Breeding success, nest site fidelity and mate fidelity in the European Storm-petrel *Hydrobates pelagicus*

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Abstract

The European Storm-petrel *Hydrobates pelagicus* is a monogamous and long-lived species with a low reproductive rate. Its nest sites are located in natural cavities under rocks or in burrows excavated by other species. Data obtained in the Molène archipelago, western France, have been analysed to study nest site fidelity and mate fidelity, and to study their relationship with breeding success and sex. Breeders were ringed and breeding success assessed from 2001–18. The influence of age and the weight of breeders on reproductive success has also been studied. Individuals were very faithful to their nest sites (94%) and to their mates (95%) from one year to the next. Breeding failure in the year t was negatively correlated with nest site fidelity and with mate retention in year t+1. Nest site fidelity was not influenced by the sex of breeding birds. Change of nest site or mate had no significant impact on the breeding success in the same year. There was a positive effect of the weight of incubating adults on reproductive success. High rates of nest site fidelity and mate fidelity may indicate good population status, with breeding habitat and mates of good quality.

Introduction

The breeding success of seabirds depends on many factors, including their habitat, breeding site, mate and experience (Bried & Jouventin 2002). The choices of nest site and mate are important because they will influence an individual's long-term reproductive performance. Thus, nest sites offering greater protection against predators and bad weather will be selected, as well as high-quality mates (Bourgeois *et al*. 2014; Michielsen *et al*. 2019). Birds use their previous breeding experience of a site, with their partner, to determine the quality of the site and the partner, which will influence their decision to retain it or to leave (Switzer 1993). Breeding success can be considered as the main factor influencing nest site fidelity and mate fidelity in Procellariiformes (Bourgeois *et al*. 2014). Breeding failure may lead to a higher probability of changing nest site and partner, in an attempt to improve the results of future breeding attempts (González-Solís *et al*. 1999). These changes make it possible to avoid the repetition of poor breeding performance with a nest site or a partner of poor quality (Bried & Jouventin 2002). But these changes only occur when their benefits outweigh their costs (Ens *et al*. 1993). Dispersal and divorce costs involve the search for a new site and a new partner, and the risk of acquiring one of lower quality (Kim *et al*. 2007), the risk of non-breeding over one or more years, and the risk of low breeding success in the first year at a new nest site or with a new partner (Naves *et al*. 2007). Nest site fidelity and mate fidelity are therefore very important for seabirds, which are mostly monogamous and long-lived species. Breeding success is associated with strong nest site fidelity and mate fidelity (Bried *et al*. 2003). High fidelity allows for a better understanding of the surrounding environment, which includes their neighbours, competitors, predators and protective nest characteristics, improved coordination between breeding adults of their incubation routine and foraging, and breeding earlier in the season (Switzer 1993; Bried & Jouventin 2002).

In Procellariiformes, fidelity is very high, especially for cavity-nesting species (Bried *et al*. 2003). Procellariiformes have a low reproductive rate, and non-breeding years, due to a change of nest or partner, can have a significant impact on individual fitness (Jouventin & Bried 2001). However, the relationship between nest and partner fidelity is not well understood. For Procellariiformes, mate fidelity may depend on nest site fidelity, as the nest is the meeting point for breeding individuals returning from their wintering areas to their colony (Davies 1957; Cézilly *et al*. 2000). However, some studies contradict this and suggest that mate fidelity does not depend on the breeding site and is instead an active process aiming to increase breeding success (Pyle *et al*. 2001; Bried & Jouventin 2003).

Site fidelity and mate fidelity influence breeding success, but these are not the only factors that come into play (Naves *et al*. 2006). The body condition of breeding adults, as well as their age and experience, can also influence breeding success. Indeed, life history theory predicts that body mass is positively correlated with reproductive effort (Williams 1966). Body mass can therefore predict breeding success (Chastel *et al*. 1995). Age also influences reproductive performance in long-lived bird species such as Procellariiformes; older individuals tend to have higher breeding success and be more faithful to their nest site and their partner (Pyle *et al*. 2001; Kim *et al*. 2007).

The European Storm-petrel *Hydrobates pelagicus* (hereafter Storm-petrel) is a procellariiform. It is a monogamous species, with a long lifespan and a low reproductive rate. It always nests under cover, in natural cavities under rocks or in burrows excavated by other species. The species is classified as "vulnerable" on the French Red List, "endangered" on the Brittany Red List and also listed in Appendix 1 of the European Birds Directive (Cadiou *et al*. 2019). The world population is estimated at between 430,000 and 520,000 pairs (IUCN 2018).

In this study, we examine breeding success and associated rates of nest site fidelity and mate fidelity in the Storm-petrel, specifically analysing the impact of breeding success in year t on fidelity in year t+1 and potential differences according to sex, the impact of fidelity in year t on breeding success in year t, as well as the impact of the age and weight of breeding adults on breeding success.

Methods

The study was conducted in the Iroise National Nature Reserve (Molène archipelago), within the Iroise Marine Nature Park in western Brittany, France. The Iroise Marine Nature Park is an area of major importance for nesting seabirds. The islands of the Molène archipelago host the most important French colonies of the Storm-petrel, with about 800 Apparently Occupied Sites (AOS) in 2018, representing three quarters of the French population of the Channel and the Atlantic coast (Cadiou *et al*. 2019). The field work described here was carried out on Enez Kreiz (48°25'N 5°0'W), which is the smallest island of the reserve (0.39 ha).

On Enez Kreiz there are 253 known Storm-petrel breeding sites and annual breeding numbers have varied over the study period between 72–87 AOS in 2007 and 143–148 AOS in 2002. Most of the nest sites are disused Rabbit *Oryctolagus cuniculus* burrows, a species that became locally extinct on Enez Kreiz in 1993 due to disease. Some of these sites have one entrance and two or more distinct nest cups. Breeding season monitoring begins in early May when the first eggs are laid and ends in October when all young have fledged. During the breeding season, the colony is visited only by day about once every two to three weeks. The different methods used for censusing are investigation by hand, observation with a torch and call-playback (see Cadiou 2001).

Since 1994, all chicks in accessible sites (about 75% of the sites) have been ringed before fledging. Since 2001, all adults in accessible sites have also been caught but only during the latter part of incubation, to avoid abandonment and breeding failure (Blackmer *et al*. 2004; Carey 2009). Thus, due to this restriction and to the delay between consecutive visits, frequently only one member of the pair is caught during the breeding season. Sometimes both members of the pair are caught, but equally sometimes neither is caught, if breeding failure has occurred at the egg stage or if the young chick had been left alone at the date of inspection of the nest site (Table 1). In a few cases, one member of the breeding pair can also be captured before egg laying, when they occupy the nest site by day. The adults are ringed or the existing ring read. Other measurements taken include wing length (to the nearest 1 mm), weight (to the nearest 1 g) and cloacal width (to the nearest 0.1 mm; Copestake *et al*. 1988). In order to reduce disturbance or sometimes due to time constraints, these measurements were not always taken. Data were available for 284 individual birds, which were involved in 187 pairings over the study period.

Due to a large overlap of the cloacal width between sexes and in the absence of molecular sexing, we allocated arbitrary fixed boundaries to assign sex. We considered birds with a cloacal width greater than 7.0 mm to be female, while birds with a cloacal width lower than 5.5 mm were classed as male. Birds with intermediate cloacal width were considered to be of unknown sex. Wing length can also be used, as females tend to be larger than males (Jakubas *et al*. 2014), and in some cases, the sex of the bird could also be deduced from the sex of the mate. However, 44 birds could not be sexed using these methods.

Estimation of age was based on data from birds ringed as chicks, i.e. of known age (n = 39). Birds caught in nest sites incubating an egg or a young chick were considered to be at least three years old at the time of first capture and ringing, and birds mist-netted at night on the neighbouring island of Banneg were considered to be at least two years old at the time of first capture and ringing (n = 245).

In addition, regurgitated pellets of the Storm-petrel's predators (gulls *Larus* sp. and Grey Heron *Ardea cinerea*) were examined to search for rings, in order to identify dead individuals. At the end of the season, breeding success was determined for all accessible sites: certain or probable success (chick observed alive at 50–65 days old or 40–50 days old respectively; success = 1), possible success (chick observed alive at 30–40 days old but not found again two weeks later; success = 0.5) or failure (unhatched egg, chick found dead or disappeared at an age too young to fledge; success = 0).

Table 1. Examples of the data available for the nest-sites and the breeders. Rg/Ct = bird ringed or recaptured in the nest-site considered on Enez Kreiz, Ra/Ca = bird ringed or recaptured in another nest-site on Enez Kreiz, Rm/Cm = bird ringed or recaptured after being caught in mist-nest on the neighbouring island of Banneg, Rc = bird ringed as a chick on Enez Kreiz, x? = bird not recaptured in the nest-site but considered to be present according to data obtained in previous and following years, ? = bird not recaptured in the nest-site and which can't be considered to be present, DP = bird found dead in a pellet; Breeding success: Cf = chick fledged, Cf? = chick possibly fledged, Fc = failure at the chick stage, Fu = failure at an unknown stage (egg or chick), Fe = failure at the egg stage, Un = unoccupied site; DS = nest-site destroyed by winter storm.

Nest-site & ring No.	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**
EK-147E																		
SA899431	Rg	x?	Ct	Ct	x?	x?	x?	x?	Ct	Ct	Ct	Ct	x?	x?	Ct	?	?	?
SA899565	Rg	Ct	Ct	x?	x?	Ct	x?	x?	Ct	x?	Ct	Ct	Ct	Ct	x?	Ct	Ct	?
Success	Fc	Cf	Cf?	Cf	Cf	Cf	Fu	Cf?	Cf	Cf?	Cf	Cf	Cf?	Cf	Fe	Cf	Cf?	Fu
EK-120D1																		
SA899433	Rg	Ct	x?	x?	x?	Ct	x?	Ct	x?	Ct	?	?	?					
SB42367	?	?	Rg	x?	Ct	x?	x?	Ct	Ct	x?	Ct	DP						
Success	Cf	Fc	Cf	Cf	Cf	Cf	Cf	Cf	Cf	Cf	Fu	Cf	Cf	DS	–	–	–	–
EK-77D																		
SA899430	Rg	?																
SB42101	?	Rg	Ct	x?	Ct	Ct	x?	x?	Ct	x?	Ct	Ct	Ct	Ct	Ct	Ct	Ct	?
SB42603		?	Rg	Ct	Ct	?												
SC34510						?	Rg											
SA897969		Rc	–	–	Cm	–	–	Ct	Ct	Ct	x?	Ct	x?	Ct	Ct	x?	Ct	Ct
Success	Fc	Cf	Fu	Cf	Cf	Cf	Cf	Cf	Cf	Fe	Cf	Cf	Cf	Cf	Cf	Cf	Cf	Fc
EK-22B																		
SC0608						Ra	–	Ct	Ct	x?	x?	Ct	Ct	x?	x?	Ct	Ct	Ct
SE10117								?	Rg	Ct	?	?						
SC0943							Rm	Ca	Ca	Ca	?	?	Ct	Ct	Ct	?	?	?
Success	Un	Un	Un	Un	Un	Un	Un	Cf	Cf	Cf	Fc	Cf	Cf	Cf	Fc	Cf	Cf	Fc

We then reconstructed the life history of breeding individuals over the study period 2001–18, and produced tables with data on ringing and recaptures of different birds at different nest sites, and corresponding annual breeding success. The next step was to perform a manual analysis of the database in order to identify years when a non-recaptured bird could effectively be considered to have been probably present according to the data obtained in the previous and following years (Table 1). A bird not recaptured can either be missed, dead, skipping breeding that year, or may have moved to an inaccessible nest site.

These tables allowed analyses of nest site fidelity or mate fidelity in year t+1 according to breeding success in year t, nest site fidelity in year t+1 according to sex and breeding success in year t, as well as breeding success in year t according to nest site fidelity or mate fidelity in year t. An individual was considered to be faithful to its nest site or to its mate if it stayed in the same site or with the same mate from one year to the next. To avoid a low sample size, age classes 16–19+ and 20–33+ years were considered for birds of uncertain age. To investigate the potential effect of weight during incubation on breeding success, each individual was considered only once a year, upon its first capture on its egg. To avoid a low sample size, one bird weighing 22 g was included in the weight class of 23 g, and two birds weighing 36 g and one bird weighing 37 g were included in the weight class of 35 g.

For the first analyses (fidelity and breeding success) only breeders present for at least two consecutive years and only birds with known breeding success were considered; those with possible breeding success (i.e. success = 0.5) were removed from analyses (n = 44). For later analyses (age, weight and breeding success) all the breeders were considered even if they were not captured in the following year. All the response variables (nest site fidelity, mate fidelity and breeding success) were binary. We used generalised linear mixed models (GLMMs), which included a nested random effect for individual and pair to account for non-independence of multiple measures on the same individuals and pairs in different years (Table 2). All initial models included interactions between the explanatory variables (Table 2). Statistical analyses were performed in R using the 'lme4' package (R Development Core Team 2018), considering analysis of deviance with associated χ^2 test when necessary (Laidlaw *et al*. 2020). Before modelling, variables were tested for collinearity using the variance inflation factors (VIF) with the 'car' package in R (Fox

Table 2. Description of the structure of initial models of nest-site fidelity, mate fidelity and breeding success and all response and explanatory variables.

Model	Response	Explanatory variables
i	Nest-site fidelity t+1	Breeding success t + sex + breeding success t × sex + (1|pair/individual)
ii	Mate fidelity t+1	Breeding success t + (1|pair/individual)
iii	Breeding success t	Nest-site fidelity t + (1|pair/individual)
iv	Breeding success t	Mate fidelity t + (1|pair/individual)
v	Breeding success t	Known age + weight + known age × weight + (1|individual)
vi	Breeding success t	Uncertain age + weight + uncertain age × weight + (1|individual)

Table 3. Results of generalized linear mixed models (see Table 2 for initial model details; none of the interactions between variables had a significant effect and they were removed from the models). Significant effects ($P < 0.05$) are highlighted in bold.

Model	Fixed effects	Estimate	SE	z value	P
i Nest-site fidelity t+1	Intercept	12.404	2.837	4.372	**<0.001**
	Breeding success t	14.424	4.799	3.005	**0.003**
	Sex	-0.223	3.265	-0.068	0.945
ii Mate fidelity t+1	Intercept	1.735	0.443	3.917	**<0.001**
	Breeding success t	2.317	0.839	2.760	**0.006**
iii Breeding success t	Intercept	0.585	0.667	0.878	0.38
	Nest-site fidelity t	0.370	0.686	0.539	0.59
iv Breeding success t	Intercept	0.511	0.730	0.699	0.484
	Mate fidelity t	0.734	0.754	0.973	0.331
v Breeding success t	Intercept	-8.376	3.258	-2.571	**0.010**
	Known age	$X^2 = 5.059$	df = 13		0.974
	Weight	0.279	0.109	2.566	**0.010**
vi Breeding success t	Intercept	-1.699	1.033	-1.644	0.100
	Uncertain age	$X^2 = 19.934$	df = 14		0.132
	Weight	0.059	0.035	1.676	0.094

& Weisberg 2019). As the sample size of birds of known age with associated data on all the variables (breeding success, nest site fidelity, mate fidelity and weight) is only five birds, analyses of collinearity were conducted on two separate samples; birds of known age with associated data on breeding success and weight, and birds of known age with associated data on breeding success, nest site fidelity and mate fidelity. The variables have low collinearity, all VIF values being smaller than 1.08.

Results

Nest site fidelity and mate fidelity were very high, at 94% and 95% respectively. Breeding failure significantly negatively impacted nest site fidelity and mate fidelity (Table 3; Figure 1). Moreover, nest site fidelity was not influenced by the sex of breeding adults (Table 3; Figure 2). Two pairs were recorded as dispersing together. The first pair moved after a breeding failure in year t to another nest site in year t+1, located about 1.7 m from the previous one, which was occupied by another pair in year t+1. The second pair also moved after a breeding failure in year t to settle in the neighbouring nest cup in the same burrow in year t+1, about 20 cm from the previous one, which remained unoccupied in year t+1.

Change of nest site and change of mate had no significant effect on breeding success (Table 3; Figure 3). A lack of significance may be attributed to the low statistical power of the tests, as the sample sizes of birds changing nest site or mate were very small (Figure 3).

There was no effect of age on breeding success, for birds of known age, i.e. ringed as chicks (Table 3; Figure 4a). But there was a significant positive relationship between the weight of incubating adults and breeding success (Table 3; Figure 5a).

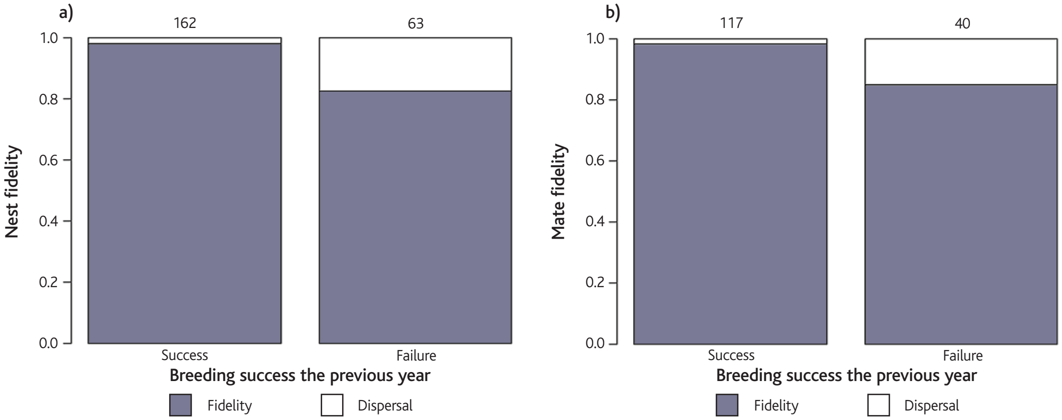

Figure 1. a) Nest site fidelity and b) mate fidelity in year t+1 according to the breeding success in year t (the sample size is shown above the graph).

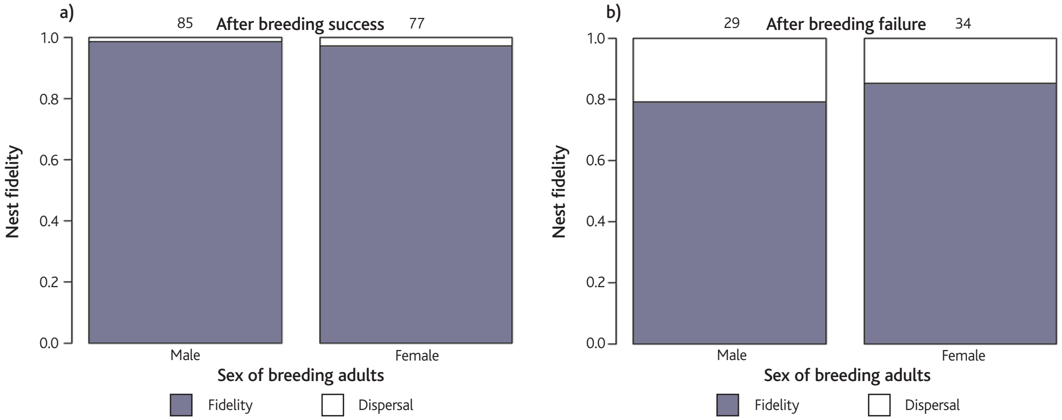

Figure 2. Nest site fidelity in year t+1 according to the sex and to a) a breeding success in year t or b) a breeding failure in year t (the sample size is shown above the graph).

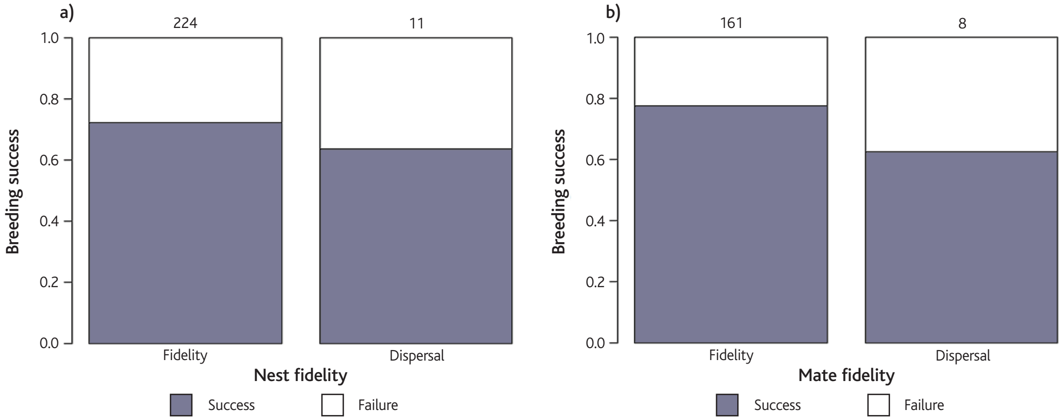

Figure 3. Breeding success in year t according to a) nest-site fidelity and b) mate fidelity in year t (the sample size is shown above the graph).

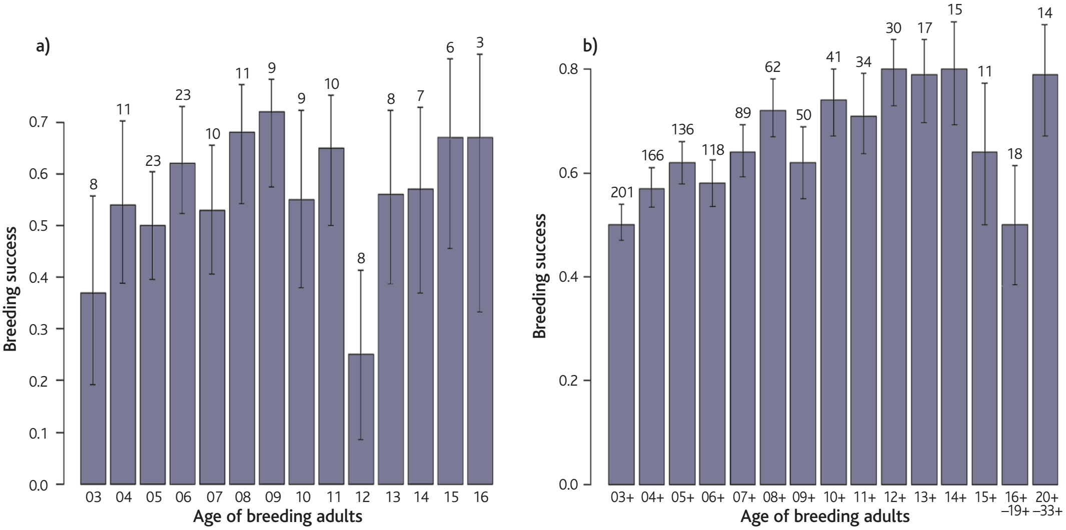

Figure 4. Mean breeding success (± S.E. and with sample size) according to age of breeding adults, a) birds of known age, i.e. ringed as chicks, and b) birds of uncertain age, i.e. mist-netted at night or ringed as breeders (the age class 20–33+ years included only one bird with 14 breeding events).

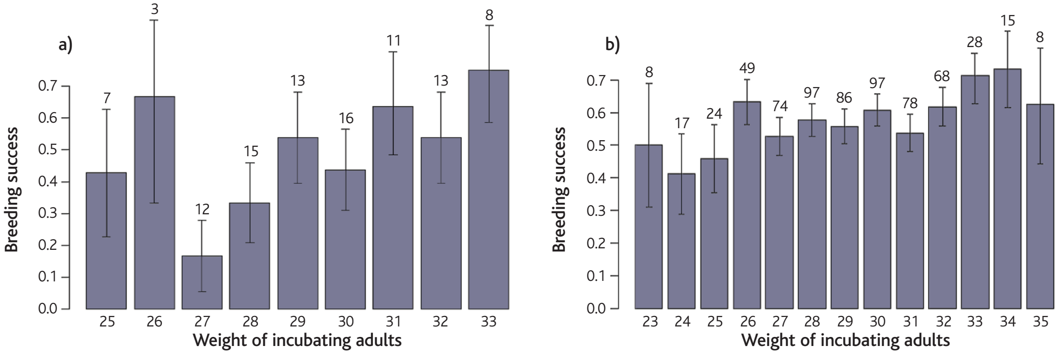

Figure 5. Mean breeding success (± S.E. and with sample size) according to the weight classes of incubating adults, a) birds of known age, i.e. ringed as chicks, and b) birds of uncertain age, i.e. mist-netted at night or ringed as breeders.

When considering all birds of uncertain age, i.e. ringed as pre-breeding prospectors or as breeders, there was no significant effect of age or weight on breeding success (Table 3; Figure 4b; Figure 5b; without the nested random effect for individual identity, age and the interaction of age × weight had significant effects). The age class 20–33+ years included only one bird with exceptionally high breeding success, which was also one of the oldest birds recorded in the Molène archipelago.

Discussion

The results showed a high level of both nest site fidelity and mate fidelity in Storm-petrels, with a very high proportion of individuals returning to the same breeding site and remaining with the same mate (Figure 1). In Procellariiformes, the high nest site fidelity and mate fidelity of breeding birds are due to the high

European Storm-petrels
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cost of divorce and the advantages of keeping the same site and the same mate (Bried *et al*. 2003). Indeed, a pair making its first breeding attempt is more likely to fail than a pair that has already bred together several times (Weimerskirch 1990). Individuals need to coordinate their incubation and foraging routines (Ollason & Dunnet 1979). Nest site fidelity and mate fidelity should then be stronger when the availability of food resources is predictable, with low individual foraging effort (Robert *et al*. 2014). The time spent at sea to acquire enough reserves to return to take over the incubation shift is on average three days for Storm-petrels, but it depends on the foraging performance of each individual. In general, the more time an individual spends at sea the more it will increase in weight (Bolton 1995). Each breeding adult must therefore decide how much time to spend at sea to acquire enough fat reserves for its incubation shift, and not leaving the mate too long at the nest. A high incidence of nest site fidelity can result from good quality breeding habitat; nest sites with better protective characteristics will be more likely to be occupied. A high proportion of mate fidelity may be due to individuals being in good condition, well-coordinated in their incubation and food search routines, or genetically compatible (Coulson 1966; Bried & Jouventin 2002; Bourgeois *et al*. 2014). Fidelity rates can be used as indicators of the state of the population, with a high rate of nest changes and divorces resulting from poor habitat and partners.

This study shows that after successful breeding, an individual remained very faithful to its nest site and its mate, whereas breeding failure significantly reduced nest site fidelity and mate fidelity, and the sex of breeding adults did not influence nest site fidelity (Figures 1 and 2). Regarding nest site fidelity, Weimerskirch (1990) and Thibault (1994) found that pairs that failed to breed were more likely to change nesting sites than those that succeed. Individuals could exchange their nest site for one with better physical characteristics for protection against the weather (Michielsen *et al*. 2019). The individuals, after a change of nest, look for a new breeding site very close to their previous nest, probably due to the bird's knowledge of their site surroundings (González-Solís *et al*. 1999). The low dispersal of breeding birds also allows them to locate their previous mate more easily (Kim *et al*. 2007). In other studies on Procellariiformes, nest changes were very often accompanied by a change of partner (Thibault 1994) and divorces were more frequent for unsuccessful breeders than for successful ones (Bradley *et al*. 1990). This higher level of divorce rate after breeding failure is also the case in our study area.

The nest can be used as a meeting point for pairs. In this way, an individual can easily locate its previous mate when it returns to the colony (Bried *et al*. 2003). As a result, mate fidelity is more likely to occur when nest site fidelity is high (Bourgeois *et al*. 2014). However, mate fidelity is not only a consequence of nest site fidelity but is an answer to different selective forces (Pyle *et al*. 2001). A change of partner may be due to the death or the dispersal of a member of the pair, to asynchronous arrival of members of the pair, or to the decision of a bird to mate with another individual (Ismar *et al*. 2010), which is related to the availability of better mating options (Ens *et al*. 1993). An individual's decision to mate with a new partner can improve breeding success by improving their compatibility through parental coordination (Coulson 1966) or by eliminating the disadvantage of consanguinity (Hatchwell *et al*. 2000). Storm-petrels will change mates after breeding failure, in order to be with a mate that is genetically compatible, or that has good parenting skills to increase reproductive performance (Robert *et al*. 2014). Our study has shown that changing nest site or mate did not significantly influence breeding success (Figure 3). In other seabird species, a change of partner has induced a decline in breeding success, which is primarily due to poor coordination of the new pair (Bradley *et al*. 1990; Naves *et al*. 2007). Having a new partner may reduce the efficacy of breeding behaviour, which may in turn decrease the likelihood of breeding success (Sommerfeld *et al*. 2015). In addition, after separating, birds will have a reduced chance of breeding the following year, due to disruption of the pair-bond and the time taken to find and bond with a new mate (Naves *et al*. 2007). Divorces can then be responsible for years of non-breeding in Storm-petrels. However, our study did not allow us to evaluate this phenomenon because not all breeding individuals were seen every year, so an individual that was not seen post-divorce did not necessarily mean a failure to breed that year.

In this study, there was an effect of the weight of incubating adults on the reproductive performance of Storm-petrels, but only for birds of known age (Figure 5). Body condition influences reproduction in pelagic seabirds (Chastel *et al*. 1995). The weight of an individual reflects its foraging efficiency, which allows it to accumulate fat reserves whilst incubating, as well as to provide sufficient food to the chick so that it fattens rapidly, and thus can cope with periods of food shortage, since the food resources for Storm-petrels in the marine environment are scarce and unpredictable (Ricklefs 1990). Individuals do not incur the risk of reproduction if the cost is such that it impacts on their own survival. Instead they may skip breeding in order to increase their chances of breeding success the following year (Boersma & Wheelwright 1979). Therefore, if their condition falls below a particular threshold at an early stage, with an insufficient food supply, birds will refrain from breeding or abandon breeding (Chastel *et al*. 1995). In our study, breeding success did not appear to be affected by the age of Storm-petrels (Figure 4), as shown in other studies on long-lived birds, related to increased breeding capacity and experience (Weimerskirch 1990). Thus, additional data should be collected in the future to increase the sample size in order to re-evaluate the potential effect of age on breeding success, as well as to investigate the effects of senescence (Pyle *et al*. 2001).

Our results suggest that breeding success positively influences nest site fidelity and mate fidelity. The high level of nest site fidelity and mate fidelity indicates good population status, with good quality breeding habitat and good quality partners (Bried & Jouventin 2002).

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