Contribution to the Theme Section 'Tracking fitness in marine vertebrates'

Annual variation in the timing of breeding, pre-breeding foraging areas and corticosterone levels in an Arctic population of black-legged kittiwakes

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ABSTRACT: Late breeding usually occurs during years of poor environmental conditions, but the proximate mechanisms underlying this phenological pattern have been poorly documented. Here, we combined the deployment of GPS devices (from 2008 to 2010) and the monitoring of breeding parameters and baseline corticosterone levels (from 2007 to 2011) during the pre-laying period to investigate the proximate regulation of breeding date in an Arctic population of black-legged kittiwake *Rissa tridactyla*. The timing of breeding varied considerably during the course of the study and late breeding was associated with reduced clutch size and low breeding success at the individual level. Foraging strategies differed considerably between males and females and among years. All but one of the females tracked using GPS during the pre-laying period foraged inside the fjord, whereas tracked males foraged both inside and outside the fjord, using the deep waters of the Greenland-Svalbard ridge. Trips lasted longer and were to greater distances in 2009, the year of late breeding, compared to 2008 and 2010, highlighting a food scarcity in 2009. Corticosterone levels differed among years, and were the lowest in 2010, the year of earliest breeding. Moreover, kittiwakes exhibiting higher corticosterone levels tended to undertake longer trips when foraging outside the fjord. Breeding decision and laying date were not related to corticosterone levels at the individual level, but were positively influenced by body condition, suggesting that complex proximate mechanisms may affect timing of breeding in kittiwakes.

KEY WORDS: *Rissa tridactyla* · Stress · Hormones · GPS · Phenology · Reproduction · Annual variations · Svalbard

INTRODUCTION

The effects of environmental fluctuations on breeding phenology have been well described in marine ecosystems and at different trophic levels (Edwards & Richardson 2004, Reed et al. 2009). In seabirds, poor environmental conditions, such as the scarcity of available food early in the season, is usually asso-ciated with delayed breeding, reduced clutch size and ultimately poor breeding success (Moe et al. 2009, Shultz et al. 2009, Votier et al. 2009). However, the proximate mechanisms that mediate this annual variation in laying date are less well documented. One hypothesis is that seabirds increase the energy and time spent foraging when food availability becomes scarce early in the season, which in turn

may postpone or even stop the progress of reproduction-related physiology (gonadal maturation) and behaviour, such as nest building, courtship and mating ('constraint hypothesis', e.g. Shultz et al. 2009). In that respect, investigating the underlying mechanisms of phenological variation requires a multidisciplinary approach by combining studies on (1) foraging behaviour, (2) physiological adjustments and (3) life-history variation during several years.

The deployment of tracking devices on seabirds, such as global positioning system loggers (GPS), offers an effective means of describing foraging behaviour (Weimerskirch et al. 2002), and of linking annual changes in foraging range with reproductive output (Boersma & Rebstock 2009, Chivers et al. 2012). However, GPS deployments have been almost exclusively conducted during the incubation and chick-rearing periods. Tracking pre-laying birds (attending the colony before the onset of egg laying) appears crucial in order to better describe their foraging strategies and to investigate the possible mechanisms mediating the adjustments of breeding schedule in response to oceanographic conditions (Mehlum 2006, Moe et al. 2009, Shultz et al. 2009, Votier et al. 2009).

At the physiological level, a reliable marker of food-related stress is the release of corticosterone: in seabirds, high baseline corticosterone levels (i.e. measured within 3 min after capture and thus unrelated to handling stress, Romero & Reed 2005) reflect low food availability and poor foraging success (Kitaysky et al. 1999, Wingfield & Kitaysky 2002, Angelier et al. 2007a, Kitaysky et al. 2007, Benowitz-Fredericks et al. 2008). In turn, corticosterone promotes the mobilization of energy reserves and foraging behaviour, but at the expense of the current reproductive attempt (Kitaysky et al. 2001, Angelier et al. 2007a,b, 2009, Breuner et al. 2008). Corticosterone is also viewed as an adaptive response that regulates and supports the metabolic demands of foraging activities (Bonier et al. 2009, 2011, Crossin et al. 2012). During the pre-laying period, recent studies have demonstrated that corticosterone can play a major role in the mediation of breeding decisions (skip or breed, timing of breeding and clutch size) in male and female seabirds (Goutte et al. 2010a,b, 2011). For instance, pre-laying females with the highest corticosterone levels did not breed or postponed the onset of egg laying in snow petrels *Pagodroma nivea* (Goutte et al. 2010a) and in black-legged kittiwakes *Rissa tridactyla* via a possible inhibition of luteinizing hormone (LH), a key driver of the onset of reproduction (Goutte et al. 2010b). The primary functional role of corticosterone in mediating breeding decisions was confirmed by a hormonal manipulation in kittiwakes: females with experimentally reduced corticosterone levels during the pre-laying period bred earlier and were more likely to be successful (Goutte et al. 2011). However, annual variation in the timing of breeding has never been related to annual variation in corticosterone levels in response to pre-laying environmental fluctuations.

One of the most appropriate seabird models for this multidisciplinary study is the black-legged kittiwake. This species is closely monitored for research on foraging behaviour, endocrine mechanisms and life history traits. In particular, an Arctic population of kittiwakes at the northwestern coast of Spitsbergen, in the Svalbard archipelago, exhibits high annual variation in the timing of breeding, although no significant long-term phenological trend was detected over the last decades (Mehlum 2006, Moe et al. 2009). In this population, late breeding generally occurs during years of low spring sea surface temperature (SST) and is associated with reduced clutch size and low breeding success (Moe et al. 2009). Hence, annual changes in timing of breeding and associated fitness consequences would be likely explained by pre-laying behavioural and physiological responses to environmental changes. In Spitsbergen, kittiwakes arrive at the breeding colonies in April and attend the colony for 2 mo before laying, which on average takes place around 10 June (Moe et al. 2009). During this pre-laying period, kittiwakes alternate foraging trips at seas with visits to a central place, their nest at the colony. This offers the opportunity to monitor foraging behaviour of pre-laying kittiwakes. In that respect, GPS loggers have been successfully deployed on this species during incubation and brooding periods (Kotzerka et al. 2010, Chivers et al. 2012). Lastly, hormonal mechanisms have been well investigated in kittiwakes, through descriptive and experimental studies of corticosterone levels (Kitaysky et al. 1999, Angelier et al. 2007a, 2009, Goutte et al. 2010b, 2011, Schultner et al. 2013).

The aim of this study is to describe the behavioural and physiological mechanisms underlying annual changes in the breeding schedule and outputs during 5 consecutive years (from 2007 to 2011) in a high Arctic population of black-legged kittiwakes. Using GPS loggers, we identified the foraging areas of pre-laying males and females during 3 yr (from 2008 to 2010). We predicted that pre-laying foraging range and trip duration would increase during 'bad' years (a year of delayed breeding and hence of reduced breeding success, Moe et al. 2009) and would be

higher in non-breeders compared to breeders, as long trips may represent a time and an energetic constraint. Concomitantly, we measured pre-laying body condition and baseline corticosterone levels, as a measure of physiological response to food-related stressors. We expected lower body condition and higher corticosterone levels during 'bad' years, and in non-breeders compared to breeders, in line with previous studies (Goutte et al. 2010a,b, 2011). Moreover, we investigated whether metrics of foraging trips were related to corticosterone levels measured before GPS deployment. Finally, we expected that skipped breeding and late laying would be related to higher corticosterone levels and would lead to low clutch size and high breeding failure, at the individual level.

MATERIALS AND METHODS

Study area and birds

Our study was conducted during 5 consecutive breeding seasons, from 2007 to 2011 in a colony of black-legged kittiwakes at Kongsfjorden (Krykkje-fjellet, 78° 54′ N, 12° 13′ E), Svalbard, 7 km east of Ny-Ålesund, Norway. Black-legged kittiwakes are colonial seabirds that breed on cliffs throughout the northern parts of the Pacific and Atlantic, including the Barents Sea region up to the Svalbard Archipelago. On the west coast of Spitsbergen, cold, relatively fresh Arctic water meets and mixes with warm, saline Atlantic water masses (Svendsen et al. 2002). Kongsfjorden-Krossfjorden is an open fjord system with no sill at the entrance, and is thereby influenced by the mix of Atlantic and Arctic water, especially at the outer part (Cottier et al. 2005). The distance between the colony and the entrance of the fjord is approximately 22 km.

Breeding phenology, skipped breeding and reproductive output

In Svalbard, kittiwakes attend the colony during the 2 mo before laying. We monitored 84 occupied nests in 2007, 80 in 2008 and 2009, 113 in 2010 and 120 in 2011, at one colony. An occupied nest is defined as a nest built, defended and occupied by a pair during the pre-laying period. Occupied nests were checked every 2 d during the laying period and every week during the incubating and chick-rearing period, using a mirror at the end of an 8 m fishing rod. We monitored proportions of birds that skipped

reproduction (no egg is laid by the pair in the occupied nest), dates of the first egg laid, clutch size (in this population, the clutch size is usually 2 eggs, with a range of 1 to 3 eggs) and breeding success (number of chicks per nest at the last nest check, between 3 August and 11 August). Chicks usually leave the nest 40 d after hatching (Roberts & Hatch 1993), in late August and early September. Loss of chicks resulted from a high predation by glaucous gulls *Larus hyperboreus* (Angelier et al. 2009).

Hormone levels and body condition

Kittiwakes were caught at their nest with a noose on the end of a 5 m fishing rod, during the pre-laying period in 2007 (21–30 May, N = 37), 2008 (20 May–15 June, N = 72), 2009 (19 May–16 June, N = 34), 2010 (20 May–13 June, N = 76) and 2011 (21 May–7 June, N = 110). Of the 329 captured kittiwakes, 34 were sampled in more than one year. Within 3 min after capture, blood samples (200 µl) were collected from the alar vein with a 1 ml heparinised syringe and a 25 gauge needle to assess baseline corticosterone levels (Romero & Reed 2005).

Within 6 h from sampling, blood samples were centrifuged and plasma was separated and stored at −20°C until subsequent analysis. Red blood cells were used for molecular sexing at the Centre d'Etudes Biologiques de Chizé (CEBC), as detailed in Weimerskirch et al. (2005). Plasma concentrations of corticosterone were determined by radioimmunoassay at the CEBC, as described in Lormée et al. (2003). The lowest detectable concentration for corticosterone was 0.5 ng ml^{-1}. Five assays (one assay per year) were performed. Intra- and inter-assay variations for corticosterone levels was within a range of 6–11% (N = 5 duplicates for intra-assay variation).

Following blood sampling, kittiwakes were weighed to the nearest 2 g using a Pesola spring balance and their skull length (head + bill) was measured to the nearest 0.1 mm with a caliper. Because male kittiwakes are larger than females (Moe et al. 2002), body condition was calculated from a standardized least-squares linear regression of body mass against head size for males and females separately.

Foraging trips

Before the onset of laying, we tracked pre-breeding males and females to determine foraging areas and maximum foraging range. We fitted individuals with a

miniaturized 7 g GPS data logger (Gipsy 3-Technosmart; flat antenna with a 250 mA battery; size = 41 × 14 × 7 mm; weight = 10 to 12 g) in 2008 (N = 6 males and 9 females), 2009 (N = 14 males and 7 females) and 2010 (N = 21 males and 12 females). Among 69 tracked kittiwakes, 3 were equipped during 2 consecutive years. The GPS was placed into a waterproof bag and attached to feathers on the bird's back using ©Tesa tape, a method successfully used for activity recorders and GPS devices in kittiwakes (Angelier et al. 2007a, Kotzerka et al. 2010). The logger's weight was about 4 % of the mass of the birds. Tagged birds generally returned to their nest immediately, or after a short (5 to 30 min) bath in the sea. The GPS device was removed 3 to 10 d after deployment, when the tracked bird returned to the nest. In this study, a foraging trip was considered to be a period outside the colony of more than 15 min at a distance from the nest >150 m (Angelier et al. 2007b). The GPS used had a circular error probability of 4 m for horizontal position (Weimerskirch et al. 2002). Because of low temperature during the pre-laying period, GPS recording was set at 5 min intervals, to save battery life. A blood sample was collected immediately after capture to assess corticosterone levels before GPS deployment.

A total of 261 trips were recorded; 224 trips were undertaken inside the fjord and 37 trips outside the fjord. A total of 78.07 ± 20.33 (mean ± SE) locations per trips were recorded. We calculated trip durations (minutes from first to last locations away from the colony site), and maximum foraging ranges (straight-line distance between the colony site and the most distant location of each central-place trip). Among these 261 trips, 9 trips were incomplete because the battery became depleted while the bird was at sea, especially in 2009 (6 incomplete trips). Hence, the trip duration and the maximum foraging range were underestimated for these incomplete trips. Note that because 2009 was characterized by unusually long trips, this underestimation makes our results more conservative. Location data were plotted with ArcView 10.1® (ESRI).

Statistical analyses

All statistical analyses were performed using R 2.15.2 (R Development Core Team 2012). We used generalised linear mixed models (GLMMs) with nest (for clustered data) or individual ID (for repeated sampling of the same individual) as a random effect. An information-theoretic approach was used to select the best models (Burnham & Anderson 2002).

Model selection criteria included the corrected version of Akaike's information criterion (AIC_c) for small sample sizes and the difference in AIC_c between each candidate model and the model with the lowest AIC_c value (ΔAIC_c; Burnham & Anderson 2002). AIC_c weight can be used as a measure of the relative probability of a model for being the best model with a given data set among other potential models. Selected models were then checked for assumptions, that is, constancy of variance and residual normality. Parameter estimates ± SE were given for models with the highest AIC_c weight and by removing interactions with covariables (Quinn & Keough 2002). Tukey's post-hoc tests were used on the selected GLMM to determine significant differences between years.

Table 1 summarises statistical hypotheses, including dependent and independent variables, sample size (N) and random effect of GLMMs. When a variable (laying date, body condition, corticosterone levels) varied among years (see 'Results'), we standardized this variable for each year, by subtracting its expected value (mean during the year t) and dividing the difference by its standard deviation during the year t.

Percentage of trips outside the fjord, trip durations outside the fjord and maximum foraging range outside the fjord, were analysed only for males since all trips of females, except one, were undertaken inside the fjord (see 'Results').

RESULTS

Breeding phenology and outputs

The laying date of the first egg differed significantly among years (Table 2A, Fig. 1A). Post hoc multiple comparisons using Tukey contrasts revealed a significantly earlier laying in 2010 compared to 2007, 2009 and 2011; significantly later laying in 2009 compared to 2007, 2008, 2010 and 2011; in 2007 compared to 2008 and 2011; and in 2011 compared to 2008 ($p < 0.042$ for post-hoc tests). The proportion of occupied nests with birds skipping reproduction differed significantly among years (Table 2B, Fig. 1B), with a significantly higher proportion in 2009 compared to 2008, 2010 and 2011 ($p < 0.008$ for post hoc tests). Clutch size differed significantly among years (Table 2C, Fig. 1C), with a significantly lower clutch size in 2009 compared to 2008, 2010 and 2011, and in 2007 compared to 2011 ($p < 0.006$ for post hoc tests). Breeding success differed significantly among years (Table 2D, Fig. 1D), with a significantly higher breeding failure in 2009 compared to 2007, 2010, 2011; in

Table 1. Biological assumptions tested and associated generalised linear mixed models (GLMMs) with kittiwake nest or individual ID as a random effect. Model selection was performed by a step down approach starting from the global model including all the independent variables. 'Metrics of foraging trip' is trip duration and maximum foraging range. 'Days before laying' is the number of days between sampling date and the median laying date for each year. 'Std LD' is the standardized laying date for each year, 'Std BC' is the standardized body condition for each year and 'Std Cort' is the standardized corticosterone levels for each year. N is the sample size

Dependent variable	Independent variables	Random effect of the GLMMs	N
Laying date	Year	Nest	411
Breeding decision	Year	Nest	473
Clutch size	Year, Std LD	Nest	410
Breeding success	Year, Std LD	Nest	374
Percentage of trips outside the fjord (males only)	Year	Individual ID	162
Metrics of foraging trip inside the fjord	Year, Sex, Year × Sex	Individual ID	224
Metrics of foraging trip outside the fjord	Year	Individual ID	37
Metrics of foraging trip inside the fjord	Year, Sex, Breeding status, Year × Breeding status, Sex × Breeding status	Individual ID	184
Percentage of trips outside the fjord (males only)	Year, Breeding status, Year × Breeding status	Individual ID	136
Metrics of foraging trip outside the fjord	Year, Breeding status, Year × Breeding status	Individual ID	31
Metrics of foraging trip inside the fjord	Year, Sex, Std LD, Year × Std LD, Sex × Std LD	Individual ID	157
Metrics of foraging trip outside the fjord	Year, Std LD, Year × Std LD	Individual ID	29
Percentage of trips outside the fjord (males only)	Year, Std LD, Year × Std LD	Individual ID	122
Body condition	Days before laying, Year, Sex, Sex × Year	Individual ID	282
Corticosterone (log-transformed)	Days before laying, Year, Sex, Std BC, Sex × Year, Sex × Std BC	Individual ID	284
Metrics of foraging trip inside the fjord	Year, Sex, Std Cort, Year × Std Cort, Sex × Std Cort	Individual ID	200
Metrics of foraging trip outside the fjord	Year, Std Cort, Year × Std Cort	Individual ID	34
Breeding decision	Year, Sex, Std Cort, Year × Std Cort, Sex × Std Cort	Individual ID	278
Breeding decision	Year, Sex, Std BC, Year × Std BC, Sex × Std BC	Individual ID	282
Laying date	Year, Sex, Std Cort, Year × Std Cort, Sex × Std Cort	Individual ID	189
Laying date	Year, Sex, Std BC, Sex × Std BC, Year × Std BC	Individual ID	194

2007 compared to 2010 and 2011 and a significantly higher breeding success in 2008 compared to 2010 and 2011 (p < 0.014 for post hoc tests). Moreover, clutch size and breeding success significantly decreased in nests with delayed laying, after taking into account the year effect (Table 2C,D).

Foraging trips

Table 3 summarises metrics of pre-laying foraging trips over 3 consecutive years. Only one female undertook a trip outside the fjord (Fig. 2). In contrast, males foraged inside and outside the fjord, using both neritic and pelagic waters (Fig. 2), but they foraged significantly more inside the fjord in 2008 compared to 2009 and 2010 (p < 0.011 for post hoc tests, Tables 3 & 4A). When performing offshore trips, males always used deep (2000–3000 m) oceanic waters, west of Svalbard, at the Greenland-Svalbard ridge (Fig. 2). Percentage of trips outside the fjord did not differ between breeders and non-breeders (Table 4B), but were related to the laying date in a 'bad' year (Table 4C). Specifically, kittiwakes that bred

later in the season foraged significantly less outside the fjord in 2009 (−23.06 ± 8.86, estimate ± SE), but this relationship was not observed in 2008 (15.56 ± 13.44) or in 2010 (6.24 ± 5.00).

When considering trips undertaken inside the fjord, trip durations differed among years (Tables 3 & 5A), with significantly longer trips in 2009 compared to 2010 (p = 0.002 for post hoc tests). Durations of trips inside the fjord did not vary between sexes, nor with breeding status or individual laying date (Table 5). When considering trips undertaken outside the fjord, trip durations differed between years, with longer trips in 2009 compared to 2008 (p = 0.032) and 2010 (p = 0.052, Table 5D). Durations of trips outside the fjord were not affected by breeding status and laying date (Table 5E,F).

When considering trips undertaken inside the fjord system, maximum foraging ranges were higher in males than in females and were significantly lower in 2010 than in 2008 and 2009 (p < 0.007 for post hoc tests, Tables 3 & 6A). Moreover maximum ranges inside the fjord differed significantly between breeders and non-breeders in an interaction with sex (Table 6B): female non-breeders stayed closer to the

Table 2. Model selection using corrected version of Akaike's information criterion (AIC_c) to explain kittiwake (A) laying date, (B) breeding decision, as a function of year (from 2007 to 2011), (C) clutch size, and (D) breeding success as a function of year (from 2007 to 2011) and standardized laying date for each year (Std LD), using GLMMs with nests as a random effect. Models with AIC_c weight less than 10% are not presented. K refers to the number of parameters and N to the sample size. **Bold** indicates the model with the best AIC_c

No.	Model	K	N	ΔAIC_c	AIC_c weight (%)
A. Laying date					
A1	**Year**	**5**	**411**	**0**	**99.99**
B. Breeding decision					
B1	**Year**	**5**	**473**	**0**	**99.95**
C. Clutch size					
C1	**Year + Std LD**	**6**	**410**	**0**	**99.99**
D. Breeding success					
D1	**Year + Std LD**	**3**	**374**	**0**	**88**
D2	Year	2	374	4.02	11.99

colony than female breeders, whereas male breeders stayed closer to the colony than male non-breeders, when foraging inside the fjord. Moreover, maximum ranges inside the fjord increased in kittiwakes breeding later in the season, especially in 2009 (1.35 ± 0.33, Table 6C). When considering trips undertaken outside the fjord, maximum foraging range was significantly higher in 2009 compared to 2008 and 2010 (Tables 3 & 6D, $p < 0.039$ for post hoc tests). In 2008, pre-laying foraging areas were situated 66–184 km at the Svalbard shelf break (Fig. 2A). In 2009, males were heading south of Svalbard along the deep oceanic Greenland-Svalbard ridge, some birds foraging as far as the Bear Island area, some 600 km south of the colony (Fig. 2B). In 2010, as in 2008, some males travelled directly 75–160 km west of Svalbard whereas others also foraged around Bear Island, 400–755 km south of the colony as observed in 2009 (Fig. 2C). Maximum foraging range of trips outside the fjord was significantly higher in non-breeders than in breeders (Table 6E, Fig. 2), but was not associated with laying date (Table 6F).
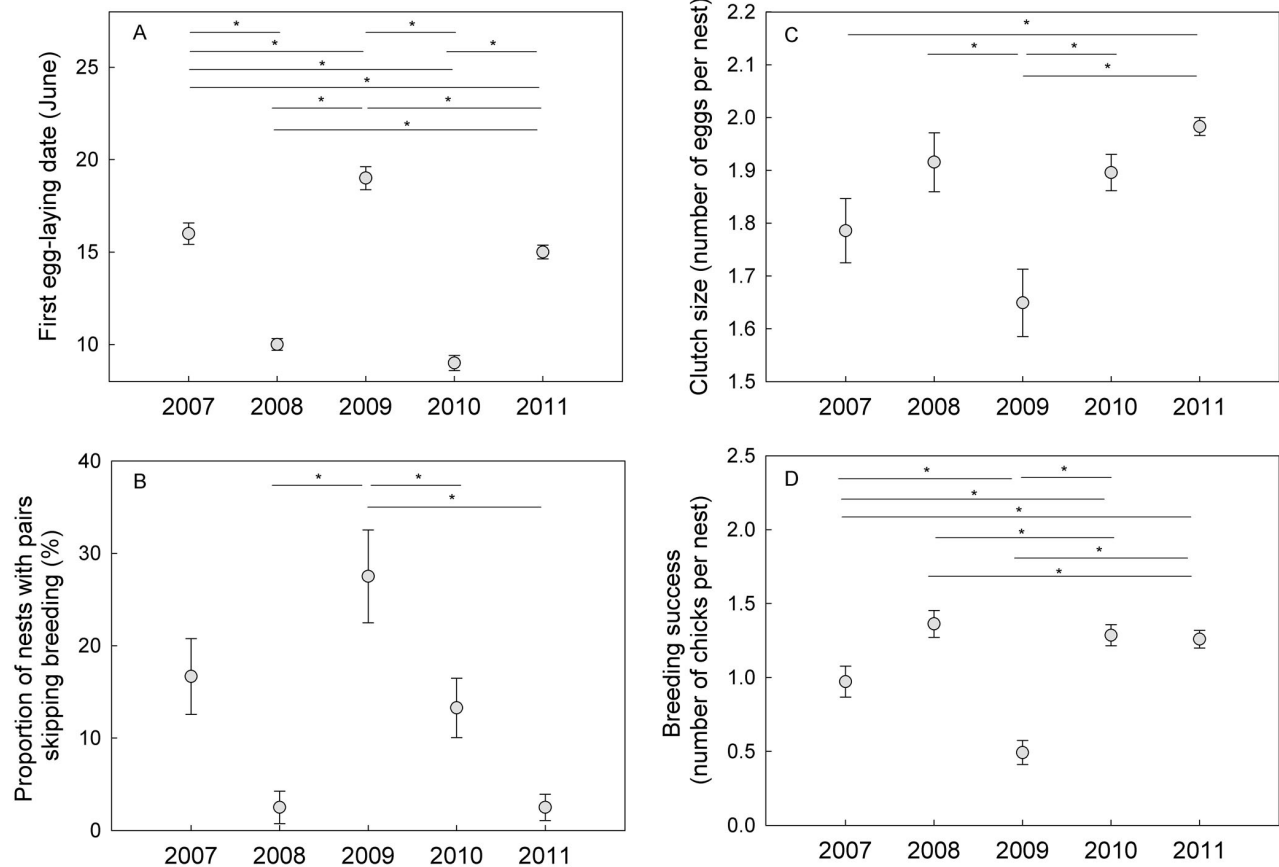

Fig. 1. *Rissa tridactyla.* Annual comparison (from 2007 to 2011) of (A) laying date of the first egg in June, (B) proportions of kittiwakes skipping reproduction (%), (C) clutch size per occupied nest and (D) breeding success per occupied nest. Means and SE are represented. The symbol '*' denotes significant differences between 2 years, using Tukey's post-hoc tests

Table 3. *Rissa tridactyla*. Metrics (mean and SE) of foraging trips of male and female kittiwakes during the 2008, 2009 and 2010 pre-laying periods

	Year	Males			Females		
		N	Mean	SE	N	Mean	SE
Percentage of trips outside the fjord	2008	16	50.00	12.91	46	0.00	0.00
	2009	33	15.15	6.34	13	0.00	0.00
	2010	113	21.24	3.86	40	2.50	2.50
Trip duration inside the fjord (h)	2008	8	2.79	0.65	46	3.01	0.65
	2009	28	11.04	6.74	13	3.54	0.82
	2010	89	1.07	0.19	39	0.57	0.07
Trip duration outside the fjord (h)	2008	8	8.15	2.88	0	–	–
	2009	5	58.57	26.20	0	–	–
	2010	24	18.34	3.74	1	43.84	–
Maximum foraging range inside the fjord (km)	2008	8	4.87	1.38	46	1.72	0.56
	2009	28	4.44	0.85	13	1.50	0.76
	2010	89	1.63	0.29	39	0.53	0.13
Maximum foraging range outside the fjord (km)	2008	8	103.39	36.55	0	–	–
	2009	5	326.27	145.91	0	–	–
	2010	24	153.86	3141	1	299.56	–

Body condition and corticosterone levels

Pre-laying body condition differed significantly among years (Table 7), with significantly higher body condition in 2010 compared to 2007 (p = 0.032 for post hoc test, Fig. 3A). Days before laying did not influence body condition (Table 7). Corticosterone levels were not related to sex and days before laying but differed significantly among years (Table 8, Fig. 3B), with lower levels in 2010 compared to 2008, 2009 and 2011 (p < 0.014 for post hoc tests). Moreover, corticosterone levels slightly increased with increasing body condition (0.06 ± 0.04, Table 8).

The percentage of trips outside the fjord was not related to standardized corticosterone levels for each year (Std Cort) measured before GPS deployment, even when considering an interaction effect with years (Table 9A). Trip durations for trips inside the fjord were related to Std Cort in an interaction with years (Table 9B): kittiwakes bearing lower levels of Std Cort in 2009 stayed longer inside the fjord (−32 801.34 ± 27 262.67), but this relationship was not detected in 2008 (−2186.75 ± 3623.34) and 2010 (578.72 ± 839.85). When considering only trips outside the fjord, trip durations increased with increasing Std Cort (Table 9C, 46 275.92 ± 23737.58). Maximum foraging ranges were not related to Std Cort, when considering trips inside and outside the fjord (Tables 9D,E).

At the individual level, breeding decision and laying date were not related to standardized corticoster-

one levels, even when considering an effect for sex and year (Table 10). However, standardized body condition influenced breeding decision in an interaction with sex: kittiwakes in good pre-laying body condition did breed compared to kittiwakes in poor body condition in females (0.12 ± 0.04), but not in males (−0.01 ± 0.04). In both sexes, kittiwakes in good pre-laying body condition bred earlier than kittiwakes in poor body condition (−0.79 ± 0.30).

DISCUSSION

By combining stress physiology and biologging, the present study investigated the possible mechanisms underlying annual differences in breeding phenology and the associated variation in reproductive decisions in response to environmental fluctuations. Significant annual variation was detected in the number of birds skipping reproduction, in the timing of breeding, in clutch size and in breeding success. Our study confirms that, at the individual level, late breeding is associated with poor breeding success and reduced clutch size. The use of miniaturized GPS loggers revealed substantial annual variation in the duration and foraging ranges of pre-laying kittiwakes and highlighted sex-specific differences in foraging strategies. Corticosterone levels differed among years, and were the lowest in the year of earliest breeding. Trip duration, but not maximum foraging range, was positively related to corticosterone
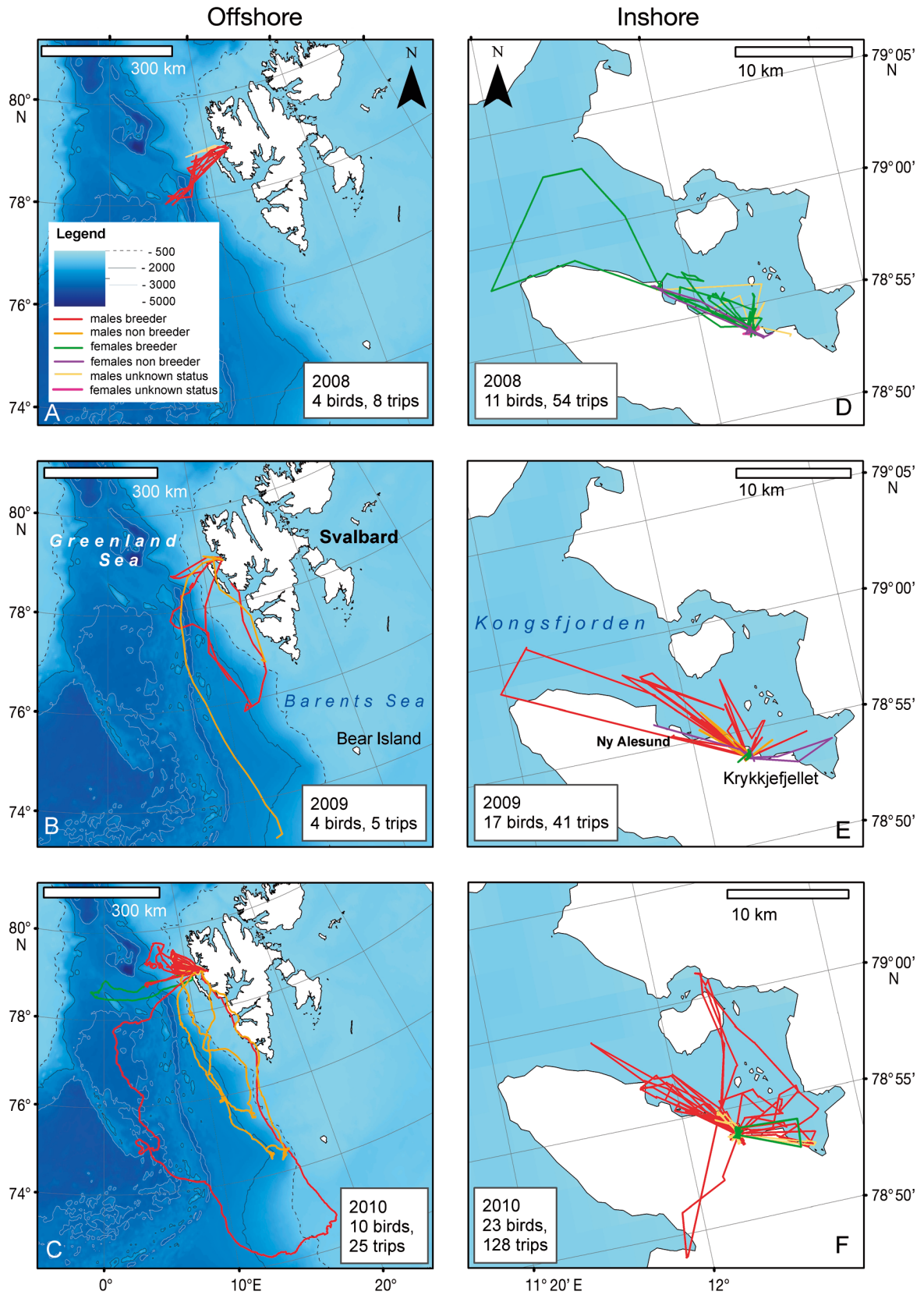
Fig. 2. *Rissa tridactyla.* Foraging tracks of pre-laying kittiwakes conducted outside (A to C) or inside (D to F) the fjord during the 2008 (A & D), 2009 (B & E) and 2010 (C & F) pre-laying periods

Table 4. Model selection using corrected version of Akaike's information criterion (AIC_c) to explain percentage of trips outside the fjord of kittiwake males as a function of (A) year (from 2008 to 2010), (B) year, breeding status and the interaction year × breeding, (C) year, standardized laying date (Std LD) and the interaction year × Std LD, using GLMMs with individual as a random effect. The null model was also tested. Models with AIC_c weight less than 10% are not presented. K refers to the number of parameters and N to the sample size. **Bold** indicates the model with the best AIC_c

	No.	Model	K	N	ΔAIC_c	AIC_c weight (%)
A.	A1	**Year**	**3**	**162**	**0**	**99.36**
B.	B1	**Year**	**3**	**136**	**0**	**69.00**
	B2	Year + Breeding status	4	136	1.94	26.14
C.	C1	**Year + Std LD + Year × Std LD**	**6**	**122**	**0**	**52.36**
	C2	Year	3	122	1.18	28.98
	C3	Year + Std LD	4	122	2.21	17.38

Table 5. Model selection using corrected version of Akaike's information criterion (AIC_c) to explain duration of kittiwake trips inside the fjord as a function of year (from 2008 to 2010), (A) sex and the interaction year × sex; (B) year, sex, breeding status and the interaction year × breeding and sex × breeding; (C) year, sex, standardized laying date (Std LD) and the interaction year × Std LD and sex × Std LD, using GLMMs with individual as a random effect. Duration of trips outside the fjord (males only) were explained as a function of (D) year; (E) year, breeding status and the interaction year × breeding; (F) year, standardized laying date (Std LD) and the interaction year × Std LD. The null model was also tested. Models with AIC_c weight less than 10% are not presented. K refers to the number of parameters and N to the sample size. **Bold** indicates the model with the best AIC_c

No.	Model	K	N	ΔAIC_c	AIC_c weight (%)
A. Trip duration inside the fjord					
A1	**Year**	**3**	**224**	**0**	**54.50**
A2	Sex + Year	4	224	1.18	30.17
A3	Sex + Year + Sex × Year	6	224	3.13	11.37
B. Trip duration inside the fjord					
B1	**Year**	**3**	**184**	**0**	**30.61**
B2	Year + Breeding status	4	184	0.24	27.20
B3	Sex + Year	4	184	1.87	12.00
C. Trip duration inside the fjord					
C1	**Year**	**3**	**157**	**0**	**41.85**
C2	Sex + Year	4	157	1.81	16.87
C3	Year + Std LD	4	157	1.89	16.30
D. Trip duration outside the fjord (males only)					
D1	**Year**	**3**	**37**	**0**	**69.71**
D2	Intercept	1	37	1.67	30.29
E. Trip duration outside the fjord (males only)					
E1	**Year**	**3**	**31**	**0**	**32.14**
E2	Year + Breeding status	4	31	0.36	26.91
E3	Intercept	1	31	0.57	24.14
E4	Breeding status	2	31	1.30	16.81
F. Trip duration outside the fjord (males only)					
F1	**Year**	**3**	**29**	**0**	**41.35**
F2	Intercept	1	29	0.86	26.88
F3	Std LD	2	29	1.59	18.64
F4	Year + Std LD	4	29	2.29	13.14

levels. However the decision to breed and laying date were not related to corticosterone levels of individuals.

Breeding phenology and reproductive performance

Breeding phenology varied greatly during the course of this study, with an interval of 10 d between the earliest (in 2010) and the latest (in 2009) median laying date. This is in agreement with a long-term study (1970–2008) of the same population, which reported large year to year variation in hatching dates in relation to oceanographic parameters (Moe et al. 2009). In addition, the proportion of birds that bred, clutch size and breeding success were lower in 2009 compared to the other years; therefore, we defined 2009 as a 'bad' year. In this high Arctic population of kittiwakes, late years are known to be associated with a reduced clutch size and poor reproductive performance (Moe et al. 2009). At the individual level, we showed that late breeders laid smaller clutches and had lower breeding success than early breeders.

Foraging strategies, sex differences and annual variations

The foraging trips of pre-laying male and female kittiwakes were tracked during 3 consecutive years using GPS devices. We defined a foraging trip as a GPS-tracked movement lasting more than 15 min and at a distance from the nest >150 m (Angelier et al. 2007b). However, some trips, especially those undertaken inside the fjord, may have included other activities, such as maintenance or roosting. We could not quantify the time spent engaged in these other activities with our GPS devices. Foraging strategies greatly differed between males and females. Although all but one of the tracked

Table 6. Model selection using corrected version of Akaike's information criterion (AIC_c) to explain maximum foraging range of kittiwake trips inside the fjord as a function of year (from 2008 to 2010), (A) sex and the interaction year × sex; (B) year, sex, breeding status and the interaction year × breeding and sex × breeding; (C) year, sex, standardized laying date (Std LD) and the interaction year × Std LD and sex × Std LD (all trips: C, trips outside the fjord: F), using GLMMs with individual as a random effect. Maximum foraging range outside the fjord (males only) were explained as a function of (D) year; (E) year, breeding status and the interaction year × breeding; (F) year, standardized laying date (Std LD) and the interaction year × Std LD. The null model was also tested. Models with AIC_c weight less than 10% are not presented. K refers to the number of parameters and N to the sample size. **Bold** indicates the model with the best AIC_c

No.	Model	K	N	ΔAIC_c	AIC_c weight (%)
	A. Maximum foraging range inside the fjord				
A1	**Sex + Year**	**4**	**224**	**0**	**54.73**
A2	Sex + Year + Sex × Year	6	224	0.43	44.11
	B. Maximum foraging range inside the fjord				
B1	**Sex + Year + Breeding status + Sex × Breeding status**	**6**	**184**	**0**	**41.31**
B2	Sex + Year + Breeding status	5	184	1.45	19.99
B3	Year	3	184	2.25	13.40
	C. Maximum foraging range inside the fjord				
C1	**Year + Std LD + Year × Std LD**	**6**	**157**	**0**	**45.71**
C2	Sex + Year + Std LD + Year × Std LD	7	157	0.42	37.06
C3	Sex + Year + Std LD + Sex × Std LD + Year × Std LD	8	157	2.52	12.94
	D. Maximum foraging range outside the fjord (males only)				
D1	**Year**	**3**	**37**	**0**	**73.30**
D2	Intercept	1	37	2.02	26.70
	E. Maximum foraging range outside the fjord (males only)				
E1	**Year + Breeding status**	**4**	**31**	**0**	**71.16**
E2	Breeding status	2	31	3.23	14.18
	F. Maximum foraging range outside the fjord (males only)				
F1	**Year**	**3**	**29**	**0**	**60.73**
F2	Year + Std LD	4	29	2.59	16.64
F3	Intercept	1	29	3.08	13.01

female kittiwakes stayed inside the fjord, males foraged both inside and outside the fjord and reached very distant foraging areas. The longest trips lasted 9 d and the farthest point during a trip was located at 755 km from the colony. The deployment of geolocators (GLS) has also revealed long pre-breeding movements in brown skuas *Catharacta lonnbergi* from Bird Island, South Georgia (Phillips et al. 2007), and in male kittiwakes breeding on the Isle of May, southeast Scotland (Bogdanova et al. 2011). This strong male bias toward long-distance foraging trips may seem surprising, as pre-laying females need to acquire resources for egg formation, while males defend the nest site. Why did female kittiwakes not forage in pelagic waters, as males did, before laying? One possible explanation is that male larids, including kittiwakes, often provision their mates as a form of courtship feeding behaviour (Kempenaers et al. 2007). As males have to forage for themselves and for their mates, they may be constrained to undertake

long-distance foraging trips to highly productive feeding areas. In fact, during their trips outside the fjord, males appeared to favour the very deep (2000–3000 m) water of the Greenland-Svalbard ridge, and never used the shallow waters of the Barents Sea, even when foraging south of the Bear Island area. In contrast, females could content themselves with courtship feeding and prey obtained inside Kongsfjorden. This sex difference in foraging strategy during the pre-laying period contrasts with other studies of kittiwakes in the Pacific (Jodice et al. 2006, Paredes et al. 2012), which reported longer distance trips in females compared to males during the chick-rearing period. This raises the possibility that sex-differences in foraging behaviour vary according to the breeding stage and localities.

Foraging strategies changed dramatically from year to year. The percentage of trips outside the fjord was much higher in 2008 than in 2009 and 2010, whereas trip duration and maximum foraging range outside

Table 7. Model selection using corrected version of Akaike's information criterion (AIC$_c$) to explain kittiwake body condition as a function of days before laying, year (from 2007 to 2011), sex and the interactions sex × year, using GLMMs with individual as a random effect. The null model was also tested. Models with AIC$_c$ weight less than 10% were not presented. K refers to the number of parameters and N to the sample size. **Bold** indicates the model with the best AIC$_c$

No.	Model	K	N	ΔAIC$_c$	AIC$_c$ weight (%)
1	**Year**	**5**	**282**	**0**	**24.28**
2	Days before laying + Year	6	282	0.46	19.27
3	Intercept	1	282	0.64	17.64
4	Days before laying + Year + Sex + Sex × Year	2	282	1.51	11.41
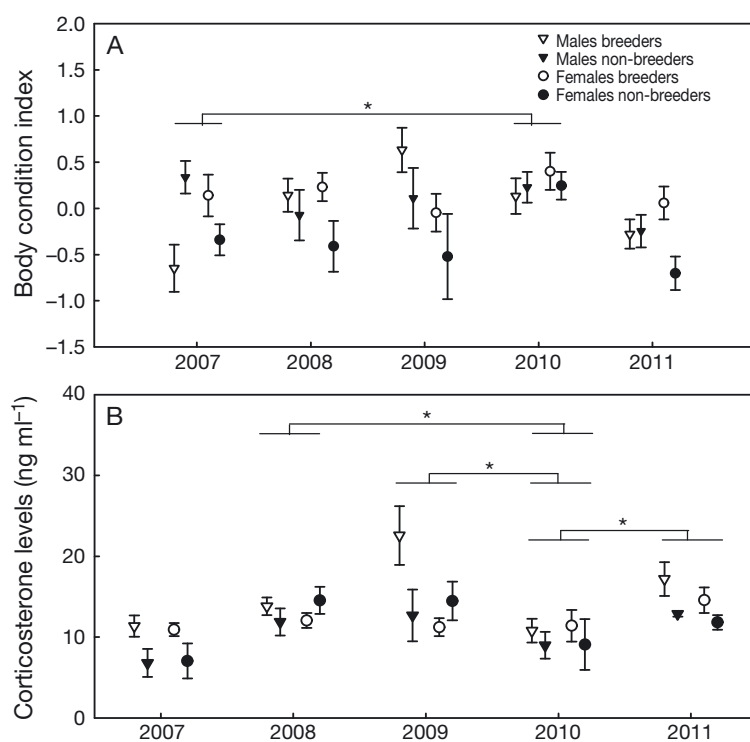
Fig. 3. *Rissa tridactyla.* Annual comparison (from 2007 to 2011) of pre-laying (A) body condition and (B) baseline corticosterone levels of males (triangles) and females (circles) that bred (open symbol) or that did not breed (filled symbol). Means and SE are represented. The symbol '*' denotes significant differences between 2 years, using Tukey's post-hoc tests

the fjord were the highest in 2009. Our results suggest food scarcity in 2009, and more abundant food available close to the colony in 2008 (about 100 km). Trip duration and maximum foraging range of all trips were the lowest in 2010, supporting the hypothesis that an early year was characterized by short-distance and short-duration foraging movements. When considering trips outside the fjord, maximum foraging range, but not trip duration, was significantly higher in non-breeders than in breeders. This

result supports the hypothesis that non-breeders were less constrained by energetic costs and time, or were less efficient at locating prey than breeders. Finally, kittiwakes breeding earlier foraged more outside the fjord than kittiwakes breeding later in the season in 2009, but not in 2008 and 2010, but maximum ranges inside the fjord increased in kittiwakes breeding later in the season. It is conceivable that a high search efficiency within a wide foraging range would be associated with early breeding. More years of GPS-tracking are needed to validate this annual shift in foraging strategies, and to understand the difference in foraging strategies between breeders and non-breeders and in relation to the timing of breeding.

Body condition, corticosterone levels and annual variations

Body condition and corticosterone levels were not related to the number of days elapsed between capture and laying. Hence, the annual differences in body condition and corticosterone levels were not due to variation in the timing of data collection. Contrary to previous studies (Kitaysky et al. 1999), in this study of black-legged kittiwakes, corticosterone levels slightly increased with increasing body condition. Elevated corticosterone has been often associated with poor energetic status (e.g. Astheimer et al. 1992). Elevated corticosterone levels can trigger the re-allocation of energy from pre-laying activities (nest building, nest defence, courtship feeding) towards self-maintenance, especially during environmental perturbations. Thus, this may explain the positive correlation found between corticosterone and body condition. This hypothesis is supported by Angelier et al. (2007b) who showed that an experimental increase of corticosterone levels in male kittiwakes promoted self-foraging and mass gain. It is likely that relationships between corticosterone and body condition are complex, non-linear and environment-dependant (Lanctot et al. 2003, Schultner et al. 2013).

Body condition differed between years, and was higher in 2010 compared to 2007; corticosterone levels also differed greatly among years, with significantly lower levels in 2010 compared to 2008,

Table 8. Model selection using corrected version of Akaike's information criterion (AIC_c) to explain kittiwake baseline corticosterone levels as a function of days before laying, year (from 2007 to 2011), sex, standardised body condition for each year (Std BC) and the interactions sex × year and sex × Std BC, using GLMMs with individual as a random effect. The null model was also tested. Models with AIC_c weight less than 10% are not presented. K refers to the number of parameters and N to the sample size. Corticosterone levels were log-transformed prior to analysis. **Bold** indicates the model with the best AIC_c

No.	Model	K	N	ΔAIC_c	AIC_c weight (%)
1	**Year + Std BC**	**6**	**284**	**0**	**37.32**
2	Year + Sex + Std BC	7	284	1.07	21.88
3	Year	5	284	1.26	19.90
4	Year + Sex	6	284	2.42	11.12

2009 and 2011. As kittiwakes undertook short-distance and short-duration foraging trips in 2010, this result supports the hypothesis that corticosterone levels reflect energetic state and sustained foraging activities in seabirds (Kitaysky et al. 2001, 2007 Angelier et al. 2007a,b, Benowitz-Fredericks et al. 2008), and that the 'good' 2010 pre-laying period (early laying date and high breeding success) was characterized by high body condition and low corticosterone levels. However and contrary to our expectations, high corticosterone levels and low body condition were not apparent during the 'bad' 2009 pre-laying period, when kittiwakes undertook longer and farther foraging trips. This lack of significance could be attributed to our relatively small sample size (only 8 male breeders sampled in 2009), but also to other sources of physiological stress, such as predation risk; to social interactions or to age and quality of individuals (Wingfield et al. 1998, Goutte et al. 2010a). Younger individuals, with potentially higher corticosterone levels (Goutte et al. 2010a), could have been less present at the colony during 'bad' years and, thus, were less sampled than older individuals. It is also likely that relationships between regional environmental conditions, corticosterone and reproductive outputs can differ according to local oceanographic features (Satterthwaite et al. 2012).

Corticosterone levels did not differ between males and females, although males undertook much longer and further trips than females. During the pre-laying period, previous study has shown strong sex-differences in the functional role of corticosterone levels on physiological regulations and on life-history traits in kittiwakes (Goutte et al. 2010b) and the present study also highlights that sex-differences in pre-laying foraging strategies were not paralleled by sex-difference in corticosterone release.

Table 9. Model selection using corrected version of Akaike's information criterion (AIC_c) to explain metrics of kittiwake foraging trips as a function of year (from 2008 to 2010), baseline corticosterone levels before the GPS deployment and standardized for each year (Std Cort) and the interaction year × Std Cort (for A, C & D), or as a function of year, sex, Std Cort and the interaction year × Std Cort and sex × Std Cort (for B & D) with individual as a random effect. The null model was also tested. Models with AIC_c weight less than 10% are not presented. K refers to the number of parameters and N to the sample size. **Bold** indicates the model with the best AIC_c

No.	Model	K	N	ΔAIC_c	AIC_c weight (%)
A. Percentage of trips outside the fjord (males only)					
A1	**Year**	**3**	**34**	**0.00**	**69.66**
A2	Year + Std Cort	4	34	1.98	25.95
B. Trip duration inside the fjord					
B1	**Year + Sex + Std Cort + Year × Std Cort**	**7**	**200**	**0**	**52.36**
B2	Sex + Year + Std Cort	5	200	1.70	22.32
B3	Year + Sex + Std Cort + Year × Std Cort + Sex × Std Cort	8	200	2.06	18.72
B4	Year + Sex + Std Cort + Sex × Std Cort	6	200	2.22	17.24
C. Trip duration outside the fjord (males only)					
C1	**Year + Std Cort**	**4**	**34**	**0**	**55.13**
C2	Year	3	34	0.77	37.48
D. Maximum foraging range inside the fjord					
D1	**Year + Sex**	**4**	**200**	**0**	**52.36**
D2	Year + Sex + Std Cort	5	200	1.85	20.73
E. Maximum foraging range outside the fjord (males only)					
E1	**Year**	**3**	**34**	**0**	**66.47**
E2	Year + Std Cort	4	34	1.48	31.69

Table 10. Model selection using corrected version of Akaike's information criterion (AIC_c) to explain kittiwake (A, B) breeding decision and (C, D) laying dates as a function of year (from 2007 to 2011), sex, and standardized baseline corticosterone levels for each year (Std Cort, A, C) or standardized body condition for each year (Std BC, B, D) and the interactions sex × Std Cort/BC and year × Std Cort/BC, using GLMMs with individual as a random effect. Models with AIC_c weight less than 10% are not presented. K refers to the number of parameters and N to the sample size. **Bold** indicates the model with the best AIC_c

No.	Model	K	N	ΔAIC_c	AIC_c weight (%)
	A. Breeding decision				
1	**Year**	**5**	**278**	**0**	**49.92**
2	Year + Std Cort	6	278	1.40	24.76
3	Year + Sex + Std Cort + Sex × Std BC	8	278	3.21	10.05
	B. Breeding decision				
1	**Year + Sex + Std BC + Sex × Std BC**	**8**	**282**	**0**	**48.98**
2	Year + Sex + Std BC + Year × Std BC + Sex × Std BC	12	282	1.19	27.01
3	Year + Std BC	6	282	2.98	11.01
	C. Laying date				
1	**Year**	**5**	**189**	**0**	**21.22**
2	Year + Std Cort	6	189	0.28	18.47
3	Year + Sex + Std Cort	7	189	0.36	17.68
4	Year + Sex + Std Cort + Sex × Std Cort	8	189	0.89	13.58
5	Year + Std Cort + Year × Std Cort	10	189	1.00	12.86
6	Year + Sex + Std Cort + Year × Std Cort	11	189	1.46	10.24
	D. Laying date				
1	**Year + Std BC**	**6**	**194**	**0**	**48.96**
2	Year **+** Sex × Std BC + Sex × Std BC	8	194	0.09	34.69
3	Year + Sex + Std BC	7	194	1.32	25.30

Corticosterone levels and foraging decisions

At the individual level, the percentage of trips undertaken outside the fjord and the maximum foraging range were not related to corticosterone levels measured before GPS deployment. Kittiwakes exhibiting lower corticosterone levels stayed longer inside the fjord in 2009, but not in 2008 and 2010, whereas trip durations outside the fjord increased with increasing corticosterone levels. As movements inside the fjord and close to the colony may have included other activities, such as roosting, it would be difficult to discuss the negative relationship be-tween those movements and corticosterone levels. Concerning foraging trips outside the fjord, elevated corticosterone level before a foraging trip may have facilitated an increase of foraging-related locomotor activity (reviewed in Wingfield et al. 1998) and forag-ing activities (Kitaysky et al. 2001, Breuner & Hahn 2003, Angelier et al. 2007a,b), thereby allowing kitti-wakes to spend more time at sea. In that respect, an experimental increase of corticosterone levels in macaroni penguins *Eudyptes chrysolophus* was asso-ciated with significantly higher levels of foraging and diving activity (Crossin et al. 2012). In wandering albatrosses *Diomedea exulans*, the level of cortico-sterone before a foraging trip is positively linked to daily distance travelled and maximum range at sea but not to time spent at sea (Angelier et al. 2007a). Hence, our findings support the idea that corticoster-one regulates the time and the metabolic demands associated with foraging activities (Bonier et al. 2009, 2011, Crossin et al. 2012).

Body condition, corticosterone levels and breeding decisions

At the individual level, our multi-year study high-lighted the effects of poor body condition on the decision to skip breeding in females, and on delayed laying in both sexes. In this population, the effect of pre-laying body condition on laying date was pre-viously detected in 2008 (Goutte et al. 2010b). Our findings support the general idea that seabirds need pre-breeding energy reserves to start breeding (Chastel et al. 1995). Previous studies have shown that elevated pre-laying corticosterone levels were associated with the decision of females to skip breed-ing (Salvante & Williams 2003, Goutte et al. 2010a, Vitousek et al. 2010), and especially in female kitti-wakes during the 2008 year (Goutte et al. 2010b). In

our multi-year study, the effect of corticosterone levels on breeding decision was not consistent, suggesting that this relationship could be environment-dependent or that other endocrine mechanisms may occur in the mediation of breeding decision. As LH levels and sex-steroids were not systematically measured in years other than 2008, we could not test an effect of these hormones on breeding decision and laying date in this study.

Laying dates were not related to corticosterone levels at the individual level and during the 5 consecutive years. Similarly in 2008, we did not detect a relationship between corticosterone levels and laying date in kittiwakes (Goutte et al. 2010b). However, the experimental reduction of corticosterone levels triggered earlier breeding in female kittiwakes but not in males (Goutte et al. 2011). A previous study on other seabird species highlights that males and females with higher corticosterone levels bred later (Goutte et al. 2010a). It has been proposed that the functional action of corticosterone levels on the timing of breeding could be environment-dependent: in female Florida scrub-jays *Aphelocoma coerulescens*, the effect of corticosterone on the first laying date was observed only during years of harsh environmental conditions (Schoech et al. 2009). This hypothesis was not supported in kittiwakes by our study since we did not find any relationship between corticosterone levels and laying date, even during the 'bad' 2009 year. This suggests that complex proximate mechanisms, including corticosterone secretion and body condition, may interact during the pre-breeding period for mediating breeding phenology in response to environmental fluctuations.

In association with other studies (Kotzerka et al. 2010, Paredes et al. 2012), our findings highlight that kittiwakes breeding in the Atlantic and Pacific are highly flexible, since they may use various foraging areas (coastal and oceanic waters) during the breeding season. In contrast, most kittiwakes breeding in various parts of the Atlantic range spend the winter in the West Atlantic, between Newfoundland and the Mid-Atlantic Ridge, including in offshore, deep-water areas (Frederiksen et al. 2012). Moreover, our kittiwake population is highly dependent on the oceanic, deep-waters areas between Greenland and Svalbard. Environmental perturbations, such as overfishing or oil spill in this area, may thus raise some serious threats to the viability of this population. A multi-colony GPS-tracking would reveal whether this oceanic area is also important for other kittiwake populations nesting in the North Atlantic.

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