Year-round video surveillance of individual nest-site attendance of Northern Fulmars (*Fulmarus glacialis*) in the Faroe Islands

Í eitt ár vórðu reiðurstaðir hjá havhesti (Fulmarus glacialis) *í Føroyum eygleiddir við vakmyndatóli*

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Abstract

Nest-site attendance was monitored on a year-round basis by using video surveillance cameras at 10 potential nest-sites in a small colony of Northern Fulmars (*Fulmarus glacialis*) in the Faroe Islands. In the colony 27-34 nests-sites were occupied each year; 25-38% contained egg and 0-10 young were fledged. Altogether 40 potential nest-sites were identified during the course of the study (2004-2007) 18 of which were actively used for breeding (i.e. egg-laying) in 1- 4 years. Although few birds were marked and individually identifiable some cases of change of partner and/or nest-site were shown to occur. Successfully breeding pairs departed the colony at the end of August or early in September, whereas those that lost eggs in June left earlier though stayed for several weeks before leaving; hence, individual length of post-breeding absence (coinciding with primary moult) varied between 105 and 180 days. First arrivals mostly occurred in second half of December, though at this time of the year the nest-sites were only intermittently attended with considerable individual variation. During the pre-breeding period nest-site attendance peaked in April immediately followed by a marked drop and a pre-laying exodus in May. This general pattern was true for one-bird-attendance and the simultaneous attendance of two birds (presumably a pair) at the nest-site. In 2006 and 2007 the pre-laying exodus (defined as no. days in a run without the presence of the pair) at the individual nest-sites started between 21 April and 4 May and lasted for 21 to 32 days. In two cases when the length of the exodus could be related to sex the male had a shorter exodus than the female. A return from pre-laying exodus did not always result in egg-laying (2 cases). In 2006 and 2007 copulations were observed between 11 and 30 April and 20 April and 1 May, respectively, though without any distinct peaks. Besides, copulations occurred at all times of the day. The total number of successful copulations (3-33), time between first and last copulation (2-19 days), and mean numbers (1.0-8.3) per day with copulations varied considerable between the sites. No eggs were laid in the two nests with the lowest mean number of copulations.

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Úrtak

Í eitt ár vórðu 10 møguligir reiðurstaðir eygleiddir við vakmyndatóli í eini lítlum havhestabøli í Føroyum. Í havhestabølinum var havhestur í 27-34 reiðurstaðum hvørt ár; í 25-38% av teimum vóru egg, og 0-10 ungar vórðu floygdir. Tilsamans 40 møguligir reiðurstaðir vórðu eyðmerktir í tíðarskeiðinum, tá ið kanningin fór fram (2004-2007), í 18 av teimum vurpu havhestar í 1-4 ár. Hóast fáir fuglar vóru merktir, sýntist tað eyðmerkjandi, at nakrir fuglar skiftu maka og /ella reiðurstað. Tey pør, ið høvdu ungar, ið komu undan, fóru úr havhestabølinum síðst í august ella tíðliga í september, men tey pør, ið mistu eggini í juni, rýmdu fyrr, hóast tey vórðu verandi í fleiri vikur, áðrenn tey rýmdu; longdin á tíðarskeiðinum, ið hvør einstakur havhestur var burturfrá eftir verpingina (ið fellur saman við tað fyrsta fjaðurskifti) skifti millum 105 og 180 dagar. Teir havhestarnir, ið komu fyrst, komu fyri tað mesta í seinnu helvt av desember, men hesa tíð á árinum høvdu reiðurstaðirnir bert við millumbilum samband við ein munandi ymisleika hjá hvørjum einstøkum havhesti. Í tíðarskeiðinum undan verpingini vóru flestir havhestar við reiðurstaðin í aprílmánaði, og beint eftir tað kom eitt tíðarskeið við nógv færri havhestum, og beint undan verpingini í maimánaði rýmdu allir havhestarnir. Hetta vanliga mynstrið var satt, tá ið tað snúði seg um ein havhest, ið var til staðar, og tá ið tað snúði seg um tveir havhestar, ið samtíðis vóru til staðar (helst eitt par) á reiðurstaðnum. Í 2006 og 2007 byrjaðu havhestarnir at rýma undan verpingini (skilmarkað sum eitt ávíst tal á døgum í einum tíðarskeiði uttan at eitt par var til staðar) á einstaklingsreiðurstaðum millum 21. april og 4. mai, og tað vardi í 21 til 32 dagar. Í tveimum førum, tá ið longdin á tíðarskeiðinum, tá ið havhestarnir vóru burturstaddir, kundi hava samband við making, var steggin styttri burtur enn bøgan. Tá ið havhesturin kom aftur, hevði tað ikki altíð við sær, at bøgan varp (í tveimum førum). Í 2006 og 2007 varð lagt merki til making ávikavist millum 11. og 30. apríl og 20. apríl og 1. mai, tó uttan nøkur týðilig hápunkt. Harumframt kom makingin fyri alla tíðir á degnum. Heildartalið á úrslitagóðari making (3-33), tíð millum fyrstu og síðstu making (2-19 dagar), og miðaltal (1.0-8.3) hvønn dag við making var sera skiftandi millum reiðurstaðirnar. Eingi egg vórðu vorpin í tey bæði reiðrini, ið høvdu lægsta miðaltal av making.

Introduction

The Northern Fulmar (*Fulmarus glacialis*) exhibits a life-history strategy that is typical for pelagic seabirds of the order Procellariiformes and includes traits such as colonial breeding, high annual survival rate, low reproductive rate, deferred first breeding, high site tenacity and mate fidelity, and small degree of sexual dimorphism with both sexes sharing parental duties (Fisher, 1952; Ollason and Dunnet, 1978; Dunnet *et al.*, 1979; del Hoyo *et al.*, 1992; Schreiber and Burger, 2001; Brooke, 2004). Hence, for the Northern Fulmar the estimated annual survival rate of adults is *c.* 0.98, adult life-expectancy *c.* 35 years, and the age at first breeding in the range of 5-12+ years, with means of 8.4 and 10.3 years for males and females, respectively (Dunnet and Ollason, 1978; Ollason and Dunnet, 1978) and the species is able to breed in consecutive years (Carrick and Dunnet, 1954). This implies that, despite the deferred maturity and low reproductive rate (clutch-size of one and no re-laying), lifetime reproduction potential of an average individual ought to be relatively high. As one might expect there is individual variation in reproductive success that can be related to e.g. age, experience, egg quality, and parental care (Ollason and Dunnet, 1978, 1986, 1988). The life strategy of the Northern Fulmar, and that of other ocean-dwelling procellariids, can be viewed as a series of inter-dependent adaptations that have evolved in response to a feeding ecology that is depending on food resources with a relatively low predictability in space and time (see Ashmole, 1963, 1971; Lack, 1968); the „seabird syndrome“ (Gaston, 2004). An obvious, major constraint for such

	2005								2006								2007				
	Nest-site								Nest-site								Nest-site				
	1	2	3	6	7	11	12	15	1	2	3	6	7	11	12	15	1	2	3	6	11
Jan.									26	19	21	14	31	31	27	31	31	31	31	31	31
Feb.									26	28	28	19	28	27	9	28	28	28	28	28	28
March									15	13	21	11	31	31	18	31	31	31	31	25	29
April									20	24	26	21	30	30	25	30	30	30	30		30
May									16	31	31	12	31	31	17	31	31	31	31		31
June									21	19	7	26	30	25	17	21	1	28	30		9
July									12	18		31	11	31	11	12		1	10		
Aug.	18	22		12			12			7		7		11							
Sept.	4						4		6	7	8	7		7							
Okt.									27	31	31	31		31							
Nov.	3	20	17	7	20	14		20	30	30	30	30		30							
Dec.	18	31	31	12	31	31	23	31	31	31	31	31		31							

Table 1. Number of days with surveillance camera observations at different Northern Fulmar nest-sites in the Faroe Islands.

species is their need to go in search of terrestrial breeding sites, and the fact that the Northern Fulmar, throughout most of its breeding range, more or less regularly visit the colony during 9-10 months of the year, underlines the significance of having access to suitable nesting sites. Furthermore, non-breeding birds that include both sexually mature individuals known to have bred in previous years and birds of pre-breeding age regularly attend the colony and because of these so-called prospectors, the total number of fulmars present at the colony is often higher, even in winter, than the breeding population (Fisher and Lockley, 1954; Coulson and Horobin, 1972; MacDonald, 1980); besides, there was no significant monthly variation in proportions of breeders and non-breeders (MacDonald, 1980).

Throughout the Boreal zone of the Atlantic, following a period of post-breeding absence, the Northern Fulmars typically begin to attend their breeding colonies intermittently from late September to early December varying between years and colonies (Fisher, 1952; MacDonald, 1977a, 1980; Mallory and Forbes, 2007). For the Faroe Islands some information on the post-breeding departure, length of autumn absence, and arrival dates of the fulmar is given by Andersen (see references in Salomonsen, 1935), who published (1899-1905) observations made by P.F. Petersen and S. Niclassen from the islands of Nólsoy and Mykines, respectively. For instance, on Nólsoy no sightings of adult fulmars were made between late September and November and in three of the years the first birds returned on De-

	Number of potential nest-sites (+/- SD)	**Number of counting days**	**Number of nests with chicks or eggs**	**Percentage of potential nest-sites occupied by breeding birds**
June 2004	34 (+/- 4,0)	3	13 (eggs or chicks)	38
June 2005	31 (+/- 4,8)	9	9 (chicks)	29
April 2006	32 (+/- 7,1)	2	8 (eggs in June)	25
June 2007	27 (+/- 3,5)	8	10 (eggs)	37

Table 2. Number of potential nest-sites (estimates from 2-9 monthly counts) and percentage nests which subsequently contained eggs or chicks.

cember 6, 18, and 28 (for more details see Fisher, 1952:348 ff). Salomonsen (1955) stated that the breeding Faroese fulmars arrive irregularly through November-December (rarely earlier) and that the breeding sites are fully occupied about New Year; though the non-breeders do not arrive until at the end of March. As egg-laying does not commence until late May and early June the pre-breeding period in the Faroes (and in other regions) extends over 5-6 months which, as suggested by Salomonsen (1955), may be a result of competion for nest-sites and lack of interspecific competitors in winter. In British colonies arrival dates seem to be associated with breeding-colony size with occupation of nest-sites taking place earlier in larger colonies than in smaller ones (Fisher, 1952), whereas in the Canadian high Arctic arrival occurs later, presumably in response to prevailing ice and climate conditions (Mallory and Forbes, 2007).

Although fulmars are present at the colonies during a prolonged pre-breeding period, the numbers vary and mostly there is a peak in nest-site attendance in April, followed by a distinct drop in May and a subsequent peak in June. The exit in May, for about three weeks prior to egg-laying, was noted by Venables (1952) at a colony in Shetland, and this so-called pre-laying exodus (or „honeymoon“) is a trait that the Northern Fulmar apparently has in common with all, or at least most, species of Procellariiformes (Fisher, 1952; MacDonald, 1977b; Warham, 1990; Mallory and Forbes, 2007). As to the Faroes, Salomonsen (1955) did not mention any pre-laying exodus but stated that the greatest number of fulmars being present was from April to June. Both sexes participate in the exodus, though some males do not take part or visit the nest-site intermittently (MacDonald, 1977b). Copulations occur through an extended period of time though just before the exodus the frequency peaks (Hatch, 1987a; Hunter, 1998). It is generally assumed that the exodus is associated with the females' need to accumulate energy required for egg-formation and for both partners to prepare for strenuous bouts of incubation (Warham, 1990; Mallory and Forbes, 2007, 2008).

In this study we examine the annual cycle of nest-site attendance at a small colony of Northern Fulmar in the Faroes, where the species is an abundant breeder (Jensen *et al.*, 2005), focusing on the non-breeding season (i.e. September to June) when the fulmars are absent for periods of time. The number of fulmars present at any time is influenced by several factors such as wind speed and direction, time of day, and state of reproduction (MacDonald, 1980; Hatch, 1989; Ojowski *et al*., 2001). We monitored attendance by employing surveillance cameras that were operated continuously at 10 nest-sites; hence allowing us to study presumed individual pairs (regrettably few birds could be marked and individually identified) and to explore topics such as (i) post-breeding absence and date of first landing, (ii) seasonal pattern in attendance, (iii) timing and frequency of copulations, and (iv) occurrence and length of a pre-laying exodus. In addition we also obtained pertinent information on numbers of breeding pairs and breeding success as well as some observations on site tenacity, and mate fidelity.

Material and methods

Observation

The study was carried out close to an abandoned quarry at Sund (N62°2´59 W6°50´46) north of Tórshavn on Streymoy, which is the largest island in the Faroes. The colony itself is located on low cliffs on the southern side of the fiord Kaldbaksfjørður. The site was choosen because of its relative accessibility, and that preliminary surveys had indicated that it hosted about 30-40 pairs of fulmars. The colony was surveyed by means of binoculars and a telescope (32x77) on a tripod from a distance of 650 m at a point on the opposite side of the fiord. Each year in June (2006 in April) fulmars sitting on the cliffs and ledges were plotted on a map of the colony (several times a day for 2-9 days each year; Table 2) allowing us to assess the number and position of potential nest-sites. During the course of the study (2004-2007) a total of 40 different potential nest-sites were identified and each was given a permanent number, and 10 were selected (mainly on the basis of their accessibility) for closer studies, using surveillance cameras (Sony LL 20); 8 of which later contained egg or chick on at least one occasion during the study. Each camera was fixed to an adjustable foot that was fastened directly on to a rock using Epoxy glue. The cameras were connected to the field computer via cables running through water pipes from the field to the computer shed, which was situated about 20 m from the nearest camera. With the aid of infrared LEDs the cameras were able to record all activites at the nests 24 hours a day, but since they were motion sensitive, it was necessary to regularly empty the field computer for various „junk data"; mainly movements of vegetation due to wind. The surveillance cameras were operated from August 2005 until July 2007 and they recorded, with some unfortunate gaps, the activity at 8 and 5 nests, respectively (Table 1).

Breeding success was assessed when in 2004, 2005, and 2007 all potential nest-sites (nos 1-40) were examined in search of breeding evidence (i.e. eggs and/or chicks), whereas in 2006, in connection with other studies taking place, only sites nos 1-15 were checked.

Marking and handling of birds

Several activities during the field work may potentially have influenced the subsequent behaviour of the birds. In 2004 fulmars were caught by *fleyg*, the traditional method of catching fulmars and other seabirds in the

Nest-site	**2004**	**2005**	**2006**	**2007**
1 (cam)	e (eph)	c (cf)	e (eph)	
2 (cam)	e (eph)	c (cf)	e (eph)	e (epc)
3 (cam)	c (cf)		e (eph)	e (epc)
4	c	(cf)		
5	e (eph)			e (?)
6 (cam)	e (eph)	c (cd)	e (eph)	
7 (cam)				
9	e (eph)		e (eph)	
10	c (cf)	c (cf)	e (eph)	e (cf)
11 (cam)			c (cpr)	e (epc)
12 (cam)		c (cf)		
15 (cam)	c (cf)		e (eph)	
16	c (cf)			
19	c (cf)			e (?)
20	c (cf)		e (?)	
22	c (cf)		e (?)	
27	c (cf)	c (cf)		e (?)
28	c (cf)			
30	c (cf)	c (cf)		e (ep)

***Table* 3.** Nests of Northern Fulmars with eggs (e), chicks (c) and/or cameras (cam) in 2004-2007.
eph = Egg loss presumably due to disturbance (handling) and subsequent abandonment of nest
epc = Egg loss by Hooded Crow
ep = Egg loss (predator unknown)
(?) = Fate of egg unknown
cpr = Chick killed by rat (*Rattus norvegicus*)
cf = Chick fledged
cd = Chick died

Faroes by means of a triangular net attached to the end of a ten-foot pole (see Williamson, 1948:149ff), at nest-sites nos 1-10. Despite considerable efforts the success of catching fulmars was disappointingly low and only 7 females and 3 males (sex determined using morphometrics; accuracy >90 % according to Furness (1983)) were captured, banded and colour-dyed on the back of their heads. In 2005 the surveillance cameras were not mounted at the nests until after the eggs had hatched. Finally, in 2006 breeding fulmars were captured by *fleyg* at nests nos 1, 2, 3, 6, 9, 10, and 15, and fitted with loggers in an eventually unsuccessful attempt (the loggers were lost because the birds abandoned their nests) to study foraging movements.

Data storage and analyses

Recorded observations were tranfered on a regular basis from the field computer to a work computer for analysis on an 250GB external harddisc. In order to facilitate the analyses the length of each recording was maximized to 3-4 minutes, with an image of what started it in a folder. As the purpose of this paper is to examine nest-site attendance on a year-round basis, and since both sexes participate in parental care and thus are present during both the incubation and food provisioning periods, detailed data from late May to early September have not been included. The analysis of the data and presentation of the results are divided into two periods: first, the post-breeding period from the birds' departure in September to December when the fulmars usually make their first landfall; secondly, the pre-breeding period extending from January, when the fulmars begin to attend the colony on a more regular basis, until late May when egg-laying normally commences. Data from the pre-breeding period were analysed on a monthly basis, and attendance is expressed as percent of days that birds were present on the nest-site. In order to examine to what extent the male and the female simultaneously attend the colony during the pre-breeding period, and only seldom being able to make use of the marked birds or video recordings to distinguish between the sexes, monthly attendance was calculated for one (could be either sex) and two (presumably male and female) birds separately. Since there were statistically no significant differences in attendance between the nests the data were pooled.

All statistical tests were done using SPSS version 15 for Windows Vista and all data were tested for homogeneity and normal distribution.Test used were: ANOVA T-tests and Mann-Whitney U-test. Only p-values for two-tailed tests of significane are given.

Results

Breeding numbers and breeding succes

As shown in Table 2 the number of occupied, potential nest-sites varied between 27 and 34 during the years of study, and the proportion of active sites (i.e. where eggs were laid) ranged from 25 to 38%. Altogether 18 of the 40 potential nest-sites were used for breeding; 2 of them (nos 2 and 10) in all four years, 5 in three years, 7 in two years, and 4 only once (Table 3). The number of fledged young was 8 and 9 in 2004 and 2005, respectively; but none in 2006 and only one in 2007 when, however, the fate of several eggs could not be established. Most of the failures were caused by abandonment at the egg stage (12 cases), though in 3 cases of egg predation Hooded Crows (*Corvus corone cornix*) were the culprits, working in pairs chasing off the incubating fulmars, and once a Norwegian rat (*Rattus norvegicus*) was video recorded when instantly killing a half-grown chick.

Nest-site and mate fidelity

Only three (possibly 5) females and one male of the adult fulmars (7 females and 3 males) that were captured and ringed on nest-sites

Nest-site	2004	2005	2006	2007
1	**FA**		**FA**	**F?**
	M		**MA**	M
3	**FB**	nb	**F?**	F
	M		M	M
6	F		**F?**	nb
	MA		M	

Table 4. Site and mate fidelity of ringed (bold letters) Northern Fulmars at three nest-sites in the study area in the Faroe Islands. ***FA*** = female 4F-0601=ring number; ***FB*** = female 4F-0603; ***F?*** = female, number on ring not established; ***MA*** = male 4F-0606; nb = no breeding.

in 2004 were re-sighted in subsequent years (Table 4). Female A bred at nest-site no. 1 in 2004 and 2006 but with different mates; it is also possible that it was the same female (ringed but number unidentifed) that in 2007 copulated with a unmarked male at the same site, though no egg-laying was recorded in that year. At nest-site no. 3 no breeding occurred in 2005 but at least two (possibly three) different females bred at the site in the other years. Furthermore, at site no. 6 different individuals formed the breeding pairs in 2004 and 2006, and not only did male A change nest-site from 2004 to 2006 but also partner.

In 2004 two failed breeders, the male from nest-site no. 7 (M7) and the female from no. 2 (F2), were observed in the colony behaving like a pair; thus having deserted their respective partners from earlier in the season. On 15 June at 16.35 hrs M7 and F2 landed at nest-site no. 8, where the incubating unmarked bird left and M7 began to incubate the egg. At 16.50 hrs he was replaced by F2 who 5 minutes later was replaced by an unmarked bird. The two marked birds (i.e. M7 and F2) then immediately proceeded to the nearby nest-site no. 5 (which contained a broken egg) and remained there until the following afternoon.

Post-breeding departure to first arrival

Breeding fulmars leave the colony before the chicks are fledged and during 2005 and 2006 the dates of departure (i.e. last record of an adult fulmar at the nest-site) could be established in 8 cases. Three pairs that lost their eggs in June stayed on for several more weeks while two pairs with chicks left 2-3 days following the loss of their chicks, whereas the three pairs with fledged chicks departed 29 August - 4 September (Table 5). The dates for first landfall later in autumn and attendance in December were recorded for 8 nest-sites, for some of them in two years. In 2005 the first arrivals occurred from 9 to 23 December and in 2006 from 30 November to 24 December. The length of the post-breeding absence at five nest-sites ranged from 105 to 180 days; shortest for sites that produced fledgelings and longest for the site where the egg was lost at an early stage. The attendance in December was 1-6 days in 2005 and 1-10 days in 2006 and the

Nest-site	Year	Last adult	First arrival	Days absent	December Days	December Total time	Remark
1	2005	4 Sep	18 Dec	105	5	50 min	Chick
1	2006	9 July	24 Dec	168	1	1 min	Egg lost[1]
2	2005	29 Aug	23 Dec	117	1	2 h 29 min	Chick
2	2006	18 July	6 Dec	141	1	4 min	Egg lost[1]
2	2007	1 July	nd	-	nd		Egg lost[1]
3	2005	nd	9 Dec	-	6	2 h 10 min	Egg[2]
3	2006	nd	30 Nov	-	10	21 h 13 min	
6	2005	14 Aug	20 Dec	128	1	1 min	Chick[3]
6	2006	21 July	17 Jan	180	0	0	Egg lost[1]
7	2005	nd	15 Dec	-	4	4 h 58 min	
11	2005	nd	9 Dec	-	1	54 min	
11	2006	5 Aug	3 Dec	120	9	11 h 27 min	Chick[3]
12	2005	1 Sep	20 Dec	110	5	14 h 27 min	Chick
15	2005	nd	20 Dec	-	4	6 h 28 min	
15	2007	9 July	nd	-	nd		Egg lost[1]

[1] Egg deserted/predated: nest-sites nos 1 and 15 between 8-17 June, nest-site no. 2 on 30 June 2006 and 10 June 2007, and nest-site no. 6 on 6 June (predated the same day).
[2] Incubating on 7 June. No further information.
[3] Died on 17 Aug (nest-site no. 6) and killed by rat on 3 Aug (nest-site no. 11).

Table 5. Dates of departure and first arrival and nest-site attendance in December of Northern Fulmars recorded by video surveillance cameras in the Faroe Islands.

total time spend at the nest-site in December varied considerably from one minute to >21 hours; thus demonstrating that, at this time of the year, the fulmars only visited the nest-sites intermittently.

Pre-breeding period

Monthly attendance by one or both partners

Throughout the period January-May monthly attendance on nest-sites never exceeded 13-15% of the total time (Fig. 1). The general pattern, with reference to two-bird-attendance, was a peak in April followed by a marked drop in May, though for one-bird-attendance in 2007 the peak was in May (Fig. 1). However, the deviation in May 2007 was caused by nest-site no. 2 and when excluding those data in the analysis the peak in April was statistically significant ($p< 0.001$) in relation to the other months; except for one-bird-attendance in February 2006.

Timing and frequency of copulations

In 2006 copulations were recorded from 11 to 30 April and in 2007 between 20 April and 1 May (Table 6). For the individual pairs the time between first and last copulation recorded at the nest-site varied considerable (2-19 days), as did the total number of successful copulations (3-33). The mean number of copulations per day varied from 1.0 to 8.3; with a statistically significantly higher num-

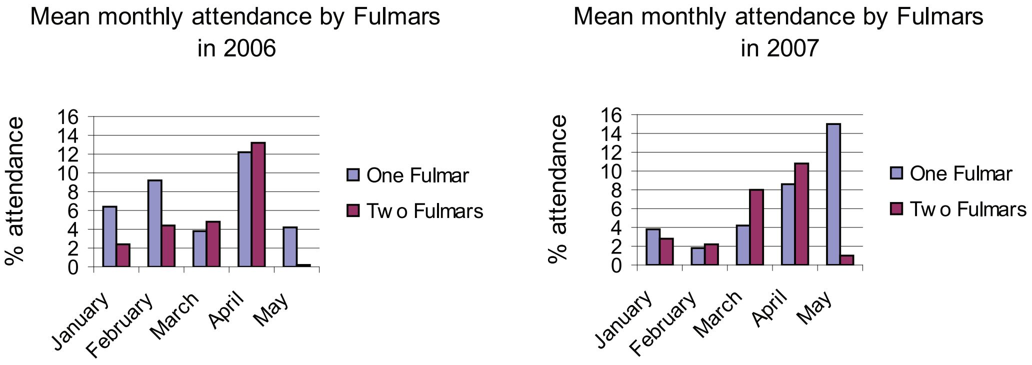

Fig. 1. Mean monthly attendance by one and two Fulmars from January to May 2006 and 2007 in the Faroe Islands.

ber of copulations at site no. 3 than at any other nest-site in 2006 ($p < 0.05$). The same was true for sites nos 2 and 15 compared to sites nos 11 and 12 ($p < 0.05$). In most cases the number of copulations in one day was in the range of 0-3, with one notable exception namely at nest no. 3 in 2006 where the birds mated 12 and 13 times on 15 and 16 April, respectively, and thereafter not until on 27 and 28 April (four times each day). The lowest mean number of copulations per day was recorded in no. 1 (2007), no. 11 (2007) and no. 12 (2006); with no eggs laid in nos 1 and 12. As to the time of the day no distinct peak was discernible and copulations occurred from 02 to 23 hrs, thus not only during daylight hours.

Pre-laying exodus

The period of relatively low attendance from late April through much of May, known as the pre-laying exodus, is presented in some

Nest-site	Date	Total	Copulations Successful	Days without	Mean no./day (SD)
1	22 Apr-1 May 2007	8	3	5	1.0 (0.0)
2	15-21 Apr 2006	22	22	1	3.7 (1.6)
2	24-27 Apr 2007	12	12	0	4.0 (1.6)
3	15-28 Apr 2006	34	33	9	8.3 (4.9)
3	24 Apr- 1 May 2007	16	15	2	3.0 (1.9)
11	19-21 Apr 2006	4	4	0	2.0 (0.6)
11	20-28 Apr 2007	9	7	3	1.4 (0.5)
12	11-30 Apr 2006	10	7	14	1.4 (0.5)
15	15-30 Apr 2006	31	17	8	2.4 (1.0)

Table 6. Copulations of Northern Fulmars at video surveilled nest-sites in the Faroe Islands, giving total numbers (attempts and successful copulations), date (first to last copulation), and mean number of copulations per day with copulation.

Nest-site	Year	Exodus	Length (days)	Days with one-bird-visits	Longest run of days without visit	Breeding remarks
1	2006	27 Apr - 21 May	(24)	7	8	21 May[1]
	2007	4 May - 26 May	(22)	12	3	no breeding
2	2006	21 Apr - 21 May	(30)	7	9	21 May[1]
	2007	29 Apr - 24 May	(25)	5	13	24 May[1]
3	2006	28 Apr - 21 May	(23)	5	9	21 May[1]
	2007	2 May - 28 May	(26)	25	1	28 May[2]
6	2006	30 Apr - 21 May	(21)	1	20	21 May[1]
11	2006	21 Apr - 23 May	(32)	8	10	24 May[2]
	2007	29 Apr - 20 May	(21)	6	10	20 May[2]
12	2006	30 Apr - 26 May	(26)	7	10	no breeding
15	2006	30 Apr - 21 May	(21)	4	10	21 May[2]

[1] Incubating (exact date of egg-laying uncertain)
[2] Egg laid

Table 7. Observations of pre-laying exodus at video surveilled nest-sites of Northern Fulmar in the Faroe Islands. Date and length of exodus is defined by the longest run of days without visits by two individuals (assumedly a pair) on the same day.

detail for 7 nest-sites in 2006 and 2007. Since the exodus may be sex-biased the length of it is here defined as the continuous run of days without the presence of the pair (i.e. two individuals) at the nest-site being recorded. In the two years exodus started between 21 April and 4 May and lasted until 20-28 May and varied in length from 21 to 32 days (Table 7). However, the longest sequence of days when no fulmar was recorded at the nest-site ranged between 1 and 20 days, but for most of the sites the period of absence was in the order of 8-10 days. Likewise, the number of days during the exodus when the nest-sites were visited by one individual varied considerably between the sites (1-25 days). In three cases the length of exodus could be related to sex since the females were ringed but not the males. Hence, at site no. 1 in 2007, the male regularly visited the nest-site during the female's exodus and maximum length of his absence was three days, whereas at sites no. 3 and 6 in 2006, the males were absent during a period of 9 and 19 -20 days, respectively; in the latter case at the same time as his partner.

Discussion

Fisher (1952), in his seminal work on the species, recognized and described in some detail the general patterns of annual cycle and colony attendance in the Northern Fulmar. Basically, across the species' breeding range, time schedule of breeding events is similar (also considering high Arctic colonies); besides, adult fulmars intermittently visit, or regularly occupy the breeding sites for much of the year, being absent from the colony only during a period in autumn and an exodus prior to egg-laying (see Mallory and Forbes (2007) and references therein). This extensive annual attendance at the breeding colony suggests that suitable nesting sites constitute a precious resource to fulmars; along with several additional key factors that are important to seabirds and other long-lived bird species (e.g. Forbes and Kaiser, 1994; Naves *et al*., 2006). By using surveillance cameras we were able to collect extensive data on the timing and duration of events going on at a number of selected nest-sites, thus enabling us to address issues and aspects of the annual cycle of the species raised by other studies. Since we did not succeed in individually marking but a few nesting fulmars, or otherwise identify individual birds, we presume that the high nest-site fidelity (even following the loss of partner; Hatch, 1987b) and mate fidelity demonstrated in previous studies (see Introduction), based on individually recognizable birds, also apply to the Faroese colonies. *Hence, we initially assumed that fulmars recorded at a given nest-site were the same individuals from time to time, although this proved not always to have been the case as shown by observations based on the few individually identifiable birds in the study colony.*

Post-breeding period

The parents stop feeding the young before it is fledged, though usually they remain in the colony or neighbourhood of it for still some time and in the Faroes the adult fulmars desert the breeding colonies from mid-August (the young from mid-September), though some may still be around at the end of September (Fisher, 1952; Salomonsen, 1955). According to our observations the timing of post-breeding departure varied considerably, presumably depending (at least partly) on breeding success; successful pairs abandoned the breeding colony in late August or in the beginning of September, whereas those that failed left much earlier (Table 5). In three cases in June 2006 nests were abandoned during egg stage (nos 1, 2, and 6), presumably due to disturbances when the birds were caught in order to be fitted with GPS-data loggers. Other studies have shown that capturing and handling incubating fulmars may cause desertion, or make the birds stay away from the nests long enough for predators to take their tolls (e.g. Furness and Bryant, 1996) and that disturbance may cause breeding failure not only in the year of capture but also reduce breeding success in the following year (Ollason and Dunnet, 1978). Hence, it is reasonable to assume that the disturbances may have affected breeding success and therefore also timing of departure and length of the autumn absence from the study colony.

Moulting is an energy-demanding process in birds (e.g. King and Murphy, 1985) and for most Procellariiformes it is more or less well separated in time from reproduction (del Hoyo *et al*., 1992). This is presumably also generally true for the Northern Fulmar that undergoes a single, complete moult, the timing of which apparently varies according to breeding status; the moult starting later among breeders than non-breeders and failed breeders (Hatch and Nettleship, 1998; Allard *et al*., 2008). At the Eynhallow colony in Orkney, Carrrick and Dunnet (1954) noted the occurrence of moulting fulmars (including primary moult) among supposedly failed-breeders, already in July, whereas in a Canadian study in High Arctic no signs of primary moult were detected (Allard *et al*., 2008). With reference to the Faroes, adult fulmars were collected at sea in 2003-2006 and examined with respect to moulting status, showing that primary- and tail moult occur from October to December (Danielsen *et al.*, unpubl.). This coincides in time with the post-breeding dispersal of Faroese fulmars suggesting that they might spend the moulting period in Faroese offshore waters. However, virtually nothing is known about the post-breeding dispersal of the Faroese population and the origin of the abovementioned fulmars collected for moult studies is not known. Since the fulmars do not shed all primaries at the same time they probably retain at least some flying ability (though see references in Bauer and Glutz, 1966; Cramp, 1977; Huettmann and Diamond, 2000:632 for somewhat conflicting views). Consequently fulmars are presumably able to travel some distance to exploit distant food resources. Although primarily considered a plankton-feeder a study of the species' diet in the Faroes has shown that the fulmar is a flexible feeder and that small-sized fishes of mesopelagic species, notably the Glacier Lanternfish (*Benthosema glaciale*), constitute an important part of the diet; though adult fulmars also feed on other items such as cephalopoda, planktonic crustacea (especially during breeding season), and fish-offal (Danielsen *et al.*, MS). The environmental conditions on the Faroe shelf and in the offshore waters ensure that rich food resources are available to the many species of seabirds that breed on the islands (Salomonsen, 1955; Gaard *et al.*, 2002). While mesopelagic fish species presumably are available in autumn to fulmars feeding in coastal waters the situation is different with regard to zooplankton. The abundance of zooplankton is generally high from late spring and through the summer with a peak at the end of August and early in September (coinciding with the main fledging-period of young fulmars) and remains at a relatively high level throughout October (Gaard, 1999:Fig. 4). Around the Faroes the dominating zooplankton is the copepod *Calanus finmarchicus*, a large species that probably constitutes most of the significant volume of plankton found in the stomachs of fulmars in spring and summer (Danielsen *et al.*, MS), which in the autumn occurs at greater depths (Gaard, pers. com.) and thus is practically inaccessible to the fulmars. Whether the seasonal dynamics in the abundance of zooplankton, or any food resource for that matter, is a key factor that determines the post-breeding behaviour of the Faroese fulmars is a subject for future studies. For instance, do the adults, despite a relative abundance of copepods, leave the colony in order to reduce competition at a time when there is a peak in number of fledged young, or to exploit more distant food resources? Because of great geographic and seasonal variability of the marine environments it has been suggested that seabirds are capable of perceiving environmental cues that may be used to predict future breeding conditions (e.g. Cairns, 1987; Erikstad *et al.*, 1998; Pinaud and Weimerskirch, 2002: Wanless *et al.*, 2007; though see Hipfner *et al.*, 2008). For several colonial and other species of birds prospecting behaviour during post-breeding dispersal has been suggested as a means of assessing the local habitat quality and to assist in choosing suitable breeding sites (e.g. Boulinier *et al.*, 1996; Doligez *et al.*, 2002; Arlt and Pärt, 2008), and it seems reasonable to propose that this might also apply to the Northern Fulmar.

Pre-breeding period

Several authors studying other species of seabirds (viz. large gulls, kittiwakes, skuas, and terns) have argued that early arrival dates and high nest-site attendances are associated with strong intraspecific competion for breeding sites, which also would prevent „prospectors" from settling and breeding (e.g. Wooller and Coulson, 1977; Duncan, 1978; Coulson, 1991; Klomp and Furness, 1992), or insufficient information about breeding site and congeners, or simply a lack of partner (Curio, 1982; Weimerskirch, 1992; Ludwigs and Becker, 2002; Dittmann and Becker, 2003). As to the Northern Fulmar, Salomonsen (1955) proposed that the early arrival was due to intraspecific competion for nest-sites and a relaxed interspecific competion for food in winter. From a study in NE Scotland, MacDonald (1980) concluded that, although the nest-sites were defended throughout the winter, there was no evidence of intra- or interspecific competion for nest-sites. Fisher (1952) compared observations from a large number of British breeding-colonies and found a slightly earlier arrivel at larger colonies than at smaller ones; though he did not explicitly suggest any explanation for this. The study colony at Sund is a relatively small one (*c.* 30 pairs), and the only other colony in the Faroes, for which relevant, comparative data on post-breeding absence exist (note that at Sund a sample of nest-sites was studied), is the much larger one (*c.* 200 pairs) in Kambsdalur, situated 19 km north of Sund and monitored for 12 years, where fulmars are to be seen in all months of the year except for October (Danielsen *et al.,* unpubl.). This is comparable to observations at the similar-sized colony at Marsden in Co. Durham, where the fulmars were absent for only 3-4 weeks in October and first days of November (Coulson and Horobin, 1972) and it is in agreement with Fisher's (1952) general observations on small *versus* large colonies in the British Isles. Non-breeding fulmars, comprising individuals that have not yet bred for the first time and intermittent breeders (the two categories are indistinguishable in the field), usually constitute a considerable portion of the adults in the colonies. At the Sund colony this fraction was about two-thirds while one-third has been recorded in other studies (see Mallory and Forbes, 2007). Ringing recoveries have shown that young birds (pre-breeders) disperse more widely and are less site faithful than fulmars that have bred (Salomonsen, 1967; MacDonald, 1977c; Dunnet *et al.*, 1979). It could be argued that competition for nest-sites is stiffer in large colonies than in smaller ones, and that prospecting pre-breeders therefore are either repelled from, or attracted to smaller colonies, which would also contribute to the colonization of new breeding sites (Coulson and Horobin, 1972). This would be consistent with Fisher's model for the timing of landfall and an example (albeit selected!) in support of the model is the island of Helgoland, where the first prospecting fulmars appeared in 1968, first successful breeding occurred 1972, and in the late 1970s the colony still only comprised about a dozen pairs that departed from the breeding grounds in August and returned in late-February and in March (Moritz, 1980). Possibly a two-step model could be applicable, where some prospectors are first attracted to a relatively old and large colony but due to competition go elsewhere (see also Coulson and Horobin, 1972). However, the surveillance cameras did not record any behaviours that indicated competition for nest-sites (no other cliff-breeding species nested within the colony area), which of course could be due to the fact that the colony was small. For the Northern Fulmar, and other long-lived seabird species, prospecting for information regarding suitable feeding areas, breeding colonies, nest-sites, and breeding success of conspecifics (the „public information" hypothesis) is probably a significant element of the species' life-history strategy (see Forbes and Kaiser, 1994). MacDonald (1980) suggested that breeding adults and other potential recruits might use the „winter assembly" to look for, and form pair-bonds with unmated birds. Although the divorce and mortality rates among fulmars are low, approximately 5% of the breeders will lose their mates annually and therefore have to search for a new partner (MacDonald, 1977a; Ollason and Dunnet, 1978). Despite scanty data, the present study indicates that divorce rate may have been higher and nest-site fidelty lower at Sund (see Results and Table 4) than previously reported for other colonies, (Ollason and Dunnet, 1978, 1988). This may be due to disturbance and a subsequent low breeding success (Table 3) or some other environmental unpredictability. In the context of the „success-stay/failure-leave" concept (Schmidt, 2004), breeding performance is thought to influence both mate and site fidelity in long-lived seabirds (Naves *et al.*, 2006); though with regard to site fidelity theory predicts that it should be inversely related to lifespan and that individuals should be site-faithful in unpredictable habitats provided there is equal site-quality (Switzer, 1993, 1997). However, not surprisingly in view of the small sample-size, no significant differences in first arrival dates and attendance patterns between nest-sites and years, or between successful and failed breeders, are discernible in the present data (Table 5). Almost invariably the first landfall occurred in December though the attendance at the individual nest-sites varied considerably from a single day (and one minute to an hour) to 9-10 days (Table 5). The fulmars continued to visit the nest-sites intermittently and with two individuals present throughout the months January-March and with two-bird-attendance reaching a peak in April (Fig. 1); thus coinciding with the period when all copulations were recorded (Table 6).

According to Hatch (1987a) fulmars copulate only at the nest-site and in his studies of the species in Alaska, the pairs began to copulate immediately upon first landfall (*c.* 50 days prior to first eggs) and on average every 2-4 hours in daylight. Furthermore, the frequency of copulations peaked about 3 weeks before the egg is laid and the female is inseminated 30-40 times before she departs for the pre-laying exodus (Hatch, 1987a). This is in sharp contrast to our study where all copulations recorded by the cameras took place during a relatively short period (11 April to 1 May), although the birds had been attending the colony since in December or January. In a study of albatrosses 96% of the observed copulations occurred in one day (Astheimer *et al.*, 1985). In our fulmar colony copulations were recorded at effectively all hours (between 02 and 23 hrs), hence not only during daylight. Besides there was no peak in frequency but a considerable variation between the pairs with regard to frequency and days between first and last copulation as well as total number of inseminations (Table 6). In all cases at least one of the birds in the pair departed for a pre-laying exodus shortly after the last copulation and all but two of the pairs laid eggs upon the return to the nest-site 3-4 weeks later. The Northern Fulmar, like Leach's Storm-petrel (*Oceanodroma leucorhoa*), Horned Puffin (*Fratercula corniculata*) and probably some other pelagic seabirds, have sperm-storage glands which allows the partners to be separated for weeks (Hatch, 1983). It is believed that fertilization occurs within a few days prior to laying and it is suggested that the probability of paternity is determined by the frequency and timing of inseminations due to physiological constraints (Hunter, 1998). Female fulmars engage in extra-pair copulations (EPCs) but the extra-pair paternity appears to be < 5% (Hatch, 1987a; Hunter *et al.*, 1992; Hunter, 1998). We did not record any EPCs, possibly because of the small sample size and too few individually marked birds.

A pre-laying exodus is a common feature to most procellariids, including the Northern Fulmar (see Introduction); though with some intra- and interspecific variation with regard to length in time and sex-biased participation (Warham, 1990, Brooke, 1990; Mallory and Forbes, 2007). In our study colony the exodus was more noticeable in 2006, when fewer birds occupied the monitored nest-sites in May than at corresponding time in 2007 (Fig. 1). However, this difference is attributable to nest-site no. 2 in May 2007 when one of the birds was present all the time, but when these data are excluded in the analysis the exodus is equally pronounced as in 2006. This also exemplifies the great between-nest variation in attendance in May. While the length of the pre-laying exodus ranged from 21 to 32 days the number of days when a given site was visiting during that period ranged from 1 to 25 days (Table 7). In two of three cases when ringed birds were involved it was the male that stayed behind and more or less regularly attended the nest-site, which is consistent with previous studies of the species and some other procellariids (Dunnet *et al.*, 1963; Hatch, 1983; Brooke, 1990). This sex-biased exodus is often discussed in terms of the females' need to build up substantial food reserves to be able to form the relatively large egg (Lack, 1966) and to participate in the incubation duties, whereas the males need to prepare for the first stints of incubation and to endure the long spells of fasting (Warham, 1990; Mallory and Forbes, 2007). In a study of Cory's Shearwaters (*Calonectris diomedea*) it was argued that the cost of forming the egg is less than 0.5% of total costs of reproduction and therefore not adequate in explaining the long pre-laying absence of the females; instead it was suggested that, since they are more at home at sea than on land and already mated, they prefer to stay out at sea until egg-laying (Jouanin *et al.*, 2001). As regards the fulmars, the fact that non-breeders also leave the colony for a period of time prior to the commencement of egg-laying seems to support the notion that the pre-laying exodus may not entirely be a matter of accumulating energy resources for forming the egg and enduring the strains of incubation (Mallory and Forbes, 2007). However, recent studies have demonstrated that, at least in High Arctic regions, fulmar activities at the nest-site between arrival and pre-laying exodus are energetically expensive and necessitate a replenishment of nutrient reserves (Mallory and Forbes, 2008). In this context it is interesting to note that at two nest-sites (nos 1 (2007) and 12 (2006); Table 7) no egg laying occurred despite a pre-laying exodus.

Concluding remarks

By and large the present study supports many findings of previous students of the species, and concurs with a picture of the Northern Fulmar as being, with regard to life-history strategies, a conservative and at the same time flexible species that has enabled it to spread over much of the northern Atlantic and become a dominant seabird in that region. As so appropriately put by Fisher (1952) in his landmark monograph on *The Fulmar*, the fulmar is „a conservative, unyielding, uncomprimising, tradition-steeped, weather-proof automaton...most predictable of all the seabirds in the North Atlantic...it certainly keeps its appointments more punctually than the ordinary farmer."; thus, referring to the time schedule of the annual cycle over geographic regions (Fisher, 1952:374-375). This makes the Northern Fulmar highly interesting as a study object in the context of climatic change (Edwards *et al.*, 2006). The purported flexibility of the species is manifested in inter-colony and between-individual (nest-sites) differences that has been recurrent themes of the above discussion. However, maybe the most important question we should try to answer nowadays is what are the fulmars doing when they are not attending their nest-site ledges but far out at sea?

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