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Unravelling dispersal patterns in an expanding population of a highly mobile seabird, the northern fulmar (*Fulmarus glacialis*)

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The northern fulmar (*Fulmarus glacialis*) is an abundant seabird whose Northeast Atlantic population has expanded dramatically over the past 100 years. Archaeological evidence suggests that Iceland and St Kilda were the ancestral populations from which essentially all other colonies in the region were derived. We collected samples from seven breeding colonies around the North Atlantic and used mitochondrial DNA analysis to ask whether population structure was present and, if so, where there was evidence about which colony was the dominant source population. Our data reveal a pattern consistent with isolation by distance, suggesting that, even though capable of flying great distances, most birds return to breed either at their own or neighbouring colonies. Interestingly, although most colonizers appear to have come originally from Iceland, our analysis also identifies St Kilda as a possible source. However, this secondary pattern appears to be largely an artefact, and can be attributed to the low haplotype diversity on St Kilda which yields a much clearer isolation by distance signal than that generated by birds dispersing from Iceland, where haplotype diversity is extremely high. Consequently, we urge caution when interpreting patterns in which populations vary greatly in the genetic diversity they harbour.

Keywords: *Fulmarus glacialis*; population bottleneck; mitochondrial control region; colonization; isolation by distance

1. INTRODUCTION

The northern fulmar (*Fulmarus glacialis*) is a large petrel belonging to the order Procellariiformes. It is one of the most numerous seabirds in the Northern Hemisphere, with the most recent estimate of population size being 10 million pairs (Lloyd *et al.* 1991). It has one of the widest distributions, breeding in the high arctic and in the low arctic of the Atlantic and Pacific. Within the Atlantic, it breeds across the boreal zone from Newfoundland east through Southwest Greenland, Iceland, the Faroe Islands and the British Isles to mainland Europe from Norway to Brittany (Warham 1990).

Arctic colonies characteristically comprise large groups consisting of 10 000 to 100 000 birds. Although records for the Arctic zones are sparse, it appears that colonial numbers have remained relatively static for the past 400 years (Salomonsen 1965). By contrast, the boreal population has reached its present distribution by undergoing a massive range expansion since the beginning of the eighteenth century (figure 1). This is exceptionally well documented owing to the birds' economic importance as a food source on remote islands and, more recently, because of extensive ornithological surveys. The ornithologist James Fisher brought together much information from a wide range of sources, giving us a clear idea of the probable route of the expansion (Fisher 1952).

Written records and excavations of human settlement suggested that the boreal population in the Atlantic was, until 350 years ago, confined to two breeding sites: Grimsey in Northern Iceland and the island of St Kilda in the Outer Hebrides (figure 1, Fisher 1952). Around the middle of the eighteenth century it appears that the Icelandic population suddenly began to form new colonies. The population spread steadily around the Icelandic mainland during the nineteenth and early twentieth centuries. Fulmars were first recorded on the Faroe Isles between 1816 and 1839 and were breeding on Foula in the Shetlands by 1878. Meanwhile Southern Norway was colonized in 1924 and the past 40 years have witnessed the colonization of Newfoundland, Labrador and Southwest Greenland as well as France and Germany (Cramp & Simmons 1977).

During the twentieth century, after their arrival on Foula, fulmars colonized almost every part of the British and Irish coastlines. Surveys show an increase of 13–19% per annum before 1939 (excluding St Kilda) which then slowed to *ca.* 4% per annum until 1985–1987. On St Kilda, however, bird counts appear to have remained relatively static until 1969 when numbers began to grow steadily at 3% per annum until 1986 (Lloyd *et al.* 1991). This delayed expansion on St Kilda may have been because of extensive hunting by local inhabitants who, until their abandonment of the island in 1930, took as many as 50% of chicks from selected colonies each year. By contrast, the Icelandic colonies continued to expand rapidly, especially in Southern Iceland (Fisher 1952).

The causes of the expansion are debated. Fisher (1952, 1966) puts forward a strong case that it corresponds to an increase in the availability of offal, first from the rapidly expanding whaling industry, and later from fishing trawlers. However, recent estimates suggest that fulmars in the North Sea obtain no more than half their food from offal discards (Camphuysen & Garthe 1997) and that breeding

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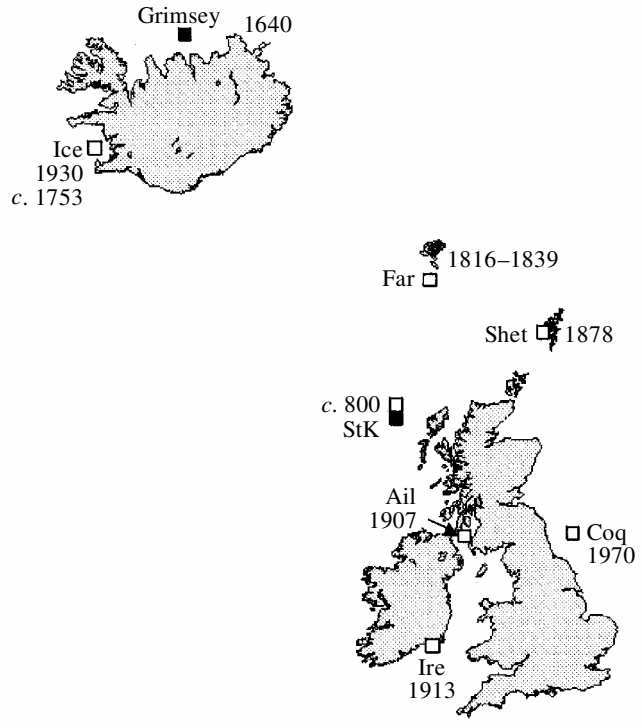

Figure 1. Location of seven fulmar sampling sites (white squares) and the two potential source populations (black squares) for the population expansion: Iceland (Ice), Faroe Islands (Far), Shetland Isles (Shet), St Kilda (StK), Ailsa Craig (Ail), Ireland (Ire) and Coquet (Coq). Dates beside Grimsey and St Kilda indicate the year since which occupation has been continuous. Dates beside sampling sites indicate approximate dates of colonization. Note that, although the Icelandic sampling site of Hvalfjordur (Ice) was colonized in 1930, the Icelandic population expansion and colonization of nearby sites started no later than 1753.

birds in Greenland at least are less dependent on fisheries offal than was previously assumed (Phillips *et al.* 1999). Furthermore, the birds breeding on St Kilda mainly feed on pelagic zooplankton (Lloyd *et al.* 1991) which could partly explain the relatively slow increase of this population. Other factors such as a shift in oceanic conditions (Brown 1970) or the appearance of a 'roving' genotype in Iceland that favoured range expansion and the formation of new, small colonies (Wynne-Edwards 1962) have also been put forward.

Based on available evidence, it is difficult to determine whether the expansion originated from Iceland or St Kilda or both. Phenotypic evidence cannot be used because, although Arctic populations differ in plumage colour and beak length from boreal populations, the boreal zone itself appears to be homogenous for both characters (Wynne-Edwards 1962; Van Franeker & Wattel 1982). Using observational data, Fisher (1952) envisaged a 'stepping stone' model of expansion, relying on the assumption that a new colony was founded by individuals from the nearest existing colony. His model suggested that Icelandic birds provided the source population that colonized Britain and Ireland via the Faroe Isles and Shetland. He considered that the pattern of the population expansion, plus the comparative stability of the St Kilda colony, made it unlikely that the St Kilda birds were involved in the expansion to any large extent before the 1950s, although he admits that such data are insufficient to rule out the possibility (Fisher 1966).

To examine this question further we employed mitochondrial DNA (mtDNA) markers. Mitochondrial DNA has proved to be a valuable tool for examining population structure, including the identification of humpback whale (*Megaptera novaeangliae*) migration patterns (Baker *et al.* 1998) and bird philopatry (Ovenden *et al.* 1991; Avise *et al.* 1992; Austin *et al.* 1994). Owing to its uniparental mode of inheritance and high mutation rate, mtDNA is an ideal marker for studying population structure. It has also been used successfully to study population bottlenecks and colonization patterns (Oakenfull & Ryder 1998; Bodkin *et al.* 1999; Glenn *et al.* 1999; Hoelzel 1999). A disadvantage of using mtDNA is that only female movements can be inferred. However, this is unlikely to be a problem for our study because, as is true of many other birds, female procellariiformes disperse more than males (Greenwood 1980; Lloyd *et al.* 1991).

The aim of this study was to determine whether Iceland or St Kilda was the source of the population expansion by using mtDNA analyses. We aim to answer two main questions:

(i) is there genetic evidence to support the idea that the St Kilda birds were involved in the colonization of other sites in the Northeast Atlantic? and
(ii) is a genetic imprint of a population expansion out of Iceland evident today?

2. MATERIAL AND METHODS

(a) *DNA samples*

Samples were collected in 1998 and 1999 from both putative source populations: Iceland and St Kilda. For Iceland, our samples were collected from Hvalfjordur, which lies *ca.* 300 km away (straight line) or 600 km (along the coast) from Grimsey, the colony thought to be the true source (Fisher 1952). We also sampled birds from five populations established during the range expansion, namely Nolsøy, Faroe Islands; Foula, Shetland Isles; Ailsa Craig, Firth of Clyde; Great Saltee, Ireland and Coquet Island, Northumberland (figure 1). Samples consisted of shed feathers, tissue or blood from young or breeding birds. In all cases the sampled young were raised successfully or the adults continued to breed at the site they were sampled. DNA was extracted from 5 mm of the feather shaft, 2 mm^3 tissue or 10 μl of ethanol-preserved blood using a modified Chelex extraction (Walsh *et al.* 1991). Blood samples were incubated at 56 °C for 20 min to allow the ethanol to evaporate. The samples were incubated for 2 hours at 56 °C in 300 μl low TE (10 mM Tris–HCl pH 8.0, 0.1 mM EDTA) containing 5% w/v Chelex, 250 μg RNase and 500 μg proteinase K. The tubes were periodically inverted to mix the solution and incubated overnight at 37 °C on a rotating wheel.

(b) *Mitochondrial DNA polymerase chain reaction*

Approximately 100 ng of genomic DNA was amplified using 200 μM dNTP, 1.5 μM $MgCl_2$, 0.2 U Taq (Hybaid), and 5 pmol of each primer ND6*-L16406 (5′-CCACCCCATAATACGGCGAAGG-3′ modified from Quinn & Wilson (1993)) and H505 (5′-GAAAGAATGGTCCTGAAGC-3′) in a 25 μl

reaction containing 1 × reaction buffer (75 mM Tris–HCl pH 9, 20 mM $(NH_4)_2SO_4$, 0.01% Tween20). Amplification consisted of one cycle of 120 s at 94 °C, 45 s at 50 °C, 120 s at 72 °C; six cycles of 60 s at 94 °C, 45 s at 50 °C, 90 s at 72 °C; 27 cycles of 60 s at 93 °C, 30 s at 55 °C, 60 s at 72 °C and one final cycle for 5 min at 72 °C. Ten microlitres of polymerase chain reaction (PCR) products were enzymatically treated with 2 U SAP (shrimp alkaline phosphatase) and 5 U of exonucleaseI at 37 °C for 30 min and 80 °C for 20 min to heat inactivate the enzymes. Treated PCR products were sequenced using ABI PRISM ReadyReaction DyeDeoxy Terminator Cycle Sequencing (FS) kit from Perkin–Elmer Cetus and 2.4 pmol of primer H505.

(c) *Genetic data analysis*

Control region sequences were manually aligned in SeqEd (Applied Biosystems 1992) and all nucleotide substitutions were confirmed by visual inspection of the chromatograms. To examine the overall distribution of haplotypes with respect to sampling sites, a minimum spanning tree (MST) was constructed (Excoffier *et al.* 1992) based on the nucleotide differences between each haplotype. The pairwise sequence divergence for each site was also calculated using the number of nucleotide substitutions between each bird, and haplotype diversity was calculated according to Nei (1987). Analysis of molecular variance (AMOVA, Excoffier *et al.* 1992) was used to calculate the variance components between populations (one group with seven populations) from 9999 permutations of the original squared distance matrix. *F*-statistics were then used to examine the levels of population differentiation and to indirectly obtain rough approximations for the levels of gene flow between sites.

3. RESULTS

Among the 115 birds, a total of 39 variable sites including seven transversions were found in 299 base pairs (bp) of control region sequence (GenBank accession numbers AY016175-AY016207, AY047691-AY047702, table 1 and presented as a MST in figure 2). Twenty-four haplotypes were found in single animals and 18 were shared between two or more individuals (Haplotypes A–R). With the exception of Haplotypes H and N found only in the Faroe Islands, the shared haplotypes were not restricted to one sampling site (see electronic Appendix A, available on The Royal Society's Publications Web site). The average intrapopulation haplotype diversity was high (0.8686) whereas the average intrapopulation nucleotide divergence was low (0.0107, table 1). Haplotype diversity in the more recent colonies was not noticeably lower than in the putative source populations, and in some cases was actually higher (electronic Appendix A). Indeed, St Kilda has significantly fewer haplotypes than other sites ($p = 0.002$ by randomization with 1000 replicates, sampling with replacement from the overall haplotype distribution, significant at $p = 0.014$ after Bonferroni correction).

Significant population differentiation was found between Iceland and St Kilda, the two possible source populations (table 2). However, no geographical clustering of haplotypes was present between the newly colonized populations and the source populations (figure 2). Significant differences were also found between the Shetland and Faroes, but even this was eliminated after Bonferroni correction, indicating high levels of gene flow between the other colonies.

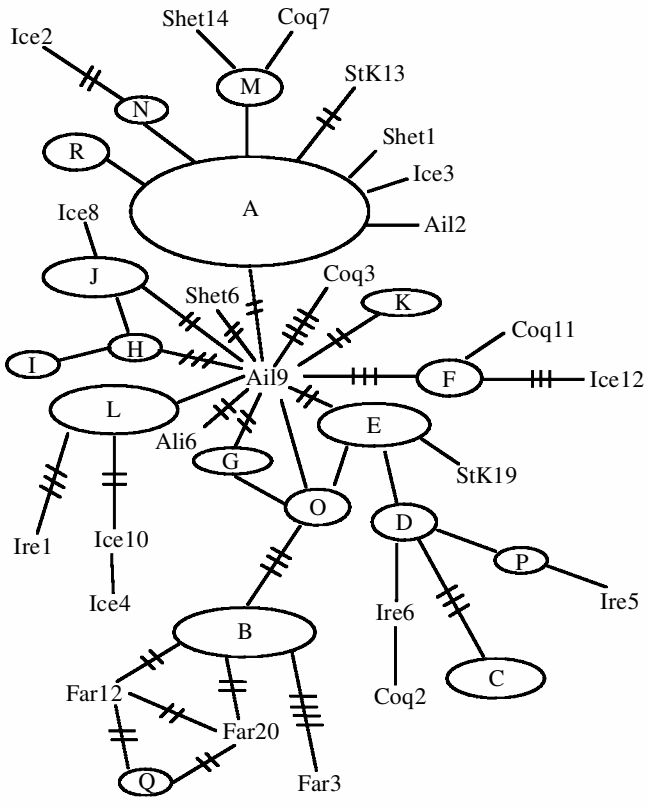

Figure 2. A minimum spanning network of the fulmar haplotypes. Haplotypes that are found in more than one bird are indicated by a single letter and are in an oval. The geographical distribution of the haplotypes is provided in table 1. Numbers of nucleotide differences larger than one are indicated by crosshatches and the size of the oval is proportional to the number of individuals sharing that haplotype.

Under Fisher's hypothesis, we would predict that genetic distance would increase with geographical distance from Iceland, but not (or at least to a lesser degree) with geographical distance from St Kilda. An all-against-all plot of genetic distance against geographical distance reveals a positive relationship which is significant by standard regression analysis ($r = 0.45$, $n = 21$, $p < 0.05$), and when non-independence is allowed for, by use of a Mantel test ($p = 0.015$; 10 000 randomizations). This result is consistent with a simple isolation by distance model. If the population has expanded from a single source population through a stepping stone colonization of ever more distant breeding sites, we might expect a pattern in which an isolation by distance model fits some sites better than others, with the most important source population showing a stronger pattern than other sites. To examine this possibility, we took each breeding site in turn and regressed genetic distance against geographical distance to all other sites. We find that St Kilda yields the strongest relationship ($r = 0.69$) followed by Ailsa ($r = 0.57$) and Faroes ($r = 0.43$). None of the regressions is significant, which is not surprising given the small number of comparisons in each case (table 3). However, given that isolation by distance does exist, the high value associated with St Kilda points to this site being an important source.

Repeating these analyses using F_{ST} as a measure of population subdivision rather than genetic distance

Table 1. Within- (bold) and between-island nucleotide divergence. Average sequence divergence is 0.0107.

	Coq	Far	Ice	Shet	Ail	StK	Ire
Coq	**0.0139**	—	—	—	—	—	—
Far	0.0123	**0.0094**	—	—	—	—	—
Ice	0.0143	0.0110	**0.0119**	—	—	—	—
Shet	0.0128	0.0097	0.0102	**0.0088**	—	—	—
Ail	0.0115	0.0086	0.0100	0.0086	**0.0079**	—	—
StK	0.0128	0.0103	0.0118	0.0099	0.0093	**0.0103**	—
Ire	0.0134	0.0105	0.0124	0.0110	0.0098	0.0113	**0.0122**

Table 2. Pairwise F_{ST} values between sites calculated from AMOVA using 9999 permutations.
(F_{ST} values are below the diagonal and p values are above the diagonal with significant values in bold.)

	Coq	Far	Ice	Shet	Ail	StK	Ire
Coq	—	0.3293	0.1198	0.1038	0.5808	0.2395	0.5749
Far	0.0112	—	0.1597	0.0279	0.7565	0.0818	0.9142
Ice	0.0379	0.0263	—	0.7824	0.3253	**0.0000**	0.2216
Shet	0.0495	0.0543	−0.0171	—	0.1982	0.1440	0.1238
Ail	−0.0034	−0.0195	0.0037	0.0275	—	0.2691	0.8218
StK	0.0104	0.0458	0.0594	0.0322	0.0142	—	0.3885
Ire	−0.0110	−0.0252	0.0297	0.0468	−0.0349	0.0034	—

Table 3. Isolation by distance correlations for each colony, calculated separately based on the genetic and geographical distances between a given site and all other sites.

	r value	significance
Coq	0.141	n.s.
Far	0.431	n.s.
Ice	0.320	n.s.
Shet	0.261	n.s.
Ail	0.574	n.s.
StK	0.685	n.s.
Ire	0.327	n.s.

revealed no significant relationships of any kind, neither for the overall isolation by distance plot ($r = 0.065$, n.s.), nor for any of the individual breeding site plots. This result is likely to be caused by the high mitochondrial haplotype diversity we find. With two-thirds of individuals carrying haplotypes found in a single individual or in one other sample, and with our rather modest sample sizes, the power of F_{ST} to reveal population subdivision is small, almost regardless of the degree of isolation that exists in reality.

4. DISCUSSION

We have examined patterns of mitochondrial diversity in seven fulmar breeding sites around the North Atlantic. Levels of gene flow appear to be high, with only one of the pairwise comparisons showing a significant F_{ST} value. By contrast, genetic distances between haplotypes reveal a pattern consistent with isolation by distance. Testing each site separately for fit to an isolation by distance model reveals the strongest pattern with St Kilda, suggesting that this population has acted as a source population.

Fulmars are capable of flying immense distances, and their recent expansion to new sites indicates that many birds have bred successfully away from their natal colonies. Such observations suggest considerable gene flow between colonies, and this appears to be born out by the generally low level of differentiation between colonies. At the same time, all of the sites carry haplotypes which, in our limited samples, were unique to a colony. Thus, although there is evidence of considerable gene flow, the population is a long way from being completely panmictic.

James Fisher (1952) proposed that the expansion occurred in a series of steps, with new colonies being founded by a few individuals from the nearest existing colony. This would result in a sequential series of bottlenecks, with haplotype diversity declining with distance from the source population. Several recent studies were able to examine the effect of founder effects on genetic diversity (Bodkin *et al.* 1999; Glenn *et al.* 1999; Clegg *et al.* 2002). Bodkin *et al.* (1999) and Glenn *et al.* (1999) found that bottlenecks caused a reduction in haplotype diversity (the number of haplotypes) in the post-bottleneck population owing to the elimination of rare haplotypes, whereas changes in nucleotide diversity (average difference between haplotypes) were more dependent on which haplotypes survived the bottleneck. Glenn *et al.* (1999) have shown that, when two-thirds of the haplotypes were lost in a severe population bottleneck in whooping cranes (*Grus americana*) at the beginning of the twentieth century, nucleotide diversity remained unchanged. Like the fulmars, Clegg *et al.* (2002) found that islands recently colonized by silvereyes (*Zosterops lateralis*) showed evidence of multiple colonization events, high levels of genetic diversity and no evidence of founder effects.

Our data suggest that any bottlenecks that did occur were too slight to impact significantly on levels of diver-

sity. Ireland, historically one of the last sites to be colonized, has approximately the same haplotype diversity as the Faroes, one of the earliest sites. Similarly Coquet, a small (about 80 pairs) colony founded around 1970 (K. Hamer, personal communication), is remote from the putative source populations of Iceland and St Kilda, but nevertheless has very high diversity (electronic Appendix A). Indeed, the very high levels of diversity found in Coquet and elsewhere argue strongly that founding events tend to involve many unrelated birds.

A further test of Fisher's hypothesis would be to look for evidence of isolation by distance. We find a significant positive relationship between genetic and geographical distance. If Fisher is correct about the stepping stone process, distances involving the true source population should show the clearest relationship with genetic distance. When tested, the strongest relationship is given by St Kilda ($r = 0.69$), with all other sites showing positive slopes, with r values ranging from 0.14 (Coquet) up to 0.57 (Ailsa). Similar tests based on F_{ST} values yield no significant relationships.

Our data thus appear contradictory. Supporting a stepping stone process we find evidence of restricted gene flow between some sites and a good isolation by a distance pattern that appears to identify St Kilda as a potential source of the expansion. Against this, there is evidence of appreciable current gene flow and the distribution of haplotype diversity bears little similarity to that expected of a series of bottlenecks radiating out from St Kilda. More importantly still, St Kilda shows significantly lower diversity than expected of random sampling from our entire samples, with four haplotypes accounting for 82% of sampled individuals. At the same time, Coquet is known to have been founded relatively recently, yet has substantially higher diversity (0.90) than St Kilda (0.76) and contains only one of the four most common St Kilda haplotypes. Even ignoring the higher diversity, the chance of sharing only one of the common haplotypes is remote (14 : 3 versus 1 : 9, $\chi^2 = 13.3$, $p < 0.001$), making it unlikely that Coquet birds are descended recently from a random sample of St Kilda emigrants.

There are two ways to reconcile the situation. Trivially, birds on St Kilda might have been sampled so as to include several close relatives, thereby distorting the pattern of haplotype diversity. This can be rejected on several grounds. First, field observations show that relatives seldom return to breed close to their natal nest site (Dunnet *et al.* 1979), making it virtually impossible to sample relatives by chance, even if sampling focused on a single area. Second, the isolation by distance seen for St Kilda is dependent on the distribution of a few more common haplotypes. If these haplotypes were not genuinely common on St Kilda, they would not have spread in such a consistent pattern to neighbouring colonies.

According to historical records, the only two colonies that were extant more than 500 years ago were St Kilda and Iceland. The records are good enough for us to assert this with some confidence. Thus, if the birds currently on Coquet did not come primarily from St Kilda, then by elimination we need to consider the possibility that they came either directly or indirectly from Iceland. Estimates of the current Icelandic population size range up to as many as 10 million birds (Lloyd *et al.* 1991), and haplotype diversity is, as expected, extremely high. Given that we have only sampled 16 Icelandic birds and yet find 13 haplotypes, it is possible that the Icelandic population embraces sufficient variability such that further sets of samples would continue to reveal mainly novel haplotypes. In other words, the apparent lack of similarity between Coquet and Iceland could be merely an artefact of small sample sizes and extreme haplotype diversity. With such high diversity, it is not surprising that rather weak patterns are found when looking for isolation by distance because only shared haplotypes are informative.

By contrast to Iceland, the St Kilda population carries substantially lower diversity, probably because of historically intensive harvesting by humans. Even with limited dispersal, this low diversity will lead to haplotype sharing between sites, which in turn will tend to generate the strong isolation by distance effect we find. A good example is Haplotype A, the most common St Kilda haplotype, which is found seven times on Shetland and three times in Iceland, in both instances being one of the few non-unique haplotypes at the site. Thus, although the most direct evidence points to St. Kilda rather than Iceland as the dominant source, this may well not be the case. Not only is dispersal from Iceland masked by the extreme haplotype diversity found there, but also, the low diversity found on St. Kilda is incompatible with this colony being the only (or even primary) source of birds founding newer colonies such as Coquet, Ailsa and Ireland.

Fisher's dismissal of the possibility that St Kilda could have been significantly involved in the colonizations before the 1950s is to some extent justified. The St Kilda fulmar population was extensively culled for food until the late 1920s (Lloyd *et al.* 1991) and remained static throughout the bulk of the expansion. However, the St Kilda population began to expand in the late 1960s and could have contributed to the population expansion in the past 40 years. There is evidence of gene flow between St Kilda and the new colonies suggesting continual migration between St Kilda and these new populations, though the direction of the movement is not known.

In conclusion, despite rather small sample sizes and the huge capacity for movement that fulmars possess, we have found evidence of isolation by distance, implying that most dispersal involves movement to neighbouring breeding sites. Exactly such a pattern of lower dispersal to further sites has been recorded in other, less dispersive Procellariiformes (see Brooke 1990; Rabouam *et al.* 1998) and indeed in other birds (Lindholm 1999). Approaching the question of which colony acted as the source population for the species' recent range expansion, we can say with confidence that birds came from both the candidate colonies on Iceland and St Kilda. The stronger pattern is shown by St Kilda, but this is probably misleading. The comparison between St Kilda and Iceland draws attention to the fact that high genetic diversity can mislead by masking even quite strong patterns of population substructure. If the excellent historical records did not tell us that Iceland was the only other possible source, it would have been extremely difficult to prove this genetically without a considerably larger sample size.

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This is an electronic appendix to the paper by Burg *et al*. 2003 Unravelling dispersal patterns in an expanding population of a highly mobile seabird, the northern fulmar (*Fulmarus glacialis*). *Proc. R. Soc. Lond.* B **270**, 979—984. (DOI 10.1098/rspb.2002.2322.)

Electronic appendices are refereed with the text. However, no attempt is made to impose a uniform editorial style on the electronic appendices.

Electronic appendix A

Variable sites from 299 bp of aligned control region sequences from 115 fulmars. Sequence identity to Coq2 is indicated by '**.**', and mixed bases by either R= A/G or Y=C/T. Haplotypes found in more than one bird are assigned a letter and the number of samples from each site are shown along with haplotype diversity estimates for each population.

	Variable sites 11111111111112222222222222 11145566789990001122366778445666678899 05845757130260172836845247459024959394	Coq	Far	Ice	Shet	Ail	Ire	StK
Coq2	ATTGATTGGTTTAAGCTAGAAGGAGGCGCAACGGTTGGG	1						
Coq3	..................G.G..R.......GT.......	1						
Coq7	..........CA.....G.G........T.G.A......	1						
Coq11	C.................GRG..........G.A......	1						
Far3	......A..........G.G....A..R..G.A......		1					
Far12	..................G.G...GR.....G.A......		1					
Far20	.....C...........G.G...GA.....G.A......		1					
Ice2	..C..........G...G.G........T.G.A..C...			1				
Ice3	........A........G.G........T.G.A......			1				
Ice4	............GG...G.G........T.GTA.....A			1				
Ice8	............GG...G.G.A........G.A......			1				
Ice10	............G....G.G........T.GTA.....A			1				
Ice12	C..........C.....GAG..........G.ACC....			1				
Shet1	..................CG.G........T.G.A......				1			
Shet6	..............C..G.G..........G.A......				1			
Shet14	..........C......G.GG.......T.G.A......				1			
Ail2	.C................G.G........T.G.A......					1		
Ail6	.........C.......G.G..........G.A......					1		
Ail9	............R....G.G..........G.A......					1		
Ire1	...R...A.........G.G....AR..T.G.A......						1	
Ire5	...............G.G...........G..A......						1	
Ire6	................................A......						1	

StK13	.................G.GG.......T.G.AT.....							1
StK19	.................G.G............A...C..							1
A	.................G.G........T.G.A.....		2	3	7	1	4	7
B	.................G.G...GA.....G.A..Y...		2	1	2		3	2
C	........................T.....A....A.				1		1	3
D	.................G.............A.....		2			1		
E	.................G.G............A.....	1	2			1		2
F	C................GAG..........G.A.....	1	1		1			
G	....G............G.G..........G.A.....			1		1	2	
H	.............G...G.G...R......G.A.....		2					
I	.............G...G.G.........GG.A.....	1	1					
J	.............GG...G.G..........G.A.....				1	1	3	
K	.............G....G.G.....A....G.A.....		3				1	
L	.............G....G.G........T.G.A.....		2	1	3	1		1
M	..........C......G.G........T.G.A.....			1	2			
N	.............G...G.G........T.G.A.....		2					
O	.................G.G..........G.A.....		1	2				
P	.................G............G..A.....	1					1	
Q	.................G.G...GA...T.G.A.....	1		1				
R	...................G........T.G.A.....	1	1				1	
Number of samples		10	24	16	20	9	19	17
Number of haplotypes		10	15	13	10	9	11	7
Haplotype diversity		0.90	0.92	0.91	0.82	0.89	0.88	0.76