DOES SEA ICE CONSTRAIN THE BREEDING SCHEDULES OF HIGH ARCTIC NORTHERN FULMARS?

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Abstract. The Northern Fulmar (*Fulmarus glacialis*) is a pelagic seabird that breeds across 25° of latitude, from the boreal to the high Arctic oceanographic zones. We examined the breeding schedule of fulmars in the remote Cape Vera colony in the Canadian high Arctic, a marine region covered by sea ice much of the year, to determine if the timing of breeding and colony attendance patterns of birds differed from the breeding phenology of fulmars in colonies farther south. Cape Vera fulmars arrived at the colony later in the year, spent less time at the colony before egg-laying, and took a significantly longer prelaying exodus from the colony compared to fulmars nesting in more southerly colonies. After egg-laying, however, patterns of colony attendance by fulmars in the high Arctic were similar to patterns for fulmars in southern colonies; this part of the fulmar breeding schedule may be inflexible. The differences in breeding schedules across the species' range might reflect behavioral adaptations by arctic-nesting birds to accommodate the physical and biological limitations imposed by extensive sea ice near arctic colonies, particularly early in the breeding season. Given that climate warming and corresponding reductions in sea ice are taking place in the Arctic, it remains to be determined whether fulmars in the high Arctic have the behavioral flexibility in their breeding phenology to compensate for rapidly occurring changes in their environment.

Key words: Arctic, breeding, Fulmarus glacialis*, Northern Fulmar, sea ice.*

¿Restringe el Hielo Marino la Fenología Reproductiva de *Fulmarus glacialis* a Altas Latitudes en el Ártico?

Resumen. Fulmarus glacialis es un ave marina pelágica que se reproduce en las zonas oceanográficas desde los 25° de latitud norte hasta altas latitudes en el Ártico. Examinamos la fenología reproductiva de individuos de *F. glacialis* en la colonia remota de Cabo Vera ubicada a altas latitudes en el Ártico canadiense, una región marina cubierta por hielo durante gran parte del año. Trabajamos allí para determinar si el inicio de la reproducción y los patrones de presencia de aves en las colonias difería de la fenología reproductiva de colonias de *F. glacialis* que se encuentran más al sur. Los individuos de Cabo Vera llegaron a las colonias más tarde, permanecieron por menos tiempo en las colonias antes de comenzar la puesta de huevos y se ausentaron antes de la postura por un período significativamente más largo que los individuos que nidificaron en colonias más sureñas. Sin embargo, después del periodo de postura de huevos, los patrones de presencia de individuos fueron similares entre las colonias del ártico y las sureñas; esta parte del periodo reproductivo podría ser inflexible. Estas diferencias en la fenología reproductiva en el área de distribución de esta especie pueden reflejar adaptaciones de comportamiento por parte de las aves que nidifican en el Ártico para hacer frente a las limitaciones físicas y biológicas impuestas por las extensas áreas de hielo en el mar cercanas a las colonias del Ártico, especialmente durante las etapas tempranas de la época reproductiva. Debido al calentamiento climático y la consecuente reducción del hielo marino que está ocurriendo en el Ártico, es aún necesario determinar si los individuos que se reproducen a altas latitudes en el Ártico tienen la flexibilidad conductual en su fenología reproductiva necesaria para compensar los cambios que están ocurriendo repentinamente en su ambiente.

INTRODUCTION

The timing of breeding by birds has received considerable attention. Timing of nesting might relate to the ability of the female to gather sufficient food for egg production (Perrins 1970), the parents' abilities to gather resources for self-maintenance during incubation (Brooke 1978), or the parents' abilities to find sufficient food to provision young while maintaining their own body condition (Lack 1954, Gaston and Hipfner 1998). Recent studies have identified

connections between breeding phenology and large-scale effects of climate change on marine ecosystems (Montevecchi and Myers 1997, Ainley 2002). Among seabirds, timing of reproduction typically reflects annual patterns of marine productivity (Cairns 1987, Abraham and Sydeman 2004). In years when marine production is low, often a result of major climatic factors, marine birds may nest later (Schreiber 2002, Gaston et al. 2005).

For seabirds nesting in polar regions, breeding phenology may be particularly affected by marine conditions (Hunt 1991), because sea-ice cover creates a physical barrier to open water access (Brown and Nettleship 1981) and also reduces light penetration, thereby reducing or delaying productivity at lower trophic levels (Raymont 1976, Welch et al. 1992). In years when sea-ice cover is extensive or persists longer into the breeding season, marine birds should experience higher foraging costs, because they have to travel farther to find food, as well as reduced food availability, because marine production is adversely affected. Both of these factors could influence reproductive decisions by breeding birds. Indeed, several studies of polar seabirds have found delayed egg-laying and reduced reproductive success in years with more severe sea-ice conditions (Ainley et al. 1983, Gaston and Hipfner 1998, Gaston et al. 2005).

Another approach for addressing the importance of ice conditions to seabird reproduction is to compare timing and duration of key breeding events within species across a range of latitudes. This reduces the contribution of interannual variation in other factors that may relate to annual variation in sea-ice cover during the breeding season. Specifically, if sea-ice cover acts as an important constraint on seabird breeding as inferred, then we would expect to find consistent differences in breeding phenology between northern (high Arctic) and southern populations of widespread species. Using published information, such a study requires comparing birds at different colonies in different years, necessitates accounting for various study designs, and assumes that breeding metrics for each colony were derived during typical annual environmental conditions.

The Northern Fulmar (*Fulmarus glacialis*) is ideal for such comparisons: it is a fulmarine petrel with a circumpolar distribution, and it breeds between 55° and 80°N in the North Atlantic Ocean (Hatch and Nettleship 1998). The Northern Fulmar is long-lived, lays one egg per clutch, and does not renest following breeding failure (Dunnet et al. 1963, Ollason and Dunnet 1978). Like all petrels, this fulmar undertakes an exodus (a key breeding event) from the breeding colony prior to egg-laying, which allows the female to gather nutrients to form her single, relatively large, energy-rich egg (Warham 1990, 1996). Additionally, breeding at fulmar colonies appears to be relatively synchronized annually, and shows little variation in mean laying dates across years (Hatch and Hatch 1990), similar to many other petrels including Sooty Shearwaters (*Puffinus griseus*; Richdale 1963), Short-tailed Shearwaters (*P. tenuirostris*; Serventy 1963), Manx Shearwaters (*P. puffinus*; Brooke 1978), Antarctic Fulmars (*Fulmarus glacialoides*), Antarctic Petrels (*Thalassoica antarctica*), Cape Petrels (*Daption capense*), and Snow Petrels (*Pagodroma nivea*; Hodum 2002).

In his seminal work on the species, Fisher (1952) deduced that Northern Fulmars throughout the boreal oceanographic zone had a similar breeding schedule, but suggested that this schedule might be different for arctic colonies. In the boreal zone of the Atlantic, fulmars typically begin to attend their breeding colony intermittently in the autumn preceding the breeding season and lay eggs in mid- to late May, with eggs hatching in early to mid-July (Fisher 1952, Dunnet et al. 1963, Coulson and Horobin 1972, MacDonald 1977, 1980). Several authors have provided some evidence that fulmars in the Arctic do indeed nest later than fulmars in the boreal zone (Freuchen and Salomonsen 1958, Falk and Møller 1997, Hatch and Nettleship 1998), but no studies to date have provided details of the first arrival of the birds at these colonies, nor measures of the duration of the prelaying exodus. These two key features of fulmar breeding should be most affected by sea ice or climatic conditions, because sea-ice extent should be greatest and pelagic marine productivity lowest early in the year.

We studied the breeding phenology of Northern Fulmars in the remote Cape Vera colony in the Canadian high Arctic. At this site, fulmars have to fly over extensive sea ice in Baffin Bay and Jones Sound for over half of
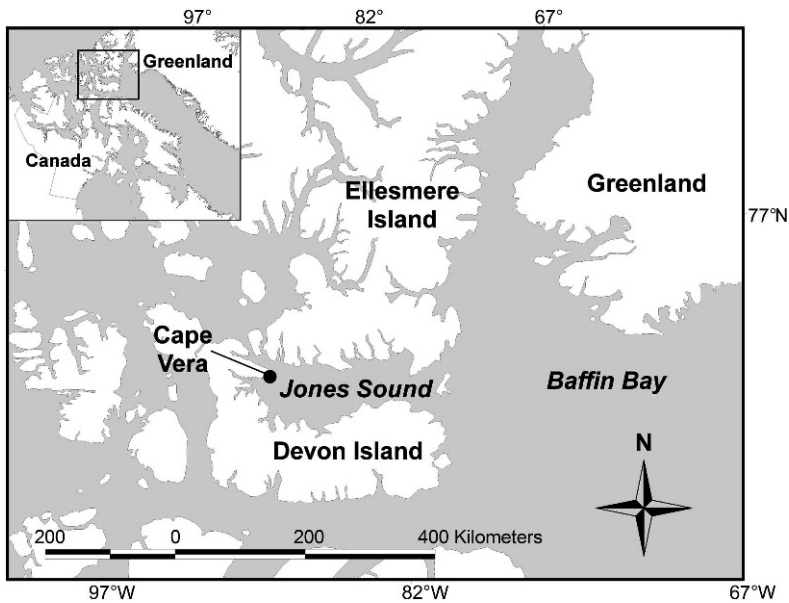
FIGURE 1.   The location of the Cape Vera study site on northern Devon Island, Nunavut, Canada.

their breeding season (first arrival at the colony to date of hatching), a constraint experienced by only a few fulmar colonies across the high Arctic (Falk and Møller 1997, Hatch and Nettleship 1998). Because of this sea-ice cover, we predicted that birds would arrive at the colony later, would have a shorter prelaying period at the colony, and would take a longer prelaying exodus than fulmars nesting in the boreal oceanographic zone. We tested these expectations, while also comparing differences in breeding phenology related to gender or breeding status as other studies have done. Our study thereby provides baseline data on timing and duration of key breeding events of fulmars nesting at this colony.

METHODS

We conducted fieldwork between 14 May and 9 August 2004 and from 20 April to 10 August 2005 at the ''Cape Vera'' fulmar colony (76°15′N, 89°15′W) on northern Devon Island, beside the Hell Gate–Cardigan Strait polynya (Fig. 1). This marine area is located in the high Arctic oceanographic zone (Salomonsen 1965), and nearby Jones Sound remains ice-covered from October through July (except for the open water near the polynya; Mallory and Fontaine

2004). We obtained data on the ice conditions of Jones Sound and Baffin Bay from the Environment Canada – Canadian Ice Service climate archives (available at <http://ice-glaces. ec.gc.ca>). Typical conditions for maximum, circumpolar extent of arctic sea ice were taken from satellite imagery (National Snow and Ice Data Center 2007).

The Cape Vera colony is the most northerly and remote fulmar colony in North America (Hatch and Nettleship 1998, Mallory 2006). The coastline at Cape Vera features prominent cliffs that rise 245–313 m above sea level, and approximately 11 000 pairs of fulmars occupy nest sites along 6.4 km of deeply incised cliffs (Gaston et al. 2006). Breeding fulmars do not appear to feed in the Hell Gate polynya, and instead fly east to forage between Ellesmere Island and Greenland (MLM, unpubl. data).

We established eight long-term monitoring plots along the breeding cliffs at Cape Vera, with each plot supporting 25–300 nest sites (Mallory and Gaston 2005). Nest sites and attending birds could be easily viewed using 10 × 42 binoculars or a 60× spotting scope from vantage points 30–300 m distant along the cliff top, meaning that birds were not disturbed during counting. Cape Vera is highly suscepti-

ble to fog and high winds, and these weather conditions meant that data on all plots were collected on only 34 of 87 (39%) days in 2004. One plot was particularly problematic, and this plot was replaced in 2005 (accounting for some of the total count differences between years). In 2005, data on all plots were collected on 93 of 107 (87%) days, and data were collected on some of the plots on days when other plots were obscured. In 2005, we also used a Canon® 20D digital camera with a 400 mm lens to produce an 8 megapixel photograph of each plot each day. These were downloaded to field computers, and counts could be conducted or confirmed in camp from these photos during poor weather. In situations where a nest could not be observed on day x, but we identified the same bird at the nest on day $x - 1$ and day $x + 1$, we assumed the bird was on the nest during day x. If the other pair member appeared on day $x + 1$, we assumed that the new bird arrived that day, and attributed the missed observation to the bird observed on day $x - 1$.

To determine which member of the pair was in attendance, we relied on several types of information. Northern Fulmars range in plumage color from very dark (DD) to intermediate (D or L) to very light (LL), which refers to increasing amounts of white on the breast, neck, and head of birds (Fisher 1952, Hatch and Nettleship 1998). Fulmars of the Canadian Arctic are mostly intermediate birds (L and D), with numerous very light morphs (LL), and relatively few very dark birds (DD). Plumage differences, along with distinct markings on the bill, allow experienced observers to distinguish members of a pair based on these characteristics. Live fulmars cannot be sexed unless measured (Mallory and Forbes 2005), or unless the position of birds during copulation is noted (Hatch 1990a). However, males are usually first to arrive at the colony (as with many other seabirds; Ainley et al. 1983), last to leave and first to return from the exodus, and they take the first long incubation shift (Fisher 1952, Hatch 1990a, 1990b, 1990c).

It is not easy to determine if a fulmar is on an egg, as nonbreeders often appear to be incubating for periods of hours, but then leave the nest site (Fisher 1952, Gaston et al. 2006). In preliminary work in 2003, we estimated that approximately one-third of the time we incorrectly assumed that observed birds at nest sites were breeding adults and then saw them fly off with no egg or chick at the site. To reduce this error, we determined that repeated observations of the same individuals for several hours each day were required.

On five of the study plots in 2004 and 2005, we conducted detailed, daily observations for 1–4 hr of selected nest sites to determine which pair member was attending the nest, and to identify whether an egg or chick was in the nest. In some cases we recorded whether the bird exhibited "egg behavior" and confirmed the status of the nest at a later date when the egg was subsequently observed. Repeated observations of the same plots by the same personnel meant that observers became familiar with the individual birds' behaviors. Thus, for these well-studied plots, "egg behavior" was incorrectly ascribed to only 1% of birds for which we later confirmed that there was no egg present. We defined the following three categories of birds: successful breeders (fulmars at nests that produced a chick which was still alive by 10 August); failed breeders (fulmars at nests that produced an egg, but either the egg or chick was lost during incubation or brood-rearing); and nonbreeders (fulmars at nests where we never observed an egg). Observing whether these types of birds differ in attendance patterns is important as it might tell us whether intercolony comparisons have to be made somewhat carefully.

In 2005, we collected six fresh fulmar eggs within one day of laying. We used the staining and yolk ring counting technique of Astheimer and Grau (1985) to determine how many days females spent developing eggs.

We followed the approach of Hatch (1990c) to divide the fulmar breeding season into stages as follows: stage 1 (pre-exodus) – 40 to 21 days before egg-laying, covering the period of prelaying colony attendance and the departure for the exodus; stage 2 (prelaying) – 20 to 1 days before egg-laying, covering most of the exodus from the colony and the return of fulmars prior to the day the egg was laid; and stage 3 (incubation) – 0 to 62 days after egg-laying, covering incubation and the posthatching guard stage where one of the parents broods the chick. We then compared the amounts of time the male and female spent at the colony in each of these stages for those fulmars that successfully reached the end of stage 3. We were not at the

colony long enough to cover Hatch's (1990c) stage 4 (chick-rearing), nor to observe young fledge.

To compare breeding schedules of fulmars at Cape Vera to those from colonies elsewhere, we reviewed the literature for published values of key phenological dates (e.g., first landing, start and end of exodus, egg-laying, date of hatching). In situations where studies were conducted over several years, we took the earliest dates from any of the years as our measure for each colony-specific date. Aside from Cape Vera, only fulmar colonies in Canada, Greenland, Spitzbergen (Norway), and Franz Joseph Land (Norway) encounter extensive sea ice at some stage of the breeding season (National Snow and Ice Data Center 2007).

For calculations, all dates were converted to ordinal dates, with 1 January = 001. In situations in which the date of first landing reported in the literature was in the autumn prior to a new breeding season, we subtracted the number of days from 1 January (e.g., 1 December = −031). Because Cape Vera data were missing for many days in 2004, we refer principally to 2005 data below, but include and describe 2004 data where appropriate. Depending on the distribution of data, we used *t*-tests, ANOVAs, Kruskal-Wallis tests, or Pearson or Spearman rank correlations to compare data among years or colonies. We used ANOVAs for comparisons with summary data from other studies, but in all cases the Bartlett's tests suggested significant differences in standard deviations among studies (all $P < 0.01$). Therefore, statistical differences among studies should be interpreted cautiously. Means are presented ± SE unless otherwise noted.

RESULTS

SEA-ICE DISTRIBUTION

During April and May, fulmars encountered >90% sea-ice cover from Disko Island, Greenland (69°30′N, 54°W) to the Cape Vera breeding colony, a distance of approximately 1200 km. The exception was a recurrent area of open water between Ellesmere Island and Greenland (the Northwater Polynya, 76°N, 75°W), which varied annually in size and could be 350–500 km away at this time. Between 1996 and 2005, the mean distance to open water at Cape Vera in the second week of June was 190
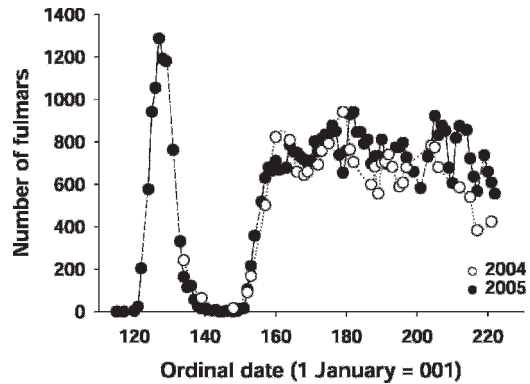

FIGURE 2. Total counts of Northern Fulmars in eight study plots at Cape Vera in 2004 and 2005, showing the early season peak in attendance, the virtual desertion of the colony following the peak, and the fluctuating attendance during incubation and early chick-rearing.

± 5 km, a distance that was consistent across years (range: 175–225 km, coefficient of variation 9%). By the third week of July, fulmars still had to cross at least 100 km of sea ice in 2004, and 300 km of ice in 2005, to reach feeding areas.

PRELAYING COLONY ATTENDANCE AND THE EXODUS

In 2005, Northern Fulmars were not observed in the nearby polynya nor landing on the cliffs before 30 April (two weeks before observations were initiated in 2004). The first birds to appear at known nesting sites in monitoring plots were observed one day later, and numbers increased rapidly to a maximum count for the year on 7 May, before declining to <5 fulmars by 21 May (Fig. 2). In 2005, the colony was effectively deserted for 14 days: only 10 fulmars were observed between 17 and 30 May at 307 nest sites. At 48 nests where we could distinguish pair members, knew the sex of the birds, and tracked attendance to hatching, 35% of the pairs arrived at the colony on the same day, with the male arriving before the female in all other cases. Thirty-three percent of pairs departed together for the exodus, while the female departed before the male in all but 6% of the remaining pairs. Collectively, males arrived earlier, spent longer at the colony prior to departing for the exodus, were away from the colony for a shorter exodus, and returned

TABLE 1. Comparison of key dates and time spent at the Cape Vera colony by paired male and female Northern Fulmars during the 2005 breeding season (paired t-tests, all $t \geq 6.7$, all $P < 0.001$). The breeding season was divided into three stages as follows: stage 1 = pre-exodus, 40 to 21 days before egg-laying; stage 2 = prelaying, 20 to 1 day before egg-laying; and stage 3 = incubation, 0 to 62 days after egg-laying. Calculations of the percentage of time spent at the colony used only pairs that had nests where incubation was completed, a chick was observed, and the identity of each member of the breeding pair was ascertained reliably.

Parameter	Male			Female		
	Mean ± SE	Range	n	Mean ± SE	Range	n
First arrival at colony (ordinal date)	123.8 ± 1.4	121–129	48	124.9 ± 1.4	122–129	48
Duration of prelaying attendance (days)	8.9 ± 2.0	5–15	48	5.7 ± 1.7	2–10	48
Duration of exodus (days)	23.1 ± 2.8	15–28	48	28.1 ± 3.1	22–39	48
Return from exodus (ordinal date)	154.7 ± 2.0	151–159	48	157.7 ± 2.5	153–165	48
Time spent at colony in stage 1 (%)	44 ± 10	25–60	38	28 ± 8	10–50	38
Time spent at colony in stage 2 (%)	11 ± 11	0–50	38	2 ± 5	0–15	38
Time spent at colony in stage 3 (%)	52 ± 5	42–61	38	44 ± 6	31–56	38
Time at colony prelaying to early chick-rearing (%)	46 ± 5	36–57	38	35 ± 4	26–43	38

earlier before egg-laying than females (Table 1). At 23 days long, the male exodus was five days shorter than the female exodus, with females away from the colony for approximately one month (Table 1).

Colony attendance from late prelaying to early incubation (14 May to 23 June) was highly correlated between counts on the same day in 2004 and 2005 (r_s = 0.86, $P < 0.05$, n = 14; Fig. 2), suggesting that the colony was synchronized across years.

EGG-LAYING, INCUBATION, DATE OF HATCHING, AND CHICK-REARING

There was no variation in counts of yolk rings among fulmar eggs; all six females took 23 days to form their egg. Mean egg-laying day for Cape Vera in 2005 was 157.9 ± 0.2 (6 June, range: 2–16 June, n = 103), with 80% of eggs laid between 4 and 9 June. This was similar to 2004, in which the egg-laying day for 16 nests averaged 157.1 ± 0.6, and the earliest egg was also observed on 2 June.

The incubation period of fulmars at Cape Vera was 49.0 ± 0.2 days (range: 46–52, n = 65), and mean day of hatching was 206.1 ± 0.3 (25 July, range: 22–31 July, n = 65). Like egg-laying, date of hatching was highly synchronized, with 80% of eggs hatching between 23 and 27 July. In 2004, we observed 39 nests hatch between 21 and 31 July (mean day = 205.8 ± 0.5), and behaviors of birds suggested that hatching occurred at a further nine nests during this period, but we were unable to confirm the presence of a chick at these nests

until 3 August. Thus, it seems probable that overall mean dates of hatching in both years were within one day of each other.

For 24 nests where the full chick-guarding stage was observed, at least one parent was with the chick for 14.6 ± 0.4 days (range: 12–18 days). At another 16 nests, an adult was observed still attending the chick 10–19 days after hatching when our observations ended (i.e., before the completion of chick-rearing).

SEASONAL PATTERN OF TIME ALLOCATION AT THE COLONY

During stage 1 (pre-exodus) of the breeding season, males spent 44% and females spent 28% of their time at the colony, although these differences were not statistically significant (Table 1). This stage was marked by high synchrony in attendance within pairs, with many pairs arriving and departing on the same day (above). Males spent only 11% of stage 2 (prelaying) at the colony, but this was significantly more than females, who attended the colony for only 2% of those days. During incubation and early chick-rearing (stage 3), males spent slightly more than half of their time at the nest, which was more than females, who attended the colony for 44% of the period (Table 1). Thus, over the entire 103-day breeding period that we observed, males spent 46% of their time at the nest and females spent 35% of their time at the nest, for an overall mean of 40% ± 1% (n = 38). During this period, birds were observed together at the nest 9% ± 1% of the time.

TABLE 2.   Values of colony attendance parameters (mean ± SE) for successful, failed, and nonbreeding Northern Fulmars nesting in the Cape Vera colony in 2005. The breeding season was divided into three stages as follows: stage 1 = pre-exodus, 40 to 21 days before egg-laying; stage 2 = prelaying, 20 to 1 day before egg-laying; and stage 3 = incubation, 0 to 62 days after egg-laying. For failed breeding adults, date of hatching was calculated as 49 days from the laying date. For nonbreeding adults, the overall mean egg-laying date, mean date of hatching, and end of observations during chick-rearing were used to calculate proportions of time spent at the colony during stage 3.

	Breeding status (n)			Statistical comparison	
Parameter	Successful (52)	Failed (48)	Nonbreeding (33)	F or K-W	P
Synchrony of prelaying arrival (days)[a]	1.2 ± 0.2	1.4 ± 0.2	1.6 ± 0.3	0.7	0.48
Synchrony of departure for exodus (days)[b]	2.0 ± 0.3	1.7 ± 0.3	1.2 ± 0.4	1.3	0.26
Proportion of days paired during prelaying (%)	76.8 ± 3.9	72.8 ± 4.8	64.1 ± 5.1	1.3	0.28
Male at colony during stage 1 (days)	8.8 ± 0.3	9.0 ± 0.4	8.7 ± 0.4	0.2	0.84
Female at colony during stage 1 (days)	5.5 ± 0.2	5.7 ± 0.3	6.0 ± 0.4	0.7	0.50
Male exodus (days)[c]	23.2 ± 0.4	23.8 ± 0.4	24.6 ± 0.7	2.0	0.14
Female exodus (days)[d]	28.4 ± 0.4	28.5 ± 0.4	28.2 ± 1.0	0.1	0.94
Synchrony of return from exodus (days)[a]	3.2 ± 0.4	2.9 ± 0.4	3.2 ± 0.6	0.1	0.86
Nest site unattended during incubation (days)	0.5 ± 0.2	3.2 ± 0.7	12.5 ± 1.3	64.8	<0.001[e]
Days pair together during stage 3 (days)	4.7 ± 0.4	8.7 ± 0.6	11.6 ± 1.0	40.7	<0.001[f]
Days pair together from prelaying to early chick-rearing (%)	9 ± 1	13 ± 1	14 ± 1	20.3	<0.001[f]

[a] Calculated as date of first arrival – date of second arrival.
[b] Calculated as date of last to depart – date of first to depart.
[c] Assumes male is last to depart and first to arrive back from exodus.
[d] Assumes female is first to depart and last to arrive back from exodus.
[e] Nonparametric Kruskal-Wallis and Dunn's multiple comparison test conducted due to significant difference in variation of each group; each group significantly different from the others (three groups tested).
[f] Nonparametric Kruskal-Wallis and Dunn's multiple comparison test conducted due to significant difference in variation of each group; successful lower than failed or nonbreeding.

BREEDING SCHEDULES AND BREEDING STATUS

At Cape Vera, males and females of known sex (above) appeared to have consistent patterns of arrival and departure, so we assumed that the first birds to arrive and the last birds to depart during prelaying were males. Using this approach, we found no significant differences for 133 apparently occupied nest sites among successful, failed, or nonbreeders in any of the following: the synchrony of arrival and departure from the colony; the amount of time the pair spent together during prelaying; the amount of time spent at the colony by males or females during stage 1; or the duration of the male or female exodus (Table 2). Fulmars attended their nest sites from prelaying to chick-rearing even if they were non- or failed breeders, but over the entire 103-day observation period, nonbreeders were more often observed together at the colony than successful breeders (Table 2). In addition, nest sites were left unattended significantly less often during incubation by successful breeders than by failed breeders, and both of these groups were at the nest more often than nonbreeders (Table 2; Kruskal-Wallis tests, all $P < 0.03$). Thus, prior to egg-laying, fulmars exhibited similar breeding schedules irrespective of breeding status, but during incubation, nonbreeders and failed breeders spent more time away from the nest site.

COMPARISONS WITH BREEDING SCHEDULES OF NORTH ATLANTIC FULMARS

For 16 fulmar colonies located across the North Atlantic and Arctic Oceans, the first landing of fulmars at the colony was significantly later at higher latitudes ($r_s = 0.68$, $P = 0.004$; Table 3, Fig. 3a). This same pattern held when the analysis was restricted to seven colonies situated around Baffin Bay ($r_s = 0.68$, $P = 0.11$), although the trend was not significant due to the small sample size. First egg dates ($r_s = 0.74$, $P = 0.04$, $n = 8$), mean egg dates ($r_s = 0.64$, P

TABLE 3. Locations, sea ice presence, and reported breeding phenology of Northern Fulmar colonies in Alaska and across the North Atlantic Ocean (Northern Fulmars are known as Fulmars in Eurasia). Parameters reported include: date of first landing (when fulmars are first observed attending the colony after the previous breeding season); M:F exodus (the length of the male and female prelaying exodus from the colony); date of the earliest reported egg-laying (first egg), mean date of egg-laying, and mean date of hatching, as well as the length of the incubation period.

Fulmar colony	Latitude	Longitude	Sea ice present?[a]	Date of first landing	M:F exodus (days)	Date of first egg	Mean egg-laying date	Mean hatching date	Incubation period (days)	Reference[c]
Alaska (Semidi Islands)	56°N	156°W	No	11 Apr	12.2:17.6	26 May	9 Jun	27 Jul	48.4	1
United Kingdom (Weybourne)	53°N	1°6'E	No	23 Oct						2
United Kingdom (Sands of Forvie)	57°18'N	1°56'W	No	22 Oct	9.3:19.6	12 May	21 May	3 Jul		3, 4
United Kingdom (St. Kilda)	57°48'N	8°36'W	No	30 Oct		5 May	12 May	21 Jun		5
United Kingdom (Orkney, Shetland)	59°30'N	2°W	No	29 Oct	14.5:15.9	12 May	22 May	24 Jun		5, 6, 7
Faeroe Islands	62°30'N	7°30'W	No	30 Oct		19 May		15 Jul		5
Iceland	65°30'N	22°30'W	No	20 Oct		11 May	16 May	7 Jul		5
Greenland (Disko)	69°N	54°W	No	8 Apr						5
Greenland (Umanaq)	71°N	52°W	Yes	12 Apr		28 May				5
Norway (Jan Mayen)	71°N	9°W	No	19 Dec				14 Jul[b]		5
Canada (Baillarge Bay)	73°24'N	84°30'W	Yes	23 Apr						5
Canada (Prince Leopold Island)	74°N	90°W	Yes	2 May		3–5 Jun	7 Jun	25 Jul	47.7	8, 9
Canada (Cape Liddon)	74°36'N	91°12'W	Yes	26 Apr						8
Norway (Bjornoya)	74°30'N	19°E	No	Dec				14 Jul[b]		5
Canada (Cape Vera)	76°12'N	89°12'W	Yes	30 Apr	23.2:28.2	3 Jun	8 Jun	25 Jul	49.0	10
Norway (Spitzbergen)	77°30'N	15°E	No	22 Jan			3 Jun			5
Norway (Franz Joseph Land)	81°N	50°E	Yes	13 Mar						5
Greenland (Mallemukfjeld)	80°12'N	16°36'W	Yes	24 Apr			31 May	19 Jul		11

[a] Extensive sea ice typically present during early breeding season (April–May).
[b] Reported hatches almost one month earlier seem highly implausible; given date substantiated by >1 study.
[c] 1 = Hatch and Hatch (1990); 2 = Slater (1990); 3 = MacDonald (1977); 4 = MacDonald (1980); 5 = Fisher (1952); 6 = Dunnet et al. (1963); 7 = Brooke (2004); 8 = Hatch and Nettleship (1998); 9 = Gaston et al. (2005); 10 = this study; 11 = Falk and Møller (1997).
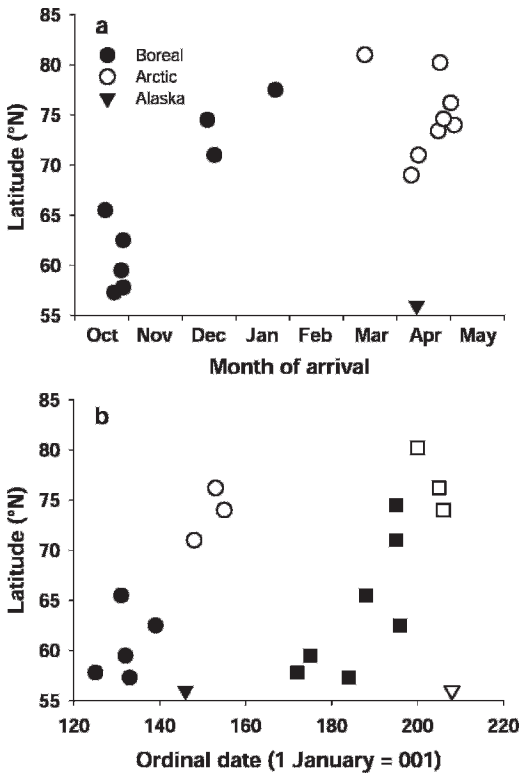
FIGURE 3. The breeding phenology of selected Northern Fulmar colonies in the North Atlantic Ocean, demonstrating earlier colony attendance, egg-laying, and hatching for birds breeding at lower latitudes. (a) First arrival by fulmars at the colony in relation to colony latitude. (b) Mean date of egg-laying (circles) and mean date of hatching (squares) for fulmar colonies in the arctic (unfilled) and boreal (filled) oceanographic zones. In both panels, data from a colony in Alaska are shown by triangles.

$= 0.01$, $n = 8$), and first observed hatching dates ($r_s = 0.78$, $P = 0.01$, $n = 10$; Table 3, Fig. 3b) also were later for fulmar colonies at higher latitudes.

Fulmars breeding at Cape Vera departed the colony for a prelaying exodus that averaged more than one week longer than fulmars at colonies farther south (Table 3). Both males (ANOVA on summary data: $F_{2,790} = 159.2$, $P < 0.001$) and females ($F_{2,779} = 113.6$, $P < 0.001$) spent significantly longer periods away from the colony, and differences among the Cape Vera, Semidi Islands, and Sands of Forvie colonies were all significant (Tukey-Kramer multiple comparisons tests, all $P < 0.05$).

The incubation period for fulmars at Cape Vera (49.0 days, $n = 65$) was slightly longer

than for fulmars in Alaska (48.4 ± 0.1 days, $n = 52$; Hatch 1990a) or Prince Leopold Island (47.7 ± 0.2 days, $n = 30$; Hatch and Nettleship 1998; ANOVA on summary data: $F_{2,144} = 11.3$, $P < 0.001$; Tukey-Kramer multiple comparisons tests, all $P < 0.05$), although the range of incubation periods was similar.

DISCUSSION

Hatch and Nettleship (1998) hypothesized that Northern Fulmars breeding in the high Arctic might exhibit adaptations to the colder, ice-covered environmental conditions, including a compressed breeding season, compared with boreal fulmars elsewhere in the Pacific and Atlantic Oceans. Results of our study of Northern Fulmars breeding at Cape Vera were similar in some respects to those of studies of breeding fulmars in the boreal zone, but we also found support for the hypothesis above. As with other fulmars, we found that females at Cape Vera took 23 days to form their eggs (Astheimer and Grau 1985). Moreover, Cape Vera fulmars completed incubation in 46–52 days (Hatch and Nettleship 1998) and guarded the chick for >14 days (Hatch 1990c), despite having to fly over extensive sea ice to forage throughout the prelaying and incubation periods. This result is similar to patterns observed by Hodum (2002), where incubation, chick-guarding, and nestling periods of four antarctic fulmarine petrels varied little for colonies separated by 21 degrees of latitude. However, Cape Vera fulmars were among the last fulmars of the North Atlantic population to begin breeding each year, with the second-latest colony arrival date and the latest mean egg-laying date. What consequences does this have for their allocation of time to different stages of their breeding schedule?

Surprisingly, both male and female fulmars breeding at Cape Vera spent about the same amount of time at the colony from arrival through chick-guarding as fulmars in the Semidi Islands in Alaska (46% and 35%, respectively; Hatch 1990c), and even similar amounts of time together at the nest site. However, time at the nest appeared to be allocated differently between these colonies. Male fulmars at Cape Vera spent proportionally more time at the colony during pre-exodus but less time during prelaying and incubation than Hatch (1990c) observed in any of six years

for male fulmars in Alaska. In contrast, female fulmars at Cape Vera spent about 6% less time at the colony during prelaying, attributable to taking a 10-day longer exodus, but were at the colony for similar proportions of time during pre-exodus and incubation compared to female fulmars in Alaska.

COMPRESSED BREEDING SEASON, THE EXODUS, AND SYNCHRONIZATION

Boreal fulmars first attend colonies six or more months prior to the annual breeding season (Fisher 1952, Coulson and Horobin 1972). However, arctic colonies surrounded by extensive sea ice are not visited by fulmars until about one month prior to egg-laying (except, occasionally, Pribilof Island colonies; S. Hatch, Alaska Science Center, pers. comm.). In northern Baffin Bay, there are no published observations of fulmars before 24–26 April (Fisher 1952), thus we suspect that there were no fulmar landings at Cape Vera before our observations on 30 April. Therefore, at Cape Vera, fulmar mates typically arrive within two days of each other and spend only six to nine days together at the colony before departing for the exodus. Unless pairs meet at sea (which is unknown), fulmars breeding in the high Arctic have a shorter period each year to choose or check nest sites, reestablish pair bonds, and copulate than fulmars breeding in boreal or low Arctic colonies (Hatch and Nettleship 1998).

The prelaying exodus of fulmars at Cape Vera is 9–14 days longer than that reported in other locations, and is characterized by a lack of intermittent, short visits to the colony which may be observed at southern colonies (Hatch 1990c). Fulmars can travel several hundred kilometers to feed (Weimerskirch et al. 2001; MLM, unpubl. data), and surveys by McLaren (1982) suggested that fulmars may leave the high Arctic completely during the exodus, perhaps to feed near southwestern Greenland or southern Davis Strait. We suspect that marine production is still too low early in the season to support the energetic needs of fulmars at this time (Welch et al. 1992, Lewis et al. 1996), thus the birds appear to move to distant, more productive waters.

If the physical and biological effects of sea ice constrain the breeding schedule of arctic fulmars (Fisher 1952, Falk and Møller 1997, Hatch and Nettleship 1998), it follows that polar colonies should be more synchronized in their schedules than southern colonies. Indeed, the range of egg-laying dates in the Canadian high Arctic (11–19 days) was shorter than the range in northeastern Greenland (24 days; Falk and Møller 1997), Alaska (18–34 days; Hatch and Hatch 1990), or the eastern North Atlantic (~30 days; Fisher 1952). Falk and Møller (1997) demonstrated how the phenology of fulmar reproduction in northeastern Greenland matched the sea-ice cycle of the nearby polynya, a pattern also found by Hodum (2002) for four species of fulmarine petrels near Antarctica. Thus, fulmars nesting in the most ice-constrained sites appear to have higher synchronization of egg-laying than fulmars breeding at colonies surrounded by open water year-round.

COMPRESSED BREEDING SCHEDULE AND EXTRA-PAIR COPULATIONS

While overall time spent at the colony from arrival through chick-guarding was similar between fulmars at Cape Vera and Alaska, fulmars breeding in Alaskan colonies may begin attending breeding cliffs up to 47 days before egg-laying, compared to 40 days for fulmars at Cape Vera (Hatch 1989). Pairs also may be observed copulating at Alaskan colonies over a 30-day period, up to 10 days before egg-laying (Hatch 1987), because the prelaying exodus is shorter in Alaska. At Cape Vera, no pairs that attempted to breed were observed at the colony after 14 May, and those same pairs laid eggs starting 5 June, meaning that no copulations occurred <22 days before egg-laying. This timing is similar to the length of the egg formation period (23 days), and the time at which copulation frequencies begin to decline at boreal colonies (20 days before egg-laying; Hunter 1998), both of which suggest that females at Cape Vera have already decided whether to breed and have secured sperm from their mates potentially much earlier than at other colonies (Hunter 1998).

During the pre-exodus period, male fulmars always arrived at the Cape Vera colony before or with their mate, and males spent 8% more time at the colony than males in Alaska (Hatch 1990c). This increased attendance may reflect a behavioral adaptation of male fulmars to the short breeding season in the high Arctic to enhance opportunities to copulate with the female, to secure extra-pair copulations, or to

guard the female from extra-pair copulation attempts by other males (Hatch 1987, Hunter 1998). If this interpretation is correct, we make the following predictions: (1) levels of extra-pair copulations by fulmars in high Arctic colonies will be more highly correlated with proportional male attendance during prelaying than is found in low Arctic or boreal colonies; (2) high Arctic fulmars will have lower egg hatchability, because there will be fewer fertilizations due to absent males during the sole opportunity to mate, and females may use older, degraded, stored sperm; and (3) male fulmars in high Arctic colonies will exhibit energetic adaptations to breeding in ice-constrained environments which require high attendance at the nest during prelaying, and specifically that they will arrive at the colony with proportionally larger energetic reserves than male fulmars at more southern colonies.

SCHEDULING DIFFERENCES BETWEEN BREEDING AND NONBREEDING FULMARS

Nonbreeding fulmars attend colonies throughout the breeding season (Fisher 1952, Coulson and Horobin 1972, Falk and Møller 1997), presumably to gain experience with potential nest sites, timing of movements, and locations of feeding areas (Warham 1990, 1996), which are critical for successful reproduction (Ollason and Dunnet 1978). At Cape Vera, nonbreeding fulmar pairs exhibited similar levels of synchrony in colony attendance as breeding birds, and spent similar amounts of time at the colony prior to the exodus, unlike nonbreeding fulmars in Alaska, which spent less time at the colony than breeding adults. With little food and extensive ice nearby, there is probably an energetic disadvantage for nonbreeders at Cape Vera to leave the breeding cliffs early in the season, whereas those in Alaska may be able to make brief foraging trips at this time.

The differences in attendance patterns between breeding and nonbreeding adult fulmars were most evident during incubation. Nonbreeders were observed either absent from the nest or with their mate at the nest site much more than breeders, a result undoubtedly attributable to the greater energetic limitations placed on breeding birds. At least one member of a breeding pair must remain at the nest to incubate the egg and protect it from inclement weather or predation. In contrast, the value of colony attendance by failed or nonbreeders declines as the season progresses, for two reasons. First, it is too late in the season for nonbreeders to initiate a nest, and failed breeders do not renest (Hatch and Nettleship 1998). Second, the high energetic costs of replacing feathers during molt, particularly primary molt, are deferred by breeding birds until late in chick-rearing, but nonbreeders initiate molt shortly after mean egg-laying dates for the colony, and failed breeders enter molt shortly after losing their egg or chick (Fisher 1952, Hatch 1990c, Hatch and Nettleship 1998).

Collectively, the data from Cape Vera and studies of other fulmar colonies affected by sea ice indicate that high Arctic fulmars have a compressed and substantially adjusted breeding schedule compared to fulmars breeding in the boreal oceanographic zone. These scheduling adaptations occur during prelaying; egg development and attendance during incubation and chick-rearing appear to be similar across the species' range.

With climate change already contributing to reductions in arctic sea ice (McBean 2004), fulmars may be less constrained in scheduling early season breeding activities near their colonies in the future. However, it is unclear whether fulmars adapted to high Arctic conditions are flexible enough to adopt a more boreal breeding schedule, or whether they can maintain a typical high Arctic breeding schedule but shift it earlier into the season. Barbraud and Weimerskirch (2006) showed that several species of antarctic seabirds have begun arriving at colonies and laying eggs later over the past 55 years. The authors noted that the birds apparently have the behavioral plasticity to accommodate the resultant shorter breeding period, perhaps by decreasing the time required for activities in the prelaying period, similar to phenology at Cape Vera. However, some studies have suggested that climate-mediated earlier production of prey items has led to a mismatch of avian breeding phenology and prey abundance (Stenseth and Mysterud 2002), which could have detrimental long-term effects if behavioral adaptations of fulmars cannot occur as rapidly as changing food supplies.

ACKNOWLEDGMENTS

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