When things go wrong:
intra-season dynamics of breeding failure in a seabird

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Abstract.   During breeding, long-lived species face important time and energy constraints that can lead to breeding failure when food becomes scarce. Despite the potential implications of intra-season dynamics in breeding failure for individual behavior, carry-over effects, dispersal decisions and population dynamics, little information is currently available on these dynamics at fine temporal scales. Here, we monitored the foraging behavior and the proportion of successful black-legged kittiwake pairs from nest construction to chick fledging in a colony of the southern Barents Sea, to relate foraging effort to the dynamics of breeding failure over an entire breeding season, and to infer the environmental conditions leading to this failure. Specifically, we tracked kittiwakes with GPS and satellite tags during incubation and early chick-rearing to document nest attendance, foraging range, time budgets and daily energy expenditures (DEE). We also monitored diet changes over time. We predicted that breeding failure would follow a non-linear trend characterized by a break point after which breeding success would drop abruptly and would be related to a substantial increase in foraging effort. Kittiwakes showed contrasting foraging patterns between incubation and chick-rearing: they extended their foraging range from 20 km during incubation to more than 450 km during chick-rearing and switched diet. They also increased their DEE and readjusted their time budgets by increasing time spent at sea. These changes corresponded to a break point in breeding dynamics beyond which the proportion of successful pairs abruptly dropped. At the end of the season, less than 10% of kittiwake pairs raised chicks in the monitored plots. This integrative study confirms that breeding failure is a non-linear process characterized by a threshold beyond which individuals face an energetic trade-off and cannot simultaneously sustain high reproductive and self-maintenance efforts. In this way, the occurrence of sudden environmental changes complicates our ability to predict population dynamics and poses conservation challenges.

Key words: breeding success; energetic trade-off; environmental change; food availability; GPS and satellite tracking; maximum working capacity; reproductive costs; *Rissa tridactyla*.

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Introduction

In long-lived species, life-history theory predicts that individuals maximize their lifetime fitness by balancing their current investment in reproduction with their probability of survival to the next breeding season (Williams 1966). In this way, parents are expected to invest a fixed amount of time and energy into reproduction to maximize the survival probability of their young, without compromising their own survival (Stearns 1992). In the marine environment, the distribution, abundance and availability of prey species fluctuate in space and time and these factors have been suggested to shape seabird life history strategies (Lack 1968). In particular, seabirds have developed highly flexible foraging strategies in response to food resource variability (Burger and Piatt 1990, Erikstad et al. 1998, Shaffer et al. 2003, Harding et al. 2007). However, climate change is likely to alter oceanographic processes and trophic interactions in marine ecosystems (Durant et al. 2005, Hoegh-Guldberg and Bruno 2010), which may contribute to spatial and/or temporal mismatches between the timing of peak energetic requirements of apex marine predators and availability of their prey (Suryan et al. 2006, Durant et al. 2007, Grémillet et al. 2008). Moreover, fishery pressure may have strong impacts on marine prey stocks (Jackson et al. 2001), which in turn can affect seabird life history traits including reproductive performance (Cury et al. 2011). Consequently, assessing foraging flexibility appears as a prerequisite to understanding seabird resilience to short-term variability in food availability, and to evaluate its consequences on population persistence.

It is well known that seabirds can compensate for local food depletion by intensifying their search effort on foraging grounds and/or increasing their foraging range (Zador and Piatt 1999, Suryan et al. 2000, Burke and Davoren 2009) or by switching prey (Croxall et al. 1999, Suryan et al. 2002, Pichegru et al. 2007). Nonetheless, as central place foragers, their time and effort at sea often remain constrained by the need to return regularly to their colony during the breeding season for nest defense, incubation duties and

chick-rearing (Orians and Pearson 1979). Consequently, they cannot indefinitely increase their foraging effort for both chick and self-provisioning (the 'prudent parent hypothesis', Drent and Daan 1980) and are expected to respond in a non-linear way to food resource variability (Cairns 1987). As long as food supplies are sufficiently abundant to cover both reproductive and self-maintenance costs, breeding success is expected to follow an asymptotic trend but when prey abundance decreases, breeding success is thought to rapidly decline (Cairns 1987, Piatt et al. 2007). Recently, Cury et al. (2011) confirmed this non-linear relationship using fourteen seabird species living in seven different marine ecosystems. They demonstrated that above a threshold of one-third of the maximum prey biomass, seabird breeding success was high and reached a plateau, whereas below this threshold, it was consistently reduced and variable. This multi-species study was among the first to highlight the strong non-linear relationship between seabird breeding failure and food depletion at large spatial and temporal scales.

At a finer temporal scale, breeding failure has been identified as a crucial factor driving individual responses to environmental changes. It has notably been shown to affect mate retention and inter-annual site fidelity (Dubois and Cézilly 2002, Naves et al. 2006, Boulinier et al. 2008, Pakanen et al. 2011), migratory movements to wintering grounds (Bogdanova et al. 2011, Hoye et al. 2012) and potentially individual behavior and time budgets. It can also affect population structure and dynamics in the long-term through dispersal (Danchin et al. 1998, Cam et al. 2004). Nevertheless, relatively little is known on how the foraging efforts of birds within a season condition the temporal dynamics of breeding failure in a colony. Such knowledge is important as it can inform us about (1) how seabirds respond to energetic constraints due to both reproductive costs and food variability and (2) how these constraints lead to breeding failure.

Black-legged kittiwakes *Rissa tridactyla* (hereafter kittiwakes) are small surface-feeding gulls that are very sensitive to variations in food availability because they often rely on only a
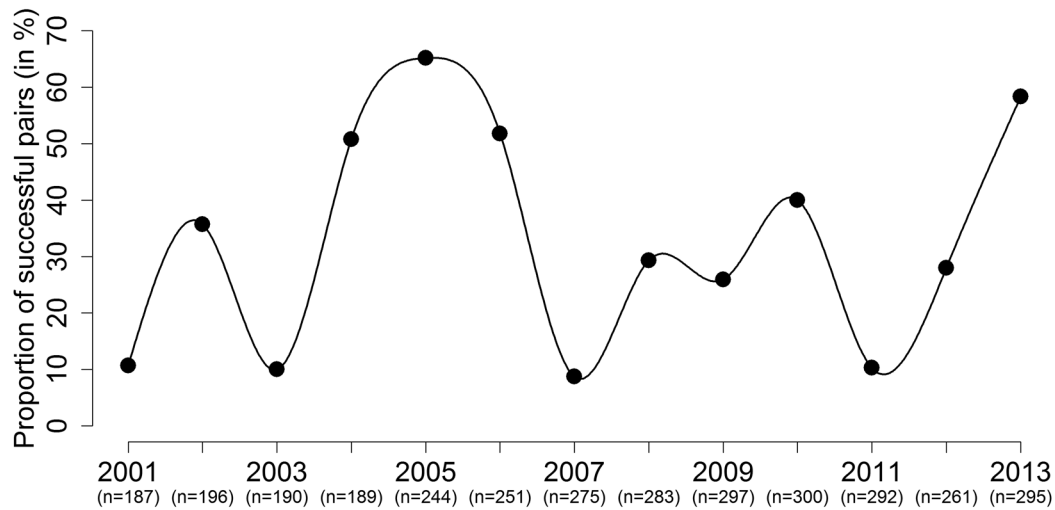
Fig. 1. Proportion of successful pairs of kittiwakes in a large monitored cliff of Hornøya from 2001 to 2013, with n representing the number of constructed nests for each breeding season.

few prey species (Barrett and Krasnov 1996, Lewis et al. 2001) and have a limited capacity to switch to alternative prey due to their surface-feeding habits (Furness and Tasker 2000, Suryan et al. 2000). The monitoring of foraging trips via land-based surveys and, more recently, the use of miniaturized electronic tracking devices, have shown that kittiwake foraging ranges vary according to colony location and food availability, but is generally between 20-60 km (Furness and Barrett 1985, Hamer et al. 1993, Suryan et al. 2000, Daunt et al. 2002, Ainley et al. 2003, Kotzerka et al. 2010, Paredes et al. 2012) and several studies examining the inter-annual variability of kittiwake breeding performance revealed that breeding failure is common when food conditions are poor (Alaska: Suryan et al. 2006; Newfoundland, Canada: Regehr and Montevecchi 1997, Carscadden et al. 2002; North Sea: Frederiksen et al. 2005; Barents Sea: Barrett and Krasnov 1996, Barrett 2007). However, such inter-annual studies do not give insights into the intra-season dynamics of breeding failure and its underlying mechanisms.

In the recent past, extensive breeding failures have repeatedly occurred in the kittiwake colony of Hornøya, Southern Barents Sea (Fig. 1), and they have been suspected to be associated with spatial shifts in local food availability (Barrett 2007). In this integrative study, we investigated foraging effort in relation to the dynamics of natural breeding failure in the kittiwake colony of Hornøya to explain how, why and when breeding failure occurs within a single breeding season. For this purpose, (1) the proportion of successful kittiwake pairs was monitored from nest construction to chick fledging (or to egg/chick loss), (2) breeding kittiwakes were tracked with GPS and Platform Terminal Transmitters (PTTs) during incubation and chick-rearing to estimate individual foraging range, time budget and energetic expenditures, which are good indicators of local food availability (Cairns 1987, Suryan et al. 2002, Piatt et al. 2007) and (3) regurgitates were collected to reconstruct kittiwake diet throughout the breeding season. We tested the hypothesis that significant changes in seabird foraging behavior and energy expenditure, potentially due to changes in food availability, would lead kittiwakes to extensive breeding failure. We predicted that breeding failure would follow a non-linear trend characterized by a break point after which breeding success would drop abruptly and that it would be related to a substantial increase in foraging effort.

METHODS

The study was conducted during the 2011 breeding season, from 26 April to 18 July on the island of Hornøya (70°23′ N, 31°09′ E), Southern

Barents Sea, where ca. 9000 pairs of kittiwakes nested in 2011 (Barrett, *unpublished data*). Kittiwakes from this colony feed primarily on capelin *Mallotus villosus* and Atlantic herring *Clupea harengus* (Furness and Barrett 1985, Barrett 2007). It seems, however, that capelin is the preferred prey. When it becomes unavailable, kittiwakes can switch to Atlantic herring and other items such as crustaceans (Barrett and Krasnov 1996, Barrett 2007), but this diet change is often negatively correlated with breeding success (Barrett 2007).

Monitoring of kittiwake breeding performance

Three sectors of the breeding colony, each composed of 4 to 7 pre-defined cliff sections (representing a total of 1191 constructed nest sites), were monitored once every three days. For each nest site, we recorded the building date, which corresponded to the day when the nest had a clear central depression within a platform of new material. We then monitored nest content at a distance using binoculars until chicks were at least 30 days-old. On a given day, a nest was considered successful if the kittiwake pair was observed incubating or rearing one or more chicks. As soon as a nest was empty (no egg or chick), the pair was considered in failure, unless it laid a replacement clutch, in which case it was considered successful again. The proportion of successful nests among those constructed within each sector was recorded at each observation day from 22 May throughout the season in order to track temporal changes in the proportion of pairs in success.

GPS and satellite tracking deployment

During incubation, from 24 May to 2 June, nine randomly chosen breeding kittiwakes from the same cliff (six females and three males) were color-ringed and equipped with 12 g MiniGPS-100 loggers (Earth & Ocean Technologies, Germany) programmed with a position acquisition frequency of 4 minutes. Individuals were captured and recaptured using a noose pole or a noose trap set on their nest and sex was determined based on behaviour and head and bill length. The loggers were attached to the lower back feathers of the birds with TESA tape. Of the nine birds equipped, eight were successfully recaptured 10 to 35 days later to retrieve the GPS loggers. All these birds were actively breeding at retrieval.

As the first two weeks of chick-rearing are crucial for chick survival (Suryan et al. 2002), we also tracked birds during this period, from 26 June to 3 July. Thirty GPS loggers were deployed in several cliffs on individual birds that were raising at least one 5–10 day old chick. To attain a higher temporal accuracy, position acquisition frequency was decreased to every 1 or 2 minutes. One week later, 28 GPS loggers were retrieved, but only six recorded complete trips with regular successive locations (two females and four males). Chicks from these six successfully tracked birds starved to death just before or after retrieval, lying dead on the nest.

Additionally, 9.5 g solar-paneled PTT-100 (Microwave Telemetry, USA) programmed with a duty-cycle 10 h on/48 h off were deployed on three breeders experimentally put in failure (two males, one female) 24 h after device deployment. These birds were primarily tracked to address different questions on habitat selection and prospecting behavior (see Ponchon et al. 2013), but they add relevant information to our understanding of foraging range and the behavior of failed breeders over the course of a breeding season, and so are included in the present study.

Time-budgets and energetics from GPS data

To calculate individual time-budgets, each GPS location was characterized by an activity based on speed, distance to the colony and position (on nest, on land or at sea). A trip was defined as all successive positions located further than 70 m from the nest (corresponding to the length of the cliff) and for a minimum duration of 20 min. Speed had a clear bimodal distribution, so birds were considered as resting or flying when speed was respectively lower or higher than 10 km·h^{-1} (see Grémillet et al. 2004 for details). Active foraging activities, characterized by high sinuosity index (Grémillet et al. 2004), were associated with flight energy expenditures, as these two activities have similar energy demands (Jodice et al. 2003, Enstipp et al. 2006).

Individual DEE were estimated from a time-energy budget analysis, with reference values for resting and flying activities taken from Enstipp et al. (2006). Specifically, DEE was calculated for each individual and for the whole period (total

DEE divided by the duration of tracking), which included nest attendance and trips. Then, for chick-rearing birds, DEE was calculated for each trip. Depending on duration and maximal distance to the colony, trips were assigned to "long" or "short" trips and DEE was averaged for each individual and then, for each category (Table 1). Individual Basal Metabolic Rates (BMR) for incubation and chick-rearing were calculated from Bech et al. (1999) to estimate the sustainable metabolic scope of the tracked birds (Drent and Daan 1980).

Diet samples from adults and chicks

Diet was determined from regurgitates of adults captured during incubation (N = 19) and of both adults and chicks during chick-rearing (N = 19) but was not sampled from birds equipped with GPS. Each regurgitate was collected in an individual plastic bag, labelled and stored at −20°C. On return to the laboratory, each sample was thawed, weighed to the nearest 0.1 g and a preliminary identification to the lowest possible taxonomic level of the remains was conducted. The samples were then further digested in a saturated solution of biological washing powder (Biotex) in an oven at 50°C for at least 24 h. The remaining hard parts (herring pro-otic bullae, otoliths, scales and vertebrae) were identified using Breiby (1985), Härkönen (1986), Watt et al. (1997) and a reference collection. Otoliths were often extracted from the undigested skulls of fish or found floating free in the sample and used in the final identification of the food remains. The taxonomic composition of each load was determined by the estimated mass (%) of each taxon. The mean diet composition (% of mass) was calculated separately for incubation and chick-rearing using Swanson et al. (1974) aggregated percentage method within five-day periods, with each period being weighted equally and averaged.

Data analysis and statistics

Satellite data were stored and managed with Satellite Tracking and Analysis Tool (STAT, Coyne and Godley 2005) and were filtered with the *argosfilter* package (Freitas 2010). Only locations corresponding to the breeding period, from 25 May to 22 July were selected for analysis. Movements from both GPS and satellite tracking were illustrated using ArcView GIS 9.3.1. To test the power of our sample size for incubation, we performed a home-range area analysis which indicated the total cumulative home range area reached a plateau when five individuals were considered, and that our sample size was therefore representative (Appendix A).

All statistical analyses were done using R 2.14.1 (R Development Core Team 2011) and results are shown as mean ± SD. Breeding parameters were analyzed at the sector level using a beta regression with the *betareg* package (Cribari-Neto and Zeilis 2010). A broken stick-model was used to test whether the proportion of successful pairs dropped suddenly during the season after day T. To estimate T, we used a profile likelihood approach: the likelihood for the model was computed for each date spanning the study period. The value of T that minimized the likelihood was thus evaluated, and an approximate confidence interval was computed with a likelihood ratio test with one df (Appendix B). Finally, conditional on the structural break T, we tested whether there was any interaction between sector and date. Models were compared with the Akaike information criterion (AIC) and the one with the smallest AIC was retained. Trip duration and maximal distance to the nest were analyzed jointly using mixture models fitted with JAGS (Plummer 2003). We used mixture models to test and identify meaningful clusters reflecting different kinds of foraging trips (for example long versus short trips). The numbers of clusters were selected with an information theoretic criterion, the Approximate Weight of Evidence (AWE; Fruhwirth-Schnatter and Pyne 2010). See Appendix C for further details on model and prior specifications. In all models, bird identity was included as a random effect. Sex was tested as a fixed effect but no difference was found between males and females, notably because of small sample sizes. As such, males and females were pooled.

RESULTS

Dynamics of kittiwake breeding performance over the season

From the profile likelihood approach, we identified a break point in breeding success on 19 June (CI: 8 June–25 June; Fig. 2; Appendix B), a
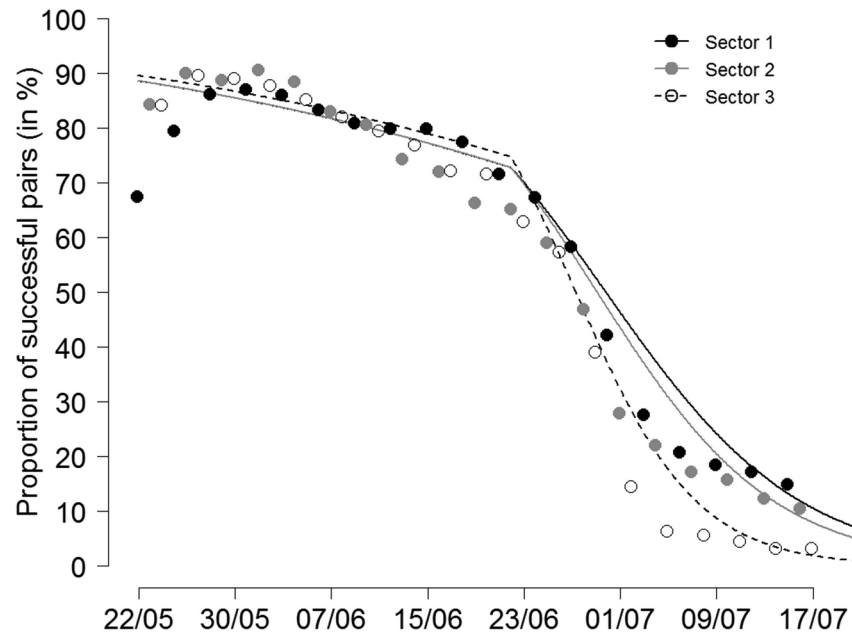
Fig. 2. Proportion of successful kittiwake pairs over the breeding season 2011 in three colony sectors on Hornøya, Southern Barents Sea. Points represent raw data whereas solid and dashed lines represent data modeled with a beta-regression.

date at which ca. 70% of the monitored pairs had one or more chicks ≥1 day old. Before this day, the proportion of successful pairs was greater than 80% and all three sectors exhibited the same trend with a mean decrease of −0.9% every 3 days. After 19 June, the decrease in the three sectors steepened, with Sector 3 decreasing significantly faster (−5.3% every 3 days) than Sectors 1 and 2 (−3.1% and −3.4% every 3 days, respectively). At the end of the season, in late July, the trend stabilized to reach a total final breeding success of 8.7 ± 4.4% (Fig. 2). Among the three sectors, Sector 3 had the lowest proportion of successful pairs, with only 3.1% of pairs fledging at least one chick.

Foraging effort over the breeding season

During egg incubation, 178 trips from eight birds were recorded over a maximum period of 7.3 days. The birds performed on average 4.0 ± 1.3 trips·day^{-1}. Trips were relatively short, both in distance and duration (Fig. 3a). The maximum average distance from the colony was 18.1 ± 1.0 km. The mean distance from the colony during a trip was 4.0 ± 1.3 km and the mean trip duration was 3.0 ± 1.0 h.

Three to four weeks later, during early chick-rearing, 29 trips from six birds were recorded for a maximum period of 3.4 days. During this period, birds performed fewer trips per day (1.6 ± 1.1) and trips were more heterogeneous in distance and duration. On the one hand, they performed very short trips, lasting on average 42 ± 30 min during which time they mainly rested on Hornøya, but away from their nest. On the other hand, each bird tracked performed one very extensive trip, lasting 39.0 ± 17.5 h for a maximum average distance of 370.9 ± 106.2 km (Fig. 3b). Incomplete trips recorded in six other successful individuals which GPS failed tracking positions continuously revealed that these individuals also travelled as far as 450 km to reach their foraging ground (Appendix D).

The mixture model discriminated three types of trips, based on trip duration and maximal distance from the nest (Fig. 4). It confirmed that foraging effort differed significantly between incubation and chick-rearing. The first group contained spatially reduced trips that were weakly correlated to trip duration ($r^2 = 0.3$). The second group included the majority of incubation trips; trip duration and maximal
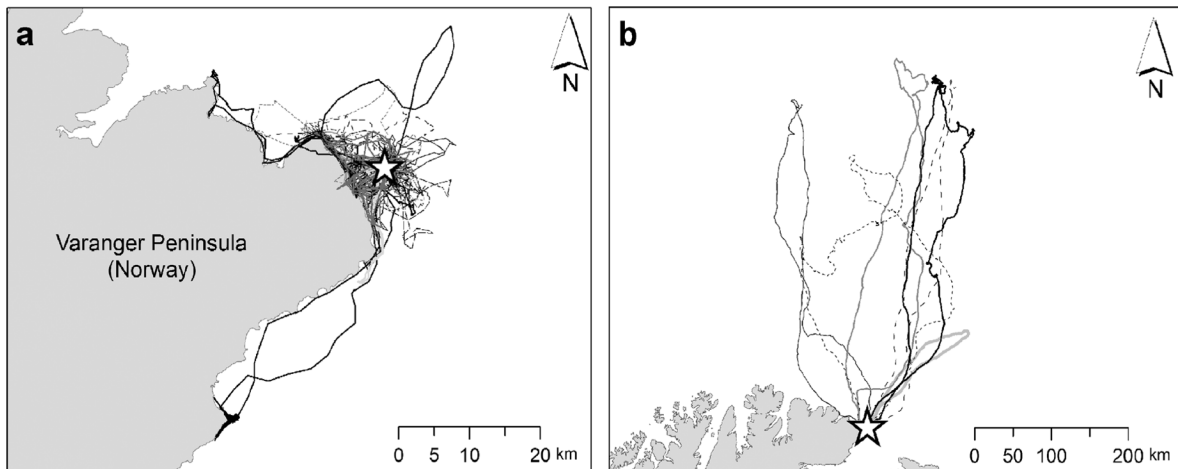
Fig. 3. Foraging trips recorded with GPS loggers from kittiwake breeders nesting on Hornøya (white star) during (a) incubation (n = 8 individuals) (b) early chick-rearing (n = 6 individuals).

distance were strongly correlated ($r^2 = 0.7$). The last group was only composed of chick-rearing trips, which were very long in both distance and time.

Despite their breeding failure during incubation, birds equipped with PTTs exhibited the same foraging strategies as successful breeders tracked with GPS and returned regularly to their nest. During the incubation period, they remained at maximum distance of 14.6 ± 12.9 km from the colony. From 15 June onward, they progressively started to travel further north. They performed the same extensive trips as individuals tracked with GPS during early chick-rearing and reached a maximal distance of 853 km in mid-July (Fig. 5; Appendix D).

Energetics and time budgets

Birds exhibited different time budgets over the season. They attended their nest significantly less during chick-rearing (26.1 ± 13.0%) than during incubation (45.7 ± 5.5%; GLMM: p < 0.001) and they did not spend the same amount of time resting and flying (Fig. 6). During incubation, or when on short trips during chick-rearing, birds spent on average 30% of their time flying/foraging and between 15% and 44% resting at sea. This latter activity represented 32% of long trips during chick-rearing. Time spent flying/foraging increased from 30% to 70% and resting on land almost completely disappeared.

Along with time budgets, individual DEE increased significantly between the two periods (incubation: 662.9 ± 59.1 kJ·day^{-1} vs. chick-rearing: 897.3 ± 88.9 kJ·day^{-1}; t-test: $t = -5.60$; df = 8.2; p < 0.001) and the highest DEE value was found for long trips performed during chick-rearing (1131.8 ± 118.8 kJ·day^{-1}; Table 1). Consequently, whereas sustainable metabolic rates were about 2 × BMR during incubation and during short trips of chick-rearing birds, these rates increased to 4 × BMR during long trips of chick-rearing birds.

Diet over the breeding season

There was a strong shift in the kittiwake diet between the incubation and chick-rearing periods (Table 2). Capelin was the most common food item consumed by kittiwakes during incubation, accounting for 81.2% of the diet. During chick-rearing, capelin was still present but represented only 26.2% of prey mass. Conversely, whereas Atlantic herring and fish offal were almost absent from kittiwake diets during incubation, their proportion reached respectively 36.7% and 16.0% during chick-rearing.

Discussion

Even if inter-annual breeding success has been related to environmental variables in numerous seabird species (e.g., Croxall et al. 2002, Pinaud and Weimerskirch 2002, Inchausti et al. 2003, Frederiksen et al. 2005), surprisingly, little infor-
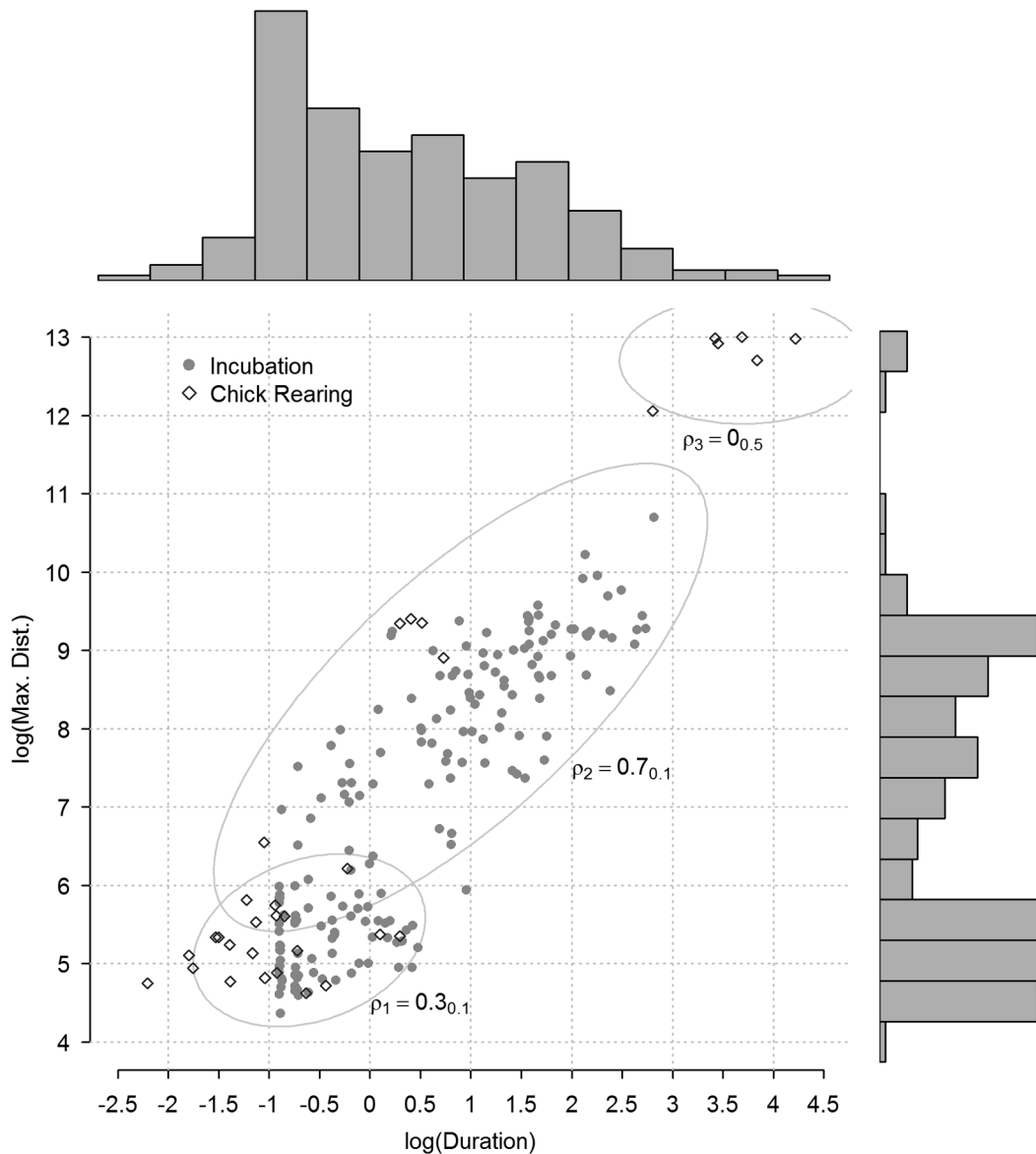
Fig. 4. Relationship between log maximum distance to the nest and log trip duration for all the trips recorded during incubation (filled circles) and early chick-rearing (open circles). ρ_1, ρ_2 and ρ_3 represent the correlation coefficient for each of the three different groups discriminated with the mixture model, with their standard error.

mation is available on the dynamics and mechanisms of breeding failure within breeding seasons (but see Lewis et al. 2001). On Hornøya in 2011, the dynamics of kittiwake breeding failure over a single breeding season was accurately described as a non-linear trend characterized by a decisive break point after which the proportion of successful pairs abruptly dropped. Extensive foraging trips of several

hundred kilometers were also recorded during the chick-rearing period, far beyond the maximum foraging range previously estimated in this species (Daunt et al. 2002). Combining the results obtained on kittiwake foraging effort, energetics and breeding performance, we infer the causes and mechanisms of breeding failure and discuss the implications that breeding failure may have on population dynamics.
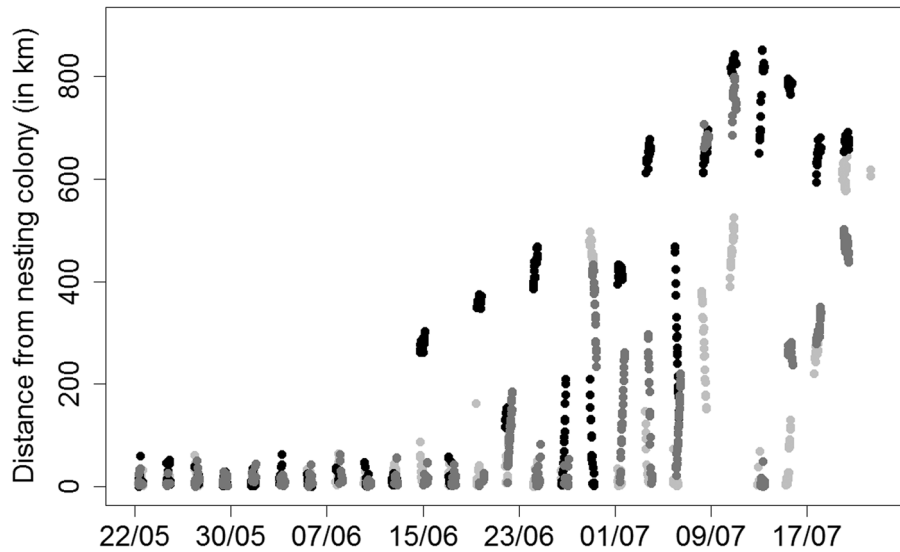
Fig. 5. Distance from the nesting colony of Hornøya recorded over the breeding season from three kittiwake breeders (black, light grey and dark grey) tracked with PTTs and put in failure just after deployment of the devices. The points correspond to locations recorded for 10 h every 48 h.

Evidence of a shift in capelin distribution and availability

Incubation and chick-rearing represent two breeding stages differing in energy demands. During incubation, seabirds only have to respond to their own energy requirements whereas after hatching, parents have to maintain both chick and self-provisioning. Increases in foraging
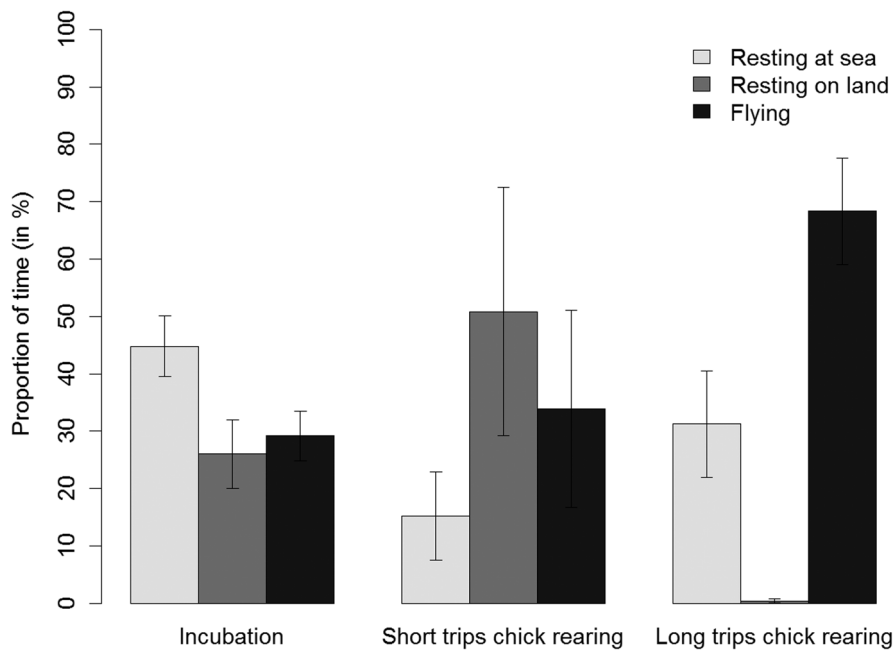

Fig. 6. Mean proportion of time spent in different activities away from the nest for kittiwake breeders tracked with GPS loggers.

Table 1. Daily energy expenditures (mean ± SD) calculated from GPS data by incubating (N = 8 individuals) and chick-rearing adults (N = 6 individuals). BMR, basal metabolic rate.

| Energy expenditure | Incubation | Chick-rearing | | |
		Total period	Short trips	Long trips
Energy budgets (kJ·day^{-1})	662.9 ± 59.1 (569.3–766.9)	897.3 ± 88.9 (775.7–993.1)	517.1 ± 45.7 (457.4–575.8)	1131.8 ± 118.8 (1004.4–1273.9)
Sustainable metabolic scope	2.0 ± 0.2 × BMR (1.8–2.4 × BMR)	3.4±0.3 × BMR (3.1–3.8)	2.0 ± 0.2 × BMR (1.8–2.5 × BMR)	4.2 ± 0.4 × BMR (3.8–4.8 × BMR)

range and energy expenditures could be interpreted as a natural response of birds facing higher energy demands (Ricklefs 1983) or taking advantage of high levels of food resources (Jodice et al. 2006, Welcker et al. 2009). However, the sudden shift observed in kittiwake diet from capelin to Atlantic herring concomitant to the steep decline in breeding success strongly suggests a spatial shift in capelin distribution and availability. Unfortunately, no independent data on coastal fish distribution and abundance are available during the kittiwake breeding period. During incubation, the high nest attendance levels, short foraging range and high proportion of capelin in diet samples indicate that kittiwakes had access to sufficient amounts of capelin around the colony and that they were able to invest energy in the laying and incubation of eggs. During chick-rearing, kittiwakes increased travel distances 15-fold to reach their foraging ground at the same time as proportion of capelin in the diet dropped.

In kittiwakes, an increase in foraging range and changes in prey selection are often associated with changes in food availability around the colony (Barrett and Krasnov 1996, Suryan et al. 2000, Suryan et al. 2002). Moreover, for kittiwakes nesting in the Southern Barents Sea, a

Table 2. Mass proportion of prey ingested by breeding kittiwakes during incubation (5–20 June; N = 19) and chick-rearing (22 June–5 July; N = 19). Samples for chick-rearing also include chick diets.

Prey ingested	End of incubation	Early chick-rearing
Capelin (Mallotus villosus)	81.2	26.2
Atlantic herring (Clupea harengus)	6.1	36.7
Fish offal	0	16
Gadidae	0	6.2
Sandeels (Ammodytes ssp.)	0	0.2
Unidentified fish	12.7	14.8

switch from capelin to Atlantic herring can reflect a decrease of capelin availability and results in a reduction of kittiwake breeding success (Barrett 2007). In our study, the proportion of successful pairs dropped over a relatively short period (2–3 weeks) and the final breeding success was among the lowest measured in the study colony over the preceding years (Fig. 1). Such a short-term spatial change may be explained by the specific hydrodynamic conditions of the southern Barents Sea (Loeng and Drinkwater 2007). This region, which is an important spawning, nursery and feeding area for capelin, is highly influenced by Atlantic water inflow. During warm years, Atlantic inflow is stronger and displaces capelin northwards, towards the Polar Front (Gjøsæter 1998). 2011 was such a warm year (Matishov et al. 2012) and the Atlantic inflow may have triggered a spatial shift in the distribution of capelin. Kittiwakes may have tracked capelin distribution far north but they ultimately had to switch to alternative prey, probably because capelin became less abundant, less accessible at the surface or too far from the colony.

Foraging effort and consequences for chick provisioning

The very long trips recorded during chick-rearing might be assimilated to self-provisioning trips, as those observed in various seabird species exhibiting bimodal foraging strategies during the same breeding stage (Chaurand and Weimerskirch 1994, Saraux et al. 2011 and references therein). This specific foraging strategy normally allows parents to alternate between extensive trips to replenish their own reserves and short trips to frequently feed their chicks. Yet, the proportion of extensive trips can be modulated according to food conditions and parental body condition (Steen et al. 2007, Saraux et al. 2011). Therefore, we hypothesize that adult kittiwakes

had a bimodal foraging strategy around hatching, but that the disappearance of capelin around the colony forced them to rapidly increase the proportion of long trips, thus finally suppressing short foraging trips dedicated to chick provisioning. At this time, most of chicks were around 5 days old, an age when they are the most vulnerable to food depletion. Chicks younger than 15 days cannot be fed large amounts of prey due to poor digestive and storage capacities (Suryan et al. 2002) and parents need to return regularly to the nest to sustain high meal delivery rates to the chicks. In 2011, it is therefore likely that parents could not compensate for low food availability around the colony and the majority of chicks starved to death. Although predation (e.g., Regehr and Montevecchi 1997) or the presence of nest parasites (Gasparini et al. 2001) may amplify breeding failure and explain some variation among colony sectors in overall breeding success, frequent observations of dead chicks on the nests suggest that food depletion was the main cause of breeding failure during our study.

Mechanisms of breeding failure: evidence for a behavioral and energetic threshold

The break point observed in the dynamics of breeding failure suggests that kittiwakes crossed a threshold beyond which they stopped investing in reproduction, leading to extensive chick mortality. First, in response to local food depletion, adults increased their foraging effort and readjusted their time-budgets and DEE. On one hand, they frequently left their nest for short periods during which they rested away from their nest, probably to reduce energy expenditure (Table 1) and avoid continuous chick begging. On the other hand, they optimized foraging search by suppressing on-land rest, considerably reducing nest attendance and travelling very far to reach their foraging areas. The only constant activity between breeding stages and trips was resting at-sea, accounting for at least 15% of individual time budgets. This could represent an uncompressible time needed by the birds while at sea to digest and assimilate prey (Hilton et al. 2000, Ropert-Coudert et al. 2004), and to recover from the high energy costs of flight and avoid overheating (Grémillet et al. 2012). Similarly, DEE increased substantially, from 663 kJ·day^{-1} during incubation to more than 1000 kJ·day^{-1} during long trips of early chick-rearing. These values are slightly higher than those estimated by previous studies for the same periods and the same species using the doubly labelled water method (Welcker et al. 2010 and references therein) but they seem reliable, especially if we assume that the breeding season was a very unfavorable year (Welcker et al. 2010; Fig. 1). Moreover, the sustainable metabolic scope calculated for each individual during long trips was just above the maximum of $4 \times$ BMR formulated by Drent and Daan (1980), confirming the possible existence of an intrinsic energetic ceiling, as already suggested by Welcker et al. (2010). This ceiling may have prevented kittiwakes from allocating more energy to reproduction, constraining them to choose between their own survival and that of their chicks (Williams 1966). Therefore, breeding failure may not have been induced directly by the potential shift in prey availability itself, but by the physiological limits imposed by increased foraging effort which jeopardized chick survival.

From single breeding failure to population dynamics

As breeding failure seems to occur regularly in the study colony (Fig. 1), we can question the impact of such regular breeding failures on population dynamics in the long-term. A single extensive breeding failure is thought to have a limited impact on seabird population dynamics, as it is adult survival that primarily drives population persistence (Stearns 1976). However, if extensive breeding failures occur regularly in the same colony, demographic processes might be affected by a direct decrease in the recruitment of young breeders. Likewise, for surviving chicks, adverse early-life conditions can have a far-reaching impact on their long-term fitness, notably via nutritional deficits, slower growth, chronic secretion of stress hormones, or decreased learning abilities, which may also affect recruitment probabilities (Lindström 1999, Cam et al. 2003, Kitaysky et al. 2006).

Extensive breeding failure can also have an indirect, but immediate, effect on population dynamics via dispersal events. Most seabirds are highly philopatric but the probability of breeding in the same colony the following year has been shown to depend on individual and conspecific breeding performance (Danchin et al. 1998, Boulinier et al. 2008). When seabirds fail among

failed conspecifics, their probability to disperse to more suitable colonies is higher (e.g., Danchin et al. 1998, Cam et al. 2004, Boulinier et al. 2008), but when birds fail late in the season, nest site fidelity the following year is favored over emigration (Danchin et al. 1998). Therefore, in addition to inter-annual variability in breeding failure among colonies, variability in the timing of breeding failure within years, due to factors such as intra-seasonal changes in food availability, may play a crucial role in conditioning dispersal decisions and immigration.

The consequences of breeding failure on population dynamics are diverse and the interactions of environmental, social and individual factors at several temporal and spatial scales are likely to affect the behavioral and physiological responses of individuals. Identifying when species reach their maximum energetic capacity and when they fail is important for conservation purposes (Cury et al. 2011), but also for a better understanding of dispersal patterns among colonies and within colony population dynamics (Grémillet and Boulinier 2009, Ponchon et al. 2013). Further studies integrating foraging effort, breeding performance and food resource dynamics at both intra-seasonal and inter-annual temporal scales are thus needed.

Acknowledgments

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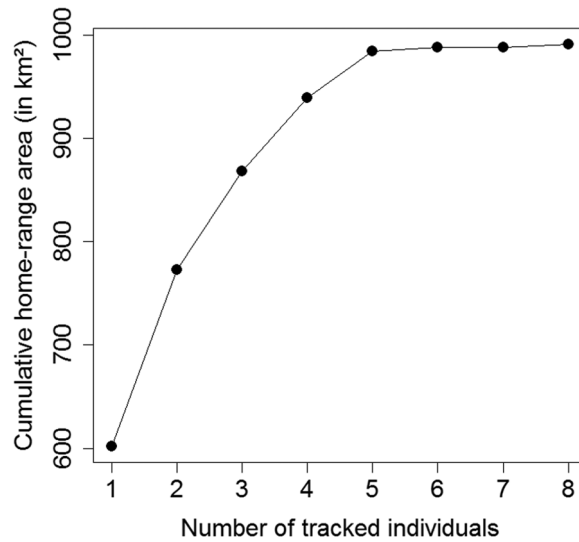
APPENDIX A

Fig. A1. Cumulative home-range area analysis to test the representativeness of sample size for the incubation period in 2011 (n = 8 individuals, total number of trips = 178). The plateau reached at five individuals shows that sample size is representative of the area used by kittiwakes during this period.
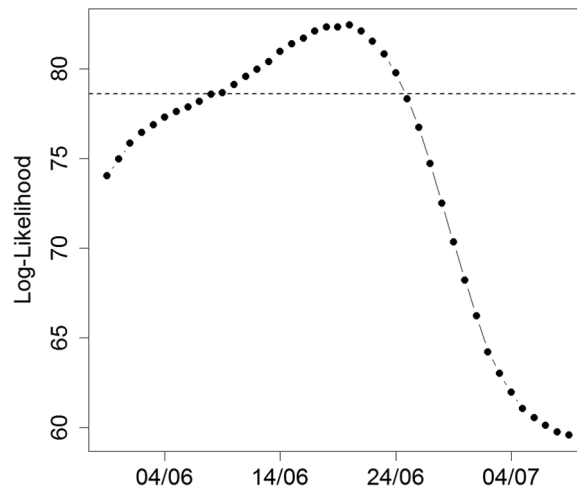
APPENDIX B

Fig. B1. Log-likelihood profile obtained from the broken stick model describing the trends of breeding failure over the season. The highest value of log-likelihood determines when the break occurs. Values above the dotted line are within the 95% confidence interval.

APPENDIX C

DETAILS ON THE MIXTURE MODEL AND PRIOR'S SPECIFICATION

Methods

We used mixture models to analyze jointly trip duration and trip distance. Let i denotes the ith datum of the jth individual in the sample and k the kth component (or cluster) of the mixture:

$$\begin{pmatrix} \log(\text{Duration}) \\ \log(\text{Distance}) \end{pmatrix}_{i,j}$$
$$\sim \sum_k \pi_k \times \text{MVN}\begin{pmatrix} \mu_{1,k} + \alpha_{1,j} \\ \mu_{2,k} + \alpha_{2,j} \end{pmatrix}, \Omega_k \end{pmatrix} \quad (\text{C.1})$$

where MVN denotes a multivariate normal distribution, π_k are the mixing proportion such that $\Sigma_k \pi_k = 1$, and $\alpha_{.,j}$ is a random intercept for individual j. Ω_k is a covariance matrix:

$$\Omega_k = \begin{bmatrix} \sigma_{1,k}^2 & \rho_k \sigma_{1,k} \sigma_{2,k} \\ \rho_k \sigma_{1,k} \sigma_{2,k} & \sigma_{2,k}^2 \end{bmatrix} \quad (\text{C.2})$$

where ρ_k is the correlation between $\log(\text{Duration})$ and $\log(\text{Distance})$ for the kth cluster and $\sigma_{.,k}$ are the residual standard deviations.

The individual-specific intercepts, $\alpha_{.,j}$ were likewise modelled as:

$$\begin{pmatrix} \alpha_1 \\ \alpha_2 \end{pmatrix}_j \sim \text{MNV}\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \begin{bmatrix} \sigma_{1,\alpha}^2 & \rho_\alpha \sigma_{1,\alpha} \ \sigma_{2,\alpha} \\ \rho_\alpha \sigma_{1,\alpha} \ \sigma_{2,\alpha} & \sigma_{2,\alpha}^2 \end{bmatrix} \end{pmatrix}. \quad (\text{C.3})$$

Mixture model fitting and priors

Models were fitted with JAGS (Plummer 2003). As it relies on Bayesian methods to draw inferences, we used weakly informative priors throughout (Gelman et al. 2008). The prior specifications for the models are detailed below.

- We used a stick-breaking construction to model the proportion π_k:

$$p_k \sim Beta(2,2)$$

$$\pi = \begin{bmatrix} p_k \\ p_k \pi_{k-1} \dfrac{1 - p_{k-1}}{p_{k-1}} \\ 1 - \sum_{l=1}^{k-1} \pi l \end{bmatrix} \begin{array}{l} \text{if } k = 1 \\ \text{if } 1 > k > K \\ \text{if } k > K \end{array}$$

- We used Student distributions with mean 0, scale 10 and 7 degrees of freedom for μ_k. For model identification purposes, we constrained $\mu_{.,1} < \mu_{.,2} < \ldots < \mu_{.,k}$. $\mu_{.,k} \sim$ Student $(0, 10, 7)$.
- We used half-Student distributions with mean 0, scale 1 and 3 degrees of freedom for $\sigma_{.,k} \sim \text{Student}^+ (0, 1, 3)$.
- We used uniform distribution for correlations $\rho_. \sim$ Uniform $(-1, 1)$.

Three chains were initialized with overdispersed starting values. After appropriate burn-in (100,000 iterations) and thinning of the chains (1 value every 50 iterations stored), convergence was assessed using the Gelman-Rubin convergence diagnostic (Cowles and Carlin 1996) with the *coda* package (Plummer et al. 2006).

Mixture model selection

Determining the number of components in a finite-mixture model is still a challenge despite a lot of research (Fruhwirth-Schnatter and Pyne 2010). The Deviance Information Criterion (Spiegelhalter et al. 2002) is a popular tool for Bayesian model selection (Barnett et al. 2010). Yet its use with mixture models is problematic (Celeux et al. 2006). One information theoretic criterion that has been found to empirically work well is the Approximate Weight of Evidence (AWE) (Fruhwirth-Schnatter and Pyne 2010). Below we detail the formulae to compute this criterion for a k-components mixture models.

$$\text{AWE} = -2\text{CL} + 2\delta\left(\frac{3}{2} + \log(n)\right)$$

where δ is the number of parameters, n the sample size. CL denotes the complete likelihood:

$$\text{CL} = \sum_{i=1}^n \log\left(\sum_{k=1}^K 1_{(k)} \pi_k \text{f}(y_i | \mu_K, \Omega_K)\right)$$

where y is the data, $\varphi(.|\mu,\Omega)$ denotes a multivariate Gaussian probability density function of mean μ and covariance matrix Ω and $1_{(.)}$ is the indicator function taking the value 1 if y_i is assigned to the kth cluster and 0 otherwise.

Table C1. Mixture model selection: Three models were considered and we kept a ratio of number of parameters to be estimated to the number of datum above 8. The Approximate Weight of Evidence (AWE) is reported. Δ_{AWE} is model AWE minus the minimum observed AWE. The selected model is in boldface.

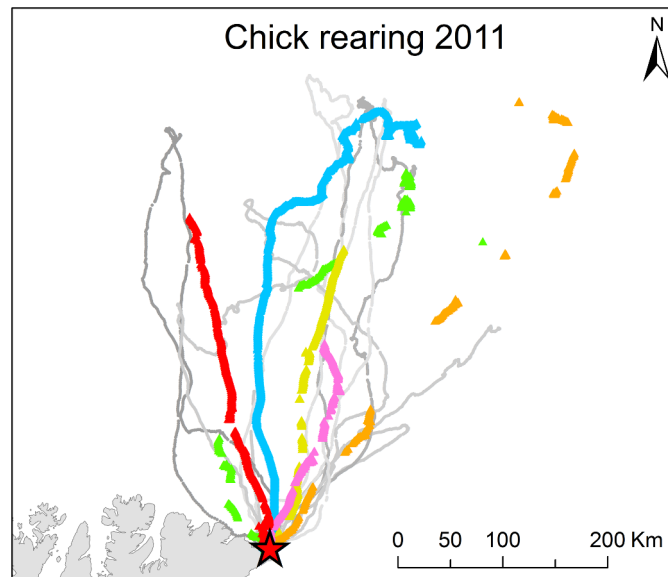| Nb clusters	Complete likelihood	δ	AWE	Δ_{AWE}	n
2	−5599	14	11389	91	210
3	**−5512**	**20**	**11298**	**0**	**210**
4	−5848	26	12052	754	210

APPENDIX D

Fig. D1. Incomplete trips recorded during chick-rearing in six successful breeders which GPS failed tracking individual locations continuously. Each color represents one individual. These data reveal the same pattern as the one presented in Fig. 3 (grey trips). The star represents the nesting colony of Hornøya.
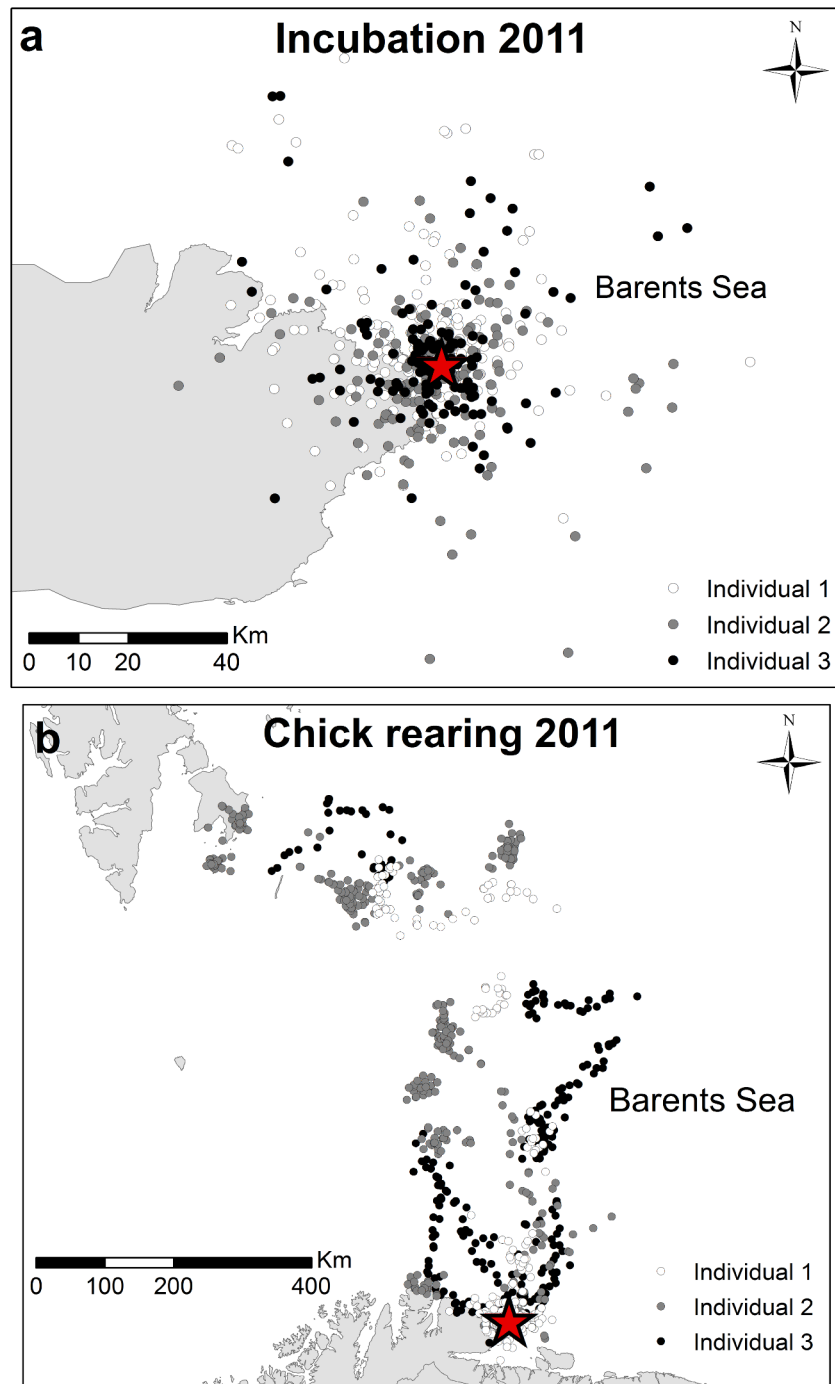
Fig. D2. Distribution of three failed breeders tracked with PTTs during (a) incubation, from 25 May to 10 June, and (b) chick-rearing, from 20 June to 22 July. The red star indicates their nesting colony, Hornøya.