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Winter distribution and foraging strategies of European shags

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Introduction

At high latitudes, long-lived, resident species face a number of challenges that must be overcome to survive the winter, including depressed food resources, increased daily energy requirements, higher frequency of extreme weather events and, for diurnal species, shortened day length. Across a species' distribution, populations experience a wide range of winter conditions. In many cases, the conditions experienced are closely tied to latitude, and latitude gradients in environmental severity are particularly marked in winter. Conditions are expected to be particularly severe for diurnal marine endotherms, because of the high costs of foraging in cold water, and greatly reduced day length and overall light levels.

An ideal candidate for studying the effects of such environmental constraints is the shag *Phalacrocorax aristotelis*, which, as a member of the cormorant family, has a wettable plumage so foraging costs are expected to be particularly high in winter. This species is therefore the target of an international study initiated in 2006 by the NERC Centre for Ecology and Hydrology in Edinburgh, Scotland and carried out in collaboration with the Institute for Natural History in Reykjavik, Iceland and projects in Norway sponsored by the Norwegian Research Council, Norsk Hydro and (from 2008) SEAPOP. Its principal objective is to identify the extrinsic and intrinsic drivers of over-wintering survival and subsequent breeding performance of shags across a latitudinal gradient. This project, that is still ongoing, addresses two main questions:

1. How do shags at high latitudes obtain sufficient food to survive the winter?

An almost complete absence of foraging at night among shags that spend the winter in temperate regions (Daunt et al. 2006) raised the question of how shags that breed and overwinter at higher latitudes obtain sufficient food to survive the winter. Three strategies are possible:

a) "Fast food" hypothesis (Grémillet et al. 1999): high latitude shags target higher quality food patches, thereby reducing time spent foraging,
b) "Night life" hypothesis (Grémillet et al. 2005): high latitude shags feed at night,
c) "Sun-chasing" hypothesis (Daunt et al. 2006): high latitude shags spend the winter south of the Arctic Circle to increase potential diurnal foraging time.

The project aims to disentangle and test these hypotheses by measuring the behavioural responses of individuals breeding in four different colonies across a latitudinal gradient of increasing environmental severity: Isle of May in south-east Scotland, Flatey in north-west Iceland, Røst in north-west Norway and Hornøya in north-east Norway. Ring recoveries indicate that while birds on the Isle of May and Flatey are largely resident and thus do not employ the sun-chasing strategy, shags on Røst and Hornøya disperse along the Norwegian coast during the autumn and winter. Although it is unclear whether dispersal to more southern latitudes and hence more daylight is sufficient to increase potential foraging time, all three strategies would appear to be potentially available to the Norwegian shags.

2. Is individual variation in winter foraging linked to latitude?

Previous work on temperate shags has shown marked differences in foraging time among individuals in autumn and spring, but not midwinter (Daunt et al. 2006). Inter-individual variation was linked to breeding performance, suggesting that the differences in foraging time were due to intrinsic foraging ability. Inter-individual variation may be less marked in higher latitude populations, since harsher conditions tend to reduce inter-individual variation. However, if individuals disperse in winter, as the Norwegian populations are known to do, then patterns of inter-individual variation in foraging time may be more complex since widely distributed individuals are likely to be experiencing a broader range of environmental conditions, which would be predicted to increase inter-individual variation. The predictive framework for latitudinal effects on individual variation is therefore not clear without prior information on winter distribution of sample individuals. However, establishing variation in performance among individuals across a latitudinal gradient was an important focus of the work since it is important in understanding the drivers of population change across a species' range.

Figure 1
One of the logger birds sitting in the colony on Hornøya. The logger is attached to the darvic ring with two cable ties. (© R. Barrett)

Methods

At each colony, miniature activity and light level data loggers from the British Antarctic Survey (model Mk4) were deployed on 20-32 breeding shags during the 2006 breeding season (Table 1). The devices weighed just 4.5 g (ca 0.25% of shag body mass). Long-term attachment was achieved by securing the logger to a darvic or acrylic colour ring placed on the birds' leg (cf. Figure 1 and cover

photo). The loggers contained a saltwater switch, which records the amount of time spent in the water, an accurate measure of daily foraging effort since shags only enter the water to feed (Daunt et al. 2006). They also recorded light intensity, such that the location of non-resident birds (from Røst and Hornøya) could be obtained by estimating latitude from day length and longitude from the timing of dawn and dusk in relation to noon (DeLong et al. 1992).

Table 1 *Details of deployment and retrieval of GLS loggers at the four colonies.*

Colony	Latitude	Deployment period	Loggers deployed			Loggers retrieved		
			2006	2007	2008	2007	2008	2009
Isle of May, E Scotland	56°11'N	Incubation	29	26	22	21	22	14
Flatey, NW Iceland	65°22'N	Incubation	20	8	0	10	9	0
Røst, NW Norway	67°28'N	Incubation + chick rearing	20	0	9	4	1	1
Hornøya, NE Norway	70°22'N	Chick rearing	32	12 [1]	0	18	9	1
All four colonies			101	46	31	53	41	16

[1] Redeployment of loggers from 2006

On visits to the study colonies in the next three summers, altogether 110 loggers (62% of those deployed or redeployed) were retrieved successfully (Table 1). One extra bird from the Isle of May was recovered dead in March 2007 and complete datasets (some covering two winters) were recovered from all but five loggers whose batteries had run out part way through the deployment.

This initial project was supplemented in 2008 by deployments of a further 9 loggers on Røst, 20 loggers on Sklinna in Central Norway and 17 loggers on Håstein in SW Norway (all BAS model Mk9). Because of near breeding failures at all three colonies, only one (of the original 20), two and one, respectively, were recovered in 2009. It is hoped that more will be retrieved in 2010.

Results

It is important to stress that the data collected from the shags is still being processed and analysed such that a complete presentation of the results is not yet possible. The following is an illustration of some of the results obtained so far.

1. How do shags at high latitudes obtain sufficient food to survive the winter?

Shags from the Isle of May and Flatey that remain in the region of the breeding colony had a broadly similar pattern of foraging time during winter, with foraging time increasing steadily to a peak of, on average, 5 h/d amongst birds from Flatey and 6 h/d amongst Isle of May birds. Most foraging took place during daylight at both colonies and night feeding was only very occasionally recorded. In midwinter, the majority of the diurnal period was used for foraging at both colonies, and on Flatey the twilight period was also used.

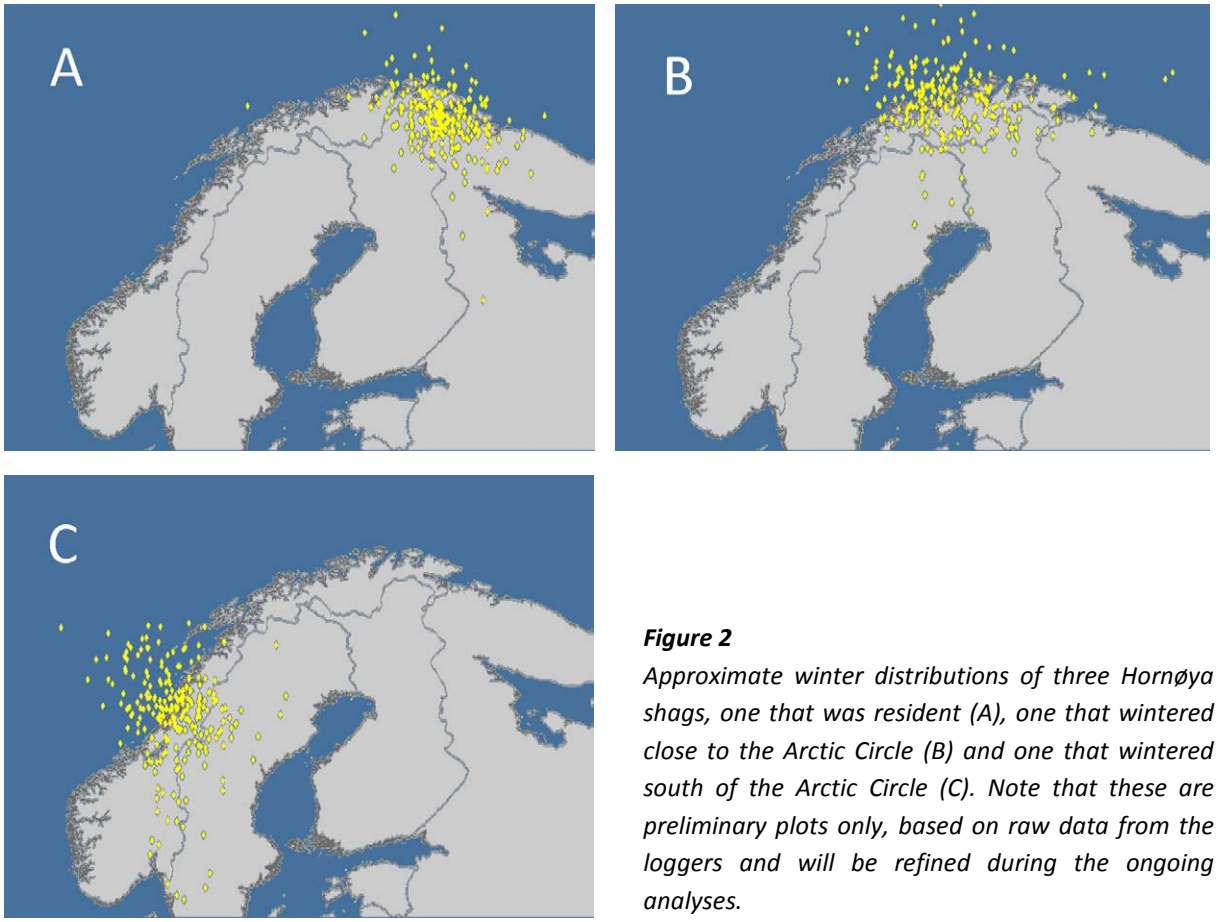

Figure 2

Approximate winter distributions of three Hornøya shags, one that was resident (A), one that wintered close to the Arctic Circle (B) and one that wintered south of the Arctic Circle (C). Note that these are preliminary plots only, based on raw data from the loggers and will be refined during the ongoing analyses.

Examples of the type of unprocessed location data retrieved from the data loggers are shown in Figure 2. Prior to this study, Hornøya shags were believed to disperse to southern latitudes in winter, but logger data from eleven study individuals revealed that only some individuals disperse (7 out of 11) whereas some remained in East Finnmark throughout the year (4 out of 11). Those that did disperse were distributed along much of the coast of Norway. However, one of the most important implications of the results is that the majority of the 11 birds wintered north of the Arctic Circle, which was also the case for the birds from Røst. This means that these birds wintered in a region of low light intensity and long periods of darkness suggesting that they may be feeding at night. This will be addressed in more detail in the final analyses of the results.

Despite the more northern distribution in winter, the pattern of winter foraging time of Hornøya birds was similar to the temperate colonies, with a steady increase through the winter and a mean foraging time in midwinter of ca. 6 hours (Figure 3). Resident and dispersive individuals showed a similar pattern throughout the winter, the main difference between them occurring in the timing of the decline in foraging time in spring, which was three weeks later among dispersers.

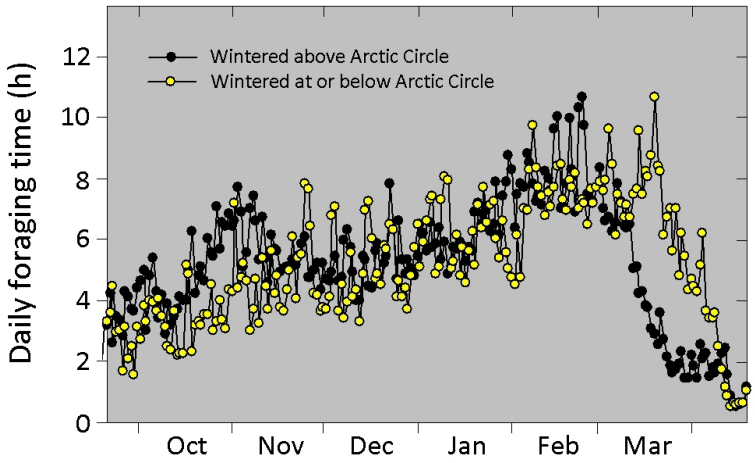

Figure 3
Mean daily foraging time of resident (black symbols, n=4) and dispersive (yellow symbols, n=7) European shags from Hornøya over the winter 2006-2007. Note also the different timing of when the birds started to spend more time onshore (likely in the colony) in spring.

2. Is individual variation in winter foraging linked to latitude?

The coefficient of variation (CV) was highest among Hornøya shags, intermediate among Flatey shags and smallest among Isle of May shags (Figure 4). Furthermore, the pattern among the former two colonies was non-linear with the smallest CV apparent in midwinter. In contrast, Isle of May CV was comparatively stable over the winter.

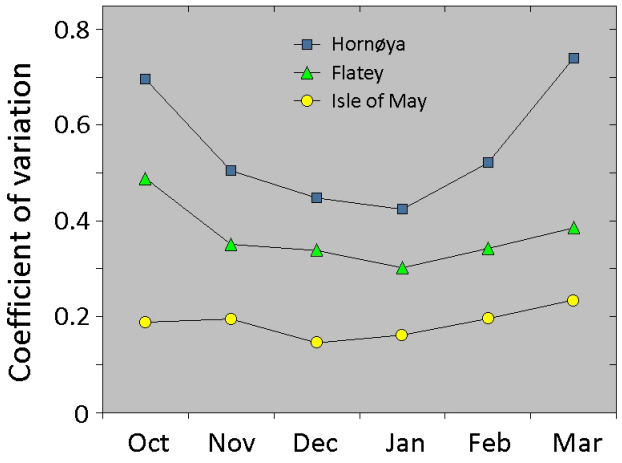

Figure 4
Monthly coefficients of variation in foraging time for individual shags from three of the four study colonies.

Discussion

This investigation of the effects of a latitudinal gradient of increasing environmental severity on the foraging dynamics of wintering European shags revealed convincing evidence for all three hypotheses. Flatey shags had shorter foraging times than Isle of May shags, despite the more severe conditions and shorter day length in winter, suggesting that they target high quality prey patches to survive the winter ("fast food" hypothesis). Hornøya shags, on the other hand, either showed night feeding ("night life" hypothesis) or dispersal to south of the Arctic Circle ("sun-chasing" hypothesis)

as methods in which to survive the winter. These data are the first to demonstrate these strategies in this species, and reveal how this species can survive the harsh conditions of northern latitudes.

There were intriguing patterns of individual variation in foraging time. Amongst the two resident populations, the patterns were in the opposite direction to that predicted, with higher values amongst Flatey birds. Whilst there is little doubt that physical conditions become more severe with increasing latitude, other factors, in particular food availability, may not follow the same pattern. The impact of latitude on individual effects may be further complicated by dispersal strategies away from the breeding colony. In accordance with this, CV was highest amongst Hornøya birds, which may be linked to the varying dispersal strategies exhibited, resulting in birds experiencing a broader range of environmental conditions than those from other colonies. Further analysis will investigate the interaction between latitude and dispersal distribution on inter-individual variation in foraging time.

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Cover photo: An adult shag carrying a GLS logger (BAS Mk9) attached to a green colour ring engraved “TJ” on its right tarsus (© T. Anker-Nilssen)

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