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Contrasted patterns of age-specific reproduction in long-lived seabirds

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While the number of studies providing evidence of actuarial senescence is increasing, and covers a wide range of taxa, the process of reproductive senescence remains poorly understood. In fact, quite high reproductive output until the last years of life has been reported in several vertebrate species, so that whether or not reproductive senescence is widespread remains unknown. We compared age-specific changes of reproductive parameters between two closely related species of long-lived seabirds: the small-sized snow petrel *Pagodroma nivea*, and the medium-sized southern fulmar *Fulmarus glacialoides*. Both are sympatric in Antarctica. We used an exceptional dataset collected over more than 40 years to assess age-specific variations of both breeding probability and breeding success. We found contrasted age-specific reproductive patterns between the two species. Reproductive senescence clearly occurred from 21 years of age onwards in the southern fulmar, in both breeding probability and success, whereas we did not report any decline in the breeding success of the snow petrel, although a very late decrease in the proportion of breeders occurred at 34 years. Such a contrasted age-specific reproductive pattern was rather unexpected. Differences in life history including size or migratory behaviour are the most likely candidates to account for the difference we reported in reproductive senescence between these sympatric seabird species.

Keywords: vertebrates; life history; senescence; breeding success; age; Antarctic seabirds

1. INTRODUCTION

The study of age-specific variation of life-history traits in vertebrates has become a popular topic (see for reviews on birds Bennett & Owens (2002) and on large mammalian herbivores Gaillard *et al.* (2003)). Of particular interest is senescence, defined as the decline in performance with age. The theory of senescence has been widely discussed (Partridge 1987; Kirkwood & Rose 1991; Ricklefs 1998; Partridge & Mangel 1999; Hughes *et al.* 2002), often from a theoretical perspective, because empirical observations *in natura* have often remained cryptic or disputed (Nisbet 2001). With the availability of both powerful statistical methods (e. g. mixed models providing the possibility to account for heterogeneity in quality among individuals Van de Pol & Verhulst 2006; Nussey *et al.* 2008) and long-term monitoring of known-aged individuals, such investigations have become possible. Moreover, age-related patterns in nature often do not follow a linear relationship with fitness traits (Weladji *et al.* 2006), which can make them difficult to describe accurately.

Owing to their generally extended lifespan (more then 60 years for albatrosses), seabirds are one of the predominant animal groups to fill the gap in knowledge of life-history patterns at old ages (Nisbet 2001; Reed *et al.* 2008). However, choosing seabirds as study species requires research programmes lasting for decades, in order to gather enough information on old birds, and due to the absence of external markers of age, birds have to be marked individually as nestlings, and recaptured throughout their lives.

Studies on ageing in wild seabirds have reported patterns of senescence, either linked to reproduction (Weimerskirch *et al.* 2005; Reed *et al.* 2008), to foraging abilities (Catry *et al.* 2006) or to survival (see Bennett & Owens (2002) for a review of case studies). On the other hand, some studies have reported an increase in reproductive performance with age (Mauck *et al.* 2004; Angelier *et al.* 2007). In the absence of comparative studies, the understanding of such contrasted age-specific variation remains scarce. To fill this gap, we provide here a first comparative study of the age-specific changes in reproductive output between two sympatric wild seabird species.

We studied populations of southern fulmar *Fulmarus glacialoides* and snow petrel *Pagodroma nivea,* which have been monitored using individual capture–mark–recapture methods since 1963. The two species are both very long-lived Antarctic seabirds, which only lay one egg per clutch and per year, and have high adult survival rates (Jenouvrier *et al.* 2003, 2005). Both species can thus be ranked close to the slow end of the slow–fast continuum of vertebrate life-history tactics (Gaillard 1989; Bielby *et al.* 2007), characterized by long generation times (Gaillard *et al.* 2005). We can therefore expect very weak senescence in both survival and reproduction in these species (Jones *et al.* 2008). However, since both species exhibit very high adult survival, the theory of life-history evolution suggests the existence of a trade-off, leading to a decreased reproductive output with increasing age. We therefore

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tested whether reproductive senescence occurred in these two closely related, sympatric species, and if so, at which age reproductive senescence begins.

2. MATERIAL AND METHODS

(a) *Study site and species*

From 1963 onwards, annual ringing and recapture sessions of adult birds and chicks of both species took place on Ile des Pétrels, Pointe Géologie Archipelago (66°40′ S, 140°01′ E), Terre Adélie, Antarctica. The three colonies of snow petrels and the only colony of southern fulmars at Pointe Géologie were intensively surveyed each year. We pooled data from the three colonies of snow petrels because no difference occurred in breeding performance. More details on the monitoring are provided in Chastel *et al.* (1993) and Barbraud & Weimerskirch (2001).

The species considered here are very long lived, have a very high adult survival (93.4%±0.3 for the snow petrel (Chastel *et al.* 1993), 92.3%±0.6 for the southern fulmar (Jenouvrier *et al.* 2003)), lay only one egg, and both sexes contribute equally to parental care. However, the species differ in other life-history traits.

The snow petrel *P. nivea* (Forster) is the smallest species (approx. 400 g) of the fulmarine petrel group. Snow petrels breed in large numbers along the coast of Antarctica, where they forage in close association with the pack ice, feeding mostly on fish (Ainley *et al.* 1984; Ridoux & Offredo 1989). They are resident in Antarctic waters throughout the year. Snow petrels are characterized by a relatively low level of philopatry compared with other petrels (Chastel *et al.* 1993). In spite of this low philopatry, once a snow petrel has selected a breeding colony, it remains faithful to this place in the future and, therefore, if not observed between two breeding events, it can be confidently assumed that it did not breed elsewhere during this period (Jenouvrier *et al.* 2003).

Southern fulmars (700–1200 g) are cliff-nesting seabirds that forage in Antarctic waters in summer, but move up to sub-Antarctic waters in winter and prey mainly on euphausiids, fishes, crustaceans and squid (Ainley *et al.* 1984; Ridoux & Offredo 1989). Unlike snow petrels, southern fulmars are highly philopatric (Jenouvrier *et al.* 2003). As for the snow petrel, if a bird is not observed between two breeding attempts, it can be confidently assumed that it did not reproduce.

(b) *Description, extraction and selection of the environmental variables*

We used one local variable, the sea ice extent (SIE), and one large-scale variable, the southern oscillation index (SOI), to account for possible confounding effects of environmental conditions. Both variables are known to influence the focal species (Jenouvrier *et al.* 2003, 2005).

The SOI was obtained for the period 1973–2004 (see http://www.bom.gov.au/climate/current/soihtml.shtml).

The SIE, expressed in units of 1000 km^2, was available from 1973 to 1990 only, for 1° latitude×10° longitude slices (see http://nsidc.org/data/g00917.html). Since Ile des Pétrels is situated at 66°40′ S, 140°01′ E, we extracted and averaged the SIE between the longitudes 130°–140° and 140°–150°. Since no SIE was available after 1990, we interpolated the second period from 1990 to 2004 using the sea ice concentration values (See http://ingrid.ldgo.columbia.edu/SOURCES/.IGOSS/.nmc/.Reyn_SmithOIv2/.monthly/.sea_ice/). These data covered a grid of 1°×1°, and a cell was considered as covered by ice when the concentration exceeded a specific value. We calculated the extent of ice (in units of 1000 km^2) for longitudinal slices (130°–140° and 140°–150°). To correct for the difference in sampling between the two time periods (1973–1990 and 1990–2004), each measure was standardized with respect to the specific mean of the period. Finally, we used the mean SIE for April–June as it has been shown that this period critically influenced the breeding ecology of the focal species (Jenouvrier *et al.* 2005). Correlation tests (using Pearson's correlation coefficient) did not show any significant collinearity between the climatic variables.

(c) *Data and statistical analysis*

For both species, our analyses included all birds of known age (i.e. ringed as chicks and later recaptured as breeders), that reached sexual maturity and for which the breeding status was observed every year since fledging (snow petrel: $n=112$; southern fulmar: $n=177$). For the snow petrel, we only included individuals that reproduced more than once, to avoid considering transient birds. Age of maturity for each species was based on previous results (Chastel *et al.* 1993; Jenouvrier *et al.* 2003). We used the breeding success at fledging, defined as the probability of a chick fledging from the laid egg. Breeding probability was defined as the proportion of breeding birds in each age group, considering that they had reached maturity and that they were alive. For both species, the detection probability of an individual was close to one, because all nests are checked several times during each breeding season. We did not perform separate analyses for sexes, since the information was unavailable for the southern fulmar, and would have dramatically reduced the sample size for the snow petrel.

The two species (especially the snow petrel; Chastel *et al.* 1993) show a marked between-year variation in breeding success and breeding probability. They are prone to skip reproduction (breeding probability) during unfavourable environmental conditions. We therefore used the mean annual breeding success and breeding probability at the population level as a proxy for year quality by adding it as a covariate in our models in order to reduce the amount of variation not due to age effect.

We first created sets of candidate models and used the Akaike information criterion (AIC) to select the most parsimonious model (Burnham & Anderson 1998). We also computed Akaike weights (w_i), which provide a measure of the relative likelihood of a given model to be the best among the models fitted.

We fitted linear, quadratic and logarithmic relationships on a logit scale to model the age-specific variation in reproductive traits (see table 1) by using generalized linear mixed models (package glmmML) in the software R, v. 2.6.2 (R Core Development Team 2005). Preliminary analyses showed that in all cases, mixed models described the data more appropriately than simple general linear models, confirming marked individual heterogeneities in reproductive traits. Such a procedure allowed us to account for the problem of pseudoreplication that occurs when using repeated measures of the same individuals (Hurlbert 1984). Note, however, that not accounting for individual variation (i.e. using GLM) led to much higher AIC but did not change the results, leading to only a small underestimation of slopes in the last life stage. Additionally, we fitted threshold models, including three stages: (i) the progressive access to reproduction from the age of maturity to a first threshold age τ_1, (ii) a prime-age stage

Table 1. Summary of the 36 candidate models tested. (The model formula presents the full model for each trend fitted. All intermediate models were tested, see appendix (table S1 and S4 in the electronic supplementary material). Bs, breeding success; Bp, breeding probability; bs_{ann}, inter-annual variations in breeding success; bp_{ann}, inter-annual variations in breeding probability; SOI, southern oscillation index; SIE_{autumn}, sea ice extent values for autumn; asterisk stands for an interaction.)

model formula	biological meaning	number
Bs (or Bp) ~ 1	no effect of age on reproduction	1
Bs (or Bp) $\sim$ age	linear effect of age on reproduction	2
Bs (or Bp) $\sim$ age + age^2 + bs_{ann} (or bp_{ann}) + SOI + SIE_{autumn}	quadratic effect of age on reproduction	3–10
Bs (or Bp) $\sim$ log(age) + bs_{ann} (or bp_{ann}) + SOI + SIE_{autumn}	logarithmic effect of age on reproduction	11–18
Bs (or Bp) $\sim$ bs_{ann} (or bp_{ann})	mean annual breeding output only explains variations of reproduction	19
Bs (or Bp) $\sim$ T1 + T2 + bs_{ann} (or bp_{ann}) + SOI + SIE_{autumn}	existence of one threshold age ($6<\tau_1<34$)	20 to 27
Bs (or Bp) $\sim$ T1 + T2 + T3 + bs_{ann} (or bp_{ann}) + SOI + SIE_{autumn}	existence of two threshold ages ($6<\tau_1<20$, $21<\tau_2<34$)	28–35
Bs (or Bp) $\sim$ T1 + T2 + T3 + bs_{ann} (or bp_{ann}) + bs_{ann} (or bp_{ann})*T3	existence of two threshold ages and an interaction between year quality and age	36

between τ_1 and τ_2 with a maximum reproductive output, and (iii) a senescent stage from the second threshold age τ_2, from which the reproductive output decreases. For each combination of threshold values (e. g. $\tau_1=12$ years and $\tau_2=23$ years for a two-threshold model), a generalized linear mixed model was fitted (see table 1). The best threshold models were determined using AIC profiles. We further tested for interactions between year quality (measured by the mean annual breeding value) and senescence rate (see table 1) when senescence occurred, to assess a possible change of senescence patterns in response to variation in environmental conditions (as recently reported in red deer (*Cervus elaphus*) according to changes of density at birth, Nussey *et al.* 2007)

3. RESULTS

(a) *Age-specific breeding success*

The breeding success of the southern fulmar was best fitted by a two-threshold model including the effects of year-to-year variations in breeding success and SOI (Model 33, table 1). The first threshold age was 6 years, and between 6 and 21 years, the reproductive success of birds increased from 55 per cent at 6 years to 75 per cent at 21 years, at an annual rate of 0.07 on a logit scale ($\pm$0.02, table 2). From 21 years of age onwards, the breeding success of birds decreased with age at an annual rate of 0.07 (slope of -0.07 ± 0.04, table 2). Towards the end of their life, southern fulmars have approximately the same breeding success as they had at 6 years of age. This model also included a positive effect of the SOI on breeding success (slope of 0.23 ± 0.09 on a logit scale, table 2) and accounted for 70 per cent of the variation observed in breeding success among individual fulmars ($w_i=0.46$; figure 1*a*; appendix, table 6 for threshold selection, and table S1 in the electronic supplementary material for details of model selection). A model including an interaction term between senescence rate and annual breeding success did not improve the fit (see appendix, model 36, table S1 in the electronic supplementary material), indicating that senescence of breeding success was not influenced by environmental conditions.

The best model (model 21, table 1) for snow petrels was a one-threshold model, including annual breeding success and showing the expected increase of breeding success throughout the early ages (threshold at 10 years), at a rate of 0.64 ($\pm$0.27, table 3) on a logit scale. After having reached a breeding success of 50 per cent at 10 years, the birds maintain high reproductive success until the oldest ages, since the slope (0.03 ± 0.02, table 3) indicates a trend of increasing success with increasing age. This model fitted the data very well, accounting for approximately 83 per cent of the observed variation in breeding success among individuals ($w_i=0.25$). No influence of either the SOI or the SIE could be detected, as the models incorporating those variables had very low w_i (figure 1*b*; appendix, table 7 for threshold selection, and table S2 in the electronic supplementary material for details of model selection).

Table 2. Effect of age on the breeding success—parameter estimates from the best model—SOUTHERN FULMAR—estimates of each parameter are presented with their standard error (s.e.). (bs_{ann}: inter-annual variations in breeding success, SOI, southern oscillation index).

	two thresholds	
term	estimate	s.e.
(intercept)	−55.772	70.526
slope before the first threshold age	8.822	11.754
slope between the first and the second threshold ages	0.072	0.022
slope after the second age threshold	−0.068	0.044
bs_{ann}	4.630	0.744
SOI	0.234	0.093

(b) *Age-specific breeding probability*

For southern fulmars, the model selected to describe breeding probability (model 29, table 1) followed the same pattern as for breeding success, except that the effects of SOI were not included. Breeding probability increased to 50 per cent at 6 years, and continued to increase (slope of 0.06 ± 0.02 on a logit scale, table 4) until 21 years of age, when it reached a peak, with 68 per cent of birds breeding. From 21 years of age onwards, breeding probability decreased at a high rate (slope of -0.10 ± 0.04 on a logit scale, table 4). The selected model ($w_i=0.41$) accounted for 41 per cent of the variation in breeding probability observed among individual fulmars (figure 2*a*; appendix, table 8 for threshold selection, and table S3 in the electronic supplementary material for details of model selection). Again the model including an interaction term

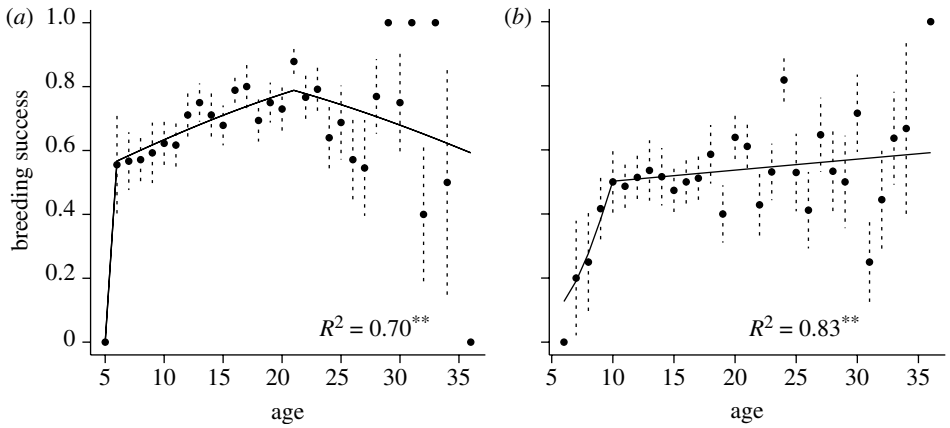

Figure 1. Breeding success in relation to age, starting at age of first breeding. (*a*) The southern fulmar and (*b*) the snow petrel. The average observed value for each age is plotted with dotted standard error bars, with predictions from the threshold model. Thresholds are at 6 years and 21 years for the southern fulmar, and at 10 years for the snow petrel. Pearson's correlation coefficients between the prediction of the best model and the averaged observed value are indicated below the curve. $^{**}p<0.01$.

between senescence rate and annual breeding probability did not improve the fit (see appendix, model 36, table S3 in the electronic supplementary material).

For snow petrels, the model including two thresholds and the year-to-year variations of breeding decision (model 29, table 1) best described individual variation in observed breeding probabilities. Breeding probabilities increased from 0 at 5 years of age to 45 per cent at 6 years, the first threshold age, then increased at an annual rate of 0.02 ($\pm$0.01 on a logit scale, table 5), but over an extended period (between 6 and 34 years of age), by the end of which, approximately 80 per cent of birds were breeding. After this, breeding probability dropped abruptly (slope of -1.28 ± 0.57 on a logit scale, table 5). This model accounted for 74 per cent of the observed variations in breeding probability of individual petrels ($w_i=0.33$; figure 2*b*; appendix, table 9 for threshold selection, and table S4 in the electronic supplementary material for details of model selection).

Table 3. Effect of age on the breeding success—parameter estimates from the best model—SNOW PETREL—estimates of each parameter are presented with their standard error (s.e.). (bs_{ann}: inter-annual variations in breeding success).

	one threshold	
term	estimate	s.e.
(intercept)	−9.253	2.714
slope before the threshold	0.642	0.273
slope after the threshold	0.027	0.017
bs_{ann}	5.227	0.554

Table 4. Effect of age on the breeding probability—parameter estimates from the best model—SOUTHERN FULMAR—estimates of each parameter are presented with their standard error (s.e.). (bp_{ann}: inter-annual variations in breeding probability).

	two thresholds	
term	estimate	s.e.
(intercept)	−68.527	302.655
slope before the first threshold age	10.908	50.443
slope between the first and the second threshold ages	0.058	0.018
slope after the second age threshold	−0.096	0.035
bp_{ann}	5.486	0.409

4. DISCUSSION

Our main goal was to examine whether senescence of reproductive traits can be detected in two populations of long-lived seabirds, using a remarkably long dataset and accounting for individual differences in quality that can prevent the detection of senescence (Cam *et al.* 2002). We found that a marked contrast occurred in age-specific changes of reproduction between the two sympatric long-lived bird species. The southern fulmar, with an annual adult survival of 0.923 (Jenouvrier *et al.* 2003), showed clear evidence of senescence in both breeding probability and breeding success from 21 years of age onwards, for a maximum longevity of more than 45 years, whereas the snow petrel, with an annual adult survival of 0.934 (Chastel *et al.* 1993), did not show any sign of senescence in breeding success, and breeding probability did not decrease before 34 years of age for a maximum longevity of more than 46 years.

(a) *Southern fulmar: evidence of senescence*

Of the two species studied, only the southern fulmar showed clear evidence of reproductive senescence. The decrease was clear for both breeding success and breeding probability. Reproductive senescence has already been shown in numerous studies carried out on a wide range of vertebrates (Bennett & Owens 2002 on birds, Gaillard *et al.* 2003 on large mammals and Reznick *et al.* 2002 on fishes), including seabirds (Weimerskirch *et al.* 2005 on wandering albatross, *Diomedea exulaus*, Reed *et al.* 2008 on common guillemot, *Uria aalge*). The pattern of age-specific breeding success found in the fulmar is very similar to that of wandering albatrosses (Weimerskirch *et al.* 2005), i.e. a progressive decline when only half the maximum longevity is reached. Since the study on guillemots did not include age-specific breeding success, but time before death (Reed *et al.* 2008), the pattern observed is not directly comparable, although this study showed an abrupt decline 3 years before death and a progressive decline 10 years before death over a study

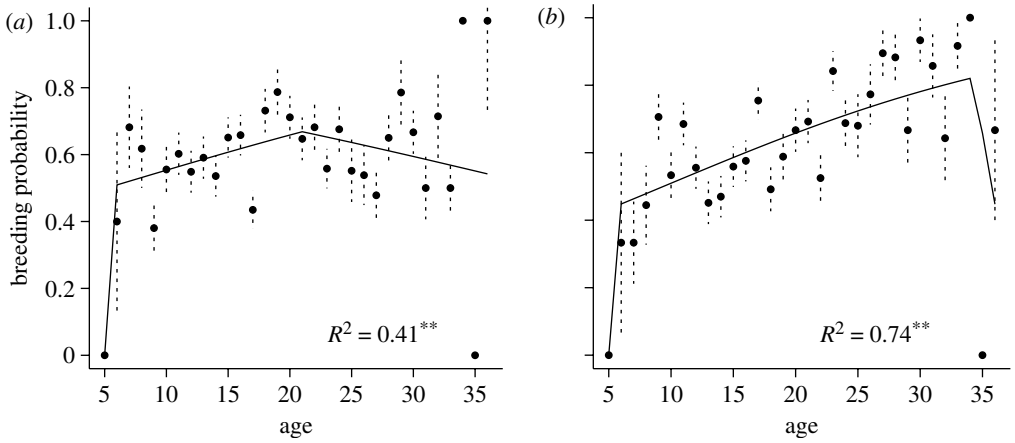

Figure 2. Breeding probability in relation to age, starting at age of first breeding. (*a*) The southern fulmar and (*b*) the snow petrel. The average observed value for each age is plotted with standard error bars, with predictions from the threshold model. Thresholds are at 6 years and 21 years for the southern fulmar, and at 6 years and 34 years for the snow petrel. Pearson's correlation coefficients between the prediction of the best model and the averaged observed value are indicated below the curve. $^{*}p < 0.05$. $^{**}p < 0.01$.

period of 23 years, a pattern similar to that reported here for fulmars. Reproductive senescence in fulmar did not seem to be influenced by variation in the year quality. This might reflect a true independence between environmental conditions and senescence patterns. Alternatively, fluctuating year quality throughout the reproductive life of individuals in this long-lived bird could have masked any effect of environmental variation on senescence in our analysis.

(b) *Snow petrel: no or very late indication for senescence*

Interestingly, we did not find any support for senescence in the breeding success of snow petrels. On the contrary, the tendency was even towards a slight continuous increase. Another study, using a measure of prolactin levels throughout life (Angelier *et al.* 2007), reported the absence of a decrease in a reproductive trait with age in snow petrels. It shows that older breeders had higher prolactin levels than younger ones, which is associated with a lower probability of neglecting the egg. Our results therefore go in the same direction. However, we found an indication that breeding probability may decline at old ages in this species. Owing to this late decline (i.e. when two-third or more of the maximum longevity has been reached), we can suspect that it represents only the trajectory of very few birds, or the possibility that after a certain age, the birds remain at sea, avoiding this way the costs of a breeding event during poor years. Thus, in old age, birds could breed successfully only when conditions are favourable, and otherwise skip a breeding attempt. Since intermittent breeding is common in petrels and albatrosses, it is important to consider also the probability of breeding as a measure of breeding performance, when studying these species. By looking at only breeding success, we would be unable to distinguish between those birds that are alive but not willing to reproduce, and birds that have died.

Senescence is widespread among seabirds, but our results showing the absence of reproductive senescence in snow petrel are in line with those from a study on Leach's storm petrel *Oceanodroma leucorhoa* (Mauck *et al.* 2004). In this species, hatching success, defined as the presence or absence of a chick after one egg was laid did not decline with increasing age, but remained constant until old age, after an initial sharp increase.

Table 5. Effect of age on the breeding probability—parameter estimates from the best model—SNOW PETREL—estimates of each parameter are presented with their standard error (s.e.). (bp_{ann}: inter-annual variations in breeding probability).

	two thresholds	
term	estimate	s.e.
(intercept)	−36.339	68.620
slope before the first threshold age	5.630	11.437
slope between the first and the second threshold ages	0.021	0.013
slope after the second age threshold	−1.281	0.568
bp_{ann}	4.714	0.435

(c) *Possible explanation for contrasted patterns of reproductive senescence between two closely related species*

Why are these two closely related species so different in the way breeding success and decision change with age? Two important differences exist between them. First, snow petrels are smaller than southern fulmars, and it is noticeable that the only other seabird species showing a similar pattern to that of the snow petrel is a small-sized storm petrel (Mauck *et al.* 2004). Although both species have similar life histories (high survival rates, low number of eggs laid, large amount of parental care, etc.), snow petrels are longer lived than fulmars and skip reproduction more frequently (Jenouvrier *et al.* 2005), leading them to have a longer generation time than fulmars. Jones *et al.* (2008) have recently shown that the magnitude of senescence is tightly linked with generation time, with slower species having later and weaker senescence. Note that although Jones *et al.* (2008) included the fulmar population analysed here in their comparative work, differences in reproductive measures considered and different analytical procedures preclude any comparison between the two studies. The between-species difference in reproductive senescence we report here could illustrate such a link between senescence and speed of the life-history cycle.

The other major difference between the two species is the migratory behaviour of the southern fulmar during winter, whereas the snow petrel is sedentary and remains closely associated with the pack ice during the whole year. Møller & De Lope (1999) found that the migratory performance of

Table 6. Breeding probability—threshold model selection—SOUTHERN FULMAR. (AIC values from the models corresponding to the first (columns) and second (rows) threshold age are shown. The lowest AIC value is given in italic.)

	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
21	*977.5115*	983.342	987.203	989.818	991.8056	993.0454	993.2465	994.0215	995.5467	996.815	997.036	998.0204	999.9394	1000.888	1001.649
22	978.5372	984.268	987.954	990.4034	992.32	993.4628	993.5284	994.2164	995.7027	996.9365	997.0619	997.9885	999.904	1000.747	1001.191
23	979.6701	985.2917	988.7886	991.0576	992.8896	993.9207	993.8375	994.424	995.8542	997.0364	997.0589	997.921	999.8055	1000.547	1000.819
24	981.1244	986.6188	989.8846	991.924	993.6393	994.517	994.2335	994.6726	996.007	997.0982	996.9584	997.7026	999.524	1000.118	1000.185
25	981.955	987.3627	990.4737	992.3611	993.999	994.7812	994.3833	994.744	996.0303	997.0806	996.8891	997.611	999.4153	1000.005	1000.126
26	982.6218	987.949	990.9244	992.6807	994.2521	994.9553	994.469	994.7733	996.0275	997.0546	996.8472	997.5778	999.384	1000.011	1000.238
27	982.6157	987.9129	990.8427	992.5703	994.1366	994.8435	994.3805	994.7243	996.0201	997.0979	997.005	997.8527	999.7137	1000.494	1000.973
28	981.6836	986.9987	989.9667	991.7594	993.3772	994.163	993.8191	994.2827	995.6783	996.8586	996.9688	997.9938	999.9212	1000.890	1001.643
29	980.206	985.5454	988.5608	990.4216	992.088	992.9443	992.6996	993.2573	994.728	995.9817	996.2377	997.3794	999.3355	1000.410	1001.305
30	980.1788	985.4833	988.4404	990.2446	991.8832	992.7063	992.4237	992.9589	994.4203	995.6688	995.9227	997.0711	999.0329	1000.117	1001.028
31	979.999	985.2826	988.2048	989.9698	991.5869	992.3863	992.0764	992.5947	994.0482	995.291	995.5426	996.6952	998.6602	999.75	1000.670
32	981.6989	986.8965	989.6652	991.2631	992.7835	993.4646	993.0127	993.4212	994.8006	995.9794	996.126	997.211	999.1652	1000.208	1001.073
33	980.844	986.0489	988.8236	990.423	991.9443	992.6277	992.1806	992.595	993.981	995.1668	995.3314	996.4319	998.3914	999.4472	1000.331
34	981.9437	987.026	989.6746	991.1377	992.5757	993.1571	992.6025	992.9308	994.2653	995.3908	995.4805	996.5204	998.4728	999.4835	1000.322

barn swallows, *Hirundo rustica*, decreased with age (delay in spring arrival on the breeding grounds), and Catry *et al.* (2006) have shown that reproductive senescence of another very long-lived seabird, the grey-headed albatross *Diomedea chrysostoma*, could be linked to reduced foraging performance at old age. Since the migratory behaviour of southern fulmars is closely associated with the search for food, a decline in migratory abilities also means a decline in foraging success. They might therefore be more strongly affected by ageing processes as compared with snow petrels.

Future studies should investigate these hypotheses to determine whether reproductive senescence is associated with a decrease in migratory ability, and whether the longest lived species show slower ageing pattern, together with possible causes for this, by comparing senescence patterns between more than two species.

The field study was approved by the ethics committee of the French Polar Institute.

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APPENDIX A

Tables 6–9.

Table 7. Breeding probability—threshold model selection—SNOW PETREL. (AIC values from the models corresponding to the first threshold age (rows) are shown. The lowest AIC value is given in italics.)

age at the first threshold	AIC
7	892.3198
8	890.8771
9	889.458
10	*888.7441*
11	889.273
12	889.578
13	890.095
14	890.8103
15	891.3826
16	891.5965
17	891.7053
18	891.6908
19	891.8913
20	891.5893
21	891.6745
22	891.991
23	892.0299
24	891.8657
25	892.361
26	892.7444
27	892.8373
28	893.0806
29	893.254
30	893.3174
31	892.5926
32	891.5535
33	891.376

Table 8. Breeding probability—threshold model selection—SOUTHERN FULMAR. (AIC values from the models corresponding to the first (columns) and second (rows) threshold age are shown. The lowest AIC value is given in italic.)

	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
21	*1771.379*	1777.174	1788.309	1793.409	1793.352	1793.514	1794.074	1794.323	1794.515	1794.436	1794.493	1794.634	1793.677	1791.614	1790.848
22	1772.353	1777.917	1789.178	1794.538	1794.370	1794.461	1795.083	1795.357	1795.600	1795.349	1795.336	1795.574	1793.660	1791.219	1790.594
23	1773.583	1778.867	1790.250	1795.864	1795.545	1795.520	1796.157	1796.394	1796.606	1796.102	1795.906	1796.051	1793.288	1790.419	1789.642
24	1774.306	1779.393	1790.847	1796.614	1796.178	1796.058	1796.68	1796.866	1797.025	1796.347	1796.022	1796.075	1793.036	1790.271	1789.768
25	1775.161	1779.990	1791.520	1797.45	1796.854	1796.6	1797.177	1797.272	1797.331	1796.410	1795.884	1795.773	1792.256	1789.259	1788.666
26	1775.580	1780.207	1791.785	1797.824	1797.098	1796.731	1797.261	1797.275	1797.246	1796.15	1795.483	1795.261	1791.540	1788.555	1788.055
27	1775.670	1780.174	1791.777	1797.873	1797.068	1796.634	1797.133	1797.100	1797.025	1795.852	1795.137	1794.887	1791.225	1788.464	1788.19
28	1775.67	1780.188	1791.786	1797.876	1797.081	1796.665	1797.175	1797.164	1797.117	1796.023	1795.400	1795.246	1791.981	1789.710	1789.807
29	1775.668	1780.202	1791.796	1797.878	1797.095	1796.694	1797.214	1797.221	1797.198	1796.165	1795.609	1795.523	1792.536	1790.588	1790.901
30	1775.633	1780.118	1791.72	1797.823	1797.007	1796.582	1797.091	1797.083	1797.047	1795.998	1795.437	1795.354	1792.429	1790.589	1790.976
31	1775.411	1779.850	1791.460	1797.583	1796.734	1796.283	1796.781	1796.757	1796.705	1795.632	1795.059	1794.969	1792.064	1790.280	1790.708
32	1775.333	1779.788	1791.395	1797.511	1796.675	1796.238	1796.744	1796.735	1796.701	1795.669	1795.139	1795.09	1792.339	1790.715	1791.233
33	1774.982	1779.432	1791.041	1797.161	1796.32	1795.882	1796.389	1796.380	1796.349	1795.324	1794.803	1794.764	1792.062	1790.496	1791.046
34	1775.311	1779.802	1791.405	1797.507	1796.697	1796.287	1796.808	1796.822	1796.816	1795.844	1795.372	1795.375	1792.812	1791.369	1791.981
35	1774.062	1778.502	1790.109	1796.240	1795.41	1794.976	1795.491	1795.517	1795.479	1794.488	1794.024	1794.017	1791.427	1789.969	1790.573

Table 9. Breeding probability—threshold model selection—SNOW PETREL. (AIC values from the models corresponding to the first (columns) and second (rows) threshold age are shown. The lowest AIC value is given in italic.)

	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
21	1338.170	1339.13	1337.555	1337.323	1340.65	1341.784	1342.233	1341.156	1340.598	1340.905	1341.303	1341.749	1340.618	1340.507	1341.193
22	1338.413	1339.387	1337.927	1337.778	1341.016	1342.081	1342.343	1341.162	1340.589	1340.894	1341.287	1341.726	1340.726	1340.778	1341.434
23	1339.022	1340.028	1338.774	1338.763	1341.834	1342.755	1342.596	1341.033	1340.263	1340.494	1340.829	1341.227	1339.771	1339.537	1339.853
24	1339.172	1340.186	1339.013	1339.055	1342.052	1342.907	1342.601	1340.946	1340.154	1340.379	1340.709	1341.099	1339.740	1339.614	1340.013
25	1339.285	1340.306	1339.215	1339.310	1342.226	1343.012	1342.539	1340.762	1339.921	1340.127	1340.44	1340.813	1339.451	1339.345	1339.744
26	1339.261	1340.305	1339.308	1339.461	1342.281	1342.977	1342.289	1340.331	1339.401	1339.566	1339.843	1340.181	1338.715	1338.562	1338.911
27	1339.029	1340.081	1339.163	1339.364	1342.097	1342.711	1341.836	1339.722	1338.714	1338.842	1339.087	1339.394	1337.854	1337.670	1337.989
28	1338.764	1339.848	1338.962	1339.184	1341.880	1342.460	1341.527	1339.394	1338.394	1338.531	1338.785	1339.102	1337.663	1337.552	1337.921
29	1338.696	1339.778	1338.887	1339.108	1341.807	1342.397	1341.515	1339.476	1338.555	1338.734	1339.028	1339.381	1338.156	1338.170	1338.615
30	1338.105	1339.168	1338.314	1338.559	1341.213	1341.761	1340.797	1338.704	1337.765	1337.938	1338.226	1338.576	1337.368	1337.395	1337.842
31	1337.865	1338.952	1338.085	1338.325	1340.993	1341.559	1340.661	1338.669	1337.805	1338.015	1338.335	1338.711	1337.670	1337.776	1338.256
32	1338.181	1339.259	1338.346	1338.561	1341.279	1341.901	1341.163	1339.362	1338.622	1338.887	1339.248	1339.653	1338.835	1339.028	1339.526
33	1337.154	1338.201	1337.296	1337.518	1340.226	1340.841	1340.095	1338.304	1337.575	1337.844	1338.208	1338.614	1337.827	1338.028	1338.522
34	*1336.985*	1338.043	1337.124	1337.339	1340.061	1340.690	1339.987	1338.243	1337.545	1337.825	1338.197	1338.607	1337.869	1338.085	1338.577
35	1338.911	1339.963	1338.973	1339.145	1341.941	1342.644	1342.135	1340.595	1340.014	1340.334	1340.729	1341.145	1340.579	1340.836	1341.308

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