Foraging trip time-activity budgets and reproductive success in the black-legged kittiwake

Lorraine S. Chivers[1],*, Mathieu G. Lundy[2], Kendrew Colhoun[3], Stephen F. Newton[4], Jonathan D. R. Houghton[2,5], Neil Reid[1]

[1]Quercus, and [2]School of Biological Sciences, Queen's University Belfast, Belfast BT9 7BL, UK
[3]Royal Society for the Protection of Birds, Belvoir Park Forest, Belfast BT8 7QT, UK
[4]Birdwatch Ireland, 20D Bullford Business Campus, Kilcoole, Co. Wicklow, Republic of Ireland
[5]Marine Laboratory, Queen's University Belfast, 12-13 The Strand, Portaferry BT22 1PF, UK

ABSTRACT: Seabirds are central place foragers during the breeding season and, as marine food resources are often patchily distributed, flexibility in foraging behaviour may be important in maintaining prey delivery rates to chicks. We developed a methodological approach using a combination of GPS data loggers and temperature-depth recorders that allowed us to describe the behaviour of surface-feeding seabirds. Specifically, we tested whether differences in foraging behaviour of black-legged kittiwakes *Rissa tridactyla* could be linked with reproductive success by comparing 2 consecutive years at 2 sites. At Rathlin Island (Northern Ireland) during 2010, foraging differed markedly from that during 2009 and from that at Lambay Island (Republic of Ireland) during both years. Birds exhibited foraging trips of greater duration, travelled a greater total distance, spent more time in transit and spent longer recuperating on the surface of the water. This notable shift was associated with a decline in breeding success, with greater loss of eggs to predation and lower prey delivery rates, resulting in the starvation of 15% of chicks. We suggest that food resources were reduced or geographically less accessible during 2010, with suitable foraging areas located further from the colony. Birds did not invest greater amounts of time attempting to catch prey. Thus, our results indicate that kittiwakes at Rathlin modulated their foraging behaviour not by increasing foraging effort through feeding more intensively within prey patches but by extending their range to increase the probability of encountering more profitable prey patches.

KEY WORDS: Breeding · Foraging effort · GPS data-logger · Prey availability · Reproductive success · Temperature-depth recorder

INTRODUCTION

Seabirds are central place foragers during the breeding season and, as marine resources are highly variable, flexibility in their foraging behaviour is important to ensure adequate provisioning of their chicks (Hamer et al. 2007). In periods when food availability is low, seabirds can increase foraging effort because they have flexible time-activity budgets and can reallocate spare time to foraging when required. Foraging effort may be increased by intensifying the number of dives and/or time spent attempting to catch prey within prey patches (hereafter, referred to as 'foraging intensity'), by extending foraging ranges to include more profitable prey patches or through a combination of both (Hamer et al. 2007, Ronconi & Burger 2008, Burke & Montevecchi 2008, Quillfeldt et al. 2010).

The black-legged kittiwake *Rissa tridactyla* (Linneaus, 1758), referred to hereafter simply as kittiwake,

has suffered low breeding success throughout most of the British Isles in recent years (Frederiksen et al. 2004, JNCC 2011a). Low reproductive success has been attributed to reduced food availability (Frederiksen et al. 2004, Mavor et al. 2008) and, therefore, understanding the foraging ecology of this species is essential if successful conservation strategies are to be implemented (Daunt et al. 2002). Kittiwakes are surface feeders and during the breeding season have limited spare time in their activity budgets to reallocate to foraging. Thus, kittiwakes are particularly sensitive to changes in food availability (Furness & Tasker 2000, Enstipp et al. 2006), and it has been suggested that they employ flexible foraging strategies to adjust to feeding conditions (Daunt et al. 2002)

In the northwestern North Sea, radio tracking has revealed that kittiwakes may increase their foraging trip duration and foraging range when food availability is low (Hamer et al. 1993, Suryan et al. 2000). Although a central tool within studies of avian behaviour, radio tracking comes with a number of caveats when assessing foraging patterns as it has a limited range and, for surface-feeding seabirds, does not provide details about changes in time allocation to different activities, specifically, flying, feeding or resting on the water. Technological advances over recent decades have greatly improved our ability to record the behaviour of seabirds away from their breeding sites. The development of miniaturised data loggers in recent years has enabled kittiwakes to be tracked throughout foraging trips and for time invested in different behaviours to be quantified (Daunt et al. 2002, Enstipp et al. 2006, Angelier et al. 2007, Kotzerka et al. 2009). However, studies limited to specific sites or within single years are not generalizable and may be of limited application. For species that forage below the surface, the use of data storage tags provides a means to define bouts of diving behaviour that move towards more refined estimates of foraging effort (Hedd et al. 2009). However, identifying such events for species that forage at or near the surface is more difficult given that such behaviour lasts only a few seconds.

The present study employed Global Positioning System (GPS) data loggers and temperature-depth recorders (TDRs) to enable foraging trip profiles to be reconstructed, providing not only position but also activity. This allowed us to link the foraging behaviour of kittiwakes at 2 sites during 2 consecutive years with reproductive success. Specifically, we investigated the hypothesis that reproductive success was indirectly related to food availability by examining changes in foraging behaviour.

MATERIALS AND METHODS

Study sites

We examined the breeding success and foraging behaviour of kittiwakes at 2 offshore sites in Ireland. Rathlin Island in the North Channel (55° 17′ 32″ N, 06° 11′ 30″ W) is designated as a Special Protection Area (SPA) for its diverse seabird assemblage, with 9900 pairs of breeding kittiwakes (Allen & Mellon Environmental 2007). Low breeding success and, in some years, complete breeding failure was observed between 2005 and 2008 (Chivers 2008). Lambay Island in the Irish Sea (53° 29′ 30″ N, 06° 01′ 00″ W) is also designated as an SPA with 4200 pairs of breeding kittiwakes (Newton 2009). In contrast to Rathlin, kittiwakes at Lambay have exhibited stable breeding success, which in 2007 was higher than the mean value for the British Isles (JNCC 2011b).

Foraging behaviour

Variance in kittiwake foraging behaviour was examined using a combination of GPS data loggers (i-gotU GT-100, MobileAction Techonology) and temperature-depth recorders (G5 TDRs, Centre for Environment, Fisheries and Aquaculture Science, UK). GPS loggers were disassembled from their external case to reduce mass and sealed within a 20 mm length of clear heat-shrink tubing to provide waterproofing. Devices were attached to the back of the breeding birds following the methods of Guildford et al. (2008). TDR devices were attached to plastic coloured rings using cable ties and fitted to the bird′s leg in the standard fashion. In total, devices weighed approximately 17.5 g and were <5% of mean (±SD) kittiwake body mass (361.4 ± 38.1 g). This was within the limits of tag mass in previous studies (e.g. 4 to 6% of body mass in Daunt et al. 2002) and the relatively low wing loadings characteristic of kittiwakes (Spear & Ainley 1997) would typically lower the putative impact of the devices. Handling time during capture and attachment was <15 min. Birds were caught during the early chick-rearing period between 3 and 19 July 2009 and 2010. Each was weighed and head-bill measurements were taken for the purposes of sexing (Coulson 2009). Data were acquired for multiple foraging trips per bird with GPS fixes obtained at least once every 120 s and TDR pressure/temperature data every 1 s. Birds were recaptured after at least 24 h and both devices were removed. At Rathlin in 2009 and 2010,

prey delivery rates (deliveries chick^{-1} h^{-1}) were recorded during three 17 h focal observation periods, from 04:00 to 21:00h (GMT+1), divided into 6 sessions between 2 and 3 h duration. Observations of prey delivery were not made at Lambay.

Data processing

Location, temperature and dive data were discarded for the first hour immediately after tag deployment and the last hour prior to re-capture to avoid recording abnormal behaviour resulting from trapping, handling or tagging. The locational accuracy of GPS devices was tested prior to deployment and the upper 95% confidence interval was 62 m. Thus, birds were considered to be on a foraging trip when they were >62 m from their nest but only if their movement trace also indicated an outward movement from the colony. Birds that stayed away from the nest between 23:00 and 02.00 h (GMT+1) were considered to be on an overnight 'roosting trip' (Daunt et al. 2002) and these data were removed from subsequent analyses. GPS data that indicated an apparent travelling speed greater than the maximum flying speed of a kittiwake, i.e. >87 km h^{-1} (Kotzerka et al. 2009) were also removed as they were likely to have been caused by locational error.

Kittiwakes use 4 methods to catch prey: (1) dipping and pattering, (2) surface plunging, (3) pursuit diving and (4) surface seizing (Ashmole 1971). Whilst performing the first 3 behaviours, kittiwakes moved in and out of the water, which was recorded as characteristic fluctuations in temperature data acquired by the TDR devices. However, during surface seizing, prey was captured whilst the bird was swimming on the sea surface with its legs constantly submerged, thus we were unable to separate this activity from when the bird was 'resting on the water'. Surface seizing is thought to be a minor part of kittiwake feeding behaviour during the breeding season (Ashmole 1971, Camphuysen & Webb 1999), and this was confirmed by observations of feeding flocks at Rathlin (n = 67 birds), which suggested that dipping and pattering was the main method employed, followed by surface plunging interspersed with a low frequency of pursuit diving. We performed simulations of these behaviours using TDRs in the sea or in air, reproducing the movement pattern typical of a kittiwake's legs. These data suggested that a temperature change over a 2 min period of >0.2°C indicated foraging behaviours, which we collapsed into the common category of 'attempting to catch prey', whereas changes <0.2°C indicated that birds were either surface seizing or 'resting on the water'. Kittiwakes were considered to be 'flying' when the GPS data suggested a travelling speed >10 km h^{-1} (Weimerskirch et al. 2005), except at the beginning and end of each trip when birds flew more slowly when leaving or approaching the nest. Thus, each GPS fix during a foraging trip was allocated to one of 3 distinct behaviours, defined using the pressure/temperature data from the TDRs, namely (1) attempting to catch prey, (2) resting on the water or (3) flying (Fig. 1).

Foraging trips were parameterised by the cumulative duration of each behaviour (also expressed as a percentage of the total trip duration), specifically, attempting to catch prey (h trip^{-1}), resting on the water (h trip^{-1}), flying (h trip^{-1}) as well as total trip duration (h), total distance travelled (km) and maximum distance travelled from the nest (km).
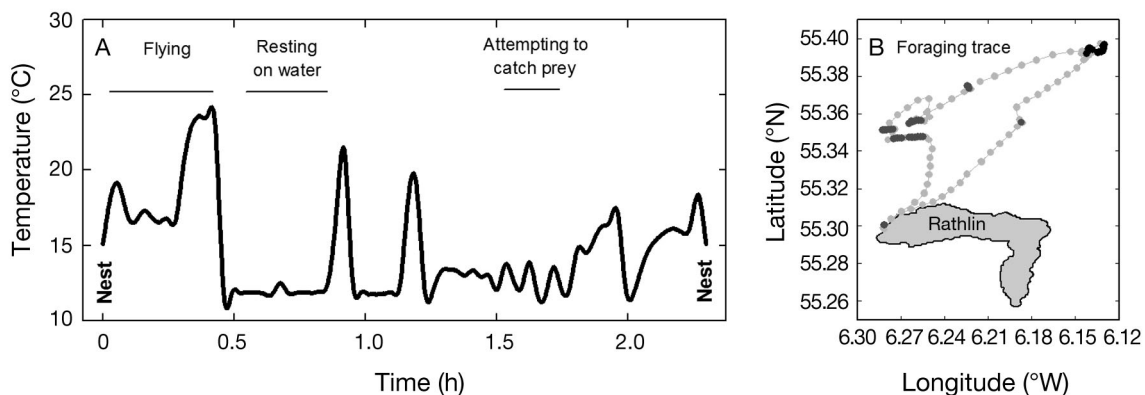

Fig. 1. *Rissa tridactyla*. (A) Temperature trace (every 2 min) derived from temperature-depth recorder (TDR) data logger for a single kittiwake foraging trip starting and ending at the nest, defining flying, resting on water and attempting to catch prey. (B) Foraging trace identifying the activity at each of the GPS coordinates (light grey dots: flying; dark grey dots: resting on water; and black dots: attempting to catch prey)

Breeding parameters

The reproductive effort and success of kittiwakes were assessed for a sub-sample of nests within each colony. Initial clutch size (1 to 3 eggs) was recorded for each nest and visits were made every 2 d to record the apparent fate of each egg or chick. Outcomes were classified as: (1) fledged, (2) nest lost, (3) eggs failed to hatch, (4) chicks starved or (5) chicks lost. Fledging was assumed when chicks were >35 d old (Gilbert et al. 1998). Reproductive success was expressed as the number of chicks fledged per nest.

Controls

To test the effect of deploying devices on bird behaviour and reproductive success, a focal study was conducted at Rathlin during 2009. Prey delivery rates were recorded as described in 'Foraging behaviour'. The first period occurred prior to deployment of devices, the second when devices were attached and the third after the devices had been removed. Mean prey delivery rate was calculated per period. We also recorded breeding success (chicks fledged nest^{-1}) of the birds that had been tagged compared with control birds that had not been tagged but had nested within the same area of the colony at Rathlin. To ensure that this area was representative of the whole colony, we also compared breeding success between the selected area and another from which observations were made but no birds had been caught or tagged.

Statistical analyses

Descriptive statistics were used to clarify trends in bird tagging and recovery. Foraging parameters including (1) attempting to catch prey (h trip^{-1}), (2) resting on the water (h trip^{-1}), (3) time spent flying (h trip^{-1}), (4) total trip duration (h trip^{-1}), (5) total distance travelled (km trip^{-1}) and (6) maximum distance travelled from the nest (km trip^{-1}) were compared between years (2009 and 2010) at Rathlin using a linear mixed model (LMM) assuming a normal error structure and an identity link function with year fitted as a fixed factor and bird ID as a random factor to account for multiple foraging trips per bird. Descriptive statistics were used to clarify trends in the same foraging parameters for birds tagged at Lambay Island. The relationships between foraging trip duration and time spent flying, total distance travelled

and maximum distance travelled from the nest were examined using Pearson correlation coefficients.

To test the effect of nest location, clutch size and reproductive success were compared between the area of the colony used to catch and tag birds with a control area in another part of the colony. A χ^2 test was used to compare clutch size and a generalized linear mixed model (GLMM) was used to compare reproductive success. The latter assumed a binomial error structure and a logit link function fitting the outcome (a binary response of success or failure of each egg) as the dependent variable with area (tagging area or control area) fitted as a fixed factor and nest ID as a random factor to account for multiple eggs per nest (thus avoiding pseudoreplication). To test the effect of tagging, reproductive success was also compared between tagged and control birds within the same area of the colony using a GLMM as before but with tagging (tagged or untagged) fitted as a fixed factor. Prey delivery rates (deliveries chick^{-1} h^{-1}) were compared before, during and after tagging using an LMM as before but fitting period (before, during and after) as a fixed factor and nest ID as a random factor.

Clutch size and reproductive success were compared between sites (Rathlin or Lambay) during 2009 using a χ^2 test and a GLMM as above but with site fitted as a fixed factor. The occurrence of both egg and chick losses was also examined using GLMMs assuming a binomial error structure and a logit link function fitting the outcome (a binary response of either success or loss of eggs or chicks) with site fitted as a fixed factor and nest ID as a random factor. Clutch size and reproductive success were also compared between years (2009 and 2010) at Rathlin Island using a χ^2 test and a GLMM as before but with year fitted as a fixed factor. The occurrence of both egg and chick losses were examined between years (2009 and 2010) at Rathlin using GLMMs as before but with year fitted as a fixed factor. Prey delivery rates (deliveries chick^{-1} h^{-1}) were compared between years (2009 and 2010) at Rathlin using an LMM as before but with year fitted as a fixed factor and chick age as a covariate.

All statistical analyses were performed using Genstat v10 (VSN International).

RESULTS

A total of 42 black-legged kittiwakes were tagged: 13 in 2009 and 10 in 2010 at Rathlin, and 12 in 2009 and 7 in 2010 at Lambay. Foraging trip data were
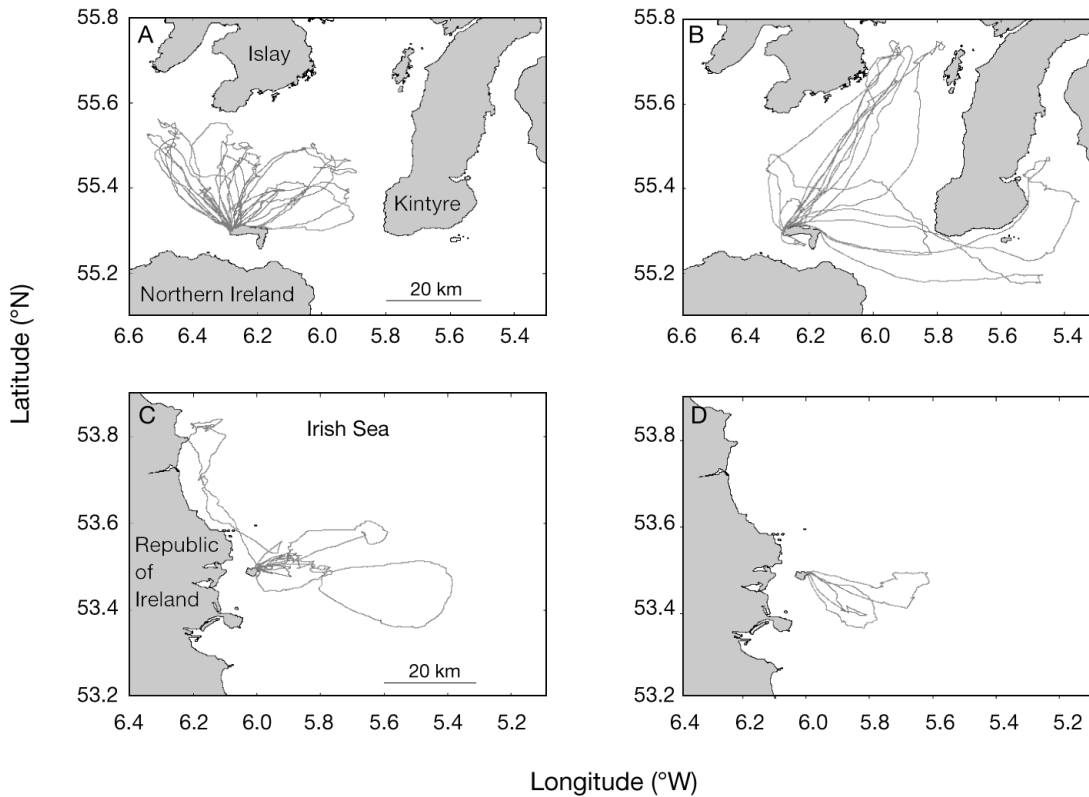
Fig. 2. *Rissa tridactyla*. Foraging traces derived from GPS data loggers of kittiwakes breeding at (A,B) Rathlin Island, Northern Ireland, and (C,D) Lambay Island, Republic of Ireland, during (A,C) 2009 and (B,D) 2010

successfully recovered from 14 birds (55 trips): 5 in 2009 (22 trips) and 5 in 2010 (17 trips) at Rathlin, and 2 in 2009 (11 trips) and 2 in 2010 (5 trips) at Lambay. A total of 15 trips were classed as overnight 'roosting trips' (4 in 2009 and 7 in 2010 at Rathlin, and 2 in 2009 and 2 in 2010 at Lambay) and were discarded from subsequent analyses. Thus, daytime foraging from a total of 13 birds (40 trips) was analysed: 5 in 2009 (18 trips) and 4 in 2010 (10 trips) at Rathlin, and 2 in 2009 (9 trips) and 2 in 2010 (3 trips) at Lambay (Fig. 2).

Foraging trip duration, time spent flying, total distance travelled and maximum distance travelled from the nest were all significantly shorter during 2009 than 2010 at Rathlin (Tables 1 & 2). Time spent resting on the water was also shorter in 2009 than in 2010, but time attempting to catch prey did not differ between years (Table 2). Insufficient GPS and TDR data were recovered from tagged birds at Lambay for statistical analysis. Nevertheless, all foraging parameters were similar during 2009 and 2010 at Lambay except the time spent attempting to catch prey, which was higher during 2010 than 2009 (Table 1). Foraging metrics were similar between Rathlin and Lambay during 2009 but were notably different during 2010 (Table 1). Specifically, tagged birds at Rathlin during 2010 exhibited foraging trips of greater duration, spent more time flying and travelled almost twice as far to reach foraging grounds as birds at Lambay. Moreover, the maximum distance travelled from their nest was also twice as great as birds at Lambay during the same year. Foraging trip duration (both sites combined) was positively correlated with time spent flying ($r = 0.928$, $p < 0.001$, $n = 40$), total distance travelled ($r = 0.654$, $p < 0.001$, $n = 40$) and maximum distance travelled from the nest ($r = 0.645$, $p < 0.001$, $n = 40$).

Clutch size ($\chi^2_1 = 0.11$, $p = 0.746$, $n = 63$) and reproductive success ($W_1 = 2.29$, $p = 0.131$, $n = 109$) at Rathlin Island did not differ between kittiwakes nesting within the area of the colony used to catch and tag birds and those within a control area used for observations only. There was also no difference in reproductive success between tagged birds and control birds within the same area of the colony ($W_1 = 0.70$, $p = 0.403$, $n = 26$). Moreover, prey delivery rates did not differ prior to, during or after tagging ($F_{2,8} = 1.66$, $p = 0.250$, $n = 5$).

Table 1. *Rissa tridactyla*. Time-activity budgets of daytime foraging trips made by kittiwakes breeding at Rathlin Island, Northern Ireland, and Lambay Island, Republic of Ireland, during 2009 and 2010. Samples sizes (n) represent foraging trips per bird. na: not applicable. Data are means ±SE. Percentages are given in parentheses

Location/date	Bird	Sex	n	Time-activity budget (h) Attempting to catch prey	Resting on water	Flying	Trip duration (h)	Total distance travelled (km)	Max. distance from nest (km)
Rathlin Island									
2009	1	M	4	0.67 ± 0.19 (20.1)	0.80 ± 0.20 (24.0)	1.86 ± 0.40 (55.9)	3.33 ± 0.50	64.87 ± 15.8	23.0 ± 3.53
	2	F	5	0.50 ± 0.06 (18.2)	0.44 ± 0.05 (16.0)	1.81 ± 0.08 (65.8)	2.75 ± 0.14	60.70 ± 4.67	23.3 ± 2.34
	3	F	2	0.70 ± 0.20 (18.7)	1.12 ± 0.71 (29.9)	1.93 ± 0.53 (51.5)	3.75 ± 1.05	64.71 ± 16.1	26.3 ± 6.42
	4	F	5	0.32 ± 0.10 (14.0)	0.44 ± 0.10 (19.2)	1.53 ± 0.31 (66.8)	2.29 ± 0.44	51.73 ± 8.85	22.0 ± 3.94
	5	M	2	0.55 ± 0.18 (12.4)	1.03 ± 0.20 (23.3)	2.85 ± 1.18 (64.3)	4.43 ± 1.57	51.75 ± 0.05	20.1 ± 0.75
	Sub-total/mean		18	0.52 ± 0.06 (17.0)	0.66 ± 0.10 (21.6)	1.87 ± 0.18 (61.3)	3.05 ± 0.27	58.58 ± 4.47	22.9 ± 1.51
2010	6	M	3	0.54 ± 0.12 (13.1)	0.67 ± 0.11 (16.2)	2.91 ± 0.18 (70.6)	4.12 ± 0.23	110.7 ± 7.55	51.4 ± 2.85
	7	F	3	0.63 ± 0.20 (13.7)	1.38 ± 0.04 (30.1)	2.58 ± 0.96 (56.2)	4.59 ± 1.18	92.96 ± 37.1	39.7 ± 17.2
	8	F	1	0.93 ± na (20.7)	1.50 ± na (33.3)	2.07 ± na (46.0)	4.50 ± na	14.50 ± na	8.90 ± na
	9	F	3	1.62 ± 0.12 (20.7)	2.31 ± 1.10 (29.6)	3.88 ± 0.40 (49.7)	7.81 ± 1.43	135.8 ± 20.4	47.3 ± 8.87
	Sub-total/mean		10	0.93 ± 0.17 (17.2)	1.46 ± 0.36 (27.0)	3.02 ± 0.34 (55.8)	5.41 ± 0.72	103.3 ± 15.9	42.4 ± 6.46
	Total/mean		28	0.66 ± 0.08 (17.0)	0.95 ± 0.16 (24.4)	2.28 ± 0.19 (58.6)	3.89 ± 0.37	74.55 ± 7.42	29.8 ± 3.02
Lambay Island									
2009	10	F	5	0.33 ± 0.04 (15.6)	0.54 ± 0.12 (25.5)	1.25 ± 0.20 (59.0)	2.12 ± 0.30	21.48 ± 6.93	7.24 ± 2.41
	11	F	4	0.86 ± 0.27 (16.1)	1.06 ± 0.14 (19.9)	3.42 ± 0.68 (64.0)	5.34 ± 0.87	90.67 ± 21.7	29.9 ± 7.18
	Sub-total/mean		9	0.56 ± 0.15 (15.8)	0.77 ± 0.12 (21.8)	2.21 ± 0.49 (62.4)	3.54 ± 0.69	52.24 ± 15.5	17.3 ± 5.10
2010	12	F	2	1.10 ± 0.07 (34.5)	0.47 ± 0.27 (14.7)	1.62 ± 0.15 (50.8)	3.19 ± 0.35	43.11 ± 3.18	17.7 ± 1.22
	13	F	1	1.83 ± na (36.1)	0.67 ± na (13.3)	2.57 ± na (50.7)	5.07 ± na	69.57 ± na	25.6 ± na
	Sub-total/mean		3	1.34 ± 0.25 (35.3)	0.53 ± 0.17 (13.9)	1.93 ± 0.50 (50.8)	3.80 ± 0.66	51.93 ± 9.01	20.3 ± 2.74
	Total/mean		12	0.76 ± 0.16 (21.1)	0.71 ± 0.10 (19.7)	2.14 ± 0.37 (59.3)	3.61 ± 0.53	52.16 ± 11.6	18.0 ± 3.83
	Grand total/mean		40	0.69 ± 0.07 (18.1)	0.88 ± 0.11 (23.1)	2.24 ± 0.17 (58.8)	3.81 ± 0.30	67.84 ± 6.38	26.3 ± 2.53

Clutch sizes were significantly larger ($\chi^2_1 = 7.40$, p = 0.007, n = 87) and reproductive success significantly higher ($W_1 = 7.68$, p = 0.006, n = 161) at Lambay than Rathlin during 2009 (Table 3). Egg loss was similar between the islands ($W_1 = 1.34$, p = 0.248, n = 161) but chick loss was significantly higher at Rathlin than Lambay ($W_1 = 7.41$, p = 0.007; Table 4). Clutch size did not differ between years ($\chi^2_1 = 1.88$, p = 0.170, n = 75) but reproductive success was higher at Rathlin during 2009 than 2010 ($W_1 = 12.75$, p < 0.001, n = 125; Table 3). No chicks starved during 2009 but during 2010 a total of 9 chicks (15%) died from starvation (Table 4). Egg loss was significantly lower during 2009 than 2010 ($W_1 = 10.63$, p = 0.001, n = 124). Chick loss did not differ between years but there was a strong trend for fewer losses during 2009 than 2010 ($W_1 = 3.68$, p = 0.055 n = 124). Mean prey delivery rates were significantly higher during 2009 than 2010 ($F_{1,46} = 12.01$, p = 0.001, n = 49; Table 3), with chick age having no effect ($F_{1,46} = 1.29$, p = 0.262, n = 49).

DISCUSSION

Here we developed a methodological and analytical approach that allowed us to overcome the problems associated with describing the foraging behaviour of a surface-feeding seabird; this approach can be transferred directly to similar species. The demonstrable utility of this approach allowed us to describe variation in the foraging behaviour of kittiwakes that may explain shifts in reproductive success. Specifically, the behaviours of birds breeding at Rathlin Island during 2010 were notably different from those breeding at the same colony during 2009 or those breeding at Lambay Island in either year. They exhibited foraging trips of greater duration, spent more time flying, travelled a greater total distance, went

further from the colony in search of food and, as a consequence, spent more time resting on the water to recuperate. The effect was a reduction in breeding success with a greater loss of eggs and lower prey delivery rates, resulting in 15% of chicks starving to death. These findings suggest that marine productivity and prey species availability (occurrence and/or

Table 2. *Rissa tridactyla*. Linear mixed model results for a comparison of daytime foraging trip parameters showing the effect of year (2009 and 2010) at Rathlin Island. *Significant (p < 0.05) results

Dependent variable	n	W	df	p
Attempting to catch prey (h trip^{-1})	28	2.76	1	0.097
Resting on the water (h trip^{-1})	28	4.55	1	0.033*
Flying (h trip^{-1})	28	10.84	1	<0.001*
Trip duration (h trip^{-1})	28	5.82	1	0.016*
Total distance travelled (km trip^{-1})	28	11.63	1	<0.001*
Maximum distance from nest (km trip^{-1})	28	14.38	1	<0.001*

Table 3. *Rissa tridactyla*. Metrics (means ± SE) describing kittiwake reproductive effort and success at Rathlin Island, Northern Ireland, and Lambay Island, Republic of Ireland, during 2009 and 2010. Sample sizes are given in parentheses. (–): no data

Location/ year	Clutch size (eggs nest^{-1})	Reproductive success (chicks fledged nest^{-1})	Food delivery rate (delivery chick^{-1} h^{-1})
Rathlin Island			
2009	1.73 ± 0.07 (37)	1.11 ± 0.11 (37)	0.27 ± 0.01 (26)
2010	1.58 ± 0.08 (38)	0.45 ± 0.08 (38)	0.18 ± 0.01 (23)
Lambay Island			
2009	1.94 ± 0.03 (50)	1.62 ± 0.08 (50)	–
2010	–	0.93 ± 0.05 (390)	–

density) was reduced or geographically less accessible during 2010, when foraging occurred much farther from the colony (in this case, off the west coast of Scotland). Birds did not invest greater amounts of time attempting to catch prey per foraging trip. Thus, we suggest that when food availability is low, kittiwakes increase foraging effort by extending their range to increase the probability of encountering more profitable prey patches.

Clutch size is an indicator of food availability in the early part of the breeding season prior to egg laying (Drent & Daan 1980, Schultz et al. 2000). As there was no difference in clutch size between 2009 and 2010 at Rathlin, we might conclude that food availability during this period was not a limiting factor in either year. In 2009, reproductive success on Rathlin was higher than the long-term (1986–2005) mean for the British Isles (Mavor et al. 2008) whereas during 2010 reproductive success was lower. During 2010, many chicks starved but none did so during 2009 and this, coupled with low provisioning rates, indicated that during 2010 some chicks did not receive sufficient food to reach fledging, which is indicative of low food availability (Wanless & Harris 1992, Hamer et al. 1993, Piatt et al. 2007). Kittiwakes are vulnerable to a number of avian predators including large gull species *Larus* spp. Gulls feed on fish but can switch to alternative food resources, including eggs and chicks, during periods of low fish availability (Uttley et al. 1989, Spear 1993, Regehr & Montevecchi 1997). Thus, higher rates of egg and chick loss at Rathlin during 2010 may have been attributed to predators increasing their reliance on non-fish prey because of low marine resource availability.

Focal observations of nest attendance (Wanless & Harris 1992) and direct observations using radio-telemetry (Hamer et al. 1993, Suryan et al. 2000) have suggested that kittiwakes can vary their forag-

Table 4. *Rissa tridactyla*. Apparent fates of kittiwake eggs laid at Rathlin Island, Northern Ireland, and Lambay Island, Republic of Ireland, during 2009 and 2010. Data are no. of eggs affected, with percentages in parentheses

Location/ year	Fate of eggs laid						
	Fledged	Nest lost	Eggs failed to hatch	Eggs lost	Chicks starved	Chicks lost	Total failure
Rathlin Island							
2009	41 (64.1)	0 (0)	5 (7.8)	3 (4.7)	0 (0)	15 (23.4)	23 (35.9)
2010	17 (28.3)	2 (3.3)	1 (1.7)	7 (11.7)	9 (15.0)	24 (40)	43 (71.7)
Sub-total	58 (46.8)	2 (1.6)	6 (4.8)	10 (8.0)	9 (7.2)	39 (31.5)	66 (53.2)
Lambay Island							
2009	81 (83.5)	0 (0)	3 (3.1)	7 (7.2)	0 (0)	6 (6.2)	16 (16.5)
Total	139 (62.9)	2 (0.9)	9 (4.1)	17 (7.7)	9 (4.1)	45 (20.4)	82 (37.1)

ing trip duration. Similarly, other seabirds have been shown to modulate their foraging effort as a form of behavioural buffering in response to food availability and distribution (Monaghan et al. 1994, Zador & Piatt 1999, Ronconi & Burger 2008). Kittiwakes with good breeding success at Shetland, Scotland, may forage as little as 5 km from their nest, but in years with poor breeding success and low food availability they may travel up to 40 km (Hamer et al. 1993). Birds breeding at Rathlin and Lambay typically travelled a maximum of 17 to 23 km when breeding success was average, but travelled twice as far from Rathlin during 2010 (42 km) when breeding success was poor. The time invested by birds in attempting to catch prey did not differ between years at Rathlin, was similar between Rathlin and Lambay during 2009 and although marginally higher at Lambay during 2010 there was a very small sample size. Thus, only foraging metrics associated with travel to foraging areas differed between years or sites. We found a positive relationship between foraging trip duration and distance travelled whereas trip duration was significantly greater during a year with poor breeding success. This supports the hypothesis that during periods of low food availability, kittiwakes modify their foraging strategy not by increasing the investment in foraging intensity but by increasing their foraging range to include more profitable prey patches. The metabolic costs of attempting to catch prey are high for kittiwakes compared with other activities and may explain why foraging range was extended rather than foraging intensity increased (Suryan et al. 2000, Jodice et al. 2003).

Despite kittiwakes shifting their foraging strategy at Rathlin during 2010, some chicks starved and breeding success was low. Thus, despite travelling further, some birds either found insufficient food or were unable to maintain high enough provisioning rates to successfully fledge their chicks. Kittiwakes have restricted time-activity budgets compared with other species of seabirds (Furness & Tasker 2000, Enstipp et al. 2006) and, in the case of individuals nesting at Rathlin during 2010, travelling further in search of prey appeared to be insufficient for some birds to compensate for lower food availability. Catching, handling and tagging kittiwakes had no effect on prey delivery rates or breeding success and there was no difference in breeding success between birds in the area used for tagging and those in a control area where only observations were made. Studies using devices of similar mass also found no effect on provisioning behaviour and our results describing foraging parameters were comparable to those of other studies that have used data loggers (Daunt et al. 2002, Kotzerka et al. 2009. Therefore, we have no reason to believe that our selection of birds or our tagging method affected either the bird's foraging behaviour or reproductive output.

The development of effective methods to identify seabird foraging areas is particularly important in Europe at present, as European Union member states have obligations to designate a network of Marine Protected Areas (92/43/EEC) within the next few years, and it is likely that the foraging areas of priority (or important) seabirds, such as the kittiwake, may be used to define the proposed boundaries. Our findings demonstrate that tracking studies are essential for this purpose and should be performed over a number of years as food availability, and thus foraging areas, can exhibit substantial interannual variability. Further research is needed to understand how kittiwake foraging habits vary temporally, geographically and with respect to diet.

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