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► **To cite this version:**

Christophe Barbraud, Karine Delord. Selection against immigrants in wild seabird populations. *Ecology Letters*, 2020, 24 (1), pp.84-93. 10.1111/ele.13624 . hal-04463032

**HAL Id: hal-04463032**

**<https://hal.science/hal-04463032v1>**

Submitted on 20 Feb 2024

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1 **Selection against immigrants in wild seabird populations**

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3

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5

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7

8 *Short title:* Immigrants have lower fitness than residents

9 *Keywords:* dispersal, fitness, immigrant, seabirds, sex-biased dispersal

10 *Type of article:* Letters

11 *Number of words in the abstract:* 150

12 *Number of references:* 57

13 *Number of figures and tables:* 6

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15

16 *Statement of authorship:* CB conceived the ideas and designed the methodology. CB and KD  
17 analyzed the data. KD collected, cleaned and managed the data. CB wrote the manuscript with  
18 input from KD.

19

20 *Data accessibility statement:* should the manuscript be accepted, the data supporting the  
21 results will be archived in an appropriate repository (Dryad, Figshare or Hal) and the data  
22 DOI will be included at the end of the article.

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26 **Abstract**

27 Immigration is a major demographic parameter shaping population dynamics and is an  
28 important driver of eco-evolutionary patterns, but the fitness consequences for individuals  
29 following their settlement to a new population (immigrants) remain poorly tested in wild  
30 animal populations, particularly among long-lived species. Here we show that immigrants  
31 have a lower fitness than residents in three wild seabird populations (wandering albatross  
32 *Diomedea exulans*, southern fulmar *Fulmarus glacialisoides*, snow petrel *Pagodroma nivea*).  
33 Across all species and during a 32-year period, immigrants made on average -9-29% fewer  
34 breeding attempts, had 5-31% fewer fledglings, had 2-16% lower breeding success and  
35 produced 6-46% fewer recruits. Female immigration and male residency were also favored  
36 through differences in breeding performance. We provide evidence for selection against  
37 immigrants in wild populations of long-lived species and our results are consistent with  
38 female-biased dispersal in birds being driven by asymmetric limiting resources and the  
39 competitive ability of dispersers *versus* non-dispersers.

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51 **INTRODUCTION**

52

53 Dispersal is a crucial driver of ecological and evolutionary patterns because of its direct  
54 implication on processes such as gene flow, effective population size, genetic drift, local  
55 adaptation, inbreeding, colonization and viability of populations and species (Clobert *et al.*  
56 2001). Among the various aspects of dispersal, theoretical and empirical studies suggest that  
57 immigrant fitness following settlement to a new population may play an important role in  
58 population genetic processes such as local adaptation and speciation (Slatkin 1985; Hendry  
59 2004; Nosil *et al.* 2005; Clobert *et al.* 2012), and in population persistence and resilience  
60 (Ward 2005; Lowe & Allendorf 2010; Schaub *et al.* 2013). Although many empirical studies  
61 have compared immigrants (successful between-population dispersers) and residents  
62 (individuals remaining in their natal population) performance in wild animals, settlement  
63 costs of dispersal are poorly documented and the overwhelming majority of these studies  
64 focused on a single demographic trait (generally survival or number of offspring) used as a  
65 fitness proxy (Bonte *et al.* 2012). However, immigrant and resident performance may be trait-  
66 specific (Bensch *et al.* 1998) and since fitness integrates several demographic components,  
67 single trait approaches may be misleading. Furthermore, the few studies that compared  
68 immigrant and resident fitness using multiple traits approaches are strongly biased towards  
69 short-lived species (Verhulst & Van Eck 1996; Bensch *et al.* 1998; Hansson *et al.* 2004;  
70 Martinig *et al.* 2020; but see Oro *et al.* 2011). This is due to a lack of empirical data which are  
71 difficult to collect in wild animal populations as it requires both identifying true immigrants in  
72 study populations and the following of their survival and fecundity over multiple years. This  
73 is extremely challenging in long-lived species, and more particularly in species with great  
74 potential for long-range dispersal such as seabirds (Inchausti & Weimerskirch 2002). In  
75 addition, contrary to species with short generation time, long-lived species generally spend

76 several years exploring their environment before recruiting (Weimerskirch 2001). During  
77 these years they may get familiarized with new environments and acquire the same skills as  
78 residents. Therefore, there is a major research gap regarding our understanding of the  
79 performance of immigrants and residents in long-lived species based on multiple trait  
80 approaches.

81       Sexes also often differ in the propensity and/or distance of dispersal (Trochet *et al.* 2016).  
82 Females disperse more frequently and further away than males in birds, the opposite pattern  
83 being typical in mammals, while unclear patterns are observed in other species. Theoretical  
84 studies have proposed several hypotheses to explain sex-biased dispersal (Greenwood 1980;  
85 Perrin & Mazalov 1999; Li & Kokko 2019), the prevailing ones being asymmetric limiting  
86 resources, within- and across-generation kin competition, inbreeding avoidance, fitness  
87 variance and effects of genetic architecture, but extremely few have explicitly integrated the  
88 reproductive value of an immigrant male or female relative to that of a philopatric individual  
89 of the same sex (Perrin & Mazalov 1999). In all cases, empirical information on the relative  
90 fitness of immigrants and residents in relation to sex is generally lacking (Martinig *et al.*  
91 2020) and is needed to test predictions from theoretical models.

92       Here, we use long-term demographic data over a 32-year period for three long-lived  
93 seabird species (the wandering albatross *Diomedea exulans*, southern fulmar *Fulmarus*  
94 *glacialoides* and snow petrel *Pagodroma nivea*) to investigate whether immigrants and  
95 residents differ in four metrics of fitness after recruitment. We first use capture-mark-  
96 recapture data to estimate four key demographic rates - probabilities of survival, breeding (i.e.  
97 laying an egg), hatching an egg and fledging a chick - of immigrants and residents by  
98 considering different breeding states and accounting for imperfect recapture probability.  
99 Second, we test whether demographic rates differ between immigrants and residents for each  
100 species and each sex. Third, we estimate and compare four metrics of individual fitness for

101 immigrants and residents: number of breeding events, defined as the total number of  
102 occasions spent by an individual in the breeding state; number of offspring fledged, defined as  
103 the total number of offspring fledged by an individual; breeding success, defined as the ratio  
104 between number of offspring fledged and number of breeding events; and number of recruits,  
105 defined for each individual as the total number of offspring fledged that recruited in the study  
106 population.

107

## 108 **MATERIALS AND METHODS**

109

### 110 **Study areas**

111 Wandering albatrosses were monitored at Ile de la Possession (46°24'S, 51°46'E), Crozet  
112 archipelago, south western Indian Ocean. Wandering albatrosses nest in loose aggregations  
113 forming eight breeding colonies that are located in flat boggy areas on the northern and  
114 eastern coasts of the island. The population had *c.* 500 breeding pairs in the 1960s, declined  
115 steeply in the 1970s to reach 260 pairs and increased progressively to 390 pairs in 2017  
116 (Weimerskirch *et al.* 2018).

117 Southern fulmars were monitored on Ile des Pétrels (66°40'S, 140°01'E), Pointe  
118 Géologie archipelago, Terre Adélie, Antarctica. Fulmars nest in a dense aggregation at a  
119 single colony on a rocky cliff on the island. The population has increased from 30 breeding  
120 pairs in the early 1960s to 55 in 2017 (Jenouvrier *et al.* 2003).

121 Snow petrels were monitored on the Pointe Géologie archipelago, Terre Adélie,  
122 Antarctica. Snow petrels nest in cracks or under boulders situated in rocky areas on eight  
123 islands (which vary in size from 2 to 20 ha) of the archipelago, either in dense colonies or in  
124 loose aggregations. The population is relatively stable with 440 breeding pairs on the Ile des

125 Pétrels and 213 pairs breeding on the other islands of the Pointe Géologie archipelago in 2017  
126 (Micol & Jouventin 2001).

127 For all species the nearest neighbouring breeding populations outside the Ile de la  
128 Possession and the Pointe Géologie archipelago are shown on Figure 1.

129

### 130 **Data collection and identification of immigrants**

131 Long-term capture-mark-recapture monitoring of wandering albatross started in 1965 and of  
132 southern fulmar and snow petrel in 1963 (Supplementary material S1). To be considered as a  
133 resident, an individual had to be born in the population (i.e. Ile de la Possession for wandering  
134 albatrosses, Ile des Pétrels for southern fulmars and Pointe Géologie archipelago for snow  
135 petrels) and recorded as having successfully recruited (i.e. acquired a nest site and breeding)  
136 or successfully returned (i.e. acquired a nest site and not breeding) to their natal population in  
137 at least one census during the years following their birth. To be considered an immigrant, an  
138 individual had to be unringed at first capture and recorded as having successfully recruited  
139 (i.e. acquired a nest site and breeding) or successfully returned (i.e. acquired a nest site and  
140 not breeding) to the studied populations defined above (i.e. Ile de la Possession, Ile des Pétrels  
141 and study colonies for wandering albatrosses, southern fulmars and snow petrels,  
142 respectively) (Supplementary material S2).

143 The accuracy with which we distinguish immigrants relies on how successfully all nests  
144 were found and all chicks were ringed in the study populations. We are confident that over the  
145 study periods during which systematic chick ringing occurred (1965-2017, 1963-2017 and  
146 1990-2017 for wandering albatrosses, southern fulmars and snow petrels, respectively) chicks  
147 in at least 99% of successful nests of wandering albatrosses, 100% of successful nests of  
148 southern fulmars and 95% of successful nests of snow petrels were ringed. Reasons for this  
149 high efficiency at ringing fledglings are: 1) fieldworkers visited the colonies of the three

150 species each year since the initiation of the long-term studies thanks to the unconditional  
151 support of the French Polar Institute; 2) all species are conspicuous and nests are unlikely to  
152 be missed by observers; 3) multiple visits were made to breeding colonies during each  
153 breeding season; 4) small area and size of the southern fulmar colony; 5) well defined area of  
154 wandering albatross colonies; 6) all detected nest sites of snow petrel in the Pointe Géologie  
155 archipelago have been marked with paint since the beginning of the monitoring of the entire  
156 archipelago in 1990. Since immigrants were unringed at their first capture, their age was not  
157 known. Therefore, we assumed immigrants were the same age as residents at return or  
158 recruitment.

159

### 160 **Modelling vital rates**

161 We considered observations of residents and immigrants monitored during the period 1985-  
162 2017 for wandering albatrosses and southern fulmars, and during the period 2004-2017 for  
163 snow petrels to build encounter histories. For every individual, its encounter history started at  
164 the first return to breed at a study population. The sex of each individual was known for  
165 wandering albatrosses and snow petrels. We analyzed the capture histories of 1748 female  
166 wandering albatrosses (335 immigrants and 1413 residents), 1665 male wandering albatrosses  
167 (234 immigrants, 1431 residents), 395 southern fulmars (160 immigrants and 235 residents),  
168 158 female snow petrels (95 immigrants and 63 residents), and 127 male snow petrels (79  
169 immigrants and 48 residents). To estimate demographic parameters and fitness while taking  
170 into account imperfect detectability of marked individuals, we used multi-state capture-mark-  
171 recapture (MSCMR) models (Brownie *et al.* 1993; Lebreton *et al.* 2009).

172 For southern fulmars and snow petrels we estimated the following demographic  
173 parameters: survival probability ( $\Phi$ ) as the probability that an individual survives from year  $t$   
174 to  $t+1$ , breeding probability ( $\beta$ ) as the probability that an individual breeds (i.e. lay an egg) in



175 year  $t+1$  given that it survived, hatching probability ( $\delta$ ) as the probability that an individual  
176 hatches its egg in year  $t+1$  given that it bred and survived, fledging probability ( $\gamma$ ) as the  
177 probability that an individual fledges a chick in year  $t+1$  given that it hatched its egg, bred and  
178 survived, and recapture probability ( $p$ ). To do so, we constructed a MSCMR model  
179 (Supplementary material S3 and Fig. S1) with five states consisting of one non-breeder state  
180 (NB), three breeder states [failed breeder at the egg stage (FBE), failed breeder at the chick  
181 stage (FBC), successful breeder (SB)], and the dead state ( $\dagger$ ). Capture histories were coded  
182 considering five events corresponding to field observations: 0 = not observed, 1 = seen as NB,  
183 2 = seen as FBE, 3 = seen as FBC, 4 = seen as SB. The dead state was not observable.

184 Since wandering albatrosses have a quasi-biennial breeding strategy (Barbraud &  
185 Weimerskirch 2012), we estimated an additional parameter for this species: the return  
186 probability ( $\rho$ ) as the probability that an individual returns to its nest in year  $t+1$  given that it  
187 survived. To do so, we constructed a MSCMR model (Supplementary material S3 and Fig.  
188 S2) with eight states consisting of one non-breeder state (NB), three breeder states [failed  
189 breeder at the egg stage (FBE), failed breeder at the chick stage (FBC), successful breeder  
190 (SB)], three non-observable states [post-non-breeder state (PNB), post-failed breeder state  
191 (PFB), post-successful breeder state (PSB)], and the dead state ( $\dagger$ ). Capture histories were  
192 coded as for the two other species. The dead state was not observable.

193 First, we developed null models for each species where all parameters were state  
194 dependent but were equal between immigrants and residents, and where all mathematical  
195 parameters were identifiable. To allow parameter identifiability, for southern fulmars and  
196 snow petrels, the underlying parameters  $\Phi$ ,  $\beta$ ,  $\delta$ ,  $\gamma$  describing the transition probabilities to and  
197 from aggregated breeding states FBE, FBC and SB (but not NB) were the same. Thus, only  
198 the underlying parameters for the non-breeding and breeding states were distinguished. For  
199 wandering albatrosses, the underlying parameters  $\Phi$  from aggregated breeding states FBE,

200 FBC, SB, PNB, PFB and PSB were the same (the state NB was kept separate), and the  
201 underlying parameters  $\rho$ ,  $\beta$ ,  $\delta$ ,  $\gamma$  were the same to and from the following state aggregations  
202 (FBE, FBC, SB), (PNB, PFB, PSB), and NB. Thus, only the non-breeding and breeding states  
203 were distinguished for parameter  $\Phi$ , and non-breeding, breeding and post-breeding states  
204 were distinguished for the other demographic parameters. Recapture probabilities were  
205 entirely state and time dependent. All the mathematical parameters were estimated for these  
206 models, which were considered as appropriate for further modelling.

207 Second, the goodness of fit tests (GOF) for multistate models (Pradel *et al.* 2003) were  
208 performed on the null models using the software U-Care (Choquet *et al.* 2009a) to test  
209 whether these models fitted the data. We ran the test on the JollyMoVe (Brownie *et al.* 1993)  
210 umbrella model for multistate data (see Supplementary material Table S1).

211 Third, we performed model selection using program E-SURGE (Choquet *et al.* 2009b) to  
212 test for the effects of group (immigrant vs resident) on demographic rates and recapture  
213 probability. Model selection was done using the Akaike Information Criterion (AICc)  
214 (Burnham & Anderson 2002). First, we considered that model  $i$  received better support  
215 compared to the null model when the  $\Delta\text{AICc}$  was  $< -2$ , where  $\Delta\text{AICc} = \text{AICc}_i - \text{AICc}_{\text{null model}}$   
216 (Burnham & Anderson 2002). Second, and following (Anderson & Burnham 2002) and  
217 (Arnold 2010), we report all models and discuss support of alternative models depending on  
218 the level of reduction in deviance vs the null model. If an alternative model was within 2  
219 AICc units from the null model and with a very similar value of the deviance we considered  
220 model  $i$  as not supported (Burnham & Anderson 2002). Thus, we considered immigrants and  
221 residents did not differ. We first modelled the recapture probability and then the demographic  
222 parameters one by one.

223

224 **Estimating fitness**

225 We estimated four parameters as different metrics for individual fitness. First, we used the  
226 total number of offspring fledged by an individual (NOF) during the study period. We used  
227 the counting algorithm to estimate NOF (Rouan *et al.* 2009). This method takes into account  
228 the uncertainty about the reproductive status when the individuals are not detected or when  
229 the reproductive status cannot be assessed. The method uses the parameters of the MSCMR  
230 model estimated using program E-SURGE and applies them to each encounter history so as to  
231 provide for each encounter history the probability that an underlying state  $s$  has occurred  $n$   
232 times between the first capture and the last capture occasion. From these, the average number  
233 of occasions in state  $s$  can be calculated. NOF is then estimated as the sum of the number of  
234 occasions in the state successful breeder during the study period.

235 Second, we used the number of breeding events (NBE), defined as the number of years  
236 spent by an individual in the breeding state. NBE was estimated using the same method as  
237 NOF, and was the sum of the number of years in any of the breeder states during the study  
238 period.

239 Third, we used average breeding success (BS), defined as the average number of  
240 offspring fledged per breeding attempt. BS was calculated as the ratio NOF/NBE.

241 We calculated NOF, NBE and BS for immigrants and residents using models where  
242 recapture probabilities were the same for immigrants and residents and all other demographic  
243 parameters differed (see model selection results). To take uncertainty of demographic  
244 parameter estimates into account and to test for differences in NOF, NBE and BS between  
245 immigrants and residents we used the parametric bootstrap for the counting algorithm with  
246 100 bootstrap samples. We then used Student's t-tests or Mann-Whitney rank sum tests to test  
247 for differences in NOF, NBE and BS between immigrants and residents. Estimates are  
248 reported as means  $\pm$  1 SE. Significance was set at  $\alpha = 0.05$ . All NOF and NBE estimates were  
249 performed using program E-SURGE.

250 Fourth, we used the number of recruits (NRC), defined for each individual as the total  
251 number of offspring fledged that recruited in the study population during the study period.  
252 Recruits are offspring recaptured as breeding at the study sites. Since recapture probability  
253 was high ( $> 0.90$ ) for breeding individuals of the three studied species, we are confident that  
254 the observed number of local recruits was close to the true number of recruits. The  
255 distribution of the number of recruits showed a high number of zero values (i.e. a high  
256 number of individuals produced no recruits). We thus fitted zero-inflated negative binomial or  
257 Poisson distribution generalized mixed effect models with ‘year’ as a random effect using the  
258 “glmmTMB” package in R (Brooks *et al.* 2017) to test for statistically significant differences  
259 in NRC between residents and immigrants while controlling for random annual variation. We  
260 used the function “fitdist” from the package DHARMA to assess the fit of residuals (see Fig.  
261 S1; Fig. S2; Fig. S3). NRC was only estimated for southern fulmars and wandering  
262 albatrosses. Indeed, snow petrel data set covered the period 2004-2017 (see above), and since  
263 mean age at first breeding is 9.9 (min: 5, max: 14) years (Chastel *et al.* 1993), there were too  
264 few recruits to perform this analysis.

265

## 266 **RESULTS**

267

268 We recorded 3134 residents and 874 immigrants for all species and sexes combined. The  
269 mean ( $\pm 1$  SE) annual immigration rate, estimated as the proportion of recruits that were  
270 immigrants as opposed to residents in the studied areas, was  $0.157 \pm 0.054$ ,  $0.623 \pm 0.036$  and  
271  $0.348 \pm 0.038$  for wandering albatrosses, snow petrels and southern fulmars, respectively.  
272 Despite annual fluctuations there was no temporal trend in immigration rates (linear models:  
273 southern fulmar,  $P = 0.085$ ; wandering albatross,  $P = 0.361$ ; snow petrel,  $P = 0.223$ ).

274

## 275 **Modelling vital rates**

276 Model selection provided strong evidence that recapture probabilities did not differ between  
277 immigrants and residents for the three species (Supplementary material Table S2). There was  
278 also strong evidence that several demographic parameters differed between immigrants and  
279 residents, including fledging probability in male snow petrels (model M17), hatching  
280 probability in female snow petrels (M24), and breeding probability in southern fulmars (M31)  
281 (Table S2). For several other parameters, although  $\Delta\text{AICc}$  were  $< 2$ , there was reduction in  
282 deviance for alternative models compared to the null models, supporting differences between  
283 immigrants and residents (Table S2). For male wandering albatrosses reduction in deviance  
284 for models M4 and M7 compared to M1, suggested that immigrant males had lower hatching  
285 ( $0.716 \pm 0.052$ ) and survival ( $0.946 \pm 0.009$ ) probabilities than residents ( $0.794 \pm 0.015$  and  
286  $0.962 \pm 0.003$ , respectively), particularly for individuals that were breeders the previous year  
287 (Fig. 2). For female wandering albatrosses, there was support for lower hatching, breeding  
288 probability and survival probabilities (but higher return probability) for immigrants (Table S2  
289 models M11, M12, M13, M14; Fig. 2). For male snow petrels, there was support for lower  
290 survival probability for immigrants, but higher breeding probability (Table S2 models M17,  
291 M18, M20; Fig. 3a). For female snow petrels, there was support for lower breeding  
292 probability for immigrants (Table S2, models M24, M25; Fig. 3b). For southern fulmars, there  
293 was support for lower fledging and hatching probabilities for immigrants (Table S2, models  
294 M29, M30, M31; Fig. 3c). Overall, differences in deviance,  $\Delta\text{AICc}$  values and parameter  
295 estimates provided moderate to strong evidence for higher demographic performance of  
296 residents, and for a few demographic parameters immigrants outperformed residents  
297 (breeding probability in male snow petrels and hatching probability in female snow petrels).

298

## 299 **Estimating fitness**

300 Across all species, immigrants made on average 4-29% fewer breeding attempts and had 6-  
301 31% fewer fledglings relative to immigrants (Fig. 4a, 4b). Only immigrant southern fulmars  
302 made 9% more breeding attempts than residents, and immigrant female snow petrels had 7%  
303 more fledglings than residents (Fig. 4a, 4b). Breeding success across all species showed that  
304 immigrants had 2-16% lower success than residents (Fig. 4c).

305 The sex ratio for immigrants was female biased (58.9% females,  $n = 569$ , binomial test  $P$   
306  $< 0.001$ ) in wandering albatrosses (but not for residents: 49.7%,  $n = 2844$ , binomial test  $P =$   
307 0.750) and the sex ratio for immigrant and resident snow petrels was not significantly biased  
308 (immigrants: 54.6%,  $n = 174$ , binomial test  $P = 0.255$ ; residents: 56.8%,  $n = 111$ , binomial  
309 test  $P = 0.184$ ), but sample sizes were relatively small. Immigrant males made on average 8-  
310 37% fewer breeding attempts and produced 17-38% fewer fledglings relative to resident  
311 males (Fig. 4a, 4b). The same differences were observed between immigrant and resident  
312 females (1-21% fewer breeding attempts and -7 to 23% fewer fledglings; Fig. 4a, 4b),  
313 although these differences were lower than in males by a factor of 1.8-13.7 and 1.6-3.4,  
314 respectively. Immigrant males had 2-10% lower breeding success than residents, immigrant  
315 female wandering albatrosses had 3% lower breeding success than residents, but immigrant  
316 female snow petrels had 7% higher breeding success than residents (Fig. 4c).

317 On average, immigrant individuals produced 6-46% fewer recruits than residents (male  
318 wandering albatrosses: 45.9%; female wandering albatrosses 16.5%; southern fulmars 6.4%;  
319 Fig. 5). However, differences were only statistically significant for wandering albatrosses  
320 (Table 1). A higher proportion of immigrant albatrosses failed to produce recruits compared  
321 to residents (females:  $P = 0.044$ ; males:  $P < 0.001$ ). Among individuals that produced at least  
322 one recruit, residents tended to produce more recruits than immigrants (Fig. 5) but the  
323 differences were not statistically significant for all species and sexes (Table 1).

324

## 325 **DISCUSSION**

326

327 Direct comparison of four fitness metrics of immigrants and residents among three seabirds  
328 enabled us to assess fitness costs after dispersal in long-lived species. Immigrants had  
329 generally lower fitness than residents. This is in line with the results from a previous study on  
330 fish (Peterson *et al.* 2014) and some studies of birds (Verhulst & Van Eck 1996; Bensch *et al.*  
331 1998) and mammals (Martinig *et al.* 2020), but is not consistent with others (birds: Gienapp  
332 & Merilä 2011; Germain *et al.* 2017; mammals: Waser *et al.* 2013). In another long-lived  
333 species, the Audouin's gull *Larus audouinii*, Oro *et al.* (2011) compared fitness components  
334 among residents and immigrants and found differences in recapture probabilities, suggesting  
335 higher site-tenacity for residents than for immigrants, but similar survival and recruitment.  
336 However, they did not use integrative metrics such as ours to estimate fitness. Since high  
337 dispersal ability is related to several aspects of fast life-history strategies (Stevens *et al.* 2012,  
338 2014; Beckman *et al.* 2018) one may expect lower costs of dispersal in short-lived species  
339 (whose life-history traits should be shaped for dispersal) than in long-lived species. Also, the  
340 predicted and observed negative co-variation between spatial and temporal dispersal across  
341 species (Buoro & Carlson 2014) may suggest lower costs of spatial dispersal for short-lived  
342 species, as long-lived species typically achieve temporal dispersal through age structure and  
343 iteroparity. However, strong association between high dispersal and high fecundity, but also  
344 positive association with survival rate, points towards complex dispersal-related life-history  
345 syndromes, whose demographic consequences remain very poorly known and require further  
346 research (Buoro & Carlson 2014; Stevens *et al.* 2014).

347 Differences in demographic parameters between immigrants and residents suggest that  
348 this selection against immigrants resulted from both immigrant inviability (Nosil *et al.* 2005)  
349 and immigrant infecundity (Smith & Benkman 2007) (most frequently, immigrants were less

350 successful at fledging chicks and, to a lesser extent, bred less frequently and hatched fewer  
351 eggs). It should be noted that these are apparent survival estimates, thus confounding true  
352 mortality and permanent emigration. Therefore, the lower apparent survival of immigrants  
353 relative to residents may be due to higher mortality and/or higher emigration from the study  
354 sites. Nevertheless, dispersal of breeding wandering albatrosses outside the study area is  
355 extremely low (Inchausti & Weimerskirch 2002). Likewise, the lower number of recruits  
356 produced by immigrants might partly result from differential emigration rather than survival if  
357 immigrants have offspring that are more likely to recruit elsewhere. This has been found in a  
358 handful of species (Hansson *et al.* 2003), including the wandering albatross although only on  
359 short spatial scales between neighboring colonies (Charmantier *et al.* 2011). Due to lower  
360 fitness of immigrants, we conclude that gene flow was lower than immigration rate. However,  
361 this is unlikely to promote genetic differentiation between populations of the studied species  
362 since the proportion of immigrant recruits was high compared to the level of gene flow  
363 necessary to maintain panmictic populations (one effective immigrant per generation). Indeed,  
364 populations of wandering albatrosses exhibit little genetic differentiation across the species'  
365 range (Milot *et al.* 2008) as do populations of snow petrels in East Antarctica (Carrea *et al.*  
366 2019). Nevertheless, our results imply a lower contribution of immigrant recruits in  
367 population dynamics as compared with resident recruits.

368       Minimum dispersal distances for immigrants belonging to the three studied species  
369 ranged from 23 to 175 km, depending on the species considered. Our analyses thus suggest  
370 that individuals potentially immigrating from relatively short distances (for seabirds) can  
371 experience lower fitness following settlement (Hansson *et al.* 2004). For wandering  
372 albatrosses, which have been marked at other breeding localities, we recorded in our study  
373 population one immigrant from Ile de l'Est (23 km, Crozet archipelago), four from Marion  
374 Island (1070 km), seven from Kerguelen Islands (1320 km) and one from South Georgia



375 (6030 km). However, these numbers are unlikely to reflect site-specific immigration rates  
376 since there are massive differences in ringing effort between the various source populations.  
377 Thus, given the dispersal pattern observed in the wandering albatross (Inchausti &  
378 Weimerskirch 2002; Charmantier *et al.* 2011) most immigrants probably came from other  
379 islands of the Crozet archipelago. We recorded one immigrant snow petrel from Casey station  
380 (1300 km east of Pointe Géologie), but snow petrels and southern fulmars were marked at  
381 only a tiny proportion of their populations.

382         The lower fitness of immigrants relative to residents may result from local adaptation  
383 with immigrants maladapted to their new environment, but also to several nongenetic effects.  
384 Immigrants might be less competitive individuals that were unable to remain in their original  
385 environment due to external conditions (Clobert *et al.* 2009), the act of dispersal itself might  
386 be costly and could have carry-over effects after settlement in the new environment, and  
387 success in the new environment might first require familiarity with the local environment and  
388 its residents (Bonte *et al.* 2012). In seabirds, costs associated with dispersal following  
389 settlement could thus be opportunity costs (e.g. loss of evolutionary acquired advantages  
390 when settling in a new habitat, unfamiliarity with new foraging areas, poor knowledge of  
391 high-quality nesting sites) and risk costs (e.g. higher predation risk in a new breeding colony,  
392 new interactions with con- or heterospecifics due to conflicts for nest occupation) (Bonte *et*  
393 *al.* 2012). Although disentangling the relative importance of these proximate causes deserves  
394 further investigation and was outside the scope of this study, our results support theoretical  
395 predictions for how selection might favor the philopatric behaviour of seabirds (Coulson  
396 2016), which has intrigued biologists due to their high mobility, particularly in albatrosses and  
397 petrels (Pinaud & Weimerskirch 2007).

398         The costs of emigrating to new colonies appear to be less for female than male seabirds.  
399 Indeed, relative to residents, fitness losses of immigrant females were relatively lower than

400 those observed in males. Immigrant female snow petrels even had higher number of chicks  
401 fledged and breeding success than residents. This smaller disadvantage (or advantage in the  
402 case of snow petrels) to immigration in females is in line with what would be expected if the  
403 benefits of remaining philopatric were sex dependent and in favor of female-biased dispersal,  
404 as generally observed in birds (Greenwood 1980; Li & Kokko 2019). The hypothesis of  
405 asymmetric limiting resources predicts that sex-biased dispersal may evolve when the  
406 familiarity with local environments benefits one sex more than the other in competition with  
407 same-sex individuals (Greenwood 1980; Li & Kokko 2019). The sex that benefits more  
408 from familiarity with local environment in competition with same-sex individuals should  
409 remain philopatric, with higher costs of dispersal for the sex that is responsible for territory  
410 acquisition, and lower competitive success of dispersers (Perrin & Mazalov 1999). In  
411 seabirds, including the three species studied here, prospecting for nest sites, defense of  
412 territories against competitors or predators are overwhelmingly performed by males (Nelson  
413 & Baird 2001). Our results are thus in line with the hypothesis of female-biased dispersal  
414 being driven by asymmetric limiting resources and the competitive ability of dispersers *versus*  
415 non-dispersers.

416 This study provides clear evidence of lower fitness of immigrants in several long-lived  
417 species. One important implication of our results is that estimates of realized gene flow can be  
418 biased if the poor reproductive performance of immigrants is not accounted for, with potential  
419 consequences for estimates of population structure (Bossart & Prowell 1998). In species such  
420 as seabirds structured in dynamic metapopulations, reduced immigrant fitness may contribute  
421 to the maintenance of intraspecific diversity in addition to previously known factors (Friesen  
422 2015). Reduction in gene flow can also help maintain local adaptation and functional diversity  
423 (Nunes & Bugoni 2018). Our definition of immigrants was straightforward for colonial  
424 nesting species such as seabirds. However, for territorial species that do not breed in colonies,

425 immigration costs may be more challenging to measure and vary as a function of dispersal  
426 distance (Hansson *et al.* 2004; Bonte *et al.* 2012). This requires further research on species  
427 with different lifestyles and across the slow-fast gradient of life-histories. Furthermore, in  
428 males, immigrants were more likely to experience proportionally greater fitness reduction  
429 than residents compared to females, supporting the idea that sex-biased dispersal patterns are  
430 understandable in light of sex-specific costs and benefits of philopatry in birds (Greenwood  
431 1980; Li & Kokko 2019). These findings raise unanswered questions about the nature of  
432 behavioral mechanisms associated with lower immigrant fitness, which poses a major  
433 challenge both logistically and methodologically.

434

## 435 **Acknowledgements**

436 We thank all the fieldworkers who participated in the long-term studies since 1963 as part of  
437 the program IPEV 109 “Seabirds and marine mammals as sentinels of global changes in the  
438 Southern Ocean” (PIs H. Weimerskirch, P. Jouventin, J.L. Mougín). We thank D. Joubert for  
439 data management. We are grateful to Y. Cherel and four anonymous reviewers for  
440 constructive comments on earlier drafts of the manuscript. Data were collected with the  
441 logistical and financial support from Institut Polaire Français, Paul-Emile Victor (IPF), Terres  
442 Australes et Antarctiques Françaises and Zone Atelier Antarctique et Terres Australes  
443 (LTSER France).

444

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587 **Figure legends**

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590 **Figure 1** Map showing the two main study areas a, Ile de la Possession within the Crozet  
591 archipelago for wandering albatrosses, and b, Pointe Géologie archipelago on the Terre  
592 Adélie coast for southern fulmars and snow petrels. Numbers are breeding pairs from  
593 Weimerskirch *et al.* (2018) [wandering albatross]; Law (1962) for LI, Barbraud *et al.* (1999)  
594 for SA, 2017 for PG [southern fulmar]; Barbraud *et al.* (1999) for CP, CJ, CH, SA, and 2017  
595 for PG [snow petrel]. PG: Pointe Géologie; CB: Cap Bienvenue; CJ: Cap Jules; CH: Cap  
596 Hunter; SA: Stillwell archipelago; LI: Lewis Island. Numbers in grey indicate southern  
597 fulmars. Stars indicate location of study colonies.

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600 **Figure 2** Demographic parameters of immigrant and resident wandering albatrosses. a, Males  
601 that were breeding the previous year. b, Females that were breeding the previous year. c, Male  
602 that were in sabbatical the previous year. d, Females that were in sabbatical the previous year.  
603 Error bars indicate 95% confidence intervals. The survival probabilities were constrained to  
604 be similar for individuals that were breeding the previous year and for those that took a  
605 sabbatical year.

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608 **Figure 3** Demographic parameters of immigrant and resident snow petrels and southern  
609 fulmars. a, Male snow petrel. b, Female snow petrel. c, Southern fulmar. Error bars indicate  
610 95% confidence intervals.

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613 **Figure 4** Fitness metrics of immigrant and resident individuals in three seabird species. a,  
614 Number of offspring fledged. b, Number of breeding events. Center line, median; box limits,  
615 lower and upper quartiles; error bars, 90<sup>th</sup> and 10<sup>th</sup> percentiles; crosses, outliers. \* indicates  
616 significant differences. FU = southern fulmar, SP = snow petrel, WA = wandering albatross.  
617 Subscripts F and M respectively indicate female and male.

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620 **Figure 5** Number of recruits produced by immigrants and residents in two seabird species. a,  
621 male wandering albatrosses. b, female wandering albatrosses. c, southern fulmars. \* indicates  
622 significant differences. R indicates that only resident southern fulmars produced more than  
623 four recruits.

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638 **Table 1** Parameter estimates from the generalized linear mixed effect models outputs with  
 639 number of recruits as a response variable for residents and immigrants of wandering  
 640 albatrosses (males and females) and southern fulmars

Fixed and random effects <sup>†</sup>	Group	Estimate	SE	Z	P
<i>Male wandering albatross, n = 1665</i>					
Conditional model	Intercept	-0.053	0.205	-0.260	0.795
	Resident	0.128	0.209	0.613	0.540
Zero-inflation model	Intercept	1.328	0.161	8.269	<0.001
	Resident	-0.632	0.170	-3.715	<0.001
Year		0.147	0.383		
<i>Female wandering albatross, n = 1748</i>					
Conditional model	Intercept	0.277	0.140	1.974	0.048
	Resident	-0.215	0.139	-1.552	0.121
Zero-inflation model	Intercept	1.001	0.123	8.125	<0.001
	Resident	-0.273	0.136	-2.012	0.044
Year		0.156	0.395		
<i>Southern fulmar, n = 321</i>					
Conditional model	Intercept	0.028	0.226	0.125	0.900
	Resident	-0.316	0.305	-1.036	0.300
Zero-inflation model	Intercept	0.818	0.172	4.768	<0.001
	Resident	-0.216	0.238	-0.910	0.363
Year		0.298	0.546		

641 <sup>†</sup> Reference category for fixed effects were set to immigrants (= intercept). Random effect  
 642 (year) estimate is variance and SE column is standard deviation. Distributions used were  
 643 negative binomial for southern fulmars and Poisson for wandering albatrosses. The zero-  
 644 inflation model estimates the probability of extra zeros such that a negative coefficient for  
 645 residents indicates a lower chance of having no recruit. The conditional model estimates the  
 646 abundance such that a positive effect for residents indicates a higher number of recruits. See  
 647 supplementary material Fig. S3, S4, S5 for model fit.