Factors Influencing Colony Attendance by Northern Fulmars in the Canadian High Arctic

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ABSTRACT. The northern fulmar (*Fulmarus glacialis*) is a common seabird of the North Atlantic Ocean and marine areas of eastern Nunavut. We studied attendance patterns of fulmars at two colonies in the Canadian High Arctic to assess variation in attendance at high latitudes, to compare these patterns to those found for fulmars breeding at colonies to the south, and to determine how weather conditions and breeding status might influence attendance. Colony attendance patterns shared similarities across the species' range, although local variation in the timing of food supplies may explain differences in the seasonal timing of peak counts at colonies. Stronger winds and extreme inclement weather resulted in lower counts of birds at colonies. Seasonal and daily variation in attendance was attributable to differences in the numbers of failed breeders or non-breeding birds. Changes toward earlier breakup and reduced extent of sea ice should lead to earlier peaks and continued short periodicities in colony attendance cycles of Arctic fulmars.

Key words: colony attendance, *Fulmarus glacialis*, marine production, northern fulmar, weather

RÉSUMÉ. Le fulmar boréal (*Fulmarus glacialis*) est un oiseau marin courant du nord de l'océan Atlantique et des régions marines de l'est du Nunavut. Nous avons étudié les tendances de fréquentation des fulmars à deux colonies situées dans l'Extrême-Arctique canadien dans le but d'évaluer les variations de fréquentation en hautes latitudes, de comparer ces tendances à celles caractérisant les fulmars se reproduisant aux colonies se trouvant plus au sud et de déterminer en quoi les conditions météorologiques et le statut de reproduction peuvent exercer une influence sur la fréquentation. Il existait des similarités entre la répartition des espèces sur le plan des tendances de fréquentation au sein des colonies, bien que les variations locales en matière de disponibilité des approvisionnements alimentaires puissent expliquer les différences entre les dénombrements saisonniers de pointe aux colonies. Les vents violents et le temps des plus incléments se sont traduits par des dénombrements d'oiseaux moins grands aux colonies. Les variations de fréquentation saisonnières et quotidiennes étaient attribuables aux différences sur le plan du nombre de reproducteurs manqués ou d'oiseaux ne se reproduisant pas. Les changements qui se manifestent, tels que l'avancement de la débâcle et une moins grande surface de glace de mer, devraient entraîner des pointes plus hâtives et des périodicités continuellement courtes pour ce qui est des cycles de fréquentation des colonies de fulmars boréaux.

Mots clés : fréquentation des colonies, *Fulmarus glacialis*, production marine, fulmar boréal, conditions météorologiques

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INTRODUCTION

Among broadly distributed bird species, reproductive traits (e.g., phenology, egg or clutch size, breeding success) may vary significantly in response to differing local environmental conditions within the breeding range (e.g., Robertson et al., 2006). Hence, proper management of such species requires knowledge of regional variation in these traits and of the factors that might lead to local adaptations. The northern fulmar (*Fulmarus glacialis*) is a petrel with a circumpolar distribution, breeding across 35° of latitude (to 80° N; Hatch and Nettleship, 1998). This seabird is a long-lived predator and scavenger that lays a single egg annually (Mallory, 2006). Its highly efficient flight is enhanced

during windier conditions (Furness and Bryant, 1996). Most northern fulmars are year-round inhabitants of the low Arctic and Boreal oceanographic zones (Salomonsen, 1965), where the birds are ubiquitous on the open ocean. However, fulmars from High Arctic colonies are found in the low Arctic or Boreal zone only over the winter; each May, they migrate north to their breeding colonies, where they remain through September (Mallory et al., 2008a).

Fulmars breeding in the High Arctic experience environmental constraints (lower temperatures, near-constant daylight, snow, and sea ice) not experienced by fulmars elsewhere in the breeding range (Hatch and Nettleship, 1998; Mallory and Forbes, 2007). Thus, we were interested in determining the variation in colony attendance by birds

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at different High Arctic colonies, and how their attendance patterns compared to attendance by conspecifics nesting in the Boreal zone, where wind and weather are known to influence fulmar attendance (Coulson and Horobin, 1972; Hatch, 1989; Furness and Bryant, 1996). An assessment of factors influencing Arctic fulmar breeding ecology is timely, as environmental conditions are changing rapidly in this region (ACIA, 2005).

We monitored colony attendance by fulmars at two colonies in the Canadian High Arctic: Prince Leopold Island and Cape Vera (Fig. 1). While some aspects of fulmar attendance at Prince Leopold Island have been described (Hatch and Nettleship, 1998; Gaston et al., 2006), we provide the first description of colony attendance at Cape Vera, the northernmost fulmar colony in Canada. We compared our observations to attendance patterns observed elsewhere and analyzed how weather affected attendance at High Arctic colonies. Although fulmars exhibit strong diurnal patterns in colony attendance at lower latitudes, Falk and Møller (1997) found no such trends at a colony in Greenland located only 4° farther north than Cape Vera, so we expected that fulmars in High Arctic Canada would exhibit weak diurnal trends in attendance. However, we predicted that their colony attendance would be consistent with the pattern observed at southern colonies: that is, attendance would be lower during stronger winds or storms, particularly for nonbreeding birds or failed breeders.

METHODS

Research was conducted at two northern fulmar colonies in the Canadian High Arctic oceanographic zone (Salomonsen, 1965; Fig. 1). Breeding phenology, behavior, and success at both colonies are influenced by annual patterns of sea-ice cover (Gaston et al., 2005; Mallory and Forbes, 2007; Mallory et al., 2008b). At the Prince Leopold Island colony (74° N, 90° W), field crews observed fulmar colony attendance during 16 June−21 August 2001; 1 June−25 August 2002; 31 May−21 August 2003; and 14 June−6 August 2005 (Gaston et al., 2005). Studies were also undertaken at the Cape Vera colony (76°15′ N, 89°15′ W), northern Devon Island, from 26 May to 22 August 2003, 14 May to 9 August 2004, and from 20 April to 10 August 2005. In this paper, we focus on the specific diurnal and seasonal fulmar attendance at Cape Vera, particularly in 2005, but we examine effects of weather on attendance at both colonies. These sites are situated on extensive, sedimentary cliffs rising more than 300 m above sea level. Fulmars nest on east-facing cliffs at Cape Vera (although deep, eroded incisions mean that nests can face most directions), but they nest all around Prince Leopold Island. Cape Vera supports approximately 9000 breeding pairs of fulmars, while Prince Leopold Island supports 16 000 or more breeding pairs (Gaston et al., 2006).

At Cape Vera in 2003−05 and at Prince Leopold Island in 2005, weather data were recorded using a Davis®
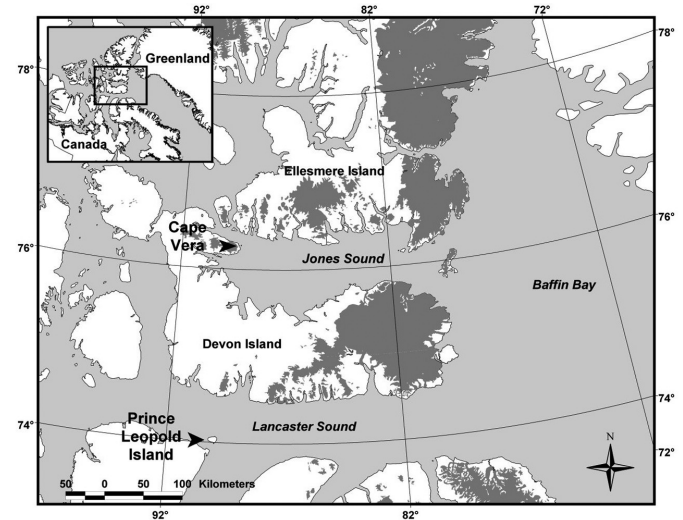

FIG. 1. The location of the Cape Vera and Prince Leopold Island study sites in the Canadian High Arctic. Shaded areas on islands represent glaciers.

Vantage Pro weather station, set to record hourly. In other years, Prince Leopold Island weather data were recorded only once a day, using a handheld weather station. Regional weather data for Resolute Bay, approximately 200 km west of both sites, were obtained from the Environment Canada's National Climate Data and Information Archive (http://www.climate.weatheroffice.ec.gc.ca/Welcome_e.html). Ice conditions near both colonies were obtained from the climate archives of the Canadian Ice Service (http://ice-glaces.ec.gc.ca).

We used "apparently occupied sites" (AOS; Lloyd et al., 1991) as our criterion for selecting nests to follow during the breeding season (Gaston et al., 2006) and counted total numbers of birds at these sites to track colony attendance. Northern fulmars have high fidelity to breeding sites (> 90% if no mortality; Hatch and Nettleship, 1998), and we assumed that observations through the season at a potential nest were observations of the same pair. Long-term population monitoring plots, each supporting 25−300 nests, were established at both Cape Vera (n = 8) and Prince Leopold Island (n = 7) (Gaston et al., 2006). Nest sites were viewed using 10 × 42 binoculars or a 60× spotting scope from vantage points 30−300 m away, so birds were not disturbed during counting. Because of poor weather (below), however, data were not necessarily collected on all plots each day.

Northern fulmars at Arctic colonies exhibit a range of plumage colour morphs, from very light (gull-like) to uniformly dark (Hatch and Nettleship, 1998). We conducted daily observations (≤ 4 hrs) on selected nest sites, where a pair consisted of one light and one dark morph, to determine which mate was attending the nest and identify whether an egg or chick (or neither) was in the nest (Gaston et al., 2006; Mallory and Forbes, 2007). Occasionally nest failures occurred during periods when we could not view the nest (e.g., fog), or when after prolonged observations of adults, we still could not determine whether the adult bird was on an egg. In these cases, we used the midpoint between the

previous and next conclusive assessments of nest contents to represent the nest failure date (typical error ± 1 day).

Using daily observation data, we defined three categories of breeding success: (a) successful breeders: fulmars at nests that produced a chick which was still alive at the post-guard stage (when both adults depart the nest to provision the chick, approximately 12–14 days after hatch; Hatch and Nettleship, 1998); (b) failed breeders: fulmars at nests that produced an egg, but lost either the egg or chick during incubation or rearing; and (c) non-breeders: fulmars at nests where we never observed an egg. For all calculations, dates were converted to ordinal dates, with 1 January = 001.

Depending on the distribution of data, we used t-tests (Welch's correction), Kruskal Wallis non-parametric ANO-VAs, or Pearson and Spearman rank correlations to compare data among years or colonies (Systat Software Inc., 2002). To examine diurnal patterns of colony attendance, we used counts collected over 24 hours from the same plots, but plots differed across months or years, and thus total counts differed substantially between sampling dates. Because we were interested in the pattern of colony attendance, and not the magnitude, we standardized all 24-hour plot counts by converting to Z-scores to compare values. We evaluated factors that influenced fulmar colony attendance using generalized linear models. We developed candidate models (Prince Leopold Island, n = 12; Cape Vera, n = 9) involving combinations of the variables ordinal date, local wind speed, regional wind speed, year (included in all Prince Leopold Island models because of known, significant differences among years; Gaston et al., 2005), and two-way interactions between year and wind variables. Akaike's Information Criterion, adjusted for small sample sizes (AIC_c; Burnham and Anderson, 2002), was used to select the best approximating models. We also used model-averaging to derive parameter estimates of continuous variables (denoted as $\theta \pm SE$) and associated variances and confidence limits from a 90% confidence set of candidate models (Burnham and Anderson, 2002). Means are presented ± SE, and all statistical tests report two-tailed probabilities.

RESULTS

Weather

At Cape Vera, temperatures were below -10°C when fulmars first arrived at the colony, and overall maximum daily temperatures during incubation and early chick-rearing (8 June–11 August) were cool (2003–05 daily means; 3.4 ± 0.4°C, n = 65 days, range -2.7–14.0°C). The mean daily maximum wind speed was 13.2 ± 1.6 km/h (8.0–62.8 km/h; n = 65), and each month experienced more than 5 cm of snowfall and wind gusts of more than 100 km/h.

At Prince Leopold Island, mean daily maximum temperatures during incubation and chick-rearing were warmer than at Cape Vera (daily means from 2002, 2003, and 2005; 6.5 ± 0.4°C, n = 65, range -0.8–26.3°C; Welch's t_{128} = 5.5,
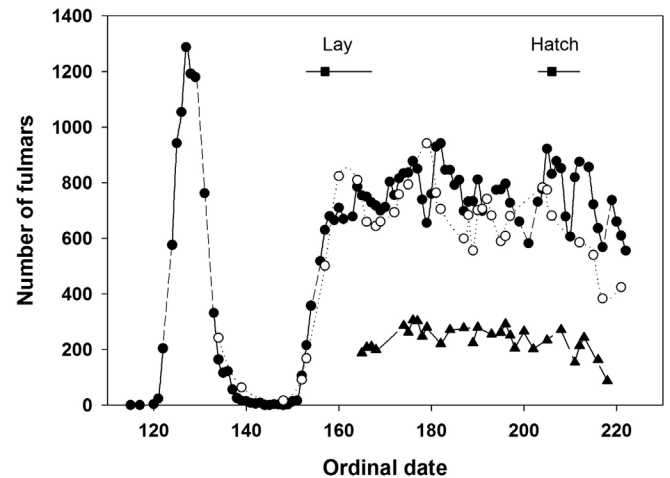

FIG. 2. Attendance patterns of fulmars at the Cape Vera colony in 2004 (open circles) and 2005 (filled circles), as measured by daily counts of birds on eight study plots, and the Prince Leopold Island colony in 2005 (filled triangles). Lower numbers of birds in 2004 are attributable to the replacement of one 2004 plot with a different plot containing more birds in 2005. The ranges of laying and hatching dates are depicted as horizontal lines, with a filled square denoting the mean lay and hatch dates (similar between the two colonies).

p < 0.001), as were mean daily maximum wind speeds (18.3 ± 1.0 km/h, range 0–70 km/h; n = 174 days; Welch's t_{128} = 2.7, p = 0.008). Blizzards were common, notably on 18–20 August 2001, 13 June, 23 July, and 13 August 2003. Fog was frequent, occurring on more than 25% of days at both colonies.

Colony Attendance and Breeding Status

At Cape Vera, fulmars arrived on the colony plots on 1 May (Fig. 2), and spent much of their time digging through snow on the nesting ledges to expose nest sites. Plot counts of fulmars increased by 183 ± 47 birds/day until 7 May, when the annual maximum count for the colony (1287 fulmars) was reached, and then declined by 128 ± 34 birds/day for the eight days following the peak. The pre-laying exodus was underway by mid-May and was most noticeable between 19 and 30 May, when not more than 16 fulmars were observed each day on the plots (< 3% of the maximum plot total or the mean count during incubation), with no fulmars observed on three of these days. Following the exodus, birds began returning to the colony on 31 May (in both 2004 and 2005), by which time most of the snow on the nesting ledges had melted, and numbers of fulmars increased by 100 ± 8 birds/day until the median laying date (Mallory and Forbes, 2007; 6 June in both years). In 2004 and 2005 at Cape Vera, the median date of hatching was 24–25 July, while at Prince Leopold Island in 2005, the median date of hatching was 26 July.

The mean total number of birds observed on the plots between 6 June and the end of observations (10 August) at Cape Vera was 753 ± 12 (n = 57; range 555–941 fulmars). The peak number of birds attending plots during incubation occurred around 1 July in both 2004 and 2005 (2005 Prince Leopold Island numbers peaked slightly earlier; Fig. 2).
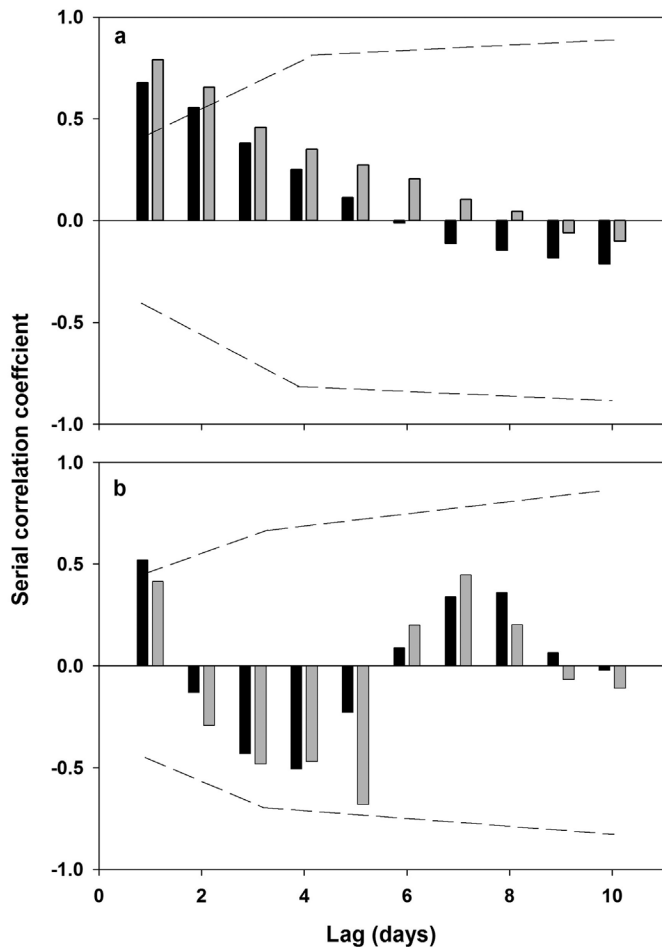
FIG. 3. Autocorrelation analysis of plot counts for fulmars at Cape Vera in 2005, for 20 June–10 July (dark bars) and 21 July–10 August (light bars), for (a) fulmars at active nests, and (b) non-breeders and failed breeders. Breeding birds did not show a cyclical pattern, but failed breeders and non-breeding birds exhibit a cyclical abundance at approximately one-week intervals. Dotted lines are 95% confidence intervals.

Hence, the peak number of birds post-laying was 73% of the maximum count for the year. At Cape Vera, daily counts of fulmars fluctuated by more than 20% over periods of three days, most strikingly after the early July attendance peak. Autocorrelation analysis on 2005 data (20 June–10 July and 21 July–10 August) found no evidence of a cyclical pattern following laying for breeding birds (Fig. 3a), but there were positive correlations at seven-day intervals for failed breeders and non-breeding birds (Fig. 3; data were insufficient for a similar analysis in 2004). Collectively, total numbers of adult fulmars counted at the colony between mean egg laying and the end of the chick-guarding period tended to decline, although patterns were inconsistent across years. At Cape Vera in 2004, numbers of fulmars declined (r_{29} = -0.45, $p = 0.01$), but in 2005 the weak declining trend was not significant (r_{58} = -0.09, $p = 0.5$), while at Prince Leopold Island in 2005, plot counts suggested a trend of declining numbers (r_{29} = -0.35, $p = 0.06$). For the two weeks following the median date of hatching, fulmar numbers declined sharply by an average of 53% for all sites and years (Fig. 2).

Through the incubation and chick-guarding stages, the number of active breeders declined as the number of failed nests increased ($|r_{54}| = 0.96$, $p < 0.001$). However, the proportion of fulmars observed each day at active nests remained stable over this period (Fig. 4a; $r_{s60} = -0.04$, $p = 0.74$), with a daily mean of 1.00 ± 0.01 birds per nest (i.e., there was usually one adult bird on the nest at active breeding sites). This proportion dropped off near the end of our observations as a higher number of active nests contained only chicks, when both adults were off the nest on foraging trips to provision their chick.

In contrast to the consistency of attendance at active nest sites (coefficient of variation 11%), non-breeders and failed breeders had higher variation in the proportion of birds attending nests each day (39% and 37%, respectively). Moreover, there was a clear decline following the mean egg-laying date in the proportion of non-breeding birds attending nest sites (Fig. 4b; $r_{s60} = -0.49$, $p < 0.0001$), with a daily mean of 0.56 ± 0.03 birds per nest (i.e., approximately half of the "no attempt" nest sites were occupied by an adult each day). For non-breeders, more nests were attended by pairs and more nests were unattended, compared to failed or active breeders (Mallory and Forbes, 2007), which generated the low proportions. As the breeding season proceeded, many non-breeders stopped attending the nest site.

For failed breeders, we analyzed trends for the period of time starting when 10 nests had been lost (24 June). The proportion of birds attending sites after nests failed declined from 24 June onwards (Fig. 5c; $r_{s42} = -0.54$, $p = 0.0002$), with a daily mean of 0.90 ± 0.05 birds per nest. The mean duration of nest attendance following egg loss was 17.0 ± 1.7 day (n = 33, range 5–39 day). In 23% of the cases where we observed that an egg was missing, no bird was present for only one day, and then an adult returned to the nest site. In a further 51% of the cases when an egg was lost, the adult attending the nest when it failed remained at the nest site until its mate returned from a foraging bout. For the remaining nests (26%), the adult remained at the nest for one or more days, but then left for two or more days before either mate returned. Following this, the nest was intermittently attended by one or both members of the pair, and then was abandoned.

Colony Attendance and Wind

We examined the relationship between colony attendance, year, ordinal date, local wind speed and regional wind speed at Prince Leopold Island for the incubation periods of 2001, 2002, 2003, and 2005 (6 June–26 July). All of the best-fitting models relating differences in fulmar colony attendance to year, date, and wind included year and local wind speed variables (Table 1), and explained 32% or more of the variation in colony attendance during incubation. However, the model-averaged parameter coefficients for date and regional wind speed did not differ significantly from zero (Table 2), indicating that neither of these parameters had a consistent, significant effect on colony attendance
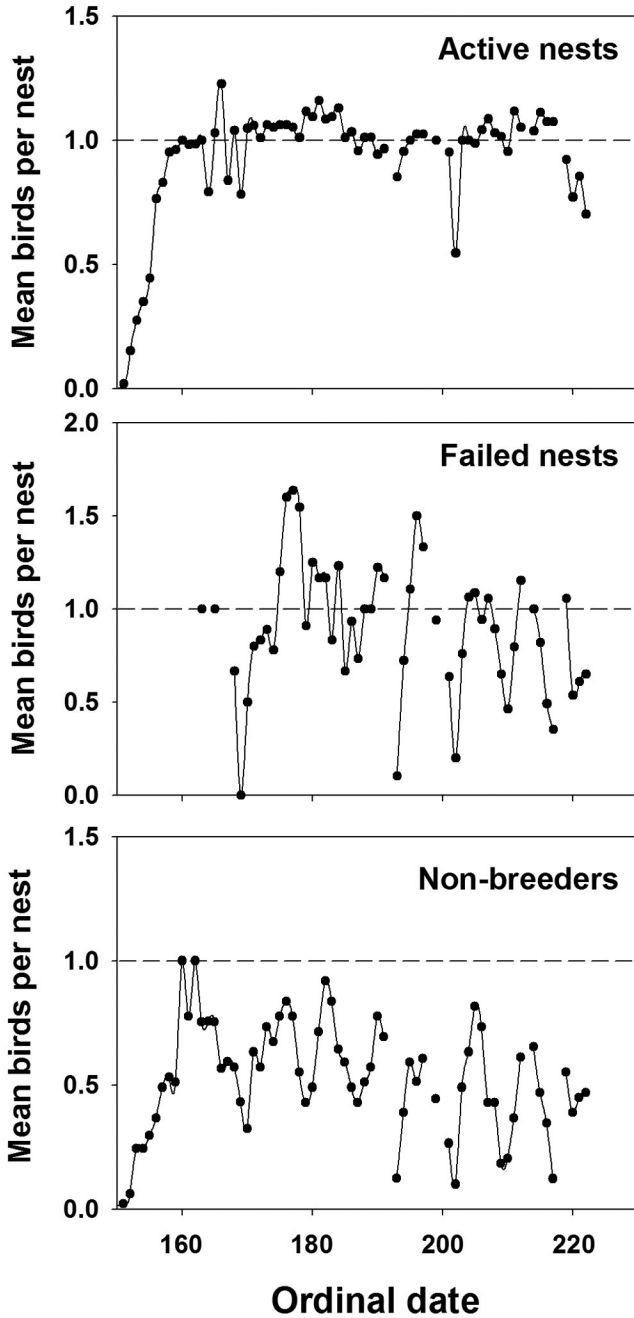
FIG. 4. Mean nest site occupancy by fulmars through the breeding period, by breeding status: a) active breeders – birds on nests containing an egg or chick; b) failed nests – the egg or chick was known to have been lost; and c) non-breeders – birds on nests where eggs or chicks were never observed during the breeding season.
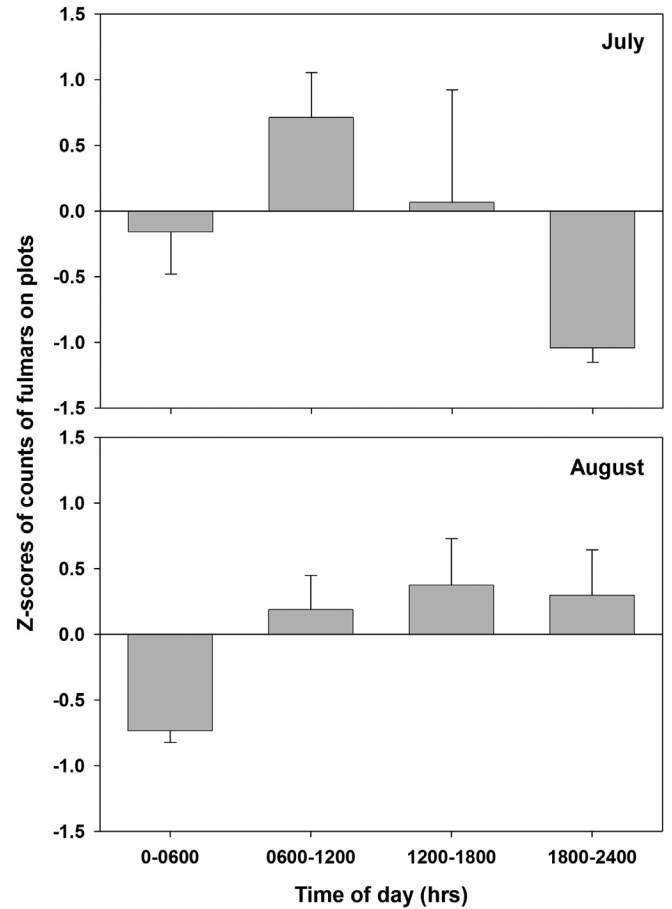

FIG. 5. Comparison of diurnal attendance patterns (means per six-hour period) of fulmars at Cape Vera in July and August 2005. The graph is based on hourly counts for three days of eight plots in July and four plots in August.

averaged parameter coefficients for ordinal date, local wind speed, and regional wind speed all encompassing zero. This result suggested that none of these parameters had a consistent influence on fulmar colony attendance during incubation at Cape Vera in 2005. Despite this, the lowest attendance by active breeders, and one of the days of lowest attendance by failed and non-breeders, occurred on 22 July 2005, when winds were consistently over 50 km/h, and gusts exceeded 100 km/h.

Diurnal Patterns of Colony Attendance

Because fulmars elsewhere are known to exhibit diurnal variation in colony attendance, we standardized daily plot counts at Cape Vera for late afternoon each year. However, on six days (11–13 August 2003, 19 July 2004, and 14–15 July 2005), we counted fulmars on plots each hour. In July, fewer fulmars tended to be observed on breeding plots between 1800 and 2400 hrs, and more were counted on the plots near 1200 hrs ($KW_{16} = 6.3$, $p = 0.09$; Fig. 5). In August, the pattern shifted, such that more fulmars were counted on the plots in the afternoon, and fewer birds attended plots between 2400 and 0600 hrs ($KW_{47} = 11.8$, $p = 0.008$; Fig. 5).

at Prince Leopold Island. In contrast, higher local wind speed had a consistently negative effect on colony attendance (i.e., smaller numbers of birds on more windy days; Table 2).

For Cape Vera (2005), we repeated the procedure above, but separated analyses for active, failed, or non-breeders. However, all models relating differences in colony attendance were poor, explaining little variation (maximum $r^2 = 0.18$), with individual models having low weight (maximum 0.31), and with 95% confidence intervals around model-

TABLE 1. Akaike's Information Criterion (AIC$_c$) values for representative models explaining variation in northern fulmar colony attendance at Prince Leopold Island, 2001 – 05. Models incorporated combinations of the parameters ordinal date (date), local wind speed (locspeed), regional wind speed (regspeed), year, and two-way interactions (year•locspeed, year•regspeed). Only candidate models of the 90% confidence set (sum of $w_i \geq 0.90$) are presented.

Model	RSS	K	ΔAIC$_c$	w_i^c	R^2
Year, regspeed, locspeed	372942.3	7	0.00	0.46	0.34
Year, locspeed	384294.9	6	1.31	0.24	0.32
Date, year, regspeed, locspeed	370859.9	8	1.63	0.20	0.34
Year, regspeed, locspeed, year•locspeed	355299.3	11	3.69	0.07	0.37
Date, year, regspeed, locspeed, year•locspeed	353563.9	12	5.58	0.03	0.37

DISCUSSION

Colony attendance by northern fulmars has now been described at sites across most of the species' breeding range (Moss, 1965; Dott, 1973; Hatch, 1989; Falk and Møller, 1997; Hatch and Nettleship, 1998; Gaston et al., 2006; this study). The schedule of colony attendance in the High Arctic (Cape Vera and Prince Leopold Island) begins later, and pre-laying colony attendance is compressed compared to Boreal colonies, as we have described elsewhere (Mallory and Forbes, 2007). Nonetheless, the general patterns of fulmar colony attendance we observed at Cape Vera were consistent with patterns observed previously (Hatch, 1989; Falk and Møller, 1997), including earlier studies from Prince Leopold Island (Hatch and Nettleship, 1998; Gaston et al., 2006). Specifically, counts of fulmars at the Cape Vera colony exhibited a rapid increase with the synchronous arrival of birds at the colony, an equally rapid decline when the birds departed for the pre-laying exodus, and then an increase when the birds returned en masse to initiate laying and incubation (Hatch and Nettleship, 1998). We also observed stable attendance by birds with active nests, but variable and cyclical attendance by failed or non-breeders, with a general decline in numbers of birds at the colony from early July onwards. Despite these overall similarities, we found that two aspects of colony attendance in the Canadian Arctic showed clear differences compared to other sites: the timing of peak colony attendance and the periodicity of the attendance cycle through the breeding period.

Seasonal peaks in fulmar attendance appear to vary by colony. For example, the post-exodus, peak colony counts at Cape Vera and Prince Leopold Island occur in early July (Gaston et al., 2006; this study), weeks after laying, whereas peak counts occur much earlier during breeding in northern Greenland (early June: Falk and Møller, 1997) and Alaska (mid- to late June; Hatch, 1989). However, fulmars at all of these colonies lay eggs within approximately one week of each other (Mallory and Forbes, 2007). The reasons for these differences among colonies are unclear, but the similarity in timing of peak attendance at Canadian sites suggests a link to common temporal patterns of marine production (e.g., Welch et al., 1992), and consequent colony attendance by non-breeders and failed breeders during times of abundant food. Gaston and Nettleship (1982) found that peak counts of thick-billed murres (*Uria lomvia*)

at Arctic colonies were driven by non-breeder attendance, which in turn was linked to marine food supplies. With peak counts of fulmars occurring earlier at other colonies, marine food availability is probably higher earlier in the breeding season at sites outside the Canadian High Arctic. This would be consistent with the fact that sea-ice cover physically precludes fulmars from feeding in many locations until it has broken up, and it also poses a barrier to light penetration, delaying the bloom of plankton in Arctic waters, and leading to a "pulsed" form of marine production (Welch et al., 1992).

Failed and non-breeding fulmars attend colonies in cycles—a social phenomenon probably influenced by weather and environmental conditions (e.g., food supplies; Hatch, 1989). The length of the cycles can vary from colony to colony, and within a colony, from year to year. In northeast Greenland, Falk and Møller (1997) found that peak counts of fulmars on breeding ledges were separated by 11.6 days, and Hatch (1989) recorded peaks of attendance 10 – 14 days apart in four of five years in Alaska. At Prince Leopold Island, Gaston et al. (2006) observed similar, long durations between peak attendance dates in 2001 (15 days) and 2003 (10 days), but found little evidence of a cycle in attendance during the late, extensive ice year of 2002, when fewer fulmars attended the colony during the breeding season (Gaston et al., 2005). In contrast, Linton and Nettleship (1977) found a short periodicity of peak attendance at Prince Leopold Island in 1976 (5.1 days), a year which had high numbers of fulmars attending the colony. At Cape Vera (2005), peaks in fulmar counts were seven days apart, closer to the 1976 pattern at Prince Leopold Island. More frequent peaks in attendance, and high numbers of birds, suggest that in 1976 and in 2005, feeding conditions during incubation were better for fulmars, so that failed breeders or non-breeders could return to the colony after shorter feeding trips. In 1976, sea ice cleared from Lancaster Sound relatively early, which would have led to higher marine productivity (Welch et al., 1992). At Cape Vera, breeding fulmars fly a long distance to feed in the productive North Water Polynya (Mallory et al., 2008a). Given that this oceanographic feature recurs annually, we posit that the periodicity in fulmar attendance is consistently short at Cape Vera.

Several studies suggest that wind direction does not play a significant role in fulmar attendance patterns (Coulson and

TABLE 2. Model-averaged ordinal date, local wind speed, and regional wind speed estimates (θ), standard errors, and 95% confidence intervals derived from the 90% confidence set of candidate models for effects of these parameters on numbers of northern fulmars attending the breeding colony during incubation at Prince Leopold Island, Nunavut, in 2001–05.

Parameter	θ	SE	95% CI
Ordinal date	0.312	0.397	-0.482 – 1.106
Local wind speed	-1.461	0.652	-2.765 – -0.158
Regional wind speed	-0.979	0.533	-2.044 – 0.086

Horobin, 1972; Dott, 1975; Hatch and Nettleship, 1998; but see Hatch, 1989), but that colony attendance is lower during periods of greater wind speed (Coulson and Horobin, 1972; Linton and Nettleship, 1977). Our observations of reduced colony attendance during stronger local winds at Prince Leopold Island were consistent with these earlier studies, but we found no statistically significant relationship between wind speed and fulmar colony attendance at Cape Vera. However, the fact that most monitoring plots at Cape Vera were protected from all but east winds may have influenced our analyses. Moreover, windstorms from the east were associated with pulses of nest failure at Cape Vera, as were snowstorms with peaks of nest failure at Prince Leopold Island (Linton and Nettleship, 1977; Hatch and Nettleship, 1998; A.J. Gaston, unpubl. data). At Cape Vera, for example, the major windstorm of 22 July 2005 not only kept non- or failed breeders away from the cliffs, but also coincided with the lowest proportional attendance by active breeders all season (Fig. 4a, ordinal date 202). Approximately half of the breeders did not attend their nests that day, which for many nests was the only day of egg neglect recorded during the entire incubation period (Mallory and Forbes, 2007), and their absence led to high depredation of nests by glaucous gulls (*Larus hyperboreus*). Strong, gusty winds may be unsafe for fulmars attempting to land at cliff ledges, and thus inexperienced, non-breeding birds or dislodged breeders may avoid the cliffs during these conditions.

Studies of fulmars in the United Kingdom (approximately 57° N, 5° W; Coulson and Horobin, 1972; Dott, 1975) and on the Norwegian island of Jan Mayen (71° N, 80° W; Cullen, 1954; Moss, 1965) have observed peak daily colony attendance in the middle of the day and generally lowest numbers overnight. With minor variations in timing, this pattern has also been found in Alaska (56° N, 156° W; Hatch, 1989), west Greenland (69°24′ N, 54°17′ W; Camphuysen, 1989), and previously at Prince Leopold Island (Hatch and Nettleship, 1998). However, in extreme northeast Greenland (80°11′ N, 16°38′ W), Falk and Møller (1997) found no obvious pattern in diurnal attendance by fulmars. Counter to our expectations, the pattern at Cape Vera (76° N, 89° W) was clearly diurnal (although samples sizes were small) and similar to that of colonies at lower latitudes, despite the continuous daylight, as in northeast Greenland, for most of the breeding season.

The consistent pattern of lower overnight numbers at fulmar colonies has been attributed to the habit of night feeding by fulmars (Furness and Todd, 1984). This daily attendance pattern suggests a common response by fulmars across their range to prey availability, such as the nocturnal migration to the ocean surface by certain zooplankton or squid (e.g., Watanabe et al., 2006). However, at Arctic colonies, foraging trips by breeding birds are usually longer than five days (Mallory et al., 2008b), and thus there would be little advantage for birds to depart at any particular time of day, if they must fly far to feed. At Cape Vera, breeding fulmars fly more than 200 km away to forage (Mallory et al., 2008a), meaning that birds departing at night would be flying over sea ice, not foraging. In contrast, many non-breeders feed along the coastline in front of the colony (Allard et al., 2008; the extent to which this behavior occurs at other colonies has not been reported). Our observations suggest that these coastline-feeding birds are among the non-breeders who visit the cliffs during the day, but return to the water at night. Therefore the diurnal attendance pattern and the role of night foraging may be largely attributable to feeding patterns of failed breeders or non-breeding fulmars, as shown for overall colony attendance patterns.

Although their breeding schedule differs (Mallory and Forbes, 2007), our data show that northern fulmars in the High Arctic exhibit diurnal and seasonal colony attendance patterns similar to those of fulmars at more southern colonies, despite foraging in constant daylight. Our findings that the periodicity in attendance counts at Cape Vera was shorter than that of most other colonies, and that windy conditions reduced the number of fulmars attending plots, support the recommendation of Gaston et al. (2006) that colony-specific attendance patterns should be accounted for when conducting population monitoring at fulmar colonies. Seasonal peaks in fulmar colony attendance and the periods between peaks appear to be influenced by marine productivity, which varies in response to annual sea-ice conditions. As the Arctic climate becomes warmer, marine food production and availability may increase earlier in the breeding season in response to reductions in the duration and extent of sea-ice cover (ACIA, 2005). Thus, in the future we should expect an earlier peak in colony attendance and relatively short periodicity in attendance cycles at Arctic fulmar colonies.

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