



## Effects of extrinsic and intrinsic factors on breeding success in a long lived seabird

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There is growing concern over the impacts of climate change on animal species. Many studies have demonstrated impacts of climate change at the population level, and density dependent effects of climate are frequently reported. However, there is an increasing recognition of the differential impact of such factors on individuals since there is marked variation in individual performance. We investigated the relationships between breeding success and environmental conditions (winter NAO and one year lagged winter NAO) and intrinsic effects (colony size, pair bond duration, past breeding success rate) in the northern fulmar *Fulmarus glacialis*, using data from a long-term study commenced in 1950. There was a negative trend in breeding success over time, and a negative relationship with winter NAO and lagged winter NAO, which themselves had shown positive increases over the study period. The effects of lagged winter NAO remained after accounting for the linear trend. There was no evidence of density dependence, with breeding success positively related to colony size. We found strong evidence that breeding success was negatively related to pair bond duration but positively related to past breeding success rate. There was also an interaction between these two intrinsic effects such that those pairs that had historically been successful maintained success with increasing pair bond duration, whereas less successful pairs showed a decline. The prediction that there would be a differential impact of extrinsic factors among pairs was supported by an interaction between past breeding success rate and winter NAO, such that pairs with low past success rate exhibited a sharp decline in breeding success with increasing winter NAO, whereas more successful pairs did not. It is critically important to understand interactions between extrinsic factors and individual heterogeneity since a differential impact on individuals will affect population structure, and hence population dynamics.

There is growing concern about the ecological effects of climate change (Hughes 2000, Walther et al. 2002). Numerous studies have demonstrated impacts on the population dynamics of animal species at both the large scale (Holmgren et al. 2001, Ottersen et al. 2001, Stenseth et al. 2002, Hallett et al. 2004) and small scale (Altwegg et al. 2006). In many cases, environmental effects on population growth rate are density dependent (Newton 1998, Godfray and Rees 2002, Berryman 2004). Typically, such studies have been carried out at the population level (Coulson et al. 2000, Jenouvrier et al. 2005). However, there is an increasing recognition that environmental conditions may have a differential impact at the individual level since there is marked variation in breeding performance and survival among individuals (Clutton-Brock 1988, Newton 1989, Gaillard et al. 2000, Coulson et al. 2006). Understanding the effect of environmental conditions and density on individual heterogeneity in demo-

graphic rates is critically important because any differential impact on individuals will affect population structure, with important consequences for population dynamics (Coulson et al. 2001, Benton et al. 2006)

Heterogeneity in individual demographic rates can result from a number of intrinsic causes. A widespread example in long-lived, iteroparous species is the effect of age on breeding success. Typically, there is an increase in reproductive performance over the first few breeding attempts, which may be due to individual improvements in competence or effort (Williams 1966, Curio 1983, Nol and Smith 1987), and a decline with old age (Mysterud et al. 2002, Orell and Belda 2002, Jones et al. 2008). Closely linked to these age-specific patterns are the effects of breeding experience and, among species with biparental care, duration of the pair bond, both of which have been generally shown to have a positive impact on breeding success, independent of age (Bradley et al. 1990, Pärt 1995, Lewis

et al. 2006). Irrespective of age, individuals vary in quality (Newton 1985, Lewis et al. 2006, van de Pol and Verhulst 2006, Stopher et al. 2008). Numerous measures of quality have been put forward (reviewed by Moyes et al. 2009), directly or indirectly linked to changing or persistent measures of fitness. Typically, individuals with greater historical breeding success are more likely to be successful in the current breeding attempt. Heterogeneity in individual quality can result in population-level increases in performance with age if breeding and survival ability are correlated within individuals (Nol and Smith 1987, Cam and Monnat 2000, van de Pol and Verhulst 2006).

There is an increasing recognition that environmental effects and density have a differential impact on demographic rates of individuals of different ages, stages or qualities e.g. plants (Horvitz and Schemske 1995, Rees et al. 2000); invertebrates (Benton and Beckerman 2005, Mueller et al. 2005); vertebrates (Clutton-Brock et al. 1987, Coulson et al. 2001). Among long-lived, iteroparous species, studies have reported interactions between age or experience and environmental conditions on breeding performance (Ratcliffe et al. 1998, Laaksönen et al. 2002, Bunce et al. 2005, but see Nevoux et al. 2007) and survival (Gaillard et al. 1993, 1998, 2000, Coulson et al. 2001, Barbraud and Weimerskirch 2005, Nevoux et al. 2007). Density dependence in age-specific reproduction (Wilson et al. 2007) and survival (Coulson et al. 2001) has also been demonstrated. Furthermore, a series of studies on red deer *Cervus elaphus* have identified interactions between certain individual quality measures and population density on birth date, calf mass and calf survival (Clutton-Brock et al. 1987, Nussey et al. 2005, Stopher et al. 2008). Typically, individual differences are more marked as conditions deteriorate, with those age/experience/quality classes with poorer intrinsic abilities more strongly affected by an increase in competition or decrease in resources (Daunt et al. 2007).

In this paper, we investigate the interrelationships between extrinsic and intrinsic factors and breeding success in a population of the long-lived, iteroparous northern fulmar *Fulmarus glacialis*. This population has been the subject of a long-term demographic study since 1950. The population increased dramatically over the first 30 years of the study before stabilising then declining slightly in recent years (Fig. 1). Previous work has shown that breeding

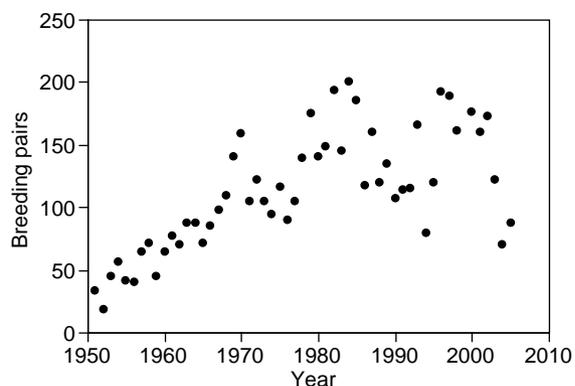


Figure 1. Number of breeding pairs of northern fulmars on Eynhallow, Orkney between 1950 and 2005.

performance increases with age and experience (Ollason and Dunnet 1978) and is negatively related to the winter NAO (Thompson and Ollason 2001). Thus, there is evidence of intrinsic and extrinsic influences on reproductive performance. Here, we examine the interactions between environmental conditions (winter NAO and lagged winter NAO) and intrinsic factors (colony size, pair bond duration and historical breeding performance) on breeding success.

## Methods

### Species and study site

The study was carried out on Eynhallow, a small uninhabited island in Orkney, Scotland (59°8'N, 3°8'W), where there is a long-established breeding colony of northern fulmars *Fulmarus glacialis*. The fulmar colony on Eynhallow has been visited each year since 1950, and approximately 60% of the birds breeding at the colony have been caught and given a numbered British Trust for Ornithology (BTO) metal ring and unique two or three colour ring combination. Our study focused on annual data between 1958 and 2005, which were collected on three standardised visits to the colony: during early incubation in late May/early June, at hatching in mid July and before fledging in mid-August. Data were available in all years except 1997, 1998 and 2000. Each year in late May/early June, we counted the number of occupied nests to provide an estimate of local density at the breeding colony. Attending birds at each nest site were identified from their unique colour ring combinations, and these data used to estimate the breeding performance of each pair in each year. Sexes were identified from a discriminant analysis of bill measurements (Dunnet and Anderson 1961), and each newly formed pairing was given a unique code. Each year, new (i.e. unringed) breeders were ringed once their chicks had hatched, when adults are less vulnerable to disturbance. Full details of the study area and methods are provided in Dunnet (1991) and Grosbois and Thompson (2005).

### Estimation of demographic parameters

As fulmars lay only one egg, breeding success for each pair in a given season (BS) was estimated by determining whether the pair did or did not produce a fledgling (1 or 0) at the end of the reproductive season. By following the success of each nest site at which both birds were colour ringed, it was possible to construct pair specific breeding histories containing 3131 breeding records from 312 unique pairs (mean pairs per year  $63.63 \pm 19.12$  SD, range 29–95; mean records per pair  $9.79 \pm 6.66$ , range 1–32). These data enabled us to examine two of the four intrinsic factors that have been widely reported to affect breeding success in biparental species (age, experience, pair bond duration and individual quality). The minimum number of previous breeding attempts (i.e. pair bond duration) and the number of previous chicks fledged per year (a measure of individual quality) could be calculated for each breeding pair. Because the relationships between these factors and breeding success may be non-linear, because of associated senescent effects, we examined both linear and quadratic

relationships in the models. Unfortunately, the age of individuals was not known. Furthermore, we support the arguments developed by Lewis et al. (2006) that past breeding success and experience with your mate are more relevant measures among biparental species than number of previous breeding attempts irrespective of success or mate identity, so did not fit breeding experience per se to the models. Note that the data contain pairs with complete and incomplete breeding histories, the latter occurring among pairs where the earliest years may have been missed due to the difficulties in capturing both members of the pair during their first breeding season. Furthermore, some of the pairs are still alive. These data also include pairs that start together as new breeders and pairs where one or both members was previously part of another pair (i.e. a new pairing following a divorce or death of partner). Of 312 pairs (comprising of 252 males and 266 females), 51 males and 42 females had more than one partner (i.e. were included in more than one pairing).

### Environmental variables

The winter North Atlantic Oscillation (WNAO), reflecting the large scale climate variation in the northern Atlantic has been found to be related to both the reproductive success (Thompson and Ollason 2001) and survival (Grosbois and Thompson 2005) of adult fulmars. The mechanism underlying these relationships remains unclear, but could be related either to known direct effects of the WNAO on weather e.g. wind speed affecting foraging costs (Furness and Bryant 1996), short-term influences of the WNAO on the availability of zooplankton prey (Planque and Taylor 1998), or a delayed influence on higher trophic level fish prey (Arnott and Ruxton 2002). We therefore considered both a direct effect of WNAO (downloaded from <<http://www.cgd.ucar.edu/cas/jhurrell/nao.stat.winter.html>>) and a lagged effect (by one year) WNAO as environmental covariates in our analyses. The use of other more local environmental indices (e.g. sea surface temperature) was not possible in these analyses due to an absence of data on the wintering or summer foraging distribution of fulmars from this or any UK colonies.

### Correlations between covariates

As expected from previous studies (Thompson and Ollason 2001, Grosbois and Thompson 2005), there were positive correlations between linear trend and WNAO, lagged WNAO and colony size (Table 1). There was also positive

Table 1. Pearson correlation coefficients (*r*) between pairs of covariates used in the model. The second values in each category represent the results of analyses on de-trended data. Corresponding *p*-values are shown in brackets.

	Lag winter NAO	Colony size	Year
Winter NAO	0.389; 0.280 (0.006; 0.054)	0.08; -0.149 (0.591; 0.319)	0.39 (0.005)
Lag winter NAO		0.159; -0.044 (0.287; 0.768)	0.380 (0.008)
Colony size			0.508 ( $<0.001$ )

temporal autocorrelation in the WNAO, resulting in a correlation between WNAO and lagged WNAO; however, WNAO and lagged WNAO were not correlated with colony size (Table 1). Following Grosbois and Thompson (2005), we also examined correlations of de-trended data (residuals of the least squares linear regression between the covariate and the linear trend) and found the positive associations to be greatly reduced (Table 1). There was a tendency for de-trended WNAO and de-trended lagged WNAO to be positively correlated, but this was not statistically significant. Thus, as previously concluded by Grosbois and Thompson (2005), the positive correlations between covariates was due to long term behaviour of the time series rather than short-term fluctuations.

### Demographic and environmental correlates of breeding success

To examine the relationship between demographic parameters and environmental correlates and breeding success, we fitted generalised linear mixed models (GLMM) with a binomial distribution and logit link function to the binary breeding success data. The following explanatory variables were examined: linear year (covariate), WNAO, lagged WNAO and linear and quadratic terms for pair bond duration and past success rate. Year (as a categorical effect) and pair id were included as multi-level random effects.

We initially ran a number of single-variable models to examine effects of explanatory variables in the absence of others. As a second step, we developed a multiple regressor model. Year (as a covariate, hereafter called linear trend) was fitted first in this model in order to account for the long-term trends in colony size, WNAO, lagged WNAO and to control for any unknown trend effects. These could include effects of unknown environmental trends, but could also capture broader scale changes in the density of birds at sea resulting from increases in UK fulmar populations over the last century (Mitchell et al. 2004). Each of the remaining explanatory variables was then fitted sequentially, after linear trend, to deduce the order of best fit for the model. In cases where both linear and quadratic effects were examined, we fitted the quadratic effect immediately after the linear effect (irrespective of significance). The most significant variable when fitted after linear trend was then fitted second followed by the remaining terms. The subsequent modelling steps involved re-fitting with a different ordering of variables (i.e. after the first and second term) to deduce the third most important term. This process was repeated with the first, second and third terms fitted first in the model, and so on, until we had the final best fit model.

The final model, omitting regression coefficients for continuous variables and denoting random categorical effects (F), was as follows:

$$\text{Logit (probability of breeding success)} = \text{linear trend} \\ + \text{past success rate} + \text{pair bond duration} \\ + \text{lag WNAO} + \text{WNAO} + \text{colony size} \\ + \text{year (F)} + \text{pair id (F)}$$

The interaction between pair bond duration and past success rate was fitted at the end of the model to examine whether any pair bond duration effects were linked to pair

Table 2. Output produced from single variable binomial generalised linear mixed models (GLMM) on breeding success for all of the fixed effects with year and pair identity as random effects, for all breeding attempts (n = 3131) from 312 pairs of fulmars followed from 1958 to 2005 (<sup>a</sup>linear trend; <sup>b</sup>past success rate + quadratic past success rate; <sup>c</sup>pair bond duration + quadratic pair bond duration; <sup>d</sup>lagged winter NAO; <sup>e</sup>winter NAO; <sup>f</sup>colony size).

Single variable models				
Fixed effects:	Estimate	SE	Wald	p
Linear trend <sup>a</sup>	-0.0145	0.007	3.78	0.052
Past success rate <sup>b</sup>	1.1330	0.168	44.20	<0.001
Past success rate (quadratic) <sup>b</sup>	-0.6330	0.460	1.89	0.169
Pair bond duration <sup>c</sup>	-0.0221	0.010	13.23	<0.001
Pair bond duration (quadratic) <sup>c</sup>	-0.0018	0.001	3.11	0.078
Lag Winter NAO <sup>d</sup>	-0.1030	0.045	5.39	0.020
Winter NAO <sup>e</sup>	-0.0976	0.044	4.95	0.026
Colony size <sup>f</sup>	0.0018	0.002	0.54	0.463

quality effects. To examine whether the environment or population density impacts on birds with longer bonds and past success rate differentially, we fitted the following two-way interactions separately at the end of the model: linear trend × pair bond duration; linear trend × past success rate; WNAO × pair bond duration; WNAO × past success rate; lagged WNAO × pair bond duration; lagged WNAO × past success rate; colony size × pair bond duration; colony size × past success rate. Finally, since climate effects themselves may be density dependent (Coulson et al. 2001, Loison et al. 2002), we fitted a WNAO × colony size interaction and a lagged WNAO × colony size interaction. Non significant interactions were omitted from the final model.

In these models, the random effects were additive in the model (thus combinations of year and pair identify data items uniquely), and the random effect distributions were assumed to be Gaussian. The models allowed for over-dispersion at the year and pair levels. The random effect factor pair id accounted for combined effects of pair-specific properties not included in the main model, thereby allowing the effects of pair-specific covariates in the model to be estimated against the correct error term and so avoiding any pseudo replication effects.

One concern with these data was that pairs present at the beginning of the study might in some way differ from pairs

recruiting into the population thereafter. For example, the early breeding years may be missing from the former, whereas we are more likely to have the full breeding histories from those pairs ringed after the study had been underway for a few years. To test for this effect, we re-ran the model only including those pairs that had entered the study post 1970 but found very little difference in the results. Consequently we present the results from the analysis of all pairs.

All models were fitted using restricted maximum likelihood (REML) methods in Genstat 8th ed. (VSN) ver. 8.2.0.158. The GLMMs allowing for interactions between pair id and covariates were fitted after modifying the code of the standard GLMM procedure: the revised code is available from the authors on request. All explanatory variables added to the fixed model were centred on their unweighted mean values.

## Results

The output from the single-variable and full binomial models examining the effect of the demographic and environmental variables on variation in breeding success are given in Table 2 and 3 respectively. There was a negative linear trend, such that breeding success declined during the

Table 3. Final binomial generalised linear mixed model (GLMM) on breeding success for all of the fixed effects with year and pair identity as random effects, for all breeding attempts (n = 3131) from 312 pairs of fulmars followed from 1958 to 2005. The significance value of sequentially adding each fixed effect to each model is shown (type I tests).

Final Model				
Fixed effects:	Estimate	SE	Wald	p
Constant	-0.4007	0.101		
Linear trend	-0.0042	0.010	1.84	0.174
Past success rate	1.3500	0.188	46.94	<0.001
Past success rate (quadratic)	-0.9825	0.561	1.65	0.199
Pair bond duration	-0.0210	0.014	10.70	0.001
Pair bond duration (quadratic)	-0.0015	0.001	1.75	0.186
Lag Winter NAO	0.0860	0.051	3.84	0.050
Winter NAO	-0.0350	0.048	1.14	0.285
Colony size	0.0056	0.003	3.78	0.052
Linear trend x Past success rate	-0.0460	0.015	3.85	0.050
Past success rate x Pair bond duration	0.0738	0.033	5.38	0.020
Past success rate x Winter NAO	0.1655	0.073	5.14	0.023
Random effects:	Variance component	SE		
Year	0.305	0.092		
Pair	0.220	0.071		

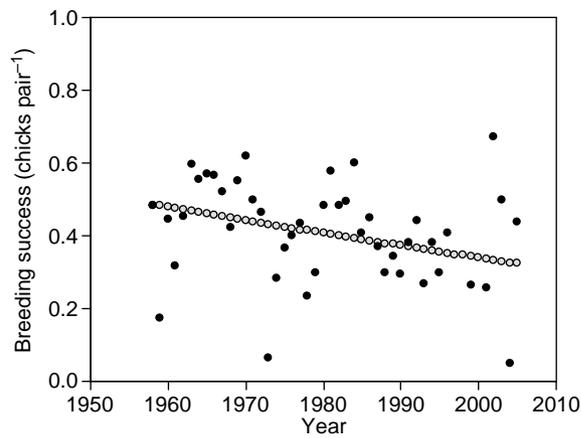


Figure 2. The relationship between year and average breeding success for 312 pairs of fulmars followed from 1958 to 2005. The fitted line (grey circles; back transformed from the single effect binomial generalised linear model) is also shown.

study from a mean of 0.49 chicks pair<sup>-1</sup> in 1958 to 0.32 chicks pair<sup>-1</sup> in 2005 (Fig. 2). There was strong evidence that breeding success was negatively related to pair bond duration but positively related to past breeding success rate (Table 2, 3). There was a significant interaction between pair bond duration and past success rate. Those pairs that had high past success rate (mean of 0.833 chicks pair<sup>-1</sup>) maintained breeding success with increasing pair bond duration at 0.5–0.55 chicks pair<sup>-1</sup>, whereas those with intermediate past success rate (mean of 0.500 chicks pair<sup>-1</sup>) and low past success rate (mean of 0.167 chicks pair<sup>-1</sup>) showed declines from 0.45 to 0.35 and 0.35 to 0.15 chicks pair<sup>-1</sup> respectively over the range of pair bond durations from 0 to 31 years (Table 3, Fig. 3). There was

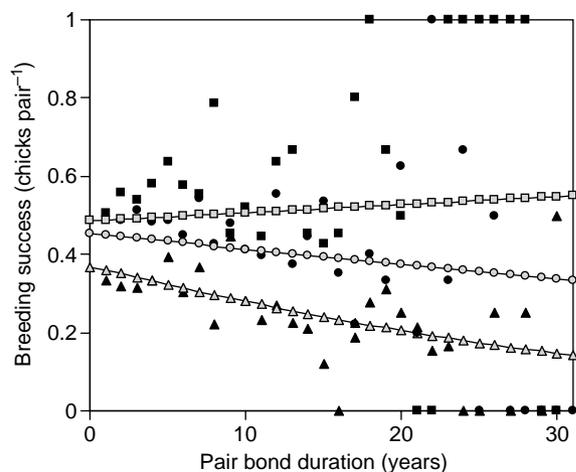


Figure 3. The relationship between pair bond duration (in years) and breeding success for northern fulmar pairs with low (black triangles; 0–0.333 chicks pair<sup>-1</sup>), medium (black circles; 0.334–0.666 chicks pair<sup>-1</sup>) and high (black squares; 0.667–1 chicks pair<sup>-1</sup>) past success rate; numbers represent annual means for each category. To aid interpretation, also shown are predicted values back transformed from the full binomial generalised linear model for past success rate values of 0.167 (grey triangles), 0.500 (grey circles) and 0.833 (grey squares) representing the mid-values for each past success rate class.

also an interaction between linear trend and past success rate on breeding success, such that pairs with higher levels of past success rate showed a decline in breeding success over the study period from ca. 0.6 to 0.35 chicks pair<sup>-1</sup>, whereas those from low past success rate increased breeding success slightly from 0.25 to 0.35 chicks pair<sup>-1</sup> (Table 3).

There was evidence for a negative relationship between breeding success and both lagged WNAO and WNAO (Table 2, Fig. 4), the former retaining its significance in the full model (Table 3). There was a significant interaction between WNAO and past success rate such that those pairs that had low levels of past success showed a decline in breeding success with increasing WNAO from 0.4 to 0.2 chicks pair<sup>-1</sup>, whereas those with high past success were unaffected by WNAO conditions (Table 3, Fig. 5).

There was no evidence of density dependence on breeding success, with colony size unrelated to breeding success in the single effect analysis (Table 2) and with a tendency to be positively associated with breeding success in the full model (Table 3).

No further interactions were apparent between extrinsic and intrinsic effects (linear trend × pair bond duration:  $W = 1.71$ ,  $p = 0.192$ ; WNAO × pair bond duration:  $W = 2.54$ ,  $p = 0.111$ ; lagged WNAO × past success rate:  $W = 0.65$ ,  $p = 0.419$ ; lagged WNAO × pair bond duration:  $W = 1.27$ ,  $p = 0.261$ ; colony size × past success rate  $W = 0.56$ ,  $p = 0.455$ ; colony size × pair bond duration:  $W = 0.33$ ,  $p = 0.565$ ).

Finally, there was no strong evidence of an interaction between WNAO and colony size ( $W = 3.29$ ,  $p = 0.070$ ), nor between lagged WNAO and colony size ( $W = 0.16$ ,  $p = 0.686$ ).

## Discussion

This study demonstrates important links between extrinsic and intrinsic factors and breeding success in the northern fulmar. Breeding success has declined steadily at a rate of ca 0.35% per annum from 1958 to 2005, and was related to lagged WNAO after accounting for this trend. Pair bond duration and past success rate were strongly related to breeding success. The significant interaction between WNAO and past success rate provides support for the general prediction of an interaction between environmental and intrinsic effects. Finally, there was no evidence that these results were density dependent.

The linear decline in breeding performance over the study period may have resulted from a trend in some unknown environmental variable, but it could also reflect density dependent effects on the foraging grounds as a result of the marked increase in the total UK population over the last century. In Orkney alone, occupied nests rose from 13 557 in 1949 (Lloyd et al. 1991) to 90 846 in 2000 (Mitchell et al. 2004). However, there is no evidence that breeding success declined in relation to measures of local density at the study colony. Rather, there was a positive tendency between local colony size and breeding success. This may be due to an Allee effect, for example from higher levels of predation during years with lower colony density. Alternatively, higher breeding population size may reflect good environmental conditions (beyond the effect of

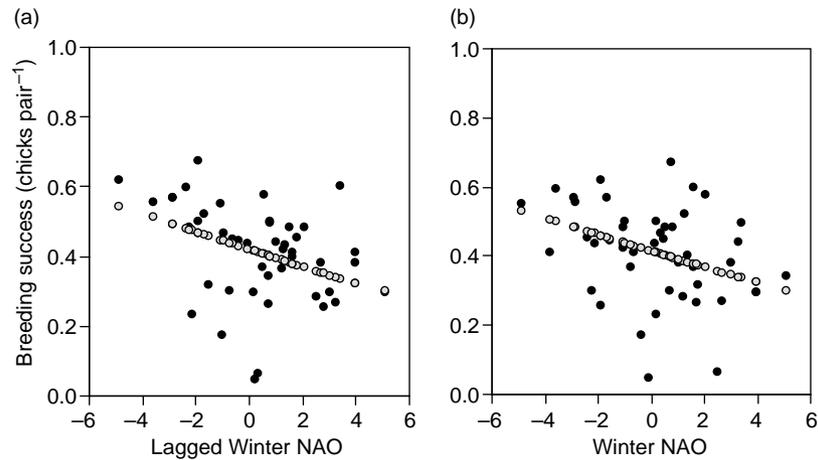


Figure 4. The relationship between a) lagged winter NAO and b) winter NAO and average breeding success. The fitted line (grey circles; back transformed from single effect binomial generalised linear models) is also shown.

WNAO, which was captured by the model), meaning that a higher proportion of breeders attend the colony (Thompson and Ollason 2001, Jenouvrier et al. 2005). However, this assertion must be set against the possibility that intermittent breeding leading to year-to-year fluctuations in breeding numbers may mean that colony size is not a particularly accurate reflection of variations in density (of breeders and non-breeders) at the foraging areas. Understanding the determinants of the decline in breeding success during the study is further complicated by the fact that there has also been a positive trend in WNAO over this period (Grosbois and Thompson 2005). However, when fitted after linear trend, the negative relationship with lagged WNAO remained, suggesting that this link did not appear to result from the long term trends in the two time series. Although

less statistically significant, there was also a negative relationship between breeding success and WNAO. However, the link with WNAO was not evident in the final model because the relationship largely disappeared when fitted after lagged WNAO. Thompson and Ollason (2001) have previously demonstrated a negative relationship between breeding success and WNAO in this population. Grosbois and Thompson (2005) showed a negative relationship between WNAO and northern fulmar survival, with female survival significantly affected by detrended NAO. Winter NAO may impact on fulmar breeding success indirectly through the availability of food. During negative NAO winters, the survival of *Calanus*, the primary prey of many of the species of fish and crustacean that fulmars feed on, is higher (Planque and Taylor 1998). The greater impact of lagged WNAO on breeding performance may reflect the time for the effect to filter up trophic levels to top predators. Alternatively, breeding success may be determined by the direct effects of weather conditions experienced under different WNAO regimes, although if direct effects are important, it is not clear why they should be lagged. These studies of northern fulmar demography are part of a growing body of evidence that suggests that the relationship between seabird demography and the NAO is complex (Forslund and Pärt 1995, Durant et al. 2003, Frederiksen et al. 2004, Crespin et al. 2006, Møller et al. 2006, Jones et al. 2008, Sandvik et al. 2008).

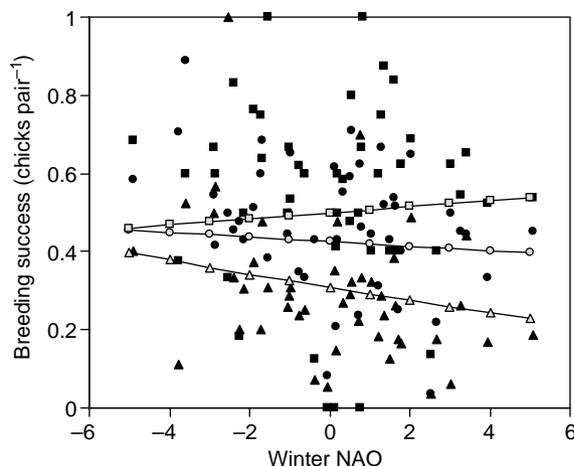


Figure 5. The relationship between winter NAO and breeding success for northern fulmar pairs with low (black triangles; 0 – 0.333 chicks pair<sup>-1</sup>), medium (black circles; 0.334 – 0.666 chicks pair<sup>-1</sup>) and high (black squares; 0.667 – 1 chicks pair<sup>-1</sup>) past success rate; numbers represent annual means for each category. To aid interpretation, also shown are predicted values back transformed from the full binomial generalised linear model for past success rate values of 0.167 (grey triangles), 0.500 (grey circles) and 0.833 (grey squares) representing the mid-values for each past success rate class.

The decline in breeding success with increasing pair bond duration contrasts with the typical age-specific pattern of reproductive performance from recruitment (Forslund and Pärt 1995). This pattern of senescence has already been reported for a smaller subset of the known-age birds from this colony (Jones et al. 2008) and may be largely due the low probability of detecting, or capturing, birds if they fail during incubation. Thus, pairs may be less likely to enter our marked population during that early phase of their breeding history when annual reproductive success is predicted to increase. There was an interaction between pair bond duration and past success rate, such that individuals with high historical success maintained breeding success with increasing pair bond duration, whereas less successful birds showed a decline. Thus, whilst it is unclear

what the cause of the decline with pair bond duration is, high quality pairs appear to be buffered against this, and can maintain their high performance. Past success rate was more closely associated with breeding success and, in contrast to pair bond duration, was positive related. Pairs that have been successful together in the past are typically more likely to do so in the current breeding attempt, as has been shown in other studies (Newton 1985, 1989, Lewis et al. 2006, van de Pol and Verhulst 2006, Stopher et al. 2008). It may seem paradoxical that low quality pairs remain together despite having a very low productivity; presumably there is a greater cost than benefit of divorce, including the energetic cost of finding a mate, the possibility of securing a poorer quality individual, and the stress of being with a new mate (Angelier et al. 2007).

We found an interaction between the linear trend and past success rate which is difficult to interpret since the linear trend could be due either to extrinsic or intrinsic factors. However, we also found that WNAO affected high and low quality pairs differently, such that those individuals with low past success rate showed a decline with increasing WNAO, whilst those with higher past success rate remained stable. This relationship supports the general finding of a greater individual heterogeneity as conditions decline. This result has important implications for our understanding of the impacts of climate change on animal populations. Differential effects of climate among individuals of different quality will affect population structure, which will have important consequences for population dynamics. Thus, it is imperative that individual heterogeneity is incorporated into models of climate effects on population size (Coulson et al. 2001, Benton et al. 2006). Whilst the population consequences of the interaction between WNAO and individual quality are unknown, this finding highlights the importance of individual-based studies in understanding the effect of environmental conditions on wild populations.

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