Seasonal interactions in the black-legged kittiwake, *Rissa tridactyla*: links between breeding performance and winter distribution

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Relationships between events in one period of the annual cycle and behaviour in subsequent seasons are key determinants of individual life histories and population dynamics. However, studying such associations is challenging, given the difficulties in following individuals across seasons, particularly in migratory species. Relationships between breeding performance and subsequent winter ecology are particularly poorly understood, yet are likely to be profoundly important because of the costs of reproduction. Using geolocation technology, we show that black-legged kittiwakes that experienced breeding failure left their colony in southeast Scotland earlier than successful breeders. Moreover, a greater proportion of unsuccessful breeders (94% versus 53% successful) travelled over 3000 km to the West Atlantic, whereas fewer visited the East Atlantic (31% versus 80% successful), less than 1000 km from the colony. The two groups did not differ in the timing of return to the colony the following spring. However, 58 per cent of males made a previously undescribed long-distance pre-breeding movement to the central Atlantic. Our results demonstrate important links between reproductive performance and winter distribution, with significant implications for population dynamics. Furthermore, macro-scale segregation associated with breeding outcome is relevant to defining important wintering areas, in particular among declining species experiencing increasingly regular breeding failure.

Keywords: annual cycle; carry-over effects; reproductive success; wintering distribution; pre-breeding exodus

1. INTRODUCTION

Many iteroparous breeders show a clear annual cycle where successive breeding events are separated by a non-breeding phase, which usually occurs during the winter and may be spatially discrete from the summer breeding area. Interactions between these phases are fundamental to a species’s population dynamics, but the opportunities to study such effects are often limited because of difficulties in following individuals across seasons [1,2]. Research has focused on the influence of winter ecology on summer breeding performance, given the opportunities to capture animals at breeding grounds and infer winter diet, habitat or distribution from stable isotope signatures [3]. These studies have demonstrated that the quality of winter habitat and diet affects body condition, and consequently the timing of arrival at breeding grounds [4], breeding performance [3,5] and survival rate [6]. Furthermore, there is evidence that these effects may operate differently in the two sexes [3].

Studying the links between reproduction and subsequent overwinter ecology of individuals is more challenging using these approaches [7]. However, this seasonal interaction is an integral component of the annual cycle. Breeding performance may impact directly on subsequent wintering ecology (so-called ‘carry-over effects’) because reproduction is costly for future survival and reproduction [1,8,9], and this effect will be mediated by winter ecology, in particular among species where peak mortality occurs in winter [10]. Alternatively, there may be repeatability in breeding performance and winter ecology within individuals determined by genetic or environmental effects (e.g. maternal effects, early life conditions [11,12]). Thus, links between performance in summer and subsequent wintering ecology may reflect carry-over effects from winter to summer, or consistencies across seasons within individuals of differing quality.

Recent technological advances in animal-borne instrumentation make it possible to obtain daily estimates of distribution throughout the year (e.g. [13,14]), allowing the investigation of associations between summer breeding and migration patterns in much greater detail than what can be achieved from, for example, colour-marking [7,15]. Previous studies have shown that unsuccessful breeders leave the breeding grounds earlier than
successful breeders (e.g. [14,16,17]). Although these
differences in the timing of departure were associated
with wintering periods that were extended for up to
several months, there were no apparent differences in
winter distribution. However, a longer migration time
window may enable unsuccessful breeders in other
species to move further, or to exploit alternative staging
areas or wintering destinations. Winter distribution may
do also differ between the sexes in association with different
breeding roles, nutritional requirements or size.

Using animal-borne loggers, we investigated associ-
ations between breeding outcome and subsequent
winter distribution of black-legged kittiwakes, Rissa
tridactyla, a species that has experienced marked popu-
lation declines over much of northern Europe in recent
decades in association with considerably reduced breeding
success [18]. Current knowledge of movements and
distribution of UK kittiwakes based on ringing
locations revealed a winter distribution across the
Atlantic outside the breeding season [19]. As with many
seasonally breeding iteroparous species, adult mortality
peaks in winter [19], and previous experimental work
has demonstrated a correspondence with reproductive
costs in the previous summer [8]. Although sexual size
dimorphism in kittiwakes is modest, there is evidence for
sex differences in breeding roles, with females incur-
ring higher energetic costs during chick-rearing than
males [20–22]. The aim of this study was to investigate
temporal and spatial variation in wintering distribution
in male and female kittiwakes that had bred successfully
and unsuccessfully in the previous breeding season.

2. MATERIAL AND METHODS

The study was carried out on the Isle of May National Nature
Reserve, southeast Scotland (56°11'N, 2°33'W). Between 1
and 13 July 2007, 80 breeding kittiwakes were fitted with a
geolocation logger (MK 14, British Antarctic Survey; 20 ×
9 × 5.5 mm; mass 1.5 g, approx. 0.4% of the mean body
mass of 350 g) attached to a leg ring. Breeding success
(number of chicks fledged per pair) of the study individuals
was determined by regular checks of nest contents. Breeding
success was also monitored at a sample of unmanipulated
nests (n = 91) to test for possible device effects. As loggers
were deployed on birds during late incubation or chick rear-
ing, these two groups excluded birds that failed earlier in the
season. However, breeding success of a further 609 unmani-
pulated pairs was followed from the onset of the breeding
season, as part of routine monitoring of this population
since 1985.

To assess any impact of the data loggers on over-wintering
survival, the proportion of birds carrying loggers that
returned the following breeding season (2008) was compared
with the proportion of returning birds carrying colour-rings
(n = 107). In 2008, loggers were retrieved from 31 birds
(39% of logger deployments). Feathers were taken from
each individual (under UK Home Office Licence) for
molecular sexing [23].

The geolocation loggers measured light intensity every
60 s and recorded the maximum value within each 10 min
interval. Data were processed in MULTITRACE-GELOCATION
(Jensen Software Systems), following Phillips et al. [24].
The timing of sunrise and sunset was estimated from
thresholds in the light curves. The coordinates of two
locations, at local noon and midnight, were obtained as fol-

ows: latitude was estimated from day length and longitude
from the timing of local noon/midnight in relation to
GMT. To reduce the error in location estimates, all retained
data were smoothed twice [24]. Locations were excluded
where there was light interference at the time of sunrise or
sunset (approx. 1% of total) and during the equinoxes,
where latitude cannot be calculated reliably (15 September
or mid-winter). The wintering period was defined as the time
between leaving the vicinity of the colony in late summer and return-
ing the following spring. Departure and return dates were
estimated with an accuracy of 1–2 days, given the error of
roughly 185 km in location estimates from the loggers [24].
Departure dates were not available for two birds because of
light interference, nor for three birds that remained in the
North Sea after the breeding season. Initial examination of
locations revealed a winter distribution across the North
Atlantic and North Sea. For the purposes of the analysis,
this range was divided into four regions: the Atlantic was
split into three parts of approximately equal size (West, Cen-
tral and East) and the North Sea, which is geographically
separate from the Atlantic Ocean, was designated the
fourth region (region boundaries shown in figure 1a).

Residency times in each region were calculated, excluding visits
of less than 2 days during which the bird was considered to
be in transit.

Associations between breeding outcome and sex, and
presence and time spent in each wintering region, were
explored using generalized linear mixed models with bino-
mal error structure and generalized linear mixed models,
respectively. As no pairs fledged more than one chick, breed-
ing outcome was a binary variable (successful versus
unsuccessful). Presence/absence and time spent in regions
were response variables, breeding outcome, sex and region
were fixed effects, and individual identity was a random
effect in the models. For the purposes of model comparison,
the models were fitted using maximum likelihood as they had
different fixed effects but the same random structure [25].
Support for different models in the candidate set was
assessed using Akaike’s information criterion adjusted for
small sample sizes (AICc) and Akaike weights. The model
in each set that had the lowest AICc value (and highest
Akaike weight) was considered to be best supported;
models were deemed strongly supported if they differed
from the best model by up to two AICc units (unless they
contained one more parameter than the best supported
model, in which case this rule of thumb is not appropri-
ate [26]). Analyses were performed in R (packages lme4 and
nlme [27]) and values are presented as mean ± s.e.

The analysis revealed differences in distribution across
regions between successful and unsuccessful birds; accord-
ingly, we determined 50 per cent kernel density contours
from the distribution of these two groups in ArcGIS [28] in
a Lambert equal-area azimuthal (North Pole) projection
with a smoothing parameter (k) of 200 km (corresponding
to the mean error of the location data [24]).

3. RESULTS

In 2007, kittiwakes at this colony had a poor breeding
season (0.24 chicks fledged per pair; average for 1985–
2007 = 0.57 ± 0.08 [29]). Average breeding success of
the study birds was 0.43 chicks/pair, which did not differ from breeding success of the sample of unmanipulated nests active at the time the loggers were deployed (0.34 chicks/pair; n = 171; Fisher’s exact test: p = 0.21).

Unsuccessful breeders left the vicinity of the colony significantly earlier than successful breeders (unsuccessful: 28 July ± 4 days, n = 13; successful: 11 August ± 3 days, n = 13; t-test: t_{24} = 2.90, p = 0.01). There was no difference in departure dates between males and females (males: 4 August ± 4 days, n = 16; females: 2 August ± 4 days, n = 10; t_{24} = 0.46, p = 0.65).

A larger proportion of unsuccessful individuals travelled to the West Atlantic (94% versus 53% successful), whereas the opposite was the case for the East Atlantic (31% versus 80% successful; figure 1b; table 1; see also electronic supplementary material for individual data). Furthermore, unsuccessful females spent significantly more time in the West Atlantic than successful females (56% versus 10% of the wintering period), whereas successful females spent longer in the East Atlantic (18% versus 42%); however, the same pattern was not apparent among males (figure 1c,d for females and males, respectively; table 1). In line with these results, kernel analyses revealed markedly different over-wintering distributions of unsuccessful and successful birds, with the former concentrated mainly in the West Atlantic and the latter in the East Atlantic, over 2000 km apart (figure 1a). Accordingly, in the West Atlantic 50 per cent kernels of successful breeders overlapped to a much greater extent with 50 per cent kernels of unsuccessful breeders than vice versa, whereas the opposite was the case in the East Atlantic (table 2).

After returning to the North Sea region in March, 13 birds (42%) made a long-distance pre-breeding movement, with 12 travelling to the Central Atlantic, of which 9 of 10 with known latitude followed a strikingly similar route via southern Iceland, returning on a southerly trajectory (figure 2). Mean departure date for these trips was 22 March ± 2 days and duration was 14 ± 1 day. The probability of making a pre-breeding movement was not related to the previous breeding outcome (n = 31; Fisher’s exact test: p = 0.28). However, males were almost four times more likely to make such trips than females (58% and 17%, respectively; Fisher’s exact test: p = 0.02).

Timing of return to the vicinity of the colony in 2008 was unrelated to breeding outcome in 2007 (unsuccessful: 9 April ± 1 day, n = 16; successful: 6 April ± 1 day, n = 15; t-test: t_{27} = 1.60, p = 0.12). Arrival dates of males and females also did not differ (males: 8 April ± 1 day, n = 19; females: 7 April ± 1 day, n = 12; t_{29} = 0.34, p = 0.74). However, birds that had undertaken a pre-breeding movement arrived significantly later than birds that had not (mean arrival date: movement: 11 April ± 1 day; non-movement: 5 April ± 1 day; n = 31, t_{29} = 3.63, p < 0.01).
Table 1. Linear mixed models testing for associations between breeding outcome (BR) and sex, and the use of winter regions by kittiwakes (*n* = 124 observations of 31 birds). Best model shown in italicized bold, strongly supported models shown in italics.

<table>
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<tr>
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</table>
In 2008, 50 (63%) of the 80 study kittiwakes were seen at the colony. This was comparable with the return rate of 107 colour-ringed control adults over the same period (66%; Fisher’s exact test: \( p = 0.64 \)). Overall return rate in 2008 was lower than the long-term average of 78 per cent [29]. Return rate did not differ between successful and unsuccessful birds (Fisher’s exact test: \( n = 31, p = 0.49 \)).

### 4. DISCUSSION

In this study, we found striking differences in winter distribution in relation to prior breeding outcome. Unsuccessful birds departed the breeding grounds significantly earlier, in line with other species [14,16,17]. Thereafter, we found strong evidence that they dispersed more widely when compared with successful breeders, with a greater proportion travelling to the West Atlantic, and females spending longer in that region than their successful counterparts. This macro-scale segregation spanned several thousand kilometres. However, unsuccessful and successful birds did not differ in the timing of return to the breeding colony the following spring. Our data obtained from geolocation loggers support conclusions from previous analysis of ringing recoveries that UK kittiwakes range widely across the North Atlantic and North Sea outside the breeding season [19]. We found no evidence that instrumented birds were unduly affected by the loggers, as breeding success and overwinter survival were comparable to unmanipulated birds. Thus, we are confident that the winter distributions are reliable.

The observed patterns may result from carry-over effects from breeding performance. Unsuccessful breeders may be more likely to migrate to the West Atlantic because they have more time available after the breeding season in which to undertake this movement. However,
movements to the West Atlantic tended to be of short duration (mean 8.0 ± 0.9 days), so it is not clear why successful breeders did not undertake this journey when they departed the colony just two weeks later. Unsuccessful breeders may also have been in better condition, as their costs of breeding will have been lower, which may have enabled them to undertake a longer migration. We also found that unsuccessful females spent more time in the West Atlantic than successful females. Carry-over effects may vary between the sexes as a result of differing size and/or breeding roles. Differences in non-breeding distributions between males and females have been identified in tracking studies or inferred from stable isotope signatures in large, sexually size-dimorphic seabirds, but not in small, sexually monomorphic seabirds [16,30,31]. However, female kittiwakes have been shown to exhibit higher metabolic rate [20] and energy expenditure [21,22] during chick-rearing than males. Thus, breeding outcome in females may produce a stronger carry-over effect on migration strategy than in males.

An alternative explanation for our results arises if there is repeatability in breeding success and winter distribution within individuals. Winter site fidelity and consistency in breeding performance could result from genetic and/or environmental factors (e.g. [11,32,33]). If so, it is possible that there is a causal link between winter distribution and breeding success, with selection against birds that travel to the West Atlantic. This would accord with studies that have demonstrated an association between winter diet, habitat and distribution, and summer breeding phenology and performance (e.g. [3–5]). Alternatively, repeatability in breeding success and winter distribution may result not from carry-over effects, but among-season correlations within individuals. Successful individuals may choose closer wintering areas because they are of better habitat quality [15]. In contrast, unsuccessful breeders may be less able to locate good wintering grounds. Unsuccessful birds may also be younger, on average, which could result in different distributions if kittiwakes show age-related spatial segregation, as demonstrated in wandering albatrosses, Diomedea exulans [34]. Alternatively, unsuccessful birds may be competitively excluded from good habitats, particularly if these are concentrated in relatively small patches. Long-term studies of year-round linkages are required to assess repeatability of breeding success and winter distribution. Furthermore, future work should aim to establish the relative quality of habitat in the East and West Atlantic, which would aid in disentangling carry-over effects from seasonal correlations. Whatever the mechanism, to our knowledge this is the first demonstration of a link between individual summer breeding performance and wintering distribution.

We expected that once kittiwakes returned to the vicinity of the colony in the spring they would remain there. However, a substantial number of birds subsequently made long-distance movements to the Central Atlantic. Similar pre-breeding movements have been observed in other species, and are typically made by females just before the egg-laying stage [14,35]. It has been suggested that these trips enable females to acquire resources for egg formation, while males guard territories and have a more limited foraging range [35]. However, in our case, the movements occurred earlier in the spring than previously recorded and, intriguingly, were carried out almost exclusively by males. It is possible that these birds used favourable winds and could thus travel large distances with relatively low energy costs. Also, the Central Atlantic may have provided profitable foraging opportunities. This region is characterized by high eddy variability and primary productivity, and recent evidence suggests that it supports significant concentrations of other seabird species [36]. However, it is currently unclear why such movements took place and why there was such a strong male bias.

Our data were collected after a poor breeding season in a winter during which adult survival was much lower than the long-term average. Although we did not find a difference in the return rate of successful and unsuccessful birds, our sample size was limited; it therefore remains possible that breeding success and subsequent survival are linked [8], mediated by variation in migration strategies. Thus, in a year with high breeding success, the overall wintering range may be smaller and the movements of individual birds restricted mainly to the East Atlantic. This may be associated with higher survival rates because of the reduced costs likely to be involved. Alternatively, this could result in increased competition for food, particularly if birds from other colonies behave in a similar way, and a greater risk from a threat that is spatially constrained, leading to reduced survival. Clearly, data from multiple years and colonies are required to establish whether these relationships occur.

Seasonal interactions and carry-over effects are a source of increasing research interest because of their potentially profound impact on population dynamics [1]. It is possible that the recent population declines recorded in this species are caused by a complex interplay between poor breeding seasons and harsher winter conditions. Our results have important implications for the identification of key wintering areas, as winter distribution is likely to be linked to breeding conditions and success in the preceding summer. Such associations will be a particular issue for declining species, such as the kittiwake, that are experiencing breeding failure with increasing regularity.

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