

## Climate fluctuations and differential survival of bridled and non-bridled Common Guillemots *Uria aalge*

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**Citation:** Reiertsen, T. K., K. E. Erikstad, R. T. Barrett, H. Sandvik, and N. G. Yoccoz. 2012. Climate fluctuations and differential survival of bridled and non-bridled Common Guillemots *Uria aalge*. *Ecosphere* 3(6):52. <http://dx.doi.org/10.1890/ES12-00031R>

**Abstract.** Climate fluctuations and its effects on ecological processes are evident in most areas worldwide but whether such climatic effects are induced phenotypic plasticity or whether animals adapt to the new environment through micro-evolutionary processes is poorly known. In this study we have analyzed long-term data (22 years) on the relationship between climatic fluctuations and the adult survival of two distinct genetic morphs of the Common Guillemot (*Uria aalge*) breeding in a colony in the southern Barents Sea. In the North Atlantic, the Common Guillemot is a genetic color dimorphic species, with a non-bridled morph, with an entirely black or dark brown head, and a bridled morph having a white eye ring and auricular groove sloping back from the eye. Our results show that the two morphs responded differently to variation in the Barents Sea winter sea-surface temperature (SST). The survival rate of the bridled morph was negatively correlated to the winter SST in the Barents Sea, while that of the non-bridled morph was slightly positively correlated to the same parameter. Over the whole study period, SSTs fluctuated between warm and cold winters and the overall mean survival rates of the two morphs remained similar (96.2% and 95.9% for the bridled and non-bridled morph, respectively). This suggests a balanced selection and a stable dimorphism of the two morphs over this time period. The contrasting trends in the survival of the two morphs with respect to temperature suggest that further warming of the sea may induce directional changes and alter the frequency of the two morphs.

**Key words:** Barents Sea; climate; color polymorphism; Common Guillemots; demography; microevolution; sea surface temperature; survival; *Uria aalge*.

**Received** 8 February 2012; **accepted** 4 May 2012; **published** 22 June 2012. Corresponding Editor: C. Lepczyk.

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### INTRODUCTION

The predicted changes in climate as a consequence of global warming are widely evident and influence both plants and animals, and knowledge of how climate fluctuations affect various life history traits has greatly improved (e.g., Parmesan 2006, IPCC 2007, Visser 2008). In

general, organisms can adapt to a changing environment through shifts of species distribution and range, through changes in migration strategies and through phenotypic plasticity and/or microevolutionary processes by altering their genetic composition (reviewed in Parmesan 2006 and Millien et al. 2006). However, empirical studies addressing whether climate fluctuations

have the potential to drive changes in selection, resulting in microevolution are scarce (Gienapp et al. 2008, Sheldon 2010).

Color polymorphism, which is the existence of two or more color variants that differ genetically in a population, can be considered as a phenotypic genetic marker, since it is often related to important fitness-related factors (Roulin 2004). One such factor is adult survival, and a recent study by Karell et al. (2011) showed that climate differentially affected the adult survival of two genetically distinct color morphs of the Tawny Owl *Strix aluco* resulting in a change in the frequency of the morphs in the population as temperature increased. Their study showed how the study of color polymorphism in birds is a promising approach to examine microevolutionary processes and demonstrates how a wild population can adapt to climate change.

Furthermore, different color patterns may be adaptive under different environmental conditions by providing behavioral or physiological advantages to their bearers (e.g., Galeotti and Cesaris 1996, Galeotti and Rubolini 2004). Galeotti et al. (2009) also suggested that the equilibrium between gene frequencies could vary under different conditions and habitats, if the lifetime fitness of different morphs differed between habitats, and that this equilibrium could be disrupted by climate change through direct and indirect effects on fitness. Thus any differences between morphs in their responses to climatic change and any differences in morph frequencies over time may indicate natural selection.

Among seabirds, there is strong evidence that climate affects life-history traits such as timing of breeding (Durant et al. 2004, Reed et al. 2009), breeding success (reviewed in Sandvik and Erikstad 2008) and adult survival (e.g., Harris et al. 2005, Jenouvrier et al. 2005, Sandvik et al. 2005, Le Bohec et al. 2008, Saraux et al. 2011). Of these, the climatic effect on adult survival is especially serious, since adult survival has a strong effect on lifetime fitness in species with “slow” life histories (Lebreton and Clobert 1991). Many seabird species have such a life history, with small clutches, delayed maturation and high adult survival (Stearns 1992). As such, any effect of climatic change observed on survival in long-lived species will, even on a small time

scale, exert a strong selective pressure (Gienapp et al. 2008).

In the North Atlantic, the Common Guillemot *Uria aalge* is a good example of a color polymorphic species; with a non-bridled morph, with an entirely black or dark brown head and a bridled morph that has a white eye ring and auricular groove sloping back from the eye. The bridled form is a recessive variant of the normal form, carried by a gene on one autosome (Jefferies and Parslow 1976). There are no apparent differences in behavior between the bridled and the non-bridled birds, and mating between them is random (Harris and Wanless 1986, Birkhead et al. 1980, Lyngbo Kristenssen 2010). The frequency of the bridled form is considered as a classic example of a stable ratio-cline polymorphism, with an increase northwards on both sides of the North Atlantic. Along the European cline, the proportion of bridled individuals increases from 0% on the Iberian Peninsula to 50% in the Arctic, whereas in Canada counts in the 1950s indicated a clear cline from 17% in southern Newfoundland to 71% in northern Labrador (Southern 1962, Birkhead and Lock 1980, Birkhead 1984). At least until the early 1980s, the overall latitudinal distribution along the European cline remained stable over many decades (Birkhead 1984). Although the current situation is uncertain, Birkhead’s study indicated a balanced polymorphism, where variable selection pressures are related to a latitudinal gradient in environmental conditions, with non-bridled individuals being more warm-tolerant than bridled birds (Southern 1951, Birkhead 1984, Jefferies and Parslow 1976). This latitudinal change in the frequency of bridling is a good example of the visualization of a clinal change in gene frequency among populations in a species. Gaston and Jones (1998) suggested that the continuous cline in bridling indicated maintenance of polymorphism by selection, presumably related to climate or water temperature.

In this study, we test the prediction that the winter adult survival rate of adult bridled Common Guillemots is higher than that of non-bridled adults under cold conditions (or vice versa), using a multi-state capture-mark-recapture framework and different climatic covariates. The results are discussed in the context of how populations adapt to climate fluctuations, and

how climate change may alter the selective balance between the two morphs, and therefore have the potential to drive microevolution.

## METHODS

### *Study species and data collection*

The Common Guillemot's distribution is circumpolar, from temperate to arctic areas. About 3 million pairs breed in the North Atlantic, with ca. 15,000 pairs (in 2005) in Norway (Gaston and Jones 1998, Barrett et al. 2006). The Norwegian population has, however, declined by >95% since the 1960s and several mainland colonies are in danger of extinction (Erikstad et al. 2007). It is thus classified as critically endangered in the Norwegian Red List (Kålås et al. 2010). A few Norwegian colonies have, however, increased in size since 1988, including that at Hornøya, an island in NE Norway (70°22' N, 31°10' E) where this study was carried out. Here the population has increased from ca. 1300 breeding pairs in 1988 (after a widespread collapse in 1986/87 due to a die-off of adult birds (Vader et al. 1990)), to ca. 10,000 breeding pairs in 2010 (R. T. Barrett, unpublished data).

Common guillemots are long-lived seabirds, with low fecundity (a single egg is laid per year). Juvenile survival is low and varies strongly between cohorts (see Harris et al. 2007) and sexual maturation is at 4–6 years (Birkhead and Hudson 1977). Common guillemots show strong nest-site fidelity, and breeding birds normally return to same site each year (Harris and Wanless 1988). Some inter-colony movements do occur, but mostly among immature birds (Gaston and Jones 1998, Harris et al. 2007). Common Guillemots forage at sea, and in NE Norway their main prey-species during the breeding season are young age-classes of cod (*Gadus morhua*) and herring (*Clupea harengus*), capelin (*Mallotus villosus*) and sandeels (*Ammodytes* sp.) (Bugge et al. 2011).

We used long-term (1988–2010) re-sightings of color-ringed breeding birds and a capture-mark-recapture framework in the analysis. Breeding birds were initially caught using a noose-pole, and ringed with a numbered stainless steel ring and a unique color-ring combination consisting of three rings. Whether the bird was bridled or non-bridled was also noted. Searches of near-

constant effort for color-ringed birds were then made in all subsequent years. Up to 2009, 209 birds had been marked, 61 bridled and 148 non-bridled guillemots. The frequency of bridling was determined five times during the period of the study through counts of birds with or without bridling in the colony in 1989, 2005, 2008, 2009 and 2010, either directly in the field (1989) or from digital photographs.

### *Capture-mark-recapture (cmr) modeling of survival*

Our capture-mark-recapture (cmr) analysis started with developments of the Cormack-Jolly-Seber model (CJS) (Lebreton et al. 1992, Cormack 1964, Jolly 1965, Seber 1965), a model that requires that all individuals should have the same probabilities of capture and survival, which is an appropriate starting point when working with live resightings of marked individuals. Since the birds were only captured once, and then later resighted, we denote the recapture rate as resighting rate.

The goodness-of-fit (GOF) of the CJS model was assessed for both the bridled and the non-bridled morph using the U-CARE software (Choquet et al. 2005) to examine if the model fitted the data, and to detect the causes of any lack of fit (transient or trap-dependent effects). Test 3.SR, a test component in the GOF test, which tests the CJS assumption that all marked birds alive at time  $i$  have the same probability of surviving to  $i + 1$  (Lebreton et al. 1992), showed that there was no transience effect (bridled morph;  $N(0, 1) = 0.44$ ,  $\chi^2 = 1.95$ ,  $df = 10$ ,  $p = 0.997$  and the non-bridled morph;  $N(0, 1) = 0.25$ ,  $\chi^2 = 3.40$ ,  $df = 17$ ,  $p = 1.0$ ). Another test component in the GOF test is the test2.CT, which tests the assumption of independence in the resighting rate, i.e., if the probability of being resighted at  $i + 1$  is a function of whether or not the bird was caught or resighted at  $i$ . The CJS was rejected in the test 2.CT, for both the bridled morph ( $N(0, 1) = -5.19$ ,  $\chi^2 = 28.11$ ,  $df = 11$ ,  $p = 0.003$ ) and the non-bridled morph ( $N(0, 1) = -4.26$ ,  $\chi^2 = 30.17$ ,  $df = 18$ ,  $p = 0.036$ ) suggesting that both morphs have trap-happiness, i.e., birds resighted in year  $t$  had a higher chance of being resighted again in year  $t + 1$ , than birds that had not been resighted in year  $t$ . We corrected for trap-happiness using the method suggested by

Gimenez et al. (2003), by using a multi-state model, with three states, considering a different resighting probability depending upon whether an animal was resighted or not in the previous year. These models take into account an unobservable state for non-resighted in the previous year (the probability of not having been seen before). An overview of the model development is given in Appendix A.

The annual survival rates of the two morphs were estimated and compared using the programme E-SURGE (Choquet et al. 2009). Model selection started with a time-dependent model (denoted  $\Phi(t)$ ,  $p(f + t)$ , where  $\Phi$  is the annual adult survival and  $p$  is the resighting probability,  $t$  is time-dependence and  $f$  is the notation for the transition between states when we corrected for trap-happiness in the model. We then looked for the appropriate model for annual adult survival and the resighting probability, comparing the time-dependent model with the constant survival ( $\Phi(i)p(f + t)$ ), constant resighting probability ( $\Phi(t)p(f)$ ), or both ( $\Phi(i)p(f)$ ) where  $i$  denotes a constant model. We also added the group effect (bridled and non-bridled birds) to the above to test for any differences in survival and resighting rate between the two morphs. This group effect is denoted  $g$ . The operators “+” and “.” were used for additive models, and for models with an interaction between groups and covariates.

All model selection was performed using the QAICc (Quasi-likelihood Akaike Information Criterion corrected for small sample size and overdispersion) (Sugiura 1978). The model with the lowest QAICc-value was considered the best model.  $\Delta$ QAICc is the difference between the QAICc of the model and the QAICc of the best model. According to Burnham and Anderson's (2002) scale of  $\Delta$ QAICc model interpretation, scores of  $\Delta$ QAICc  $\leq 2$  are strongly plausible, 4–7 are considerably less plausible and  $\geq 10$  are improbable. Survival and resighting probability estimates are given with 95% CI.

#### *Climatic and density-dependence effects*

Climatic variables were included as covariates in the models to examine whether any of these could explain the variation observed in the survival and resighting probabilities. We used the large scale North Atlantic Oscillation (NAO) winter index (Hurrell 1995, Hurrell 2010) (avail-

able at: <http://www.cgd.ucar.edu/cas/jhurrell/indices.html>) and winter SST (December–March) from the Barents Sea, and SST for May and June (around the colony) lagged by 0 to 4 years. Winter, when food abundance is depressed, weather conditions are generally poor and sometimes extreme and shortened day length restrict foraging opportunities, is a critical period for the survival of seabirds, and most mortality occurs then (Daunt et al. 2006, Harris et al. 2010). As such, winter climate conditions may be an important factor affecting Common Guillemot survival. Winter SST in the Barents Sea is used because Common Guillemots spend most of the winter in this area (Nikolaeva et al. 1996). Having returned to the colony in early spring to breed, the birds are more restricted to the areas around the colony in their search for food. Therefore we also used SST close to the colony for May and June, the months when the birds lay eggs and incubate at Hornøya. To test whether climate affected the survival directly or indirectly, we also lagged the climatic variables with 0–4 years. The covariates were added to both groups (bridled and non-bridled guillemots) both separately and together, and both additive models and models with interactions between groups were run. When incorporating covariates into the models, the winter NAO and SST and the May and June SST (all with lags 0 to 4) were denoted as NAO, SST, SSTJune and SSTMay respectively.

May and June SST was an optimum interpolation of SST data available on a  $1^\circ \times 1^\circ$  grid NE around Hornøya (Reynolds et al. 2002, NOAA 2010). Winter SST was interpolated in the same way, but for a larger area, covering the ice free parts of the Barents Sea (between  $80^\circ$  N,  $50^\circ$  E,  $70^\circ$  N and  $15^\circ$  E). Since the guillemot population at Hornøya has increased since 1987, we also added the effect of the population size to the models. The population size was log-transformed prior to analysis, in order to compare it relatively to the other covariates.

#### RESULTS

The most parsimonious model corrected for trap-happiness both before and after climatic covariates was added (Appendix B: Table B1). The best model structure before covariates were added (here noted as general model) consisted of

Table 1. Alternative models explaining variation in survival ( $\Phi$ ) and resighting probabilities ( $p$ ) of the bridled (B) and the non-bridled (NB) Common Guillemots, and the neighbour models of the best model. Notations: SSTL2, winter sea surface temperature in the Barents Sea with a lag of two years; SSTJune, sea surface temperature around Hornøya in June; SSTMay, sea surface temperature around Hornøya in May;  $f$ , a model that has been corrected for trap-happiness in the resighting probabilities;  $i$ , a constant model;  $g$ , a group effect;  $t$ , a time dependent model; operators “.” and “+”, a model with an interaction between the groups and an additive model, respectively.

No.	Model	Par	Dev.	QAICc	$\Delta$ QAICc	QAICc wt
1	$\Phi(\text{SSTL2(B).SSTL2(NB)})$ $p(\text{SSTJune} + f)$	7	1592.80	1606.86	0.00	0.38
2	$\Phi(\text{SSTL2(B).SSTL2(NB)})$ $p((\text{SSTJune(B)} + \text{SSTJune(NB)}) + f)$	8	1592.36	1608.44	1.58	0.17
3	$\Phi(\text{SSTL2(B).SSTL2(NB)})$ $p(\text{SSTMay} + f)$	7	1595.22	1609.26	2.42	0.11
4	$\Phi(\text{SSTL2(B).SSTL2(NB)})$ $p((\text{SSTMay(B)} + \text{SSTMay(NB)}) + f)$	8	1594.90	1610.98	4.12	0.05
5	$\Phi(\text{SSTL2(B).SSTL2(NB)})$ $p((\text{SSTJune(B).SSTJune(NB)}) + f)$	10	1591.06	1611.19	4.32	0.04
11	$\Phi(i(\text{B}).\text{SSTL2(NB)})$ $p(\text{SSTJune} + f)$	6	1602.46	1614.51	7.65	0.01
13	$\Phi(g)$ $p(\text{SSTJune} + f)$	5	1605.86	1615.90	9.04	0.00
14	$\Phi(\text{SSTL2})$ $p(\text{SSTJune} + f)$	5	1606.11	1616.14	9.28	0.00
16	$\Phi(\text{SSTL2(B)+SSTL2(NB)})$ $p(\text{SSTJune} + f)$	6	1605.82	1617.87	11.01	0.00
19	$\Phi(\text{SSTL2(B).SSTL2(NB)})$ $p(f + t)$	27	1564.71	1619.54	12.68	0.00
21	$\Phi(\text{SSTL2(B).SSTL2(NB)})$ $p(t + g) + f)$	28	1564.13	1621.03	14.17	0.00
29	$\Phi(\text{SSTL2(B).SSTL2(NB)})$ $p(f)$	6	1612.25	1624.30	17.44	0.00
33	$\Phi(i)$ $p(f + t)$	24	1577.32	1625.98	19.12	0.00
54	$\Phi(\text{SSTL2(B).i(NB)})$ $p(\text{SSTJune} + f)$	6	1655.57	1667.62	60.76	0.00

a constant survival and a time dependent resighting rate (Table 1). Adding climatic covariates to the survival probabilities, a model containing winter sea surface temperature (winter SST) in the Barents Sea with a lag of two years, and an interaction between the bridled and the non-bridled guillemot survival proved to be the best model (Table 1 and Fig. 1). This model contained a time-dependent resighting rate that covaried with the SST in June around the colony (Fig. 2). The second best model had a  $\Delta$ QAICc that was 1.58 units higher than the best model and differed only in having an additive group effect in the resighting rate (Table 1). This model had one parameter more than the best model, but did not add any more information over the simpler model. Based upon parsimony and lack of any biological reason to include the extra parameter we chose the simpler model (Table 1). The mean resighting rate in the model with differential

resighting between the two morphs did not differ (mean resighting rate for bridled birds = 0.71 ( $\text{CI}_{95\%} = [0.59, 0.78]$ ), mean resighting rate for non-bridled birds = 0.73 ( $\text{CI}_{95\%} = [0.63, 0.81]$ )). We therefore considered that the group-effect in the resighting rate was unsupported. Based on QAICc weight, the likelihood that the top rank model was best was 38%, whereas the likelihood that the second best model proved to be the best was only 17% (Table 1). Thus winter sea surface temperature two years earlier explained best the variation in the survival, and showed that the two morphs responded differently to winter SST (Fig. 1). The survival of bridled Common Guillemots was negatively correlated ( $\beta = -1.9$  ( $\text{CI}_{95\%} = [-3.09, -0.71]$ )) to the winter SST in the Barents Sea, whereas that of the non-bridled Common Guillemots was slightly positively correlated ( $\beta = 0.77$  ( $\text{CI}_{95\%} = [-0.16, 1.69]$ )) to the same parameter. However the overall mean survival rates of the

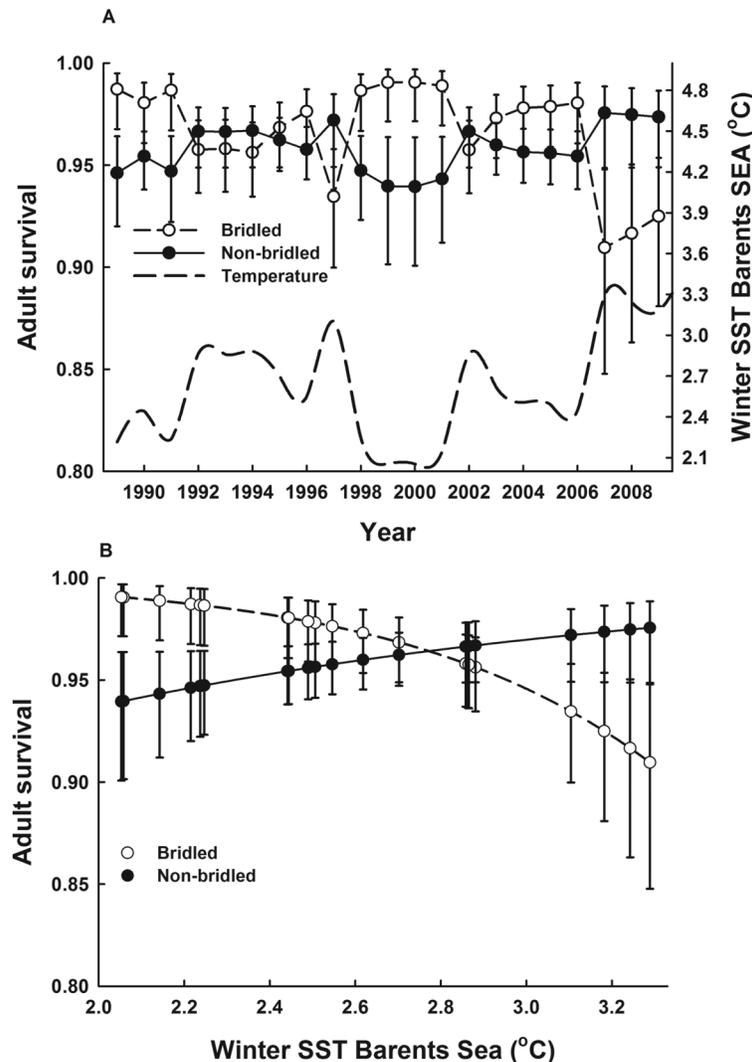


Fig. 1. The variation in estimated survival ( $\Phi$ ) for bridled and the non-bridled Common Guillemots with 95% CI at Hornøya, NE Norway. (A) Yearly variation in survival and yearly variation in winter sea surface temperature (SST) lagged by two years in the Barents Sea, 1988 to 2009. (B) The same data as in (A) but the estimated survival lagged by two years are plotted against the variation in winter SST.

two morphs remained similar (96.2% and 95.9% for the bridled and non-bridled morph, respectively).

The model selection did not give any support for the NAO index having an effect on survival or resighting rate ( $\Delta\text{QAICc} = 8.64$ ). Nor was there any evidence that the population size affected survival and resighting rate ( $\Delta\text{QAICc} = 4.40$ ). Table 1 only includes the 5 top rank models together with some neighbour models of interest. A total overview of the model selection can be

seen in Appendix B: Table B1. There were no significant changes in the frequencies of bridling at Hornøya during the period of this study ( $\chi^2 = 2.8$ ,  $df = 4$ ,  $p = 0.60$ ; Table 2).

## DISCUSSION

Our results show contrasted demographic responses to climate between two genetically different color morphs within a population of Common Guillemots in the Barents Sea. The

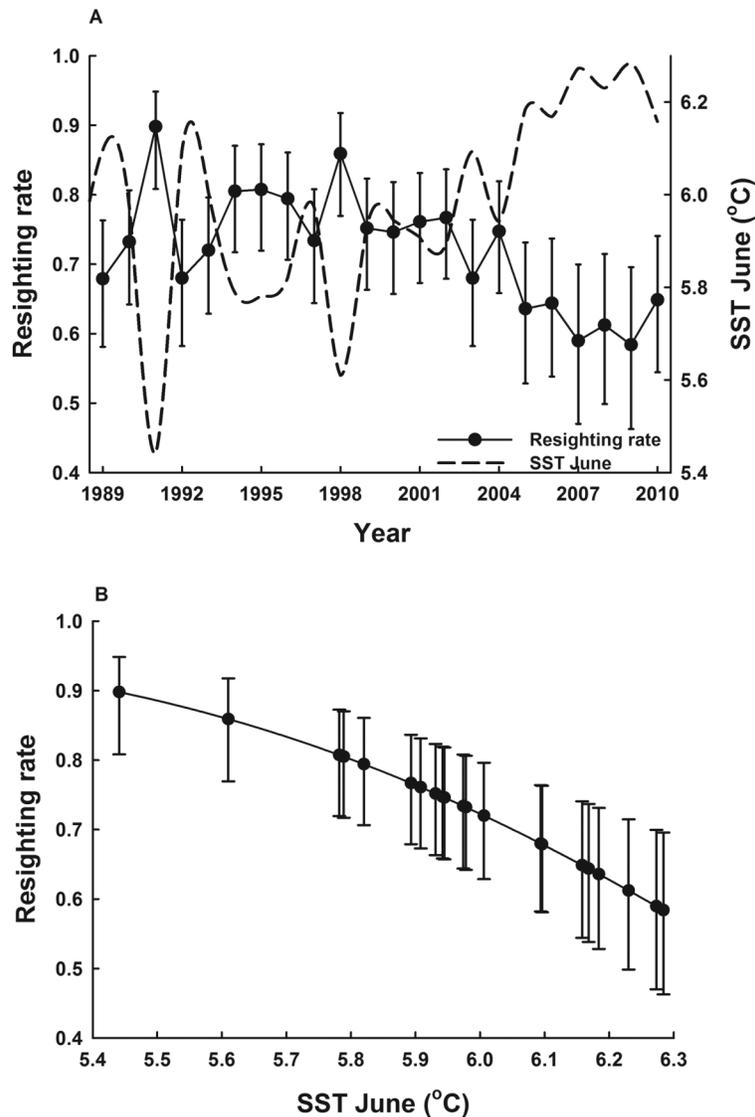


Fig. 2. The variation in the estimated resighting rate ( $p$ ) of Common Guillemots with 95% CI at Hornøya, NE Norway. (A) Yearly variation in resighting rate and the yearly variation in SST in June (SST June) near Hornøya, 1988 to 2010. (B) The same data as in (A) but the estimated resighting rate is plotted against the variation in June SST.

survival of the bridled morph was negatively correlated to winter SST in the Barents Sea two years prior to breeding while that of the non-bridled morph was slightly positively affected by the same factor. Such contrasted demographic responses to temporal environmental variations have previously been documented between closely related bird species (Forcada et al. 2006, Rolland et al. 2010, Barbraud et al. 2011) and

between different populations of the same species (Frederiksen et al. 2005), but rarely within a single population (but see Karell et al. 2011). For the Common Guillemot it has been suggested that bridling is a balanced polymorphism with the bridled form being better adapted to cold conditions (Southern 1951, Jefferies and Parslow 1976, Birkhead 1984). There is, however, hitherto scarce evidence for any relationship between life

Table 2. Frequency (number of birds) of bridled and non-bridled Common Guillemots at Hornøya in 1989–2010.

Year	Bridled	Non-bridled	% bridled birds
1989	39	66	37, 1
2005	75	138	35, 2
2008	86	180	32, 3
2009	138	270	33, 8
2010	139	317	30, 5

history traits in bridled and non-bridled guillemots and the variance in temperature. The only study to our knowledge is that by Harris et al. (2003) at the Isle of May, Scotland, where the frequency of the bridled morph is 3.5–5.9% (range between 1946 and 2000). They found small and non-significant differences in adult survival and small but significant differences in hatching success (83.8% for a pair including at least one bridled bird vs. 79.5% in non-bridled pairs). The differences in breeding success contributed, however, relatively little to the increase of bridling observed in the Scottish population, and no association with a decrease in air or sea temperatures over the period was found.

Our documentation of differential survival of the two morphs on Hornøya supports the hypothesis that the bridled morph is better adapted to a colder climate, which is consistent with the increase in frequency of bridling towards the north (Southern 1951, Jefferies and Parslow 1976, Birkhead 1984). However, we have, as yet, no direct evidence of the underlying mechanisms and, in the lack of any conclusive evidence, we discuss two possible pathways which need to be considered in more detail in the future.

(1) Different color patterns may be adaptive under different environmental conditions by providing behavioral or physiological advantages (Galeotti and Cesaris 1996, Galeotti and Rubolini 2004, Galeotti et al. 2009). In the Common Guillemot genes for bridling may have a pleiotropic effect, such that color dimorphism may be associated with another property that is the real target of selection. Several studies of both birds and other animals have suggested that differential performance of morphs across environments are caused by genetic co-variation between coloration and a physiological or be-

havioral trait (Roulin 2004, Brommer et al. 2005, Ducrest et al. 2008, Pault et al. 2009). However, our study gives no support for any physiological differences related to temperatures. We show that winter SST two years earlier affected the survival, implying an indirect effect.

(2) Any lagged climatic effects on adult survival in seabirds as shown here is most likely an indirect effect of the temporal variation in the prey availability (e.g., Sandvik et al. 2005). The two-year lagged effect on the winter SST in the Barents Sea on adult survival suggests differences in prey selection among the two morphs. The fish community in the Barents Sea is dominated by a few but very abundant species with strong interspecific interactions (Hamre 1994) driven by climatic interactions (e.g., Hjermann et al. 2004, Stige et al. 2010). Among the dominant fish species in the region are the Northeast Arctic cod, Norwegian spring-spawning herring and capelin, all of which are important prey species for the guillemots during the pre-breeding (Erikstad and Vader 1989) and breeding season (Bugge et al. 2011). The winter diet of Common Guillemots in the Barents Sea is unknown, but detailed studies of fish stock interactions in the Barents Sea have shown that climate indirectly influenced the population dynamics of capelin through its influence on the reproduction of herring and cod (Hjermann et al. 2004). In warm years, the spawning conditions for cod and herring are good and as the fish become older their predation on their main prey, capelin, increases. This increase, combined with extensive fisheries (in the first instance), have contributed to repeated collapses in the capelin stocks (in 1986/87, 1995/96 and 2003–06). That the bridled guillemot's survival is negatively correlated to the winter SST in the Barents Sea two years prior to breeding season could indicate that the bridled morph depends more on cold-water species such as capelin as a food resource. Conversely, the slightly positive correlation between the survival of the non-bridled morph and the winter SST could indicate that non-bridled birds forage more on warmer water species such as young age classes of cod and herring. To confirm this, we need detailed studies of both the winter diet of the two morphs and their spatial distribution outside the breeding season.

Another important question arising from the

present study is whether climate fluctuations and a future global warming have the potential to alter the selective balance between the morphs, and therefore the potential to drive microevolutionary changes. Such changes depend on a temporal change in the frequency of bridling in the population. Although the survival of the two morphs showed opposite trends in response to the winter SST in the Barents Sea (Fig. 1B), the mean adult survival of the two morphs did not differ over the 22 years of this study (96.2% and 95.9% for the bridled and non-bridled morph respectively), suggesting that the variance in temperature during the present study was insufficient to upset a stable and balanced selection of the two morphs over time. This is also consistent with the frequency of the bridled morph in the present study population which did not change during the study period. However further warming of the Barents Sea is expected over the next decades (IPCC 2007) and such warming may result in selection for the non-bridled morph in our study area. An alternative mechanism which may balance or alter the frequency of bridled and non-bridled birds is gene flow due to immigration of bridled recruits from more southern populations when the temperature increases. Such a scenario also needs to be considered in the future.

The resighting rates were similar for the two morphs, but were negatively related to the SST around the colony in June. The effort to read color rings was the same each year, and the variance in resighting may reflect the rate of deferred breeding (the frequency of birds who are alive, but skip breeding in any year, e.g., Jenouvrier et al. 2003). For long-lived seabirds, the strategy to skip breeding is common in years of poor breeding conditions in order to maximize their residual fitness and thereby buffer their life histories against environmental variability by trading current reproduction for future reproduction (Erikstad et al. 1998, Jenouvrier et al. 2003, Breton et al. 2006). A high frequency of non-breeding birds is often associated with poor body condition at the start of the breeding season (Chastel et al. 1995) and a general lower breeding success, (Schreiber and Schreiber 1989, Catry et al. 1998, Nur and Sydeman 1999). In the only, to us, known study of the breeding success of the two morphs, Harris et al. (2003) showed a small

but significant higher breeding success among bridled Common Guillemots but concluded that these small differences could not explain the slight increase in the frequency of bridled birds in their study area (Isle of May). At Hornøya there are detailed data on breeding success for three years only (2009–2011), but no differences between the two morphs were evident (*unpublished data*). All in all, this suggests that there is no differential selection on the two morphs during the breeding season. Instead, the adult winter survival is plausibly the target for selection on the frequency of the two morphs.

### Conclusion and prospects

Our study provides strong evidence for contrasting effects of climatic fluctuations on the adult survival of two genetic morphs of the Common Guillemot. Adult survival is the trait that has the largest potential impact on lifetime fitness in a long-lived species such as the Common Guillemot. This suggests that climatic factors, even on a small time scale, are able to exert selection pressure, and hence could induce microevolutionary processes for adaptations to a new environment. A main challenge for future studies of climatic effects on population changes would be to separate the effect of phenotypic plasticity from that of microevolutionary processes. Such studies are so far scarce and fragmentary (reviewed in Gienapp et al. 2008), but see Karell et al. (2011). There are three conditions that need to be fulfilled in order to demonstrate that a population has responded adaptively to climatic change (reviewed in Parmesan 2006). One is that the selection on a trait related to fitness has to be documented. Second, there should be evidence that this trait is linked to climatic change and third that a genetic change in the trait is demonstrated. Our study gives strong evidence of the first two conditions. Although the frequency of bridling over time shows no trend so far, the predicted warming of the sea may pose directional changes in favor of the non-bridled morph in the years to come.

### ACKNOWLEDGMENTS

The Norwegian Coastal Administration is thanked for the use of the lighthouse on Hornøya as a base for the field work. This study was funded by the University of Tromsø, and the Norwegian Directorate

for Nature Management. Since 2005 the study has also been financed through the Norwegian Seabird Program (SEAPOP). Author contributions; field work was performed by RTB, data was analyzed by TKR, NGY and HS. The paper was written by TKR, KEE and RTB. We thank Tony Gaston and an anonymous reviewer for comments that improved this manuscript.

## LITERATURE CITED

- Barbraud, C., P. Rivalan, P. Inchausti, M. Nevoux, V. Rolland, and H. Weimerskirch. 2011. Contrasted demographic responses facing future climate change in Southern Ocean seabirds. *Journal of Animal Ecology* 80:89–100.
- Barrett, R. T., S.-H. Lorentsen, and T. Anker-Nilssen. 2006. The status of breeding seabirds in mainland Norway. *Atlantic Seabirds* 8:97–126.
- Birkhead, T. R. and P. J. Hudson. 1977. Population parameters for the Common Guillemot *Uria aalge*. *Ornis Scandinavica* 8:145–154.
- Birkhead, T. R. and A. R. Lock. 1980. Changes in the proportion of bridled murrelets in Northern Labrador. *Condor* 82:473–474.
- Birkhead, T. R. 1984. Distribution of the bridled guillemot *Uria aalge* in the North Atlantic. *Journal of Zoology, London* 202:165–176.
- Birkhead, T. R., J. D. Biggins, and D. N. Nettleship. 1980. Non-random, intra-colony distribution of bridled guillemots *Uria aalge*. *Journal of Zoology, London* 192:9–16.
- Breton, A. R., A. W. Diamond, and S. W. Kress. 2006. Encounter, survival, and movement probabilities from an Atlantic Puffin (*Fratercula arctica*) meta-population. *Ecological Monographs* 76:133–149.
- Brommer, J. E., K. Ahola, and T. Karstinen. 2005. The color of fitness: plumage coloration and lifetime reproductive success in the tawny owl. *Proceedings of the Royal Society, London* 272:935–940.
- Bugge, J., R. T. Barrett, and T. Pedersen. 2011. Optimal foraging in chick-raising Common Guillemots (*Uria aalge*). *Journal of Ornithology* 152:253–259.
- Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.
- Catry, P., R. A. Phillips, K. C. Hamer, N. Ratcliffe, and R. W. Furness. 1998. The incidence of nonbreeding by adult great skuas and parasitic jaegers from Foula, Shetland. *Condor* 76:448–455.
- Chastel, O., H. Weimerskirch, and P. Jouventin. 1995. Body condition and seabird reproductive performance: a study of three petrel species. *Ecology* 76:2240–2246.
- Choquet, R., A. M. Reboulet, J. D. Lebreton, O. Gimenez, and R. Pradel. 2005. U-CARE 2.2 user's manual. CEFE, Montpellier, France.
- Choquet, R., L. Rouan, and R. Pradel. 2009. Program E-SURGE: a software application for fitting multi-event models. Pages 845–865 in D. L. Thomson, E. G. Cooch, and M. J. Conroy, editors. *Modeling demographic processes in marked populations*. Springer, New York, New York, USA.
- Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. *Biometrika* 51:429–438.
- Daunt, F., V. Afanasyev, J. R. D. Silk, and S. Wanless. 2006. Extrinsic and intrinsic determinants of winter foraging and breeding phenology in a temperate seabird. *Behavioural Ecology and Sociobiology* 59:381–288.
- Ducrest, A.-L., L. Keller, and A. Roulin. 2008. Pleiotropy in the melanocortin system, coloration and behavioural syndromes. *Trends in Ecology and Evolution* 23:502–510.
- Durant, J. M., N. C. Stenseth, T. Anker-Nilssen, M. P. Harris, P. M. Thompson, and S. Wanless. 2004. Marine birds and climate fluctuation in the North Atlantic. Pages 95–105 in N. C. Stenseth, G. Ottersen, J. W. Hurrell, and A. Belgrano, editors. *Marine ecosystems and climate variation: the North Atlantic—a comparative perspective*. Oxford University Press, Oxford, UK.
- Erikstad, K. E. and W. Vader. 1989. Capelin selection by Common and Brünnich's Guillemots during the prelaying season. *Ornis Scandinavica* 20:151–155.
- Erikstad, K. E., P. Fauchald, T. Tveraa, and H. Steen. 1998. On the cost of reproduction in long-lived birds: the influence of environmental variability. *Ecology* 79:1781–1788.
- Erikstad, K. E., T. K. Reiertsen, T. Anker-Nilssen, R. T. Barrett, S.-H. Lorentsen, H. Strøm, and G. H. Systad. 2007. Levedyktighetsanalyser for norske lomvibestander. Report 240. NINA, Trondheim, Norway. (In Norwegian with English summary).
- Forcada, J., P. N. Trathan, K. Reid, E. J. Murphy, and J. P. Croxall. 2006. Contrasting population changes in sympatric penguin species in association with climate warming. *Global Change Biology* 12:411–423.
- Frederiksen, M., M. P. Harris, and S. Wanless. 2005. Inter-population variation in demographic parameters: a neglected subject? *Oikos* 111:209–214.
- Galeotti, P. and C. Cesaris. 1996. Rufous and grey color morphs in the Italian tawny owl: geographical and environmental influences. *Journal of Avian Biology* 27:15–20.
- Galeotti, P. and D. Rubolini. 2004. The niche variation hypothesis and the evolution of color polymorphism in birds: a comparative study of owls, nightjars and raptors. *Biological Journal of the Linnean Society* 82:237–248.
- Galeotti, P., D. Rubolini, R. Sacchi, and M. Fasola. 2009. Global changes and animal phenotypic responses:

- melanin-based plumage redness of scops owls increased with temperature and rainfall during the last century. *Biology Letters* 5:532–534.
- Gaston, A. J. and I. L. Jones. 1998. *The auks—Alcidae*. Oxford University Press, Oxford, UK.
- Gienapp, P., C. Teplitsky, J. S. Alho, J. A. Mills, and J. Merilä. 2008. Climate change and evolution disentangling environmental and genetic responses. *Molecular Ecology* 17:167–178.
- Gimenez, O., R. Choquet, and J.-D. Lebreton. 2003. Parameter redundancy in multistate capture-recapture models. *Biometrical Journal* 45:704–722.
- Hamre, J. 1994. Biodiversity and exploitation of the main fish stocks in the Norwegian-Barents Sea ecosystem. *Biodiversity and Conservation* 3:473–492.
- Harris, M. P. and S. Wanless. 1986. A comparison of the biology of the normal and bridled forms of the Guillemot *Uria aalge* at a single colony. *Journal of Zoology, London* 210:121–130.
- Harris, M. P. and S. Wanless. 1988. The breeding biology of Guillemots *Uria aalge* on the Isle of May over a six year period. *Ibis* 130:172–192.
- Harris, M. P., P. Rothery, and S. Wanless. 2003. Increase in frequency of the bridled morph of the Common Guillemot *Uria aalge* on the Isle of May, 1946–2000: a return to former levels? *Ibis* 145:22–29.
- Harris, M. P., T. Anker-Nilssen, R. H. McCleery, K. E. Erikstad, D. N. Shaw, and V. Grosbois. 2005. Effect of wintering area and climate on the survival of adult Atlantic puffins *Fratercula arctica*. *Marine Ecology Progress Series* 297:283–296.
- Harris, M. P., M. Frederiksen, and S. Wanless. 2007. Within- and between-year variation in the juvenile survival of Common Guillemots *Uria aalge*. *Ibis* 149:472–481.
- Harris, M. P., F. Daunt, M. Newell, R. A. Phillips, and S. Wanless. 2010. Wintering areas of adult Atlantic puffins *Fratercula arctica* from a North Sea colony as revealed by geolocation technology. *Marine Biology* 157:827–836.
- Hjermann, D. Ø., N. C. Stenseth, and G. Ottersen. 2004. Indirect climatic forcing in the Barents Sea capelin: a cohort effect. *Marine Ecology Progress Series* 273:229–238.
- Hurrell, J. W. 1995. Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. *Science* 269:676–679.
- Hurrell, J. W. 2010. Climate indices. <http://www.cgd.ucar.edu/cas/jhurrell/indices.html>.
- IPCC. 2007. *Climate change 2007: the physical science basis*. Contribution of Working Group I to the Fourth Assessment. Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- Jefferies, D. J. and J. L. F. Parslow. 1976. The genetics of bridling in guillemots from a study of hand-reared birds. *Journal of Zoology, London* 179:411–420.
- Jenouvrier, S., C. Barbraud, and H. Weimerskirch. 2003. Effects of climate variability on temporal population dynamics of southern fulmars. *Journal of Animal Ecology* 72:576–587.
- Jenouvrier, S., C. Barbraud, and H. Weimerskirch. 2005. Long-term contrasted responses to climate of two Antarctic seabird species. *Ecology* 86:2889–2903.
- Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration stochastic model. *Biometrika* 52:225–247.
- Karell, P., K. Ahola, T. Karstinen, J. Valkama, and J. E. Brommer. 2011. Climate change drives microevolution in a wild bird. *Nature Communications* 2. doi: 10.1038/ncomms1213
- Kålås, J. A., Å. Viken, S. Henriksen, and S. Skjelseth. 2010. The 2010 Norwegian red list for species. Norwegian Biodiversity Centre, Trondheim, Norway.
- Le Bohec, C., J. M. Durant, M. Gauthier-Clerc, N. C. Stenseth, Y.-H. Park, R. Pradel, D. Gremillet, J.-P. Gendner, and Y. LeMaho. 2008. King penguin population threatened by Southern Ocean warming. *Proceedings of the National Academy of Sciences* 105:2493–2497.
- Lebreton, J. D. and J. Clobert. 1991. Bird population dynamics, management and conservation: the role of mathematical modelling. Pages 105–125 in C. M. Perrins, J.-D. Lebreton, and G. J. M. Hirons, editors. *Bird population studies: Relevance to conservation and management*. Oxford University Press, Oxford, UK.
- Lebreton, J. D., K. P. Burnham, J. Clobert, and D. Anderson. 1992. Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monograph* 62:67–118.
- Lygbo Kristensen, D. 2010. Sex allocation and reproductive strategies in a population of Common Guillemots (*Uria aalge*). Thesis. University of Copenhagen, Copenhagen, Denmark.
- Millien, V., S. K. Lyons, L. Olson, F. A. Smith, A. B. Wilson, and Y. Yom-Tov. 2006. Ecotypic variation in the context of global change: revisiting the rules. *Ecology Letters* 9:853–869.
- Nikolaeva, N. G., J. V. Krasnov, and R. T. Barrett. 1996. Movements of Common *Uria aalge* and Brünnich's Guillemots *Uria lomvia* breeding in the southern Barents Sea. *Fauna norvegica Serie C, Cinclus* 19:9–20.
- NOAA [National Oceanic and Atmospheric Administration]. 2010. Optimum interpolation sea surface temperatures. Version 2. Accessed 29 September 2010. National Center for Atmospheric Research, Boulder, Colorado, USA. <http://dss.ucar.edu/datasets/ds277.0/>

- Nur, N. and W. J. Sydeman. 1999. Survival, breeding probability, and reproductive success in relation to population dynamics of Brandt's Cormorants *Phalacrocorax penicillatus*. *Bird Study* 46(supplement): S92–S103.
- Parmesan, C. 2006. Ecologically and evolutionary responses to recent climatic change. *Annual Review of Ecology, Evolution and Systematics* 37:637–669.
- Piault, R., J. Gasparini, P. Bize, S. Jenni-Eiermann, and A. Roulin. 2009. Pheomelanin-based coloration and the ability to cope with variation in food supply and parasitism. *American Naturalist* 174:548–556.
- Reed, T. E., P. Warzybok, A. J. Wilson, R. W. Bradley, S. Wanless, and W. J. Sydeman. 2009. Timing is everything: flexible phenology and shifting selection in a colonial seabird. *Journal of Animal Ecology* 78:376–387.
- Reynolds, R. W., N. A. Rayner, T. M. Smith TM, D. C. Stokes, and W. Wang. 2002. An improved in situ and satellite SST analysis for climate. *Journal of climate* 15:1609–1625.
- Rolland, V., H. Weimerskirch, and C. Barbraud. 2010. Relative influence of fisheries and climate on the demography of four albatross species. *Global Change Biology* 16:1910–1922.
- Roulin, A. 2004. The evolution, maintenance and adaptive function of genetic color polymorphism in birds. *Biological Review* 79:815–848.
- Sandvik, H., K. E. Erikstad, R. Barrett, and N. G. Yoccoz. 2005. The effect of climate on adult survival in five species of North Atlantic seabirds. *Journal of Animal Ecology* 74:817–831.
- Sandvik, H. and K. E. Erikstad. 2008. Seabird life histories and climatic fluctuations: a phylogenetic-comparative time series analysis of North Atlantic seabirds. *Ecography* 31:73–83.
- Saraux, C., C. Le Bohec, J. M. Durant, V. A. Viblanc, M. Gauthier-Clerc, D. Beaune, Y.-H. Park, N. G. Yoccoz, N. C. Stenseth, and Y. LeMaho. 2011. Reliability of flipper-banded penguins as indicators of climate change. *Nature* 469:203–206.
- Schreiber, E. A. and R. W. Schreiber. 1989. Insights into seabird ecology from a global “natural experiment.” *National Geographic Research Report* 5 64–79.
- Seber, G. A. F. 1965. A note on the multiple-recapture census. *Biometrika* 52:249–259.
- Sheldon, B. C. 2010. Genetic perspectives on the evolutionary consequences of climate change in birds. Pages 149–168 *in* P. Berthold, W. Fiedler, and A. P. Møller, editors. *Effect of climate change on birds*. Oxford University Press, Oxford, UK.
- Southern, H. N. 1951. The status and problem of the bridled guillemot. *Proceedings of Zoological Society of London* 121:657–671.
- Southern, H. N. 1962. Survey of Bridled Guillemots, 1959–1960. *Proceedings of Zoological Society of London* 138:455–472.
- Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press, New York, New York, USA.
- Stige, L. C., G. Ottersen, and P. Dalpadao. 2010. Direct and indirect climate forcing in a multi-species marine system. *Proceedings of the Royal Society of London B* 277:3411–3420.
- Sugiura, N. 1978. Further analysis of the data by Akaike's information criterion and the finite corrections. *Communications in Statistics: Theory and Methods* 7:13–26.
- Vader, W., R. T. Barrett, K. E. Erikstad, and K.-B. Strann. 1990. Differential responses of Common and Thick-billed Murres to a crash in the Capelin stock in the southern Barents Sea. *Studies in Avian Biology* 14:175–180.
- Visser, M. E. 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proceedings of the Royal Society London B* 275:649–659.

SUPPLEMENTAL MATERIAL

APPENDIX A

MODEL DEVELOPMENT

Models were developed according to Gimenez et al. (2003), where the effects of trap-dependence on resighting probabilities were taken into account. The models were written in a multi-state framework.

$$\Phi = \begin{matrix} & \begin{matrix} \text{seen} & \text{not seen} & \text{dead} \end{matrix} \\ \begin{matrix} \text{seen before} \\ \text{not seen before} \\ \text{dead} \end{matrix} & \begin{bmatrix} \alpha & 1 - \alpha & 0 \\ \alpha & 1 - \alpha & 0 \\ 0 & 0 & 1 \end{bmatrix} \end{matrix}$$

States:

- 1) the probability of being seen before
- 2) the probability of not being seen before
- 3) dead

$$T = \begin{matrix} & \begin{matrix} \text{seen} & \text{not seen} & \text{dead} \end{matrix} \\ \begin{matrix} \text{seen before} \\ \text{not seen before} \\ \text{dead} \end{matrix} & \begin{bmatrix} \Psi & 0 & 1 - \Psi \\ 0 & \Psi & 1 - \Psi \\ 0 & 0 & 1 \end{bmatrix} \end{matrix}$$

Events:

- 1) Not seen
- 2) Seen

Events

$$B = \begin{matrix} & \begin{matrix} \text{not seen} & \text{seen} \end{matrix} \\ \begin{matrix} \text{seen before} \\ \text{not seen before} \\ \text{dead} \end{matrix} & \begin{bmatrix} 0 & \beta \\ \beta & 0 \\ \beta & 0 \end{bmatrix} \end{matrix}$$

Model-pattern:

Survival and transitions

APPENDIX B

Table B1. A total overview of the model selection.  $\Phi$  is survival,  $p$  is the capture (resighting) probability,  $i$  is the notation for a constant model,  $t$  is the time-dependent model,  $g$  is a model with a group effect between the two morphs, the bridled Common Guillemot (B) and the non-bridled Common Guillemot (NB),  $f$  is a model with a correction for trap-dependency. SST, SSTL1, SSTI2, SSTL3 and SSTL4 are the winter sea surface temperature in the Barents Sea, with and without lags. SSTMay and SSTJune are the sea surface temperature for May and June around the colony with and without lags. NAO, NAOL1, NAOL2, NAOL3 and NAOL4 represent the North Atlantic Oscillation index, with and without lags. Popsizel is the yearly population size for the time-period 1989 to 2010.

No	Model	Par	Dev.	QAICc	$\Delta$ QAICc	QAICc wt
1	$\Phi(\text{SSTL2}(\text{B}), \text{SSTL2}(\text{NB}))$ $p(\text{SSTJune} + f)$	7	1592.80	1606.86	0.00	0.38
2	$\Phi(\text{SSTL2}(\text{B}), \text{SSTL2}(\text{NB}))$ $p((\text{SSTJune}(\text{B}) + \text{SSTJune}(\text{NB})) + f)$	8	1592.36	1608.44	1.58	0.17
3	$\Phi(\text{SSTL2}(\text{B}), \text{SSTL2}(\text{NB}))$ $p(\text{SSTMay} + f)$	7	1595.22	1609.28	2.42	0.11
4	$\Phi(\text{SSTL2}(\text{B}), \text{SSTL2}(\text{NB}))$ $p(\text{SSTMay}(\text{B}) + \text{SSTMay}(\text{NB})) + f)$	8	1594.90	1610.98	4.12	0.05
5	$\Phi(\text{SSTL2}(\text{B}), \text{SSTL2}(\text{NB}))$ $p((\text{SSTJune}(\text{B}), \text{SSTJune}(\text{NB})) + f)$	10	1591.06	1611.19	4.32	0.04
6	$\Phi(\text{popsizel}(\text{B}), i(\text{NB}))$ $p(\text{SSTJune} + f)$	6	1599.21	1611.26	4.40	0.04
7	$\Phi(\text{SSTL2}(\text{B}), \text{SSTL2}(\text{NB}))$ $p(\text{SSTMay}(\text{B}), \text{SSTMay}(\text{NB})) + f)$	9	1594.33	1612.42	5.57	0.02
8	$\Phi(\text{popsizel}(\text{B}), \text{popsizel}(\text{NB}))$ $p(\text{SSTJune} + f)$	7	1598.49	1612.55	5.70	0.02

Table B1. Continued.

No	Model	Par	Dev.	QAICc	$\Delta$ QAICc	QAICc wt
9	$\Phi(i)$	4	1606.19	1614.22	7.36	0.01
10	$p(\text{SSTJune} + f)$ $\Phi(\text{SSTL2(B),SSTL2(NB)})$	7	1600.19	1614.25	7.39	0.01
11	$p(\text{NAOL4} + f)$ $\Phi(i(\text{B}),\text{SSTL2(NB)})$	6	1602.46	1614.51	7.64	0.01
12	$p(\text{SSTJune} + f)$ $\Phi(\text{popsize})$	5	1605.85	1615.89	9.03	0.00
13	$p(\text{SSTJune} + f)$ $\Phi(g)$	5	1605.86	1615.90	9.03	0.00
14	$p(\text{SSTJune} + f)$ $\Phi(\text{SSTL2})$	5	1606.11	1616.14	9.28	0.00
15	$p(\text{SSTJune} + f)$ $\Phi(\text{popsize(B)} + \text{popsize(NB)})$	6	1605.59	1617.63	10.77	0.00
16	$p(\text{SSTJune} + f)$ $\Phi(\text{SSTL2(B)} + \text{SSTL2(NB)})$	6	1605.82	1617.86	11.01	0.00
17	$p(\text{SSTJune} + f)$ $\Phi(\text{SSTL2(B),SSTL2(NB)})$	7	1604.06	1618.13	11.27	0.00
18	$p(\text{SST} + f)$ $\Phi(\text{SSTL2(B),SSTL2(NB)})$	7	1605.17	1619.23	12.37	0.00
19	$p(\text{SSTJuneL2} + f)$ $\Phi(\text{SSTL2(B),SSTL2(NB)})$	27	1564.71	1619.54	12.68	0.00
20	$p(f + t)$ $\Phi(\text{SSTL2(B),SSTL2(NB)})$	7	1605.52	1619.58	12.72	0.00
21	$p(\text{SSTL2} + f)$ $\Phi(\text{SSTL2(B),SSTL2(NB)})$	28	1564.13	1621.03	14.17	0.00
22	$p((t + g) + f)$ $\Phi(\text{SSTL2(B),SSTL2(NB)})$	7	1607.40	1621.46	14.60	0.00
23	$p(\text{SSTJuneL1} + f)$ $\Phi(\text{SSTL2(B),SSTL2(NB)})$	7	1607.43	1621.49	14.63	0.00
24	$p(\text{SSTJuneL4} + f)$ $\Phi(\text{SST(B),SST(NB)})$	27	1568.16	1622.99	16.14	0.00
25	$p(f + t)$ $\Phi(\text{SSTL2(B),SSTL2(NB)})$	7	1609.28	1623.34	16.48	0.00
26	$p(\text{NAOL3} + f)$ $\Phi(\text{SSTL4(B),SSTL4(NB)})$	27	1569.29	1624.12	17.26	0.00
27	$p(f + t)$ $\Phi(\text{SSTL2(B),SSTL2(NB)})$	7	1609.92	1623.98	17.12	0.00
28	$p(\text{NAOL2} + f)$ $\Phi(\text{SSTL2(B),SSTL2(NB)})$	7	1610.13	1624.20	17.34	0.00
29	$p(\text{SSTL1} + f)$ $\Phi(\text{SSTL2(B),SSTL2(NB)})$	6	1612.25	1624.30	17.44	0.00
30	$p(f)$ $\Phi(\text{SSTL2(B),SSTL2(NB)})$	7	1610.46	1624.52	17.66	0.00
31	$p(\text{NAOL1} + f)$ $\Phi(\text{SSTL2(B),SSTL2(NB)})$	7	1611.11	1625.18	18.32	0.00
32	$p(\text{SSTL3} + f)$ $\Phi(\text{SSTL1(B),SSTL1(NB)})$	27	1571.15	1625.98	19.12	0.00
33	$p(f + t)$ $\Phi(i)$	24	1577.32	1625.98	19.12	0.00
34	$p(f + t)$ $\Phi(i)$	25	1575.32	1626.04	19.18	0.00
35	$p((t + g) + f)$ $\Phi(\text{SSTL2(B),SSTL2(NB)})$	7	1612.00	1626.07	19.20	0.00
36	$p(\text{SSTL4} + f)$ $\Phi(g)$	26	1574.42	1627.20	20.34	0.00
37	$p((t + g) + f)$ $\Phi(g)$	25	1576.90	1627.61	20.76	0.00
38	$p(f + t)$ $\Phi(\text{SSTL2(B)} + \text{SSTL2(NB)})$	27	1573.29	1628.12	21.27	0.00
39	$p((t + g) + f)$ $\Phi(\text{SSTL3(B),SSTL3(NB)})$	27	1573.62	1628.45	21.59	0.00
40	$p(f + t)$ $\Phi(\text{NAOL1(B),NAOL1(NB)})$	27	1574.55	1629.38	22.53	0.00
41	$p(f + t)$ $\Phi(\text{NAOL2(B),NAOL2(NB)})$	27	1575.19	1630.03	23.17	0.00
42	$p(f + t)$ $\Phi(\text{NAOL4(B),NAOL4(NB)})$	27	1575.52	1630.35	23.49	0.00

Table B1. Continued.

No	Model	Par	Dev.	QAICc	$\Delta$ QAICc	QAICc wt
43	$\Phi$ (NAO(B).NAO(NB))	27	1576.22	1631.05	24.19	0.00
44	$p(f+t)$ $\Phi$ (NAOL3(B).NAOL3(NB))	27	1576.63	1631.46	24.61	0.00
45	$p(f+t)$ $\Phi(t+g)$	26	1582.79	1635.57	28.70	0.00
46	$p(\text{SSTJune} + f)$ $\Phi(t)$	25	1585.81	1636.53	29.66	0.00
47	$p(\text{SSTJune} + f)$ $\Phi(i)$	46	1545.08	1639.48	32.63	0.00
48	$p((t,g) + f)$ $\Phi(g)$	47	1543.15	1639.65	32.80	0.00
49	$p((t,g) + f)$ $\Phi(t)$	44	1553.65	1643.85	36.99	0.00
50	$p(f+t)$ $\Phi$ (SSTL2(B).SSTL2(NB))	6	1631.69	1643.73	36.88	0.00
51	$p(\text{popsize} + f)$ $\Phi(t+g)$	46	1553.44	1647.84	40.98	0.00
52	$p(f+t)$ $\Phi(t,g)$	47	1552.67	1649.19	42.33	0.00
53	$p(\text{SSTJune} + f)$ $\Phi(t,g)$	66	1523.79	1660.76	53.91	0.00
54	$p(f+t)$ $\Phi$ (SSTL2(B).i(NB))	6	1655.57	1667.62	60.76	0.00
55	$p(\text{SSTJune} + f)$ $\Phi(i)$	23	1622.17	1668.77	61.92	0.00
56	$p(t)$ $\Phi(i)$	2	1672.87	1676.88	70.02	0.00
57	$p(i)$ $\Phi$ (SSTL4(B) + SSTL4(NB))	27	1629.03	1683.86	77.00	0.00
58	$p((t+g) + f)$ $\Phi$ (SSTL2(B).SSTL2(NB))	7	1669.18	1683.24	76.38	0.00
59	$p(\text{SSTJuneL3} + f)$ $\Phi(t)$	43	1599.74	1687.84	80.98	0.00
60	$p(t)$ $\Phi(t)$	23	1645.46	1692.07	85.21	0.00
61	$p(i)$ $\Phi$ (SSTL1)	25	1733.13	1783.84	176.98	0.00
	$p(f+t)$					