig. E.3.4. Also, graphical summaries of the colony-specific productivity rates are provided in Fig. E.3.5. Effective size of the posterior distributions were all >2400. Each 95% posterior credible interval was calculated as the highest posterior density interval.

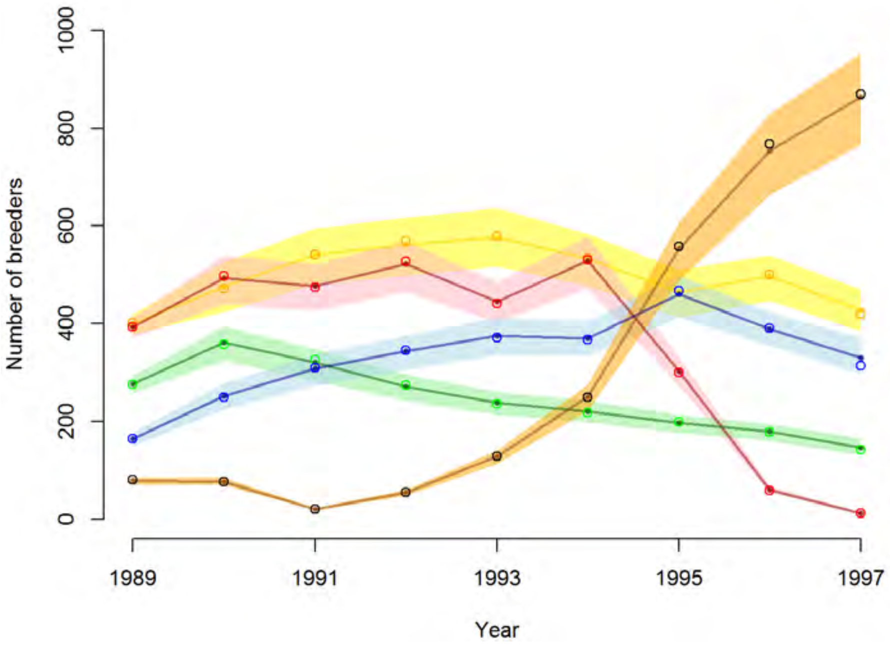

Figure E.3.1. Dynamics of the kittiwake breeding population in each colony of the Cap Sizun over 1989–1997. Colony 1 is in red, colony 2 in green, colony 3 in blue, colony 4 in yellow, colony 5 in orange. Lines indicate posterior means, color backgrounds indicate 95% confidence intervals, and colour circles indicate the observations (i.e. count data).

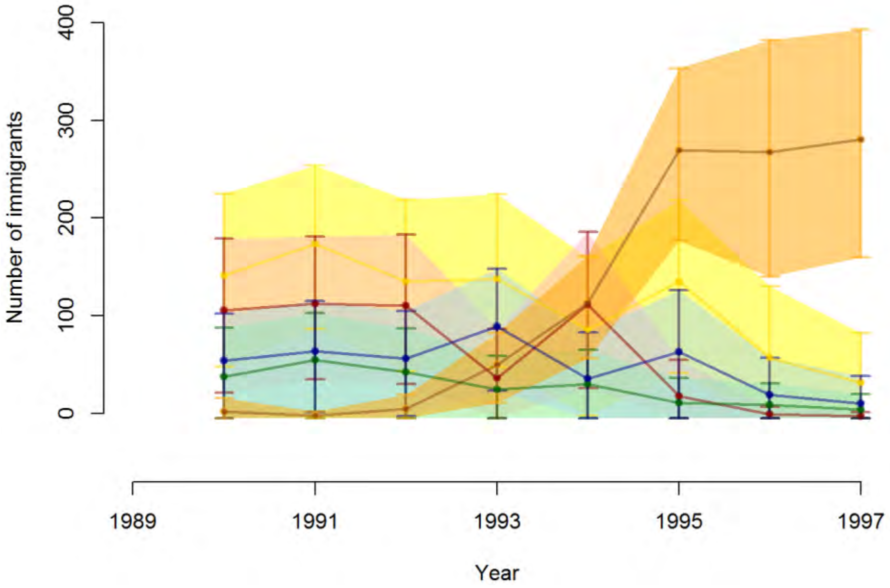

Figure E.3.2. Annual number of immigrants in each colony of the Cap Sizun over 1989–1997. Colony 1 is in red, colony 2 in green, colony 3 in blue, colony 4 in yellow, colony 5 in orange. Lines indicate posterior means and color backgrounds indicate 95% confidence intervals.

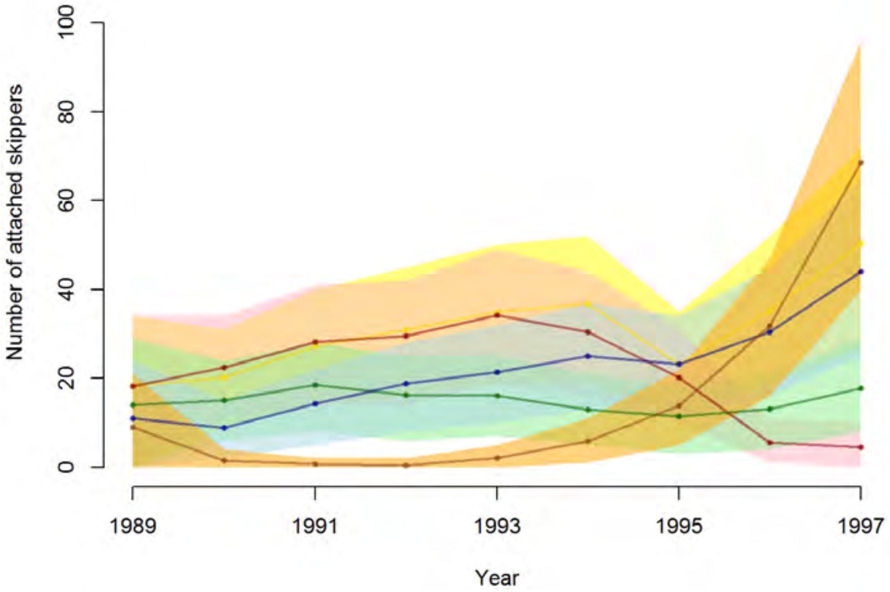

Figure E.3.3. Annual number of attached skippers in each colony of the Cap Sizun over 1989–1997. Colony 1 is in red, colony 2 in green, colony 3 in blue, colony 4 in yellow, colony 5 in orange. Lines indicate posterior means and color backgrounds indicate 95% confidence intervals.

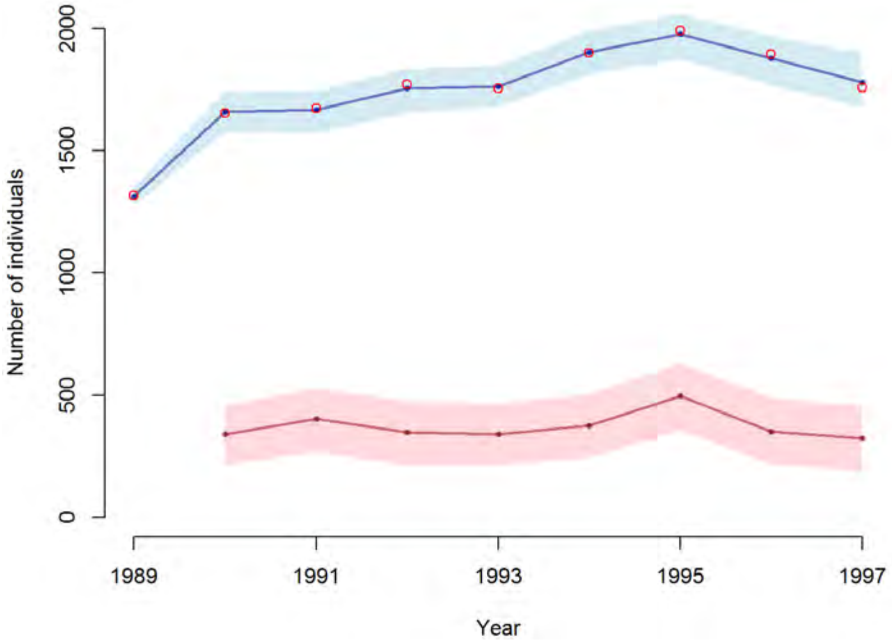

Figure E.3.4. Annual number of breeders (blue) and immigrants (red) in the kittiwake Cap Sizun population over 1989–1997. Lines indicate posterior means, color backgrounds indicate 95% confidence intervals, and red circles indicate observations of the number of breeders (i.e. count data).

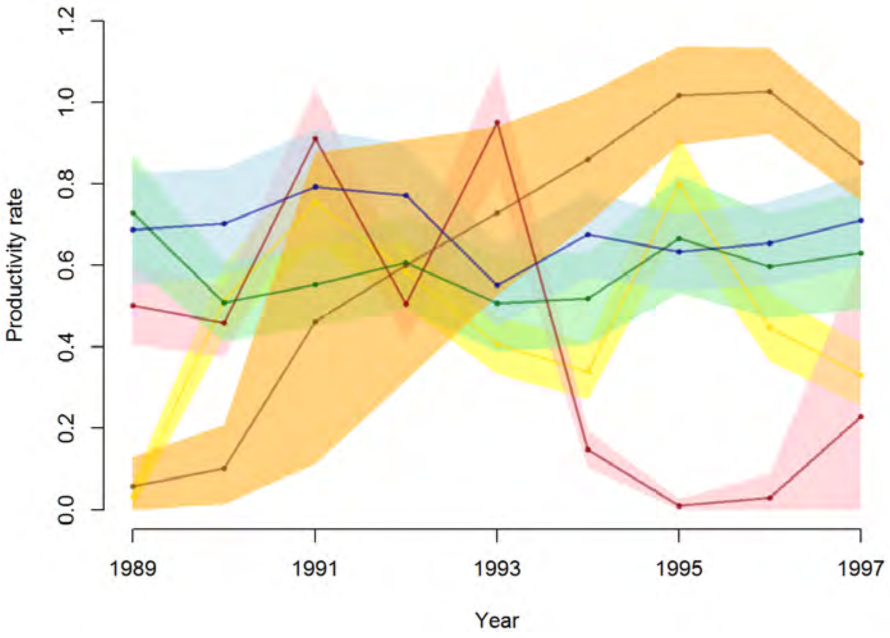

Figure E.3.5. Annual *per capita* productivity rates in each colony in the kittiwake Cap Sizun population over 1989–1997. The productivity rate summarized here is the average of the productivity of first-time breeders and experienced breeders weighted by their respective proportion in the focal colony. Colony 1 is in red, colony 2 in green, colony 3 in blue, colony 4 in yellow, colony 5 in orange. Lines indicate posterior means and color backgrounds indicate 95% confidence intervals.

E.4 Derived habitat selection analyses

E.4.1 Methods

To study the link between (i) the choice of a colony of reproduction (or a colony of attendance for individuals that will finally not attempt breeding) in the different states of the population (see section E.1), and (ii) social information in that colony in the previous year, I calculated partial correlations in each posterior sample.

First, I calculated partial correlations between (i) either colony-specific numbers of immigrants or colony-specific immigration rates, and (ii) productivity, number of breeders, and number of attached skippers in the colony of immigration in the previous year. For this purpose, the colony-specific immigration rate in a given colony i ($i \in \{1,2,\ldots,5\}$) was calculated as the number of immigrants in that colony divided by the number of breeders in the population (i.e. first-time breeders plus breeders summed up over all colonies):

$$\omega_t^i = \frac{N_{I,t}^i}{\sum_{i=1}^{5}(N_{F,t}^i + N_{E,t}^i)} \quad .$$

The colony-specific productivity rate Π_t^i used here (and also for the following partial correlations) is the *per nest* average of the productivity of first-time breeders and experienced breeders weighted by their respective proportion in the focal colony *i*:

$$\Pi_t^i = 2\left(\pi_{f,t}^i \frac{N_{F,t}^i}{N_{F,t}^i + N_{E,t}^i} + \pi_{e,t} \frac{N_{E,t}^i}{N_{F,t}^i + N_{E,t}^i}\right) \quad .$$

Second, I calculated partial correlations between (i) the probability of leaving the previous colony (that is, 1 minus the probability of “dispersing” towards the previous colony) in either former first-time breeders (i.e. $1 - \delta_F^{i,i}$, where *i* is the colony, $i \in \{1,2,\ldots,5\}$), former experienced breeders (i.e. $1 - \delta_E^{i,i}$), or former attached skippers (i.e. $1 - \delta_S^{i,i}$), and (ii) the productivity, number of breeders, and number of attached skippers in that colony in the previous year.

Third, I calculated partial correlations between (i) the probability of settling in a colony (conditional on having left the previous colony for non-floating individuals) in either former first-time breeders, former experienced breeders, former attached skippers, first-time breeders, or former floating skippers, and (ii) the productivity, number of breeders, and number of attached skippers in that colony in the previous year. For first-time breeders (i.e. former prebreeders), all the probabilities of dispersal ($\delta_P^{i,j}$, $i \in \{1,2,\ldots,5\}$, $j \in \{1,2,\ldots,5\}$) are probabilities of settling in a new colony because individuals do not settle before recruitment. Note that for these preliminary analyses, I did not consider the probability of ‘going back to the colony of birth’ in a different framework. For former floating skippers, all the probabilities of dispersal ($\delta_S^{\emptyset,i}$) are probabilities of settling in a new colony *i*. For former first-time breeders, former experienced breeders, and former attached skippers, the probabilities of settling in a new colony are conditional on leaving the previous colony. Accordingly, these probabilities $\zeta_K^{i,j}$ of settling in a new colony *j* for an individual in state *K* that was previously in colony *i* ($K \in \{\mathrm{F,E,S}\}$, $i \in \{1,2,\ldots,5\}$, $j \neq i$ & $j \in \{1,2,\ldots,5\}$) were each calculated as the probability of dispersal from colony *i* to the colony *j* divided by the probability of leaving colony *i*:

$$\zeta_{K,t}^{i,j} = \frac{\delta_{K,t}^{i,j}}{1 - \delta_{K,t}^{i,i}} \ .$$

Because there is not enough information in the first year to properly estimate the number of immigrants and the number of skippers (classes that cannot be counted in the field), I did not consider social information in the first year (1989) and probabilities of leaving or settling in a colony in the second year (based on social information in the first year). Samples sizes for each partial correlation are given with results in Table E.4.1, E.4.2, E.4.3.

E.4.2 Results

Decisions of settling in a colony made by immigrants— According to 95% credible intervals of partial correlations (Table E.4.1), there was evidence for a positive association between (i) either the number of immigrants or the immigration rate in a colony, and (ii) productivity and the number of breeders in that colony in the previous year. There was also evidence for a negative association between (i) either the number of immigrants or the immigration rate in a colony, and (ii) the number of attached sabbatical in that colony in the previous year (Table E.4.1). Partial correlation plots illustrating these results are provided in Fig. E.4.1.

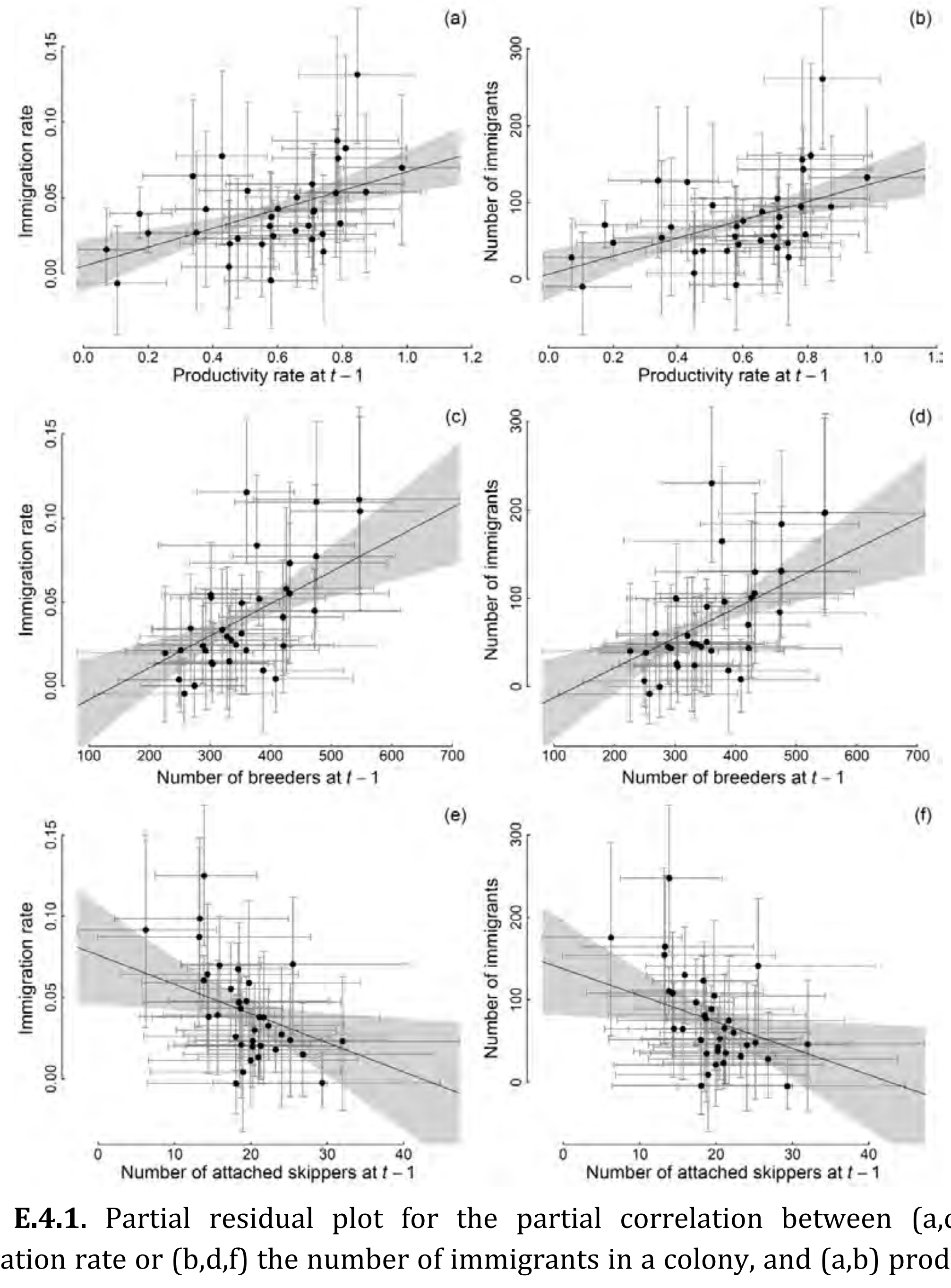

Figure E.4.1. Partial residual plot for the partial correlation between (a,c,e) the immigration rate or (b,d,f) the number of immigrants in a colony, and (a,b) productivity rate, (c,d) number of breeders, or (e,f) number of attached skippers in that colony at *t-1*. Residuals were centered on the variable mean to rescale variation within the original range. Points indicate posterior means and segments indicate 95% credible intervals. The solid line is the posterior mean of the corresponding OLS regression line, along with the 95% credible interval in grey background.

Table E.4.1. Partial correlations between the colony-specific number of immigrants or the immigration rate (first variable), and an information component on breeding habitat quality in the focal colony (second variable), while controlling for the set of remaining second variables.

First variable (year *t*)	Second variable (year *t-1*)		
	Productivity rate	Number of breeders	Number of skippers
Immigration rate	0.426 [0.232,0.606]	0.521 [0.290,0.731]	-0.371 [-0.642,-0.082]
Number of immigrants	0.429 [0.238,0.610]	0.500 [0.266,0.713]	-0.356 [-0.623,-0.063]

Estimates are given as the posterior mean with 95% credible interval between brackets. Scatter plots of the relationships are provided in Fig. E.4.1. Sample size is 5×7=35 (5 colonies, 7 years) for each partial correlation.

Decisions of leaving a colony made by locals— According to 95% credible intervals of partial correlations (Table E.4.2), there was evidence for a negative association between (i) the probability of leaving the previous colony in former first breeders and former experienced breeders, and (ii) productivity in that colony in the previous year. There was also evidence for a negative association between probability of leaving the previous colony in former experienced breeder and the number of breeders in that colony in the previous year (Table E.4.1). Partial correlation plots illustrating these results are provided in Fig. E.4.2.

Table E.4.2. Partial correlations between the probability of leaving the previous colony in former first-time breeders, former experienced breeders, and former attached skippers (first variable), and an information component on breeding habitat quality in the focal colony (second variable), while controlling for the set of remaining second variables.

First variable (year *t*):	Second variable (year *t-1*)		
Probability of changing colony in former…	Productivity rate	Number of breeders	Number of skippers
First-time breeders	-0.528 [-0.672,-0.375]	-0.221 [-0.473,0.046]	-0.041 [-0.334,0.243]
Experienced breeders	-0.552 [-0.694,-0.400]	-0.286 [-0.497,-0.061]	-0.227 [-0.469,0.015]
Attached skippers	-0.043 [-0.304,0.224]	-0.044 [-0.333,0.253]	-0.180 [-0.480,0.130]

Estimates are given as the posterior mean with 95% credible interval between brackets. Scatter plots of the relationships are provided in Fig. E.4.2. Sample size is 5×7=35 (5 colonies, 7 years) for each partial correlation.

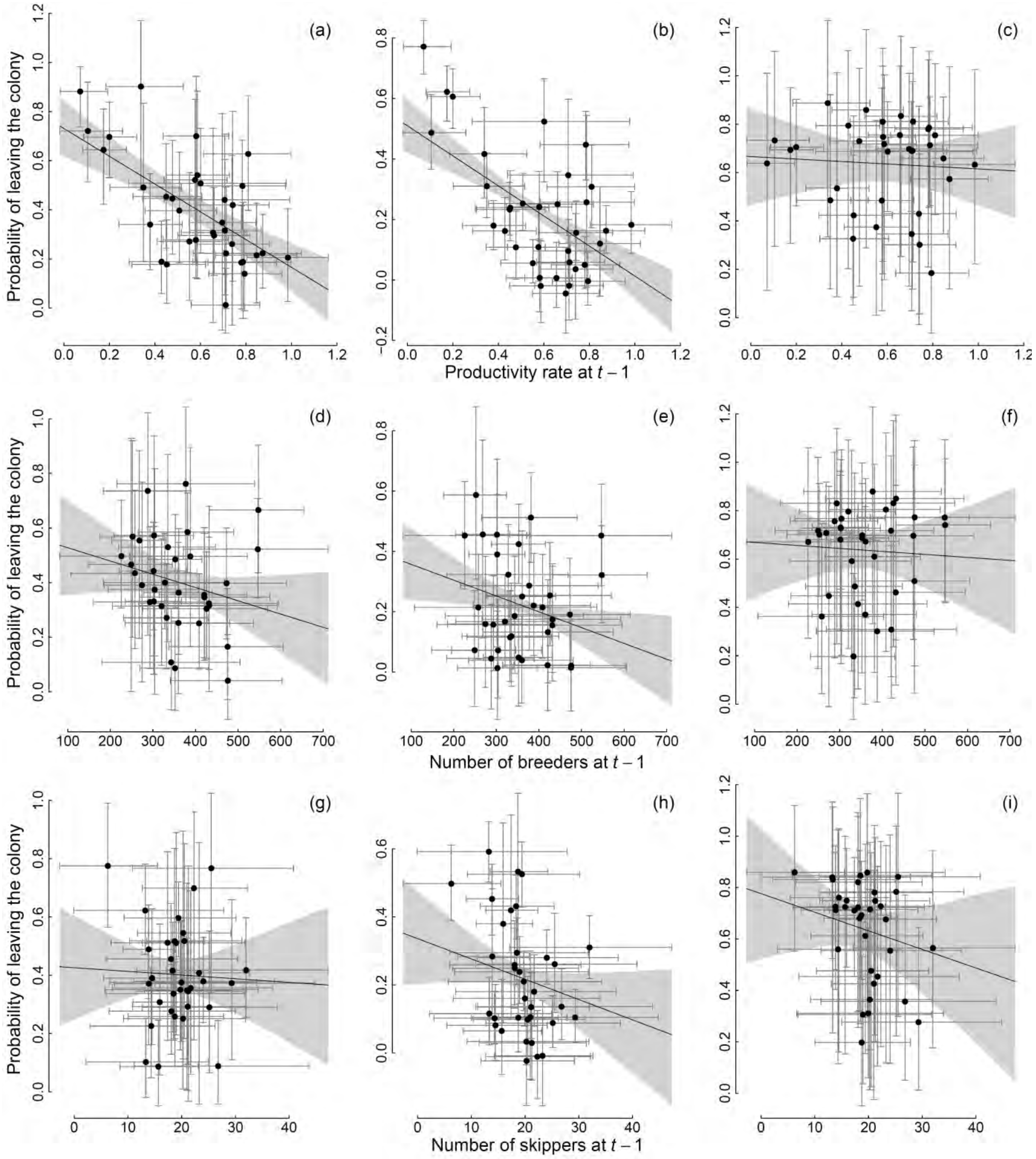

Figure E.4.2. Partial residual plot for the partial correlation between [i] the probability of leaving the previous colony in (a,d,g) former first-time breeders, (b,e,h) former experienced breeders, or (c,f,i) former attached skippers, and [ii] (a,b,c) productivity rate, (d,e,f) number of breeders, or (g,h,i) number of attached skippers in that colony at *t-1*. Residuals were centered on the variable mean to rescale variation within the original range. Points indicate posterior means and segments indicate 95% credible intervals. The solid line is the posterior mean of the corresponding OLS regression line, along with the 95% credible interval in grey background.

Decisions of settling in a colony made by locals— According to 95% credible intervals of partial correlations (Table E.4.3), there was evidence for a negative association between (i) the probability of settling in a colony in first-time breeders, former first-time breeders, and former experienced breeders, and (ii) productivity in that colony in the previous year. Partial correlation plots illustrating these results are provided in Fig. E.4.3 and E.4.4.

Table E.4.3. Partial correlations between the probability of settling in a new colony (conditional on having left the previous colony in former "attached" individuals) in first-time breeders, former first-time breeders, former experienced breeders, former attached skippers, and former floating skippers (first variable), and an information component on breeding habitat quality in the focal colony (second variable), while controlling for the set of remaining second variables.

First variable (year *t*):	Second variable (year *t-1*)		
Probability of settling in a colony in …	Productivity rate	Number of breeders	Number of skippers
First-time breeders	0.159 [0.035,0.283]	0.026 [-0.110,0.162]	0.063 [-0.065,0.192]
Former first-time breeders	0.152 [0.001,0.298]	0.103 [-0.056,0.260]	-0.084 [-0.239,0.070]
Former experienced breeders	0.189 [0.047,0.329]	0.118 [-0.041,0.274]	-0.149 [-0.307,0.005]
Former attached skippers	0.034 [-0.128,0.191]	0.032 [-0.126,0.190]	0.010 [-0.138,0.159]
Former floating skippers	0.231 [-0.006,0.464]	0.103 [-0.170,0.375]	0.103 [-0.182,0.386]

Estimates are given as the posterior mean with 95% credible interval between brackets. Scatter plots of the relationships are provided in Fig. E.4.3 and E.4.4 when the 95%CI excludes zero, and in Appendix C.5 when the 95%CI includes zero. Sample size is 5×7=35 (5 colonies, 7 years) for each partial correlation in the first and last lines, 5×(4-1)×7=140 (5 colonies of departure, 4 colonies of arrival in each case, 7 years) for each partial correlation in the three middle lines.

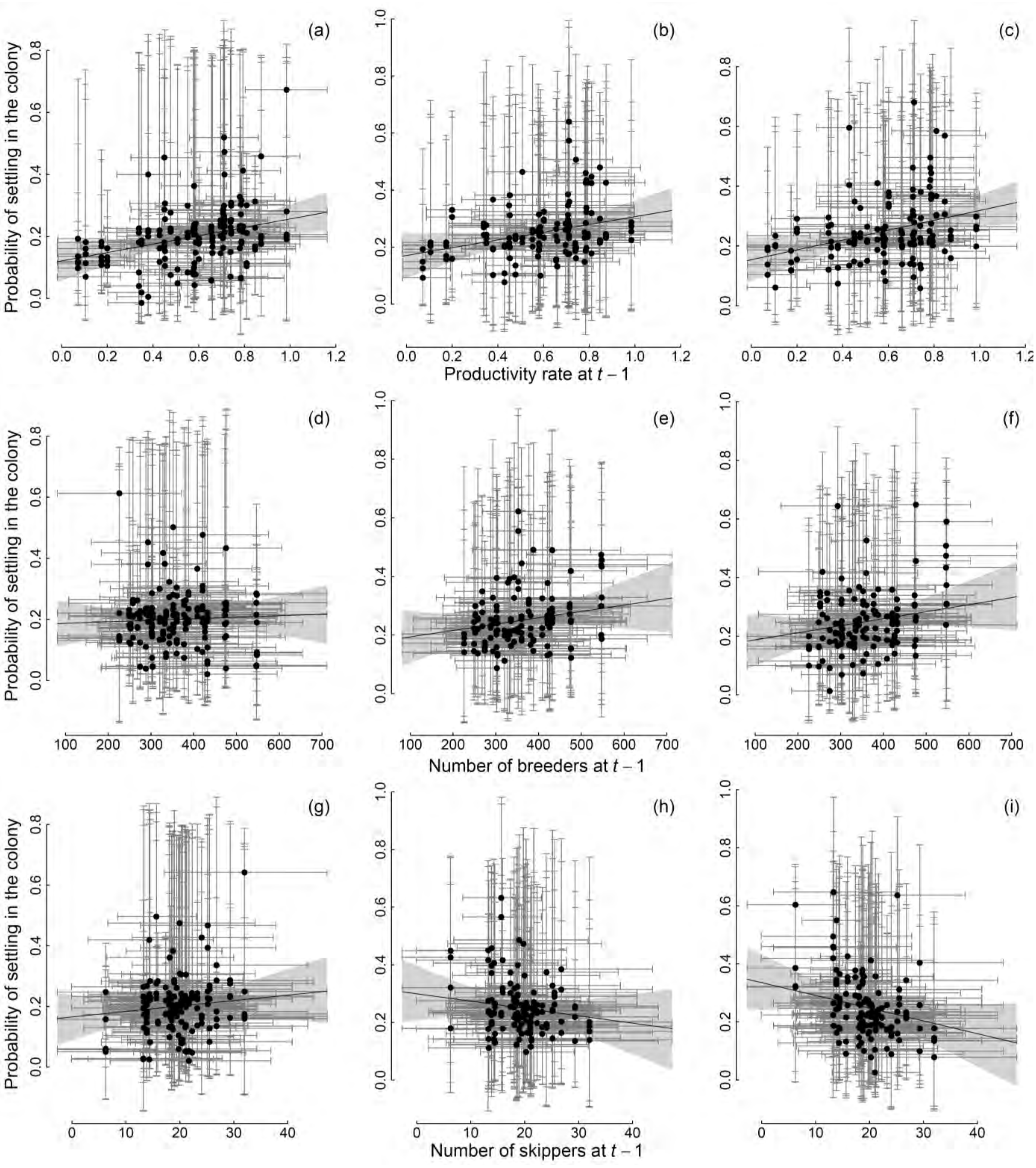

Figure E.4.3. Partial residual plot for the partial correlation between [i] the probability of settling in a given colony in (a,d,g) former first-time breeders, (b,e,h) former experienced breeders, or (c,f,i) former attached skippers, and [ii] (a,b,c) productivity rate, (d,e,f) number of breeders, or (g,h,i) number of attached skippers in that colony at *t-1*. Residuals were centered on the variable mean to rescale variation within the original range. Points indicate posterior means and segments indicate 95% credible intervals. The solid line is the posterior mean of the corresponding OLS regression line, along with the 95% credible interval in grey background.

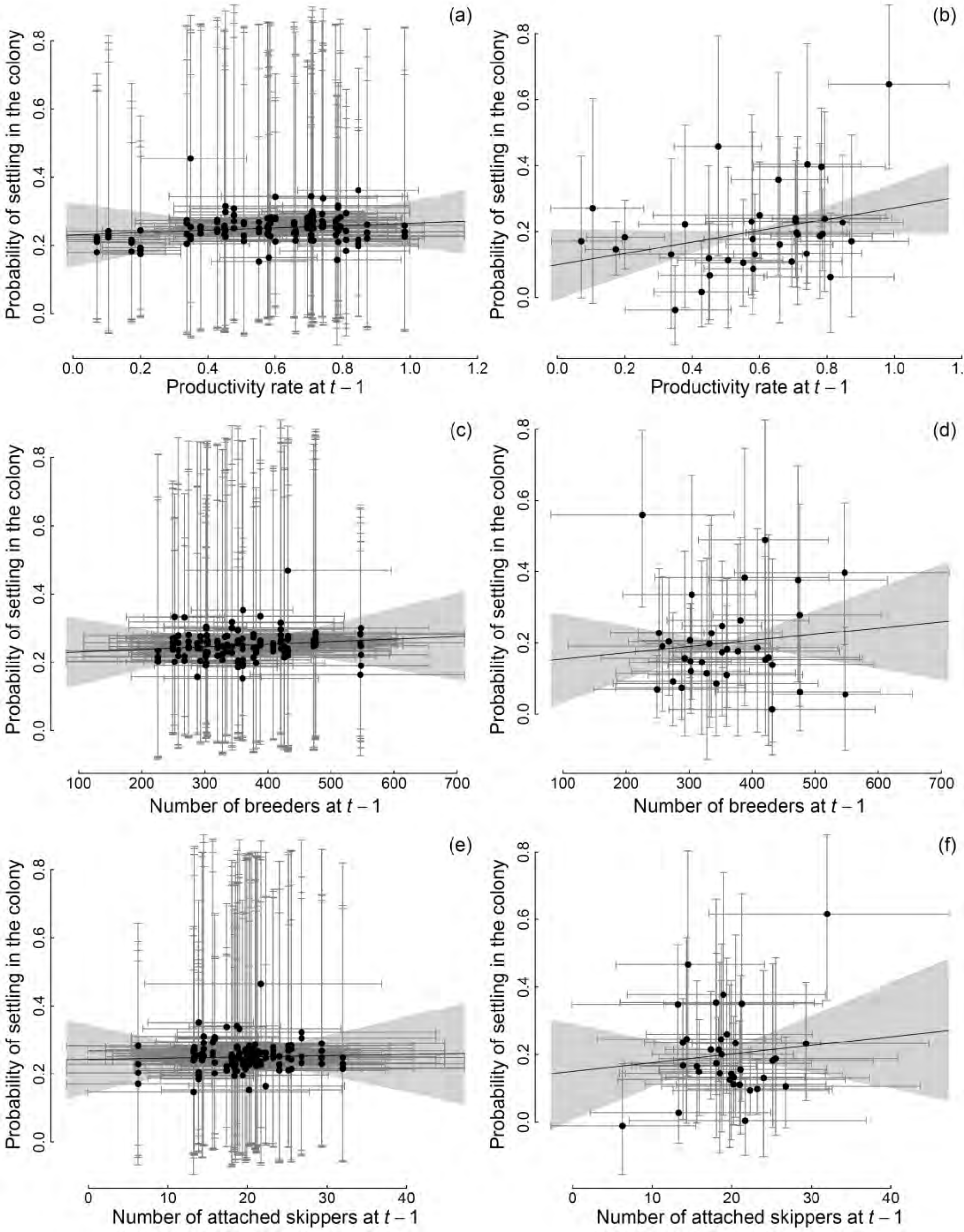

Figure E.4.4. Partial residual plot for the partial correlation between the probability of settling in a given colony in (a,c,e) former attached skippers or in (b,d,f) former floating skippers, and (a,b) productivity rate, (c,d) number of breeders, or (e,f) number of attached skippers in that colony at *t-1*. Residuals were centered on the variable mean to rescale variation within the original range. Points indicate posterior means and segments indicate 95% credible intervals. The solid line is the posterior mean of the corresponding OLS regression line, along with the 95% credible interval in grey background.

E.4.3 Discussion

This multi-colony model proved to be useful to get more precise estimates of the number of immigrants, and to show that immigrants do use social information to select their habitat. This suggest that immigrants are prospecting colonies the year before their effective establishment as breeders in the population, and that they select breeding habitats where productivity is higher than in other habitats and where breeders are more abundant. The results also indicate that former experienced breeders prefer not to leave the largest colonies. Moreover, first-time breeders and former breeders (experienced or not) choose their breeding colony according to conspecific when deciding whether or not to leave their previous colony (for former breeders), and where to settle (for all). However, there was no evidence that former skippers used social information in habitat selection. These conclusions are exposed and discussed in *General Discussion* (Chapter 5, section 5.3.2).

The analyses depicted here are preliminary and concern only nine years of study. Therefore, only seven years were used to address hypotheses on habitat selection. These analyses have to be continued to refine the way hypotheses were addressed, and to extend the study period to more years in order to fully benefit from the large dataset available (as done in Chapter 3). It would also be needed to provide an assessment of model fit to the data (as done in Chapter 3), though Fig. E.3.1 and E.3.4 indicate that estimates of the number of breeders in each colony and in the population as a whole closely matched the count data.

These preliminary results may also be useful to consider the limit of the model. For example, it is clear from Fig. E.4.3 and E.4.4 that probabilities of settlement are often difficult to estimate with great precision: 95% credible intervals of these rates were often large, especially for skippers. This may notably stem from the fact that the number of marked individuals in each state in each colony in each year is often small. Consequently, it is hard to estimate the proportion of individuals in a given state and a given colony that go to one or another colony, which is itself a subpart of the proportion of individuals that leave the colony. Here, we modeled all these substates because we were interested in detecting differences that could be related to peculiar individual circumstances (e.g. first-time breeders are less experienced, might be less competitive and frailer than older, etc.). Further, dispersal probabilities are necessarily different in each colony and this point must be addressed. In addition, some classes have a peculiar habitat selection behavior (e.g. prebreeders and floating skippers do not attend a particular colony). It might be hard to overcome the problems of stratification (small precision, huge number of parameters, general complexity, etc.), because dispersal probabilities inherently vary between colonies – this is the subject of habitat selection studies. However, we could consider different ways of grouping individual states and select the most appropriate (which might be less stratified than in the model presented here). For example, we could consider a model in which dispersal probabilities of former first-time breeders and former experienced breeders are grouped together. We could also consider a model in which dispersal probabilities at first-time breeding is independent from the colony of birth (notably because prebreeders do not settle on a nest site in a specific colony, as breeders and attached skippers do).

The colony scale might also be appropriate to explore the factors driving permanent emigration. Adult kittiwakes are rarely predated and colonies in the Cap Sizun share much of their environment in common. The only two predators that are known to hunt adult kittiwakes in the study area are the peregrine falcon (*Falco peregrinus*) that re-colonized the study areas after year 2000, and the American mink (*Neovison vison)* whose sign of presence has been found in the 1990's. Further, there is no hypothesis suggesting that mortality at sea could be colony-dependent. Unless individuals are distributed among colonies according to their survivorship, differences in apparent adult survival between colonies should reflect differences in permanent emigration. It would thus be necessary to control for potential sources of differences in (apparent) survivorship (e.g. age, breeding status; Cam et al. 1998, Cam and Monnat 2000a, 2000b, Cam et al. 2002) to test for differences in colony-specific survival. If differences in apparent survival among colonies correlate with dispersal within the population, and with productivity, this would support the hypothesis that the kittiwake population exports individuals depending on habitat quality. We might then be able to get an idea of the minimum number of individuals involved in emigration.

I think that such analyses are promising because studies in the Cap Sizun kittiwake population do not suggest a cost of reproduction, but apparent survival is lower in failed breeders (and notably when individual heterogeneity in survival is taken into account;

Aubry et al. 2011). Failed breeders should have less invested in reproduction than successful breeders at the end of the season (because they had less parental duties) and should thus not incur any higher survival cost of reproduction than successful breeders. Therefore, the lower apparent survival in failed breeders is likely to have resulted from a higher probability of permanent emigration. This is further supported by habitat selection mechanisms described in the kittiwake (Danchin and Monnat 1992, Danchin et al. 1998) and throughout my dissertation.

The integrated multi-colony model could also be refined to address how differences between colonies affect transitions towards the breeder state. We might thus increase the understanding of the link between habitat selection and the decision to breed in this population. For this purpose, it would probably be necessary to consider recruitment and intermittent breeding in a different framework. In the case of intermittent breeding, we could assess whether there is an association between social information in the colonies where individuals decide to disperse and transition towards the breeder state, and thus whether higher competition or lower productivity in a given colony induce lower breeding (see Chapter 3). This might be more difficult in the case of recruitment because prebreeders are not assigned to a particular colony. When we study dispersal of first-time breeders, the dispersal probabilities are conditioned by recruitment. We could however merge the recruitment probability and the probabilities to disperse in each of the different colonies at first-time breeding into probabilities for prebreeders of recruiting in each of the colonies (the probability of not recruiting being the complement, i.e. 1 minus the sum of the probabilities of recruiting in each of the colonies). We could then test for an association between the probabilities of recruiting in a colony and social information in the previous year in that colony (see Aubry et al. 2009 for other types of tests of the same hypotheses at the cliff scale in the Cap Sizun).

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E.5 *BUGS* code

```
model {

# --------------------------
#  PARAMETERS IN THE MODEL
# --------------------------
# C is the number of colonies (here, C=5)
# nocc is the number of occasions (here 9 years)
## a) Parameters which are not colony-dependent
# phi.0: first and second year survival probability
# phi.2: adult survival probability
# rho.3: probability to start breeding when 3 years old
# rho.4: probability to start breeding when 4 years old
# rho.5: probability to start breeding when 5 years old
# rho.6: probability to start breeding when 6 years old
# probability to start breeding when 7 years old is 1
# psi.b: probability that a breeder at t breeds at t+1
# psi.s: probability that a skipper at t breeds at t+1
# p.y: recapture probability of yearlings
# p.p: recapture probability of pre-breeders (age > 1)
# p.bs: recapture probability of breeders and skippers (very close to 1)
# alpha: probability that a skipper is “attached” to a specific colony
## b) Parameters which are colony-dependent
# pi.f[i]: productivity of first-time breeders in colony i
# pi.e[i]: productivity of experienced breeders in colony i
# disp.p[i,j]: probability of dispersing towards colony j at first-breeding for
#              individuals born in colony i
# disp.f[i,j]: probability of dispersing towards colony j for former first-time
#              breeders that bred in colony j
# disp.e[i,j]: probability of dispersing towards colony j for former experienced
#              breeders that bred in colony j
# disp.sa[i,j]: probability of dispersing towards colony j for former skippers that
#               were attached to colony j
# disp.sf[j]: probability of dispersing towards colony i for former floating
#             skippers
```

```
# ----------------------
#  STATES & OBSERVATIONS
# ----------------------
# States:
# 1+10*(i-1): fledgling from site i
# 2+10*(i-1): yearling (not yet breeding, born in site i)
# 3+10*(i-1): not yet breeding at age 2 years (born in site i)
# 4+10*(i-1): not yet breeding at age 3 years (born site i)
# 5+10*(i-1): not yet breeding at age 4 years (born site i)
# 6+10*(i-1): not yet breeding at age 5 years (born site i)
# 7+10*(i-1): not yet breeding at age 6 years (born site i)
# 8+10*(i-1): first-time breeder in site i
# 9+10*(i-1): experienced breeders in site i
# 10+10*(i-1): attached sabbatical individuals (experienced breeders skipping
reproduction) in site i
# 1+10*C: free sabbatical individuals
# 2+10*C: dead individuals
# Observations:
# i: seen as fledgling in colony i
# C+1: seen as pre-breeder in the study area
# C+1+i: seen as first-time breeder in colony i
# 2*C+1+i: seen as experienced breeder in colony i
# 3*C+1+i: seen as sabbatical individual in colony i
# 4*C+2: seen as free sabbatical individual
# 4*C+3: not seen
# ---------------------------------

# ----------------------------
#    PRIORS AND CONSTRAINTS
# ----------------------------


for (t in 1:(nocc-1)) {

  logit(phi.0[t]) <- ep.phi.0[t]
  logit(phi.2[t]) <- ep.phi.2[t]
  logit(rho.3[t]) <- ep.rho.3[t]
  logit(rho.4[t]) <- ep.rho.4[t]
  logit(rho.5[t]) <- ep.rho.5[t]
  logit(rho.6[t]) <- ep.rho.6[t]
  logit(psi.b[t]) <- ep.psi.b[t]
  logit(psi.s[t]) <- ep.psi.s[t]
  logit(alpha[t]) <- ep.alpha[t]
  logit(p.y[t]) <- ep.p.y[t]
  logit(p.p[t]) <- ep.p.p[t]

  ep.phi.0[t] ~ dnorm(mu.phi.0, tau.phi.0)T(-10,10)
  ep.phi.2[t] ~ dnorm(mu.phi.2, tau.phi.2)T(-10,10)
  ep.rho.3[t] ~ dnorm(mu.rho.3, tau.rho.3)T(-10,10)
  ep.rho.4[t] ~ dnorm(mu.rho.4, tau.rho.4)T(-10,10)
  ep.rho.5[t] ~ dnorm(mu.rho.5, tau.rho.5)T(-10,10)
  ep.rho.6[t] ~ dnorm(mu.rho.6, tau.rho.6)T(-10,10)
  ep.psi.b[t] ~ dnorm(mu.psi.b, tau.psi.b)T(-10,10)
  ep.psi.s[t] ~ dnorm(mu.psi.s, tau.psi.s)T(-10,10)
  ep.alpha[t] ~ dnorm(mu.alpha, tau.alpha)T(-10,10)
  ep.p.y[t] ~ dnorm(mu.p.y, tau.p.y)T(-10,10)
  ep.p.p[t] ~ dnorm(mu.p.p, tau.p.p)T(-10,10)

  mean.alpha ~ dunif(0,1)
  mu.alpha <- log(mean.alpha / (1 - mean.alpha))
  tau.alpha <- pow(sigma.alpha, -2)
  sigma.alpha ~ dunif(0,10)

  mean.phi.0 ~ dunif(0,1)
  mu.phi.0 <- log(mean.phi.0 / (1 - mean.phi.0))
  mean.phi.2 ~ dunif(0,1)
  mu.phi.2 <- log(mean.phi.2 / (1 - mean.phi.2))

  tau.phi.0 <- pow(sigma.phi.0, -2)
  sigma.phi.0 ~ dunif(0,10)
  var.phi.0 <- pow(sigma.phi.0, 2)
  tau.phi.2 <- pow(sigma.phi.2, -2)
  sigma.phi.2 ~ dunif(0,10)
  var.phi.2 <- pow(sigma.phi.2, 2)

  mean.rho.3 ~ dunif(0,1)
  mu.rho.3 <- log(mean.rho.3 / (1 - mean.rho.3))
  mean.rho.4 ~ dunif(0,1)
  mu.rho.4 <- log(mean.rho.4 / (1 - mean.rho.4))
  mean.rho.5 ~ dunif(0,1)
  mu.rho.5 <- log(mean.rho.5 / (1 - mean.rho.5))
  mean.rho.6 ~ dunif(0,1)
```

```
   mu.rho.6 <- log(mean.rho.6 / (1 - mean.rho.6))
   mean.psi.b ~ dunif(0,1)
   mu.psi.b <- log(mean.psi.b / (1 - mean.psi.b))
   mean.psi.s ~ dunif(0,1)
   mu.psi.s <- log(mean.psi.s / (1 - mean.psi.s))

   tau.rho.3 <- pow(sigma.rho.3, -2)
   sigma.rho.3 ~ dunif(0,10)
   var.rho.3 <- pow(sigma.rho.3, 2)
   tau.rho.4 <- pow(sigma.rho.4, -2)
   sigma.rho.4 ~ dunif(0,10)
   var.rho.4 <- pow(sigma.rho.4, 2)
   tau.rho.5 <- pow(sigma.rho.5, -2)
   sigma.rho.5 ~ dunif(0,10)
   var.rho.5 <- pow(sigma.rho.5, 2)
   tau.rho.6 <- pow(sigma.rho.6, -2)
   sigma.rho.6 ~ dunif(0,10)
   var.rho.6 <- pow(sigma.rho.6, 2)
   tau.psi.b <- pow(sigma.psi.b, -2)
   sigma.psi.b ~ dunif(0,10)
   var.psi.b <- pow(sigma.psi.b, 2)
   tau.psi.s <- pow(sigma.psi.s, -2)
   sigma.psi.s ~ dunif(0,10)
   var.psi.s <- pow(sigma.psi.s, 2)

   mean.p.y ~ dunif(0,1)
   mu.p.y <- log(mean.p.y / (1 - mean.p.y))
   mean.p.p ~ dunif(0,1)
   mu.p.p <- log(mean.p.p / (1 - mean.p.p))
   p.bs ~ dunif(0,1)

   tau.p.y <- pow(sigma.p.y, -2)
   sigma.p.y ~ dunif(0,10)
   var.p.y <- pow(sigma.p.y, 2)
   tau.p.p <- pow(sigma.p.p, -2)
   sigma.p.p ~ dunif(0,10)
   var.p.p <- pow(sigma.p.p, 2)

for (i in 1:C) {
for (j in 1:(C-1)) {

   l.disp.p[i,j,t]  ~ dnorm(0,0.315)T(-10,10)
   l.disp.f[i,j,t]  ~ dnorm(0,0.315)T(-10,10)
   l.disp.b[i,j,t]  ~ dnorm(0,0.315)T(-10,10)
   l.disp.sa[i,j,t] ~ dnorm(0,0.315)T(-10,10)
   el.disp.p[i,j,t]  <- exp(l.disp.p[i,j,t])
   el.disp.f[i,j,t]  <- exp(l.disp.f[i,j,t])
   el.disp.b[i,j,t]  <- exp(l.disp.b[i,j,t])
   el.disp.sa[i,j,t] <- exp(l.disp.sa[i,j,t])
   disp.p[i,j,t]  <- el.disp.p[i,j,t]  / (1 + sum(el.disp.p[i,1:(C-1),t]))
   disp.f[i,j,t]  <- el.disp.f[i,j,t]  / (1 + sum(el.disp.f[i,1:(C-1),t]))
   disp.b[i,j,t]  <- el.disp.b[i,j,t]  / (1 + sum(el.disp.b[i,1:(C-1),t]))
   disp.sa[i,j,t] <- el.disp.sa[i,j,t] / (1 + sum(el.disp.sa[i,1:(C-1),t]))

} #j

   disp.p[i,C,t]  <- 1-sum(disp.p[i,1:(C-1),t])
   disp.f[i,C,t]  <- 1-sum(disp.f[i,1:(C-1),t])
   disp.b[i,C,t]  <- 1-sum(disp.b[i,1:(C-1),t])
   disp.sa[i,C,t] <- 1-sum(disp.sa[i,1:(C-1),t])

} #i

 for (i in 1:(C-1)) {

   l.disp.sf[i,t]  ~ dnorm(0,0.315)T(-10,10)
   el.disp.sf[i,t]  <- exp(l.disp.sf[i,t])
   disp.sf[i,t] <- el.disp.sf[i,t] / (1 + sum(el.disp.sf[1:(C-1),t]))

 } #i

   disp.sf[C,t] <- 1-sum(disp.sf[1:(C-1),t])

 } #t

 for (i in 1:C) {
 for (t in 1:nocc){

   log(prod.f[i,t]) <- ep.prod.f[i,t]
   log(prod.e[i,t]) <- ep.prod.e[i,t]

   ep.prod.f[i,t] ~ dnorm(mu.prod.f[i], tau.prod.f[i])T(-10,10)
```

```
   ep.prod.e[i,t] ~ dnorm(mu.prod.e[i], tau.prod.e[i])T(-10,10)

   nrIM[i,t] ~ dunif(-5,750)
   IM[i,t] <- round(nrIM[i,t])

 } #t

 mean.prod.f[i] ~ dunif(0, 2)
 mu.prod.f[i] <- log(mean.prod.f[i])
 mean.prod.e[i] ~ dunif(0, 2)
 mu.prod.e[i] <- log(mean.prod.e[i])

 tau.prod.f[i] <- pow(sigma.prod.f[i], -2)
 sigma.prod.f[i] ~ dunif(0,10)
 var.prod.f[i] <- pow(sigma.prod.f[i], 2)
 tau.prod.e[i] <- pow(sigma.prod.e[i], -2)
 sigma.prod.e[i] ~ dunif(0,10)
 var.prod.e[i] <- pow(sigma.prod.e[i], 2)

 } #i

 nrY[1]  ~ dnorm(96, 0.01)T(0,)
 nrY[2]  ~ dnorm(67, 0.01)T(0,)
 nrY[3]  ~ dnorm(40, 0.01)T(0,)
 nrY[4]  ~ dnorm(98, 0.01)T(0,)
 nrY[5]  ~ dnorm(19, 0.01)T(0,)
 nrP2[1] ~ dnorm(68, 0.01)T(0,)
 nrP2[2] ~ dnorm(48, 0.01)T(0,)
 nrP2[3] ~ dnorm(29, 0.01)T(0,)
 nrP2[4] ~ dnorm(70, 0.01)T(0,)
 nrP2[5] ~ dnorm(14, 0.01)T(0,)
 nrP3[1] ~ dnorm(53, 0.01)T(0,)
 nrP3[2] ~ dnorm(37, 0.01)T(0,)
 nrP3[3] ~ dnorm(22, 0.01)T(0,)
 nrP3[4] ~ dnorm(54, 0.01)T(0,)
 nrP3[5] ~ dnorm(11, 0.01)T(0,)
 nrP4[1] ~ dnorm(28, 0.01)T(0,)
 nrP4[2] ~ dnorm(20, 0.01)T(0,)
 nrP4[3] ~ dnorm(12, 0.01)T(0,)
 nrP4[4] ~ dnorm(29, 0.01)T(0,)
 nrP4[5] ~ dnorm(6, 0.01)T(0,)
 nrP5[1] ~ dnorm(12, 0.01)T(0,)
 nrP5[2] ~ dnorm(8, 0.01)T(0,)
 nrP5[3] ~ dnorm(5, 0.01)T(0,)
 nrP5[4] ~ dnorm(12, 0.01)T(0,)
 nrP5[5] ~ dnorm(2, 0.01)T(0,)
 nrP6[1] ~ dnorm(4, 0.01)T(0,)
 nrP6[2] ~ dnorm(2, 0.01)T(0,)
 nrP6[3] ~ dnorm(1, 0.01)T(0,)
 nrP6[4] ~ dnorm(4, 0.01)T(0,)
 nrP6[5] ~ dnorm(1, 0.01)T(0,)
 nrF[1]  ~ dnorm(50, 0.01)T(0,)
 nrF[2]  ~ dnorm(35, 0.01)T(0,)
 nrF[3]  ~ dnorm(21, 0.01)T(0,)
 nrF[4]  ~ dnorm(51, 0.01)T(0,)
 nrF[5]  ~ dnorm(10, 0.01)T(0,)
 nrE[1]  ~ dnorm(344, 0.01)T(0,)
 nrE[2]  ~ dnorm(241, 0.01)T(0,)
 nrE[3]  ~ dnorm(143, 0.01)T(0,)
 nrE[4]  ~ dnorm(351, 0.01)T(0,)
 nrE[5]  ~ dnorm(70, 0.01)T(0,)
 nrSA[1] ~ dnorm(18, 0.01)T(0,)
 nrSA[2] ~ dnorm(12, 0.01)T(0,)
 nrSA[3] ~ dnorm(7, 0.01)T(0,)
 nrSA[4] ~ dnorm(18, 0.01)T(0,)
 nrSA[5] ~ dnorm(4, 0.01)T(0,)

for (i in 1:C) {
   NY[i,1] <- round(nrNY[i])
   NP2[i,1] <- round(nrNP2[i])
   NP3[i,1] <- round(nrNP3[i])
   NP4[i,1] <- round(nrNP4[i])
   NP5[i,1] <- round(nrNP5[i])
   NP6[i,1] <- round(nrNP6[i])
 } #i

 nrSF[1] ~ dnorm(sad10, 0.01)T(0,)
 SF[1] <- round(nrSF[1])
 NB[i,1] <- NF[i,1] + NE[i,1]

 tau.obs ~ dgamma(0.001, 0.001)
 var.obs <- 1/tau.obs
```

```
sigma.obs <- pow(var.obs,0.5)

# ---------------------------------------------------------
#   LIKELIHOOD OF THE STATE-SPACE MODEL FOR COUNT DATA
# ---------------------------------------------------------

    ## State process

for (i in 1:C) {
for (t in 1:(nocc-1)) {

  NY[i,t+1] ~ dpois(mu1[i,t])
  mu1[i,t] <- NF[i,t] * prod.f[i,t] * phi.0[t] + NE[i,t] * prod.e[i,t] * phi.0[t]

  NP2[i,t+1] ~ dbin(mu2[i,t], NY[i,t])
  mu2[i,t] <- phi.0[t]

  NP3[i,t+1] ~ dbin(mu3[i,t], NP2[i,t])
  mu3[i,t] <- phi.2[t] * (1-rho.3[t])

  NP4[i,t+1] ~ dbin(mu4[i,t], NP3[i,t])
  mu4[i,t] <- phi.2[t] * (1-rho.4[t])

  NP5[i,t+1] ~ dbin(mu5[i,t], NP4[i,t])
  mu5[i,t] <- phi.2[t] * (1-rho.5[t])

  NP6[i,t+1] ~ dbin(mu6[i,t], NP5[i,t])
  mu6[i,t] <- phi.2[t] * (1-rho.6[t])

for (j in 1:C) {

  NF3[i,j,t+1] ~ dbin(mu7[i,j,t], NP2[j,t])
  mu7[i,j,t] <- phi.2[t] * rho.3[t] * disp.p[j,i,t]

  NF4[i,j,t+1] ~ dbin(mu8[i,j,t], NP3[j,t])
  mu8[i,j,t] <- phi.2[t] * rho.4[t] * disp.p[j,i,t]

  NF5[i,j,t+1] ~ dbin(mu9[i,j,t], NP4[j,t])
  mu9[i,j,t] <- phi.2[t] * rho.5[t] * disp.p[j,i,t]

  NF6[i,j,t+1] ~ dbin(mu10[i,j,t], NP5[j,t])
  mu10[i,j,t] <- phi.2[t] * rho.6[t] * disp.p[j,i,t]

  NF7[i,j,t+1] ~ dbin(mu11[i,j,t], NP6[j,t])
  mu11[i,j,t] <- phi.2[t] * disp.p[j,i,t]

  # Note: NI[i,t] is given in another loop (that covers all time steps)

  NEF[i,j,t+1] ~ dbin(mu12[i,j,t], NF[j,t])
  mu12[i,j,t] <- phi.2[t] * psi.b[t] * disp.f[j,i,t]

  NEE[i,j,t+1] ~ dbin(mu13[i,j,t], NE[j,t])
  mu13[i,j,t] <- phi.2[t] * psi.b[t] * disp.b[j,i,t]

  NESA[i,j,t+1] ~ dbin(mu14[i,j,t], NSA[j,t])
  mu14[i,j,t] <- phi.2[t] * psi.s[t] * disp.sa[j,i,t]

  NSAF[i,j,t+1] ~ dbin(mu15[i,j,t], NF[j,t])
  mu15[i,j,t] <- phi.2[t] * (1 - psi.b[t]) * disp.f[j,i,t] * alpha[t]

  NSAE[i,j,t+1] ~ dbin(mu16[i,j,t], NE[j,t])
  mu16[i,j,t] <- phi.2[t] * (1 - psi.b[t]) * disp.b[j,i,t] * alpha[t]

  NSASA[i,j,t+1] ~ dbin(mu17[i,j,t], NSA[j,t])
  mu17[i,j,t] <- phi.2[t] * (1 - psi.s[t]) * disp.sa[j,i,t] * alpha[t]

} #j

  NESF[i,t+1] ~ dbin(mu18[i,t], NSF[t])
  mu18[i,t] <- phi.2[t] * psi.s[t] * disp.sf[i,t]

  NSASF[i,t+1] ~ dbin(mu19[i,t], NSF[t])
  mu19[i,t] <- phi.2[t] * (1 - psi.s[t]) * alpha[t] * disp.sf[i,t]

  NSFF[i,t+1] ~ dbin(mu20[i,t], NF[i,t])
  mu20[i,t] <- phi.2[t] * (1 - psi.b[t]) * (1-disp.f[i,i,t]) * (1-alpha[t])

  NSFE[i,t+1] ~ dbin(mu21[i,t], NE[i,t])
  mu21[i,t] <- phi.2[t] * (1 - psi.b[t]) * (1-disp.b[i,i,t]) * (1-alpha[t])

  NSFSA[i,t+1] ~ dbin(mu22[i,t], NSA[i,t])
  mu22[i,t] <- phi.2[t] * (1 - psi.s[t]) * (1-disp.sa[i,i,t]) * (1-alpha[t])
```

```
} #t
} #i

for (t in 1:(nocc-1)) {

    NSFSF[t+1] ~ dbin(mu33[t], NSF[t])
    mu33[t] <- phi.2[t] * (1 - psi.s[t]) * (1-alpha[t])

} #t

## Observation process

for (t in 2:nocc) {

  NSF[t] <- sum(NSFF[,t]) + sum(NSFE[,t]) + sum(NSFSA[,t]) + NSFSF[t]

for (i in 1:C) {

  NF[i,t]  <- sum(NF3[i,,t]) + sum(NF4[i,,t]) + sum(NF5[i,,t]) + sum(NF6[i,,t])
            + sum(NF7[i,,t]) + NI[i,t]
  NE[i,t]  <- sum(NEF[i,,t]) + sum(NEE[i,,t]) + sum(NESA[i,,t]) + NESF[i,t]
  NSA[i,t] <- sum(NSAF[i,,t]) + sum(NSAE[i,,t]) + sum(NSASA[i,,t]) + NSASF[i,t]

  NB[i,t] <- NF[i,t] + NE[i,t]     # total breeding size in each colony

} #t
} #i

for (i in 1:C) {
for (t in 1:nocc) {

  NPB[i,t] <- NY[i,t] + NP2[i,t] + NP3[i,t] + NP4[i,t] + NP5[i,t] + NP6[i,t]

  lNB[i,t] <- log(NB[i,t])
  C[i,t]    ~ dnorm(lNB[i,t], tau.obs)

} #t
} #i

#----------------------------------------------------------
#  LIKELIHOOD FOR PRODUCTIVITY DATA: POISSON REGRESSIONS
#----------------------------------------------------------

for (i in 1:C) {
for (t in 1:nocc) {

  JF[i,t] ~ dpois(rho.f[i,t])
  log(rho.f[i,t]) <- log(RF[i,t]) + log(prod.f[i,t]*2)

  JB[i,t] ~ dpois(rho.b[i,t])
  log(rho.b[i,t]) <- log(RB[i,t]) + log(prod.e[i,t]*2)

  JU[i,t] ~ dpois(rho.u[i,t])
  log(rho.u[i,t]) <- log(RU[i,t]) + log(prod.f[i,t]*2*prop[i,t]
                       + prod.e[i,t]*2*(1-prop[i,t]))
  prop[i,t] <- F[i,t]/NB[i,t]

} #t
} #i

# ---------------------------------------------------------
#   LIKELIHOOD OF THE MULTISTATE CAPTURE-RECAPTURE MODEL
# ---------------------------------------------------------

## Define the state-transition matrix

for (t in 1:(nocc-1)){
for (i in 1:C) {

  for (j in 1:(i-1)) {

    for (k in 1:2) {
    for (l in 1:10) {
      ps[k+10*(i-1),t,l+10*(j-1)]  <- 0  } } #k,l
    for (k in 3:7) {
    for (l in 1:7) {
      ps[k+10*(i-1),t,l+10*(j-1)]  <- 0  } #l
      ps[k+10*(i-1),t,9+10*(j-1)]  <- 0
      ps[k+10*(i-1),t,10+10*(j-1)] <- 0  } #k

      ps[3+10*(i-1),t,8+10*(j-1)]  <- phi.2[t] * rho.3[t] * disp.p[i,j,t]
```

```
         ps[4+10*(i-1),t,8+10*(j-1)]  <- phi.2[t] * rho.4[t] * disp.p[i,j,t]
         ps[5+10*(i-1),t,8+10*(j-1)]  <- phi.2[t] * rho.5[t] * disp.p[i,j,t]
         ps[6+10*(i-1),t,8+10*(j-1)]  <- phi.2[t] * rho.6[t] * disp.p[i,j,t]
         ps[7+10*(i-1),t,8+10*(j-1)]  <- phi.2[t] * disp.p[i,j,t]

    }   #j

         ps[1+10*(i-1),t,1+10*(i-1)]  <- 0
         ps[1+10*(i-1),t,2+10*(i-1)]  <- phi.0[t]
       for (k in 3:10) {
         ps[1+10*(i-1),t,k+10*(i-1)]  <- 0 } #k

       for (k in 1:2) {
         ps[2+10*(i-1),t,k+10*(i-1)]  <- 0 } #k
         ps[2+10*(i-1),t,3+10*(i-1)]  <- phi.0[t]
       for (k in 4:10) {
         ps[2+10*(i-1),t,k+10*(i-1)]  <- 0 } #k

       for (k in 1:3) {
         ps[3+10*(i-1),t,k+10*(i-1)]  <- 0 } #k
         ps[3+10*(i-1),t,4+10*(i-1)]  <- phi.2[t] * (1 - rho.3[t])
         ps[3+10*(i-1),t,5+10*(i-1)]  <- 0
         ps[3+10*(i-1),t,6+10*(i-1)]  <- 0
         ps[3+10*(i-1),t,7+10*(i-1)]  <- 0
         ps[3+10*(i-1),t,8+10*(i-1)]  <- phi.2[t] * rho.3[t] * disp.p[i,i,t]
         ps[3+10*(i-1),t,9+10*(i-1)]  <- 0
         ps[3+10*(i-1),t,10+10*(i-1)] <- 0

       for (k in 1:4) {
         ps[4+10*(i-1),t,k+10*(i-1)]  <- 0 } #k
         ps[4+10*(i-1),t,5+10*(i-1)]  <- phi.2[t] * (1 - rho.4[t])
         ps[4+10*(i-1),t,6+10*(i-1)]  <- 0
         ps[4+10*(i-1),t,7+10*(i-1)]  <- 0
         ps[4+10*(i-1),t,8+10*(i-1)]  <- phi.2[t] * rho.4[t] * disp.p[i,i,t]
         ps[4+10*(i-1),t,9+10*(i-1)]  <- 0
         ps[4+10*(i-1),t,10+10*(i-1)] <- 0

       for (k in 1:5) {
         ps[5+10*(i-1),t,k+10*(i-1)]  <- 0 } #k
         ps[5+10*(i-1),t,6+10*(i-1)]  <- phi.2[t] * (1 - rho.5[t])
         ps[5+10*(i-1),t,7+10*(i-1)]  <- 0
         ps[5+10*(i-1),t,8+10*(i-1)]  <- phi.2[t] * rho.5[t] * disp.p[i,i,t]
         ps[5+10*(i-1),t,9+10*(i-1)]  <- 0
         ps[5+10*(i-1),t,10+10*(i-1)] <- 0

       for (k in 1:6) {
         ps[6+10*(i-1),t,k+10*(i-1)]  <- 0 } #k
         ps[6+10*(i-1),t,7+10*(i-1)]  <- phi.2[t] * (1 - rho.6[t])
         ps[6+10*(i-1),t,8+10*(i-1)]  <- phi.2[t] * rho.6[t] * disp.p[i,i,t]
         ps[6+10*(i-1),t,9+10*(i-1)]  <- 0
         ps[6+10*(i-1),t,10+10*(i-1)] <- 0

       for (k in 1:7) {
         ps[7+10*(i-1),t,k+10*(i-1)]  <- 0 } #k
         ps[7+10*(i-1),t,8+10*(i-1)]  <- phi.2[t] * disp.p[i,i,t]
         ps[7+10*(i-1),t,9+10*(i-1)]  <- 0
         ps[7+10*(i-1),t,10+10*(i-1)] <- 0

    for (j in (i+1):C) {

        for (k in 1:2) {
        for (l in 1:10) {
          ps[k+10*(i-1),t,l+10*(j-1)]  <- 0  } } #k,l
        for (k in 3:7) {
        for (l in 1:7) {
          ps[k+10*(i-1),t,l+10*(j-1)]  <- 0  } #l
          ps[k+10*(i-1),t,9+10*(j-1)]  <- 0
          ps[k+10*(i-1),t,10+10*(j-1)] <- 0  } #k

          ps[3+10*(i-1),t,8+10*(j-1)]  <- phi.2[t] * rho.3[t] * disp.p[i,j,t]
          ps[4+10*(i-1),t,8+10*(j-1)]  <- phi.2[t] * rho.4[t] * disp.p[i,j,t]
          ps[5+10*(i-1),t,8+10*(j-1)]  <- phi.2[t] * rho.5[t] * disp.p[i,j,t]
          ps[6+10*(i-1),t,8+10*(j-1)]  <- phi.2[t] * rho.6[t] * disp.p[i,j,t]
          ps[7+10*(i-1),t,8+10*(j-1)]  <- phi.2[t] * disp.p[i,j,t]

     } #j

     for (j in 1:C) {

        for (k in 1:8) {
          ps[8+10*(i-1),t,k+10*(j-1)]   <- 0
          ps[9+10*(i-1),t,k+10*(j-1)]   <- 0
```

```
       ps[10+10*(i-1),t,k+10*(j-1)]  <- 0   } #k

       ps[8+10*(i-1),t,9+10*(j-1)]  <- phi.2[t] * psi.b[t] * disp.f[i,j,t]
       ps[8+10*(i-1),t,10+10*(j-1)] <- phi.2[t] * (1-psi.b[t]) * disp.f[i,j,t]
                                     * alpha[t]

       ps[9+10*(i-1),t,9+10*(j-1)]  <- phi.2[t] * psi.b[t] * disp.b[i,j,t]
       ps[9+10*(i-1),t,10+10*(j-1)] <- phi.2[t] * (1 - psi.b[t]) * disp.b[i,j,t]
                                     * alpha[t]

       ps[10+10*(i-1),t,9+10*(j-1)]  <- phi.2[t] * psi.s[t] * disp.sa[i,j,t]
       ps[10+10*(i-1),t,10+10*(j-1)] <- phi.2[t] * (1 - psi.s[t]) * disp.sa[i,j,t]
                                      * alpha[t]

   } #j

     for (k in 1:7) {
       ps[k+10*(i-1),t,1+10*C]  <- 0   }  #k
       ps[8+10*(i-1),t,1+10*C]  <- phi.2[t] * (1 - psi.b[t]) * (1-disp.f[i,i,t])
                                 * (1 - alpha[t])
       ps[9+10*(i-1),t,1+10*C]  <- phi.2[t] * (1 - psi.b[t]) * (1-disp.b[i,i,t])
                                 * (1 - alpha[t])
       ps[10+10*(i-1),t,1+10*C]  <- phi.2[t] * (1 - psi.s[t]) * (1-disp.sa[i,i,t])
                                 * (1 - alpha[t])

     for (k in 1:8) {
       ps[1+10*C,t,k+10*(i-1)]   <- 0 } #k
       ps[1+10*C,t,9+10*(i-1)]   <- phi.2[t] * psi.s[t] * disp.sf[i,t]
       ps[1+10*C,t,10+10*(i-1)]  <- phi.2[t] * (1 - psi.s[t])
                                  * alpha[t] * disp.sf[i,t]

   } #i

       ps[1+10*C,t,1+10*C]  <- phi.2[t] * (1 - psi.s[t]) * (1 - alpha[t])


## Prepare the matrix of resighting probabilities for calculations
## of expected frequencies in the m-array

   for (i in 1:C) {
     for (k in 1:10) {
       for (j in 1:C) {

          po[k+10*(i-1),t,1+10*(j-1)] <- 1
          po[k+10*(i-1),t,2+10*(j-1)] <- p.y[t]

    for (l in 3:7) {

          po[k+10*(i-1),t,l+10*(j-1)]  <- p.p[t]

     } #l

          po[k+10*(i-1),t,8+10*(j-1)]  <- p.bs
          po[k+10*(i-1),t,9+10*(j-1)]  <- p.bs
          po[k+10*(i-1),t,10+10*(j-1)] <- p.bs

        } #j

          po[k+10*(i-1),t,1+10*C] <- p.bs

      } #k

          po[1+10*C,t,1+10*(i-1)]  <- 1
          po[1+10*C,t,2+10*(i-1)]  <- p.y[t]

      for (k in 3:7) {

          po[1+10*C,t,k+10*(i-1)] <- p.p[t]

      } #k

          po[1+10*C,t,8+10*(i-1)]  <- p.bs
          po[1+10*C,t,9+10*(i-1)]  <- p.bs
          po[1+10*C,t,10+10*(i-1)] <- p.bs

   } #i

   po[1+10*C,t,1+10*C] <- p.bs

   } #t

   qo <- 1 - po
```

```
## Define the multinomial likelihood

for (t in 1:((nocc-1)*ns)){
  marray[t,1:(nocc*ns-(ns-1))] ~ dmulti(pr[t, ], rel[t])
}

 # Define matrix Q: product of probabilities of survival and non-capture

for (t in 1:(nocc-2)){

  Q[((t-1)*ns+1):(t*ns), ((t-1)*ns+1):(t*ns)] <- ones

for (j in (t+1):(nocc-1)){

  Q[((t-1)*ns+1):(t*ns),((j-1)*ns+1):(j*ns)] <-
              Q[((t-1)*ns+1):(t*ns),((j-2)*ns+1):((j-1)*ns)] %*% (ps[,t,]*qo[,t,])

 } #j
 } #t

 Q[((nocc-2)*ns+1):((nocc-1)*ns),((nocc-2)*ns+1):((nocc-1)*ns)] <- ones

# Define the expected frequencies in the m-array
for (t in 1:(nocc-2)){

  pr[((t-1)*ns+1):(t*ns),((t-1)*ns+1):(t*ns)] <-
                   Q[((t-1)*ns+1):(t*ns),((t-1)*ns+1):(t*ns)] %*% (ps[,t,]*po[,t,])

  # Above main diagonal
  for (j in (t+1):(nocc-1)){

     pr[((t-1)*ns+1):(t*ns),((j-1)*ns+1):(j*ns)] <-
                  Q[((t-1)*ns+1):(t*ns), ((j-1)*ns+1):(j*ns)] %*% (ps[,j,]*po[,j,])

   } #j
} #t

pr[((nocc-2)*ns+1):((nocc-1)*ns),((nocc-2)*ns+1):((nocc-1)*ns)] <-
                                                           ps[,nocc-1,]*po[,nocc-1,]

  # Below main diagonal
for (t in 2:(nocc-1)){
  for (j in 1:(t-1)){

    pr[((t-1)*ns+1):(t*ns),((j-1)*ns+1):(j*ns)] <- zero

 } #j
 } #t

# Last column: probability of non-recapture
for (t in 1:((nocc-1)*ns)){

  pr[t,(nocc*ns-(ns-1))] <- 1-sum(pr[t,1:((nocc-1)*ns)])

} #t

} #model
```

Titre : Où et quand se reproduire ? Décisions d'histoire de vie des laridés en habitats variables dans l'espace et le temps.

Résumé : Tout au long de leur vie, les individus sont confrontés à deux décisions qui ont des conséquences majeures sur leur succès reproducteur : où et quand se reproduire. Cette thèse étudie les mécanismes sous-jacents à ces décisions, à travers trois études basées sur des données de suivis individuels chez la mouette tridactyle (*Rissa tridactyla*) et le goéland railleur (*Chroicocephalus genei*). La première étude porte sur la dispersion chez la mouette tridactyle. La probabilité de quitter le site de reproduction est décomposée selon une structure hiérarchique des patchs d'habitat. Une hypothèse synthétique est exposée pour expliquer la stratégie de sélection de l'habitat en intégrant les coûts de la dispersion et l'utilisation de l'information sur la qualité de l'habitat. La seconde étude s'appuie sur un modèle de population intégré chez la mouette tridactyle pour estimer l'immigration, le recrutement, et la reproduction intermittente. Cette étude interroge la relation entre information sociale sur l'habitat et décision de se reproduire dans une population qui est située en bordure d'aire de répartition. La troisième étude porte sur le recrutement et la dispersion chez le goéland railleur, caractérisé par un fort nomadisme de reproduction. Des modèles de capture-recapture multi-évènements sont employés pour quantifier les variations liées à l'âge et au sexe. Ces exemples permettent d'aborder l'importance des contraintes imposées par la variabilité de l'habitat et la compétition intraspécifique dans le processus d'accès à la reproduction.

Mots-clés : sélection de l'habitat, dispersion, histoire de vie, étude à long terme, modèle bayésien.

Title: Life-history decisions of larids in spatio-temporally varying habitats: where and when to breed.

Abstract: Throughout their lifetime, individuals face two decisions which have major consequences on the reproductive success: where and when to breed. This thesis explores the mechanisms underlying these decisions through three studies based on individual monitoring data in the black-legged kittiwake (*Rissa tridactyla*) and the slender-billed gull (*Chroicocephalus genei*). The first study addresses hypotheses on dispersal in the kittiwake. The probability of leaving the nest site is sequenced according to the hierarchical structure of habitat patches. A synthetic hypothesis that integrates the costs of dispersal and the use of information on habitat quality is suggested to explain the strategy of habitat selection. The second study uses a population integrated model in the kittiwake to estimate immigration, recruitment, and intermittent reproduction. This study investigates the relationships between social information on the habitat and the decision to breed in a population which is located at the edge of the species range. The third study focuses on recruitment and dispersal in the slender-billed gull which is characterized by a high degree of nomadic breeding. Multievent capture-recapture models are used to quantify sex- and age-dependent variations. These examples enable to address how important the constraints of habitat variability and intraspecific competition are in the process of obtaining a breeding position.

Keywords: habitat selection, dispersal, life history, long-term study, bayesian model.