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Timing and extent of primary moult in breeding Black-legged Kittiwakes *Rissa tridactyla* at different colonies in the north-east Atlantic

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ABSTRACT
Timing of moult of the inner primaries by breeding Black-legged Kittiwakes is very similar among colonies ranging from southern England to northern Norway, but can be much later at very high-latitude colonies, such as at Svalbard, where breeding is delayed by the late spring thaw. Breeding adult Black-legged Kittiwakes almost all replaced the first and second (innermost) primary feathers on their wings while breeding.

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The progression of feather moult in birds is an important aspect of their ecology, with the timing and patterns of moult differing among bird species, and sometimes within species. It is necessary to study timing and patterns of moult in order to understand the extent to which it may constrain or be constrained by other energy-expensive activities, such as breeding (Jenni & Winkler 2020). However, it is also important to understand moult to underpin the increasing use of feathers as sampling tools for biological markers, such as pollutants or stable isotopes (Leat *et al.* 2013, Atkins *et al.* 2023). Investigating relationships between stable isotope signatures in feathers and bird diet (Furness *et al.* 2006, Morkūnė *et al.* 2016) or migration (Cherel *et al.* 2000, González-Solís *et al.* 2011, Leat *et al.* 2013) requires accurate information on species-specific timing and patterns of moult (Quinn *et al.* 2016, Atkins *et al.* 2023), because isotopes are incorporated from blood circulating into feathers as they grow, and remain unchanged once feather growth has been completed (Bearhop *et al.* 2002, Hobson & Bond 2012).

The Black-legged Kittiwake *Rissa tridactyla* (hereafter Kittiwake) is an abundant oceanic gull that breeds on sea cliffs across much of the higher latitudes around the North Atlantic and North Pacific. However, it is Red-listed due to its severe population decline since 1990 throughout the North Atlantic (OSPAR Commission 2008, 2019). The main threats to Kittiwakes in the North Atlantic are depletion of forage fish stocks and climate change (OSPAR Commission 2008, 2019, Burnell *et al.* 2023). However, the species is also subject to several new but probably smaller threats: the Kittiwake is one of the seabirds considered to be at greatest risk of collision mortality at offshore wind farms (Furness *et al.* 2013, Burnell *et al.* 2023), and has recently been subject to mortality caused by highly pathogenic avian influenza (HPAI) (Burnell *et al.* 2023, Scottish Government 2023). Understanding the moult of Kittiwakes will help to develop the use of markers in feathers as a tool to study movements of different populations, so will help in the development of a conservation strategy for this threatened species.

The Kittiwake's moult of the primary wing feathers has been studied in detail at North Shields (Tyne & Wear), in north-east England. Moult starts with the first, innermost primary ('primary one') which is moulted by immatures during spring (late April or May) but by breeding adults in late May or early June when these birds are incubating eggs (Coulson 2011). Primary feathers are moulted sequentially from primary one (innermost) to primary 10 (the longest outer primary), with moult normally being

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symmetrical on each wing. In the Kittiwakes at North Shields, the two innermost primaries on each wing (primaries one and two) are often shed at the same time, followed by primaries three and four once the preceding two are close to being fully regrown (Coulson 2011).

The rate of progress of primary renewal was found to be essentially the same in males and females but progressed marginally faster in immatures than in breeding adults, and in breeding adults the rate slowed during the second half of primary moult (Coulson 2011). Most breeding adults at the North Shields colony replaced the inner five primaries between early June and late August, during which time birds are attending the breeding colony, whereas the outer five primaries regrew between early August and December or even January (Coulson 2011), by which time birds are in wintering areas away from the colony. At North Shields, Kittiwakes laying eggs before 10 May began primary moult on 20 May, whereas those laying after 8 June started primary moult on 12 June; birds that began egg-laying later moulted slightly faster than those laying early, so tended to close the gap in the timing of moult progress (Coulson 2011). Among years, the timing of primary moult was influenced by the timing of breeding, with earlier moult occurring when breeding was earlier (Coulson 2011). However, based on examination of study skins in museums and on the extent of moult in birds killed in winter wrecks, Coulson (2011) concluded that the timing and pattern probably differs elsewhere, especially at higher latitudes, and that there was a need to study the Kittiwake's moult in the more northerly regions of the species' distribution. Of 64 Kittiwakes killed by an oil spill in Shetland in early January 1993, half were still growing primaries eight to 10. This suggested that their primary moult would not be completed until late January or February, apparently later than in birds from North Shields (Coulson 2011), and it was thought that many of these birds probably originated from northern Norway to Greenland rather than from the UK (Weir *et al.* 1996). In Shetland, the timing of breeding by Kittiwakes varies between years, probably according to local food availability (Lesser Sandeel *Ammodytes marinus* abundance) at the time (Pennington *et al.* 2004). This suggests that moult may be later in years, or regions, of poor food abundance (Adekola *et al.* 2021), or in regions where climate forces Kittiwakes to breed later than in north-east England (Belopolskii 1961, Barrett 1996).

This study uses data for Kittiwake moult at several colonies, with particular emphasis on Kittiwakes breeding in the northern part of their North Atlantic range, to investigate how timing of primary moult differs among populations and among individuals, and to assess whether sampling feather material from Kittiwake primaries for isotopic or elemental analysis provides reliable information on the presumed location of individual birds at the time of feather synthesis.

Data for 411 adults of known breeding status caught at nests at North Shields (55.00° N, 1.45° W) from 1954 to 2009 have been published by Coulson (2011). To add to those data, breeding adult Kittiwakes were caught (using a noose on a fishing pole) at nests containing eggs or chicks at a number of other colonies, with over 1100 breeding adults sampled at eight colonies/areas (Appendix 1): Lowestoft (Suffolk, England 56.01° N, 2.52° W) in 2023 ($n = 15$); Gateshead Saltmeadows Tower (Tyne & Wear 54.97° N, 1.59° W) in 2023 ($n = 15$); Dunbar (East Lothian, Scotland 56.01° N, 2.52° W) in 1984 or 1985 ($n = 65$); colonies in Orkney (Scotland 59° N, 3° W) in 2014 ($n = 56$); Fair Isle (Shetland, Scotland 59.52° N, 1.64° W) in 1984 ($n = 30$); Foula (Shetland 60.12° N, 2.08° W) in 1984 ($n = 84$); Hornøya (northern Norway 70.39° N, 31.16° E) from 29 June to 18 July 1983 ($n = 331$) and also 18 June to 13 July 1989 ($n = 465$); and at Hopen (Spitsbergen, Norway 76.58° N, 25.23° E) on 24–30 June 1984 ($n = 72$).

For all individuals, the moult of each primary feather in the right wing was scored on the internationally recognized six-point (0–5) scale where a score of 0 is an old feather, 1 is for a feather just starting to regrow (in 'pin'), 2 for a feather up to one-third grown, 3 for a feather between one-third and two-thirds grown, 4 for a feather more than two-thirds but not yet fully grown, and 5 for a completely regrown new feather (Ginn & Melville 1983, Jenni & Winkler 2020). The total primary moult score for each bird was calculated as the sum of each of the scores for the 10 primaries, so it varied from zero (all 10 primaries old) to 50 (all 10 primaries fully regrown). Total primary moult scores were then plotted against calendar date expressed as day from 31 May, for consistency following the method developed by Coulson (2011) for analysis of Kittiwake moult at North Shields.

The results showed that, at all colonies except Hopen (Svalbard), primary moult data from breeding adults caught at nests were consistent with moult starting at the end of May. The rate of moult during the first half of the primary moult averaged a score increase of 0.241–0.516 per day at the different colonies (Table 1). In contrast to this consistent pattern, a study of a sample of 72 adults caught at nests at Hopen (Svalbard) on 24–30 June 1984 found that only seven

Table 1. Summary of moult score progression of breeding adult Kittiwakes at different colonies. The regression equation refers to the estimated daily increase in moult score from 31 May.

Colony	Latitude (N)	Years	Sample size	Regression of moult score on days after 31 May	Correlation coefficient (Pearson r)	Predicted mean score on 1 July (observed mean score for Hopen)	Predicted mean score on 1 August
Lowestoft	52.5	2023	15	Y = 0.516x	0.99	16.0	32
Gateshead	55.0	2023	15	Y = 0.280x	0.96	8.7	17
N Shields	55.1	1954 to 2009	411	Y = 0.420x	0.77	13.0	26
North Shields	55.1	1984	16	Y = 0.260x	0.90	8.1	16
Dunbar	56.0	1984 & 1985	65	Y = 0.343x	0.94	10.6	21
Orkney	59.0	1984	45	Y = 0.293x	0.92	9.1	18
Fair Isle	59.5	1984	30	Y = 0.409x	0.97	12.7	25
Foula	60.1	1984	84	Y = 0.241x	0.87	7.5	15
Hornøya	70.4	1983	331	Y = 0.343x	0.96	10.6	21
Hornøya	70.4	1989	465	Y = 0.394x	0.98	12.2	24
Hopen	76.6	1984	72	n/a	n/a	0.0	n/a

of these birds had begun their primary moult, with moult scores of 5, 3, 2 (two birds) or 1 (three birds).

Excluding Hopen, the differences among colonies in the slope of moult score against days after 31 May could result from differences in the rate of primary moult of individual birds, or from differences in the mean date of the start of moult among colonies. The data suggest very little difference in primary moult progress between colonies as distant as Lowestoft at 52.5° N and Hornøya at 70.4° N (Table 1). Within that wide geographical range, birds from Foula (Shetland) in 1984 showed the slowest progression of primary moult (score increase of 0.241 per day).

There was much greater variability in the data from North Shields (collected over 55 years) than at any of the other colonies, which could be due to variation in the start of moult among years and/or the rate of moult; the correlation coefficient was 0.77 at North Shields, but higher for data from this site in 1984 alone (0.90), and at all other colonies where data were mostly collected in a single season (Table 1). Furthermore, at Hornøya in northern Norway, the data collected in 1983 differed from those collected in 1989, with the data suggesting an earlier start of primary moult in 1983 but slightly faster progress of moult in 1989, but with the timing and rate of primary moult being closely similar between breeding adults at Hornøya and at Dunbar in south-east Scotland. Figure 1 shows the mean moult scores on each date when birds were caught at these colonies.

At most colonies (excluding Hopen), all birds had regrown primary one to a moult score of at least 3 by late June or July (Table 2). However, 15 birds out of 133 sampled at Orkney and Shetland in 1984 had not reached that threshold. At most colonies (excluding Hopen), completely or nearly all of the sampled breeding adults had regrown primary two to a moult score of at least 3 by late June or July, but that percentage was much lower at Foula (Shetland). Excluding Hopen, most birds had begun to regrow primary three, but only a small proportion had begun to regrow primary four, and very few had begun to regrow primary five when sampled in late June or July (Table 2).

Coulson (2011) concluded that the timing of primary moult in breeding Kittiwakes was strongly influenced by the timing of breeding. Coulson suggested that the timing (and possibly pattern) of primary moult might, therefore, be significantly later in Kittiwakes breeding at high latitudes, and indicated that museum material further suggested this may be the case. Our results support this conclusion, with evidence that the timing of primary moult was about a month later at Hopen (Svalbard) than further south, as was the timing of egg-laying (Barrett 1996).

The timing of moult in Kittiwakes breeding at Hornøya in northern Norway was almost the same as at colonies in the UK (Table 1 and Figure 1), suggesting that variation in the timing of moult may be small across most of the breeding range of this species. This is consistent with evidence on the timing of breeding; the mean egg-laying date at North Shields was 18 May (Coulson 2011), while it was 22 May at Foula in Shetland in 1976 (Furness 1979) and 20 May in 1980 at Hornoya (Barrett 1983). In contrast, Kittiwakes breeding at Hopen (Svalbard) were much later, with a mean laying date of 14 June in 1984 (Barrett 1996). Kittiwakes breeding at the northern extreme of their breeding range in the North Atlantic and Barents Sea, at Svalbard (Løvenskiold 1964), Novaya Zemlya and Franz Josef Land (Belopolskii 1961), are constrained by the timing of spring melt of snow and ice, with the first eggs often appearing in mid-June, but this is variable among years and can be as late as early July (Belopolskii 1961). Svalbard,

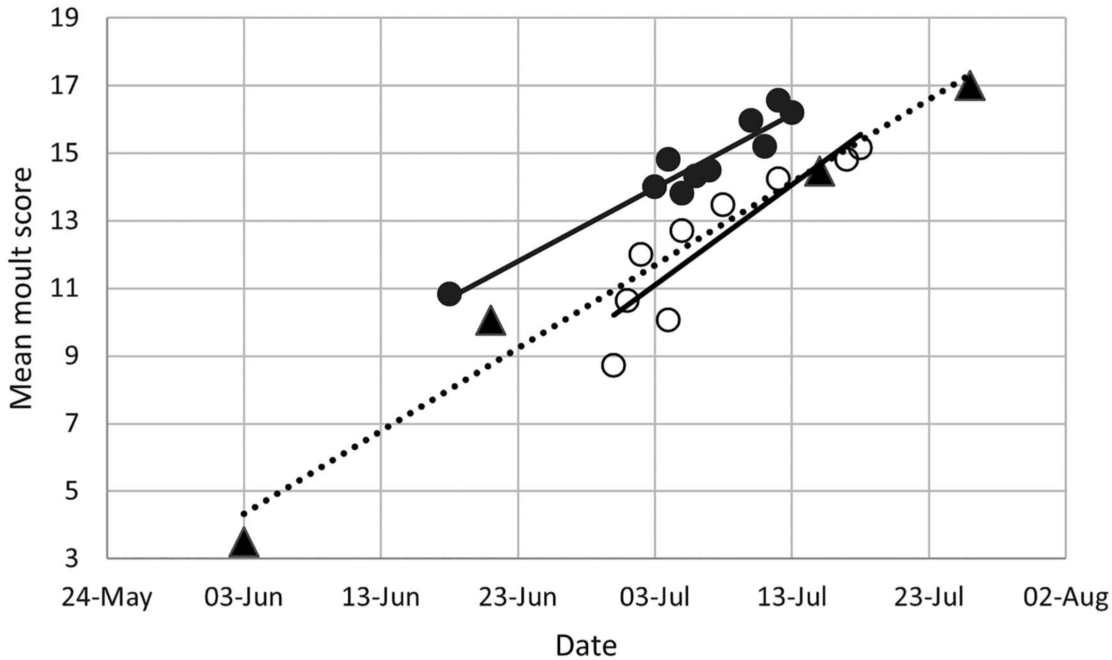

Figure 1. Mean moult scores on different dates of adult Black-legged Kittiwakes caught at nests at Hornøya, in northern Norway (331 birds sampled on 10 dates in 1983: grey dots and grey solid line; and 465 birds sampled on nine different dates in 1989: black open circles and black solid line), and at Dunbar (East Lothian) in Scotland (66 birds sampled on four different dates in 1984 or 1985: black triangles and black dotted line).

Novaya Zemlya, and Franz Josef Land lie close to the northernmost limit of breeding Kittiwakes (see Figure 1.1 in Coulson 2011), suggesting that climate extremes may delay both the timing of breeding and of moult in this region, although there is little influence of climate on the timing of breeding and moult further south in Europe. It would be interesting to analyse moult data from colonies in Canada, where sea ice progresses much further south than in Europe, and therefore the timing of breeding and onset of moult may differ in the western North Atlantic.

The data indicate relatively consistent moult scores among breeding adult Kittiwakes on a particular date at a given colony, but indicate some variation among years, shown by the lower correlation coefficient at North Shields over a period of decades, rather than in a single year, and lower than at other colonies studied within one season, and by the consistent difference seen at Hornøya between 1983 and 1989. The timing of moult may be influenced by food availability, with birds in colonies subject to food shortages tending to breed later (Pennington *et al.* 2004), and late breeding therefore resulting in late onset of primary moult (Adekola *et al.* 2021). The presence of a small number of breeding adults at Orkney and Foula (Shetland) that had not started primary moult by early July may also relate to the declining abundance of Lesser Sandeels in those areas in the mid to late 1980s, which led to greatly reduced survival of adult Kittiwakes (Oro & Furness 2002) and a collapse in breeding numbers (Pennington *et al.* 2004, Burnell *et al.* 2023).

Table 2. Percentage of breeding adult Kittiwakes where the regrowth of primary feathers has progressed to a moult score of 3 or more by sampling dates in late June or July. P1–P5 refers to the primary feather from the innermost (P1).

Colony	Sampling date	Sample size	P1	P2	P3	P4	P5
Lowestoft	27 June	15	100	100	80	7	0
Gateshead	10 July	15	100	87	33	0	0
Dunbar	21 June	20	100	90	15	0	0
Dunbar	15 July	15	100	100	80	0	0
Dunbar	26 July	6	100	100	83	33	17
Orkney	15 July	33	94	88	55	18	0
Fair Isle	28 June to 4 July	27	100	96	59	0	0
Foula	3 to 5 July	73	82	60	22	3	0
Hornøya	10 to 18 July	323	100	99	81	21	0
Hopen	24 to 30 June	72	1	0	0	0	0

Extrapolating the rate of primary moult to predict the mean moult score of breeding adults at each colony by 1 August (Table 1) suggests that the score would be between 15 and 32 by that date. That is equivalent to having the three to six innermost primaries fully regrown. Kittiwake chicks tend to fledge in late July and disperse by early August (Coulson 2011), and breeding adult Kittiwakes tend to disperse from the colony during August. However, the departure of breeding adults from the colony at North Shields varied considerably from year to year, being as late as

November in some years and as early as August in others (Coulson 2011). Most of the Kittiwakes breeding in northern Norway and in other areas in the Barents Sea disperse from the colonies in late August or early September (Anker-Nilssen *et al.* 2000). It can be concluded from this that most adult breeding Kittiwakes at UK and Norwegian colonies will grow most of the four innermost primary feathers while attending the colony, so that isotopic signatures in those feathers will reflect the local environment of the foraging range around the breeding colony. It is highly likely that primaries one and two are regrown while the bird is attending the colony, and also likely for primaries three and four. However, some failed breeders may depart from the colony before primaries three and four are regrown, and a few individuals may start moulting much later than most adults.

There is a low risk of the innermost primaries having an isotopic signal influenced by locations away from the colony foraging area, and that risk will be higher for primaries three and four than for primaries one and two. Some or all of the outer primary feathers (primaries five to 10) are likely to grow while the bird is on migration or in its wintering area, and therefore will be likely to have different isotopic signatures that are unrelated to the breeding colony from which the bird had departed. Instead, they will reflect the environment in which the bird was feeding as those feathers were growing. However, the locations represented by primaries five to 10 may vary considerably from year to year, as Kittiwake migration appears to vary considerably in timing and extent under different circumstances. For example, Kittiwakes breeding in northern Norway tend to move first to Svalbard before migrating south-west towards Newfoundland, whereas some Kittiwakes breeding at colonies in Britain and Ireland remain in European waters while others migrate to Canada (Frederiksen *et al.* 2012). Individuals make these migratory movements at rather different times and possibly with different rates of primary moult. Kittiwakes breeding at the Isle of May, in eastern Scotland, that migrate rapidly towards Newfoundland after breeding tend to be birds that have bred unsuccessfully, whereas those that remain in European waters are predominantly birds that bred successfully (Bogdanova *et al.* 2011). Outer primaries are therefore likely to be grown by some individuals in Canadian waters and by others from the same colony in European waters.

Kittiwakes using a roost at Bear Island (so possibly a mixture of immature birds and breeding adults) moulted inner primaries at the colony, but none had moulted primaries 8 to 10 before the end of July, indicating that the outermost primaries were most likely grown in the wintering area (Meissner 2002). Hobson & Bond (2012) used the outer primaries of Kittiwakes to infer winter diet from stable isotopes. Carbon and nitrogen isotopic signatures in Kittiwakes breeding in northern Norway differed progressively between primary feathers as the birds moved from their breeding colony to overwintering areas in the West Atlantic, leading the authors of that study to conclude that stable isotope analysis of outer primary feathers can be used to trace migratory movements of individuals (González-Solís *et al.* 2011).

Sampling the tips of the innermost primaries of breeding adult Kittiwakes should provide material derived from food ingested by these birds from waters around the breeding site. Sampling of the outermost primaries will most likely provide material derived from food ingested by these birds in their wintering area, but that latter conclusion seems slightly less reliable given the variation in the rate of moult and the extent of migratory movements of different individuals, and would best be supported by deployment of geolocators. It seems that these conclusions hold good for Kittiwakes breeding at most colonies in the north-east Atlantic, with the exception of those at the very northernmost limit of the breeding range, where there is an uncertain extent of primary regrowth while birds are attending the colony.

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Appendix 1

Map of North East Atlantic and Barents Sea showing locations of the eight study colonies (red dots) in relation to the coastline where Black-legged Kittiwake colonies are present (black line) or absent (white coastline). Data on the breeding distribution of kittiwakes is redrawn from Coulson (2011).