The effect of the 2023 bird flu outbreak on the population biology of Common Guillemots on Skomer Island

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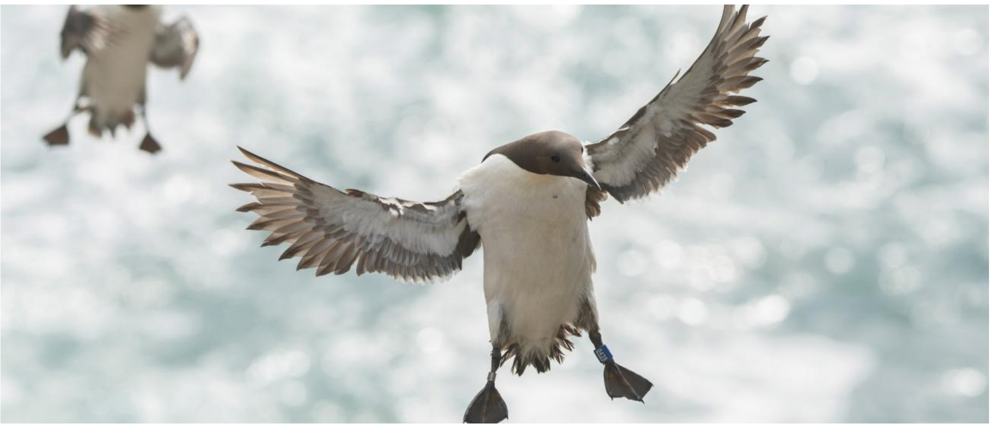

Abstract The outbreak of Highly Pathogenic Avian Influenza (HPAI, 'bird flu') first detected in the UK in 2021 has resulted in the deaths of millions of birds, both domesticated and wild, and is a major conservation threat to seabirds. During the summer of 2023, HPAI killed many Common Guillemots *Uria aalge* in Britain. Amongst the birds killed on Skomer Island, Pembrokeshire, were a number of ringed individuals from a long-term population study there. This paper makes a preliminary assessment of the impact of HPAI-driven mortality on the Skomer Guillemot population. This assessment was complicated by the fact that, for the first time in the 50-year history of the study, there was clear evidence that in 2023, prior to the HPAI outbreak later that summer, Guillemots were short of food, evidenced by a late breeding season, unusually low off-duty partner attendance during chick-rearing, and underweight chicks. The number of recoveries of Skomer-ringed Guillemots during July and August 2023 – assumed to be due to HPAI – was greater than in any previous year of the study. To assess the impact of events in 2023, we monitored the breeding population in 2024 and found that sightings of ringed Guillemots (indicative of adult survival) were 20–30% lower than in previous years. There was also clear evidence of 'compensatory recruitment' in 2024, with younger birds moving into the colony to occupy sites left vacant by HPAI deaths. This, together with a reduction in breeding density, resulted in relatively low breeding success (0.68 chicks/pair) in 2024 compared with previous recent years (0.80 chicks/pair). The timing of egg-laying and off-duty partner attendance were both apparently normal in 2024, suggesting that food supplies were not compromised. Overall, we estimate that the 2023 bird flu outbreak resulted in the loss of 20–30% of the Guillemot population on Skomer, a figure presumably mirrored across other colonies in South Wales. The full impact of the HPAI outbreak on the Guillemot population, however, will take several years to elucidate.

Introduction

H5N1, a highly pathogenic strain of avian influenza (HPAI, 'bird flu'), originated from intensive poultry-farming facilities in Asia in 1996 (Cunningham *et al*. 2002; Klaasen & Wille 2003; Adlhoch *et al.* 2022, 2023) and was first detected in the UK in 2021. To date, over 70 species have been affected, notably Barnacle Geese *Branta leucopsis*, Black-headed Gulls *Chroicocephalus ridibundus,* Common Terns *Sterna hirundo* and Great Skuas *Stercorarius skua*. In 2022, bird flu also affected Northern Gannets *Morus bassanus* and, in 2023, the virus appeared in other seabirds, including Common Guillemots *Uria aalge*, Razorbills *Alca torda* and Kittiwakes *Rissa tridactyla* (Pearce-Higgins *et al.* 2023; Tremlett *et al*. 2024).

In the 1930s, the Common Guillemot population on Skomer Island, Pembrokeshire, comprised around 100,000 individuals, but it showed a dramatic decline after the Second World War, probably as a result of oil pollution, and numbers had fallen to just 2,000 individuals by the early 1970s (Birkhead 2016). A population study of Guillemots on Skomer has been running since 1972, with detailed monitoring of numbers, timing of breeding, breeding success, chick diet and adult and immature survival since the 1980s (Hatchwell & Birkhead 1991; Votier *et al*. 2005, 2008, 2009; Meade *et al*. 2012; Birkhead 2023). This study showed that, between 1980 and 2022, the population started to recover from the post-war declines, increasing at an average rate of around 5% per annum and, by 2022, 31,790 individuals –or about 21,000 pairs –were recorded on the annual whole island census (Newman *et al.* 2022; Birkhead & Montgomerie 2023).

Common Guillemot

Klaus Nigge

3. Common Guillemot *Uria aalge*, Skomer, Pembrokeshire, July 2023.

In the late summer of 2023, just after most Guillemots had left the colony at the end of the breeding season, hundreds of dead Guillemots, including an unprecedented number of ringed individuals from the Skomer study, were found washed up on Welsh beaches; in total, 1,600 dead Guillemots were found between 11th July and 23rd August (L. Morgan pers. comm.). This mirrored events at a Guillemot colony on the German North Sea island of Helgoland in mid to late May, where hundreds of adult and juvenile Guillemots were found dead; many of these birds tested positive for HPAI (Jochen Dierschke & Elmar Ballstaedt pers. comm.).

In this paper, we provide a preliminary assessment of the effect of the 2023 HPAI outbreak on the Common Guillemot population on Skomer Island.

Methods

The population parameters measured and the methods employed each year in the Guillemot study have been described elsewhere (e.g. Birkhead 2023). Briefly, these include: numbers, monitored at selected study plots and from whole island counts; timing of breeding, monitored for a sample of c. 100–130 pairs at a single study plot and recorded as the median laying date; breeding success, measured for the same sample of 100–130 pairs (one or both pair members being individually ringed) and recorded as chicks surviving to leave the colony per pair; chick diet, fish species fed to chicks identified visually and from specimens recovered from adults feeding chicks (see Riordan & Birkhead 2018); and adult and immature annual survival measured from re-sightings of individually ringed birds (c. 12,000 ringed up to 2023) and calculated using Capture-Mark-Recapture (CMR) methodology (see Votier *et al.* 2005, Meade *et al.* 2012 and Birkhead 2023).

In 2023, we also recorded off-duty parental attendance throughout the chick-rearing phase for all pairs that were also monitored for breeding success, using methods previously employed on Skomer (Birkhead 1976; Hatchwell 1988) and on the Isle of May (Wanless *et al.* 2023). This index of parental effort comprised recording the presence of 'neither', 'one' or 'both' parents at noon each day at each of 100–120 sites with a chick throughout the chick-rearing period. Normally, one parent is present continuously with the egg or chick. In periods when food is plentiful, off-duty parents spend more time at their breeding site with their partner. If food is in short supply, the off-duty partner spends less time at the site and more time at sea and, when food is extremely short, both parents may temporarily abandon their egg or chick and spend time at sea foraging.

The index of parental effort and the ratio of breeding pairs to number of individuals present during the census period (known as the ‘k value’; Birkhead & Nettleship 1980) both provide an index of food availability. The difference is that the k value includes attendance by both breeding birds and non-breeding birds. We also recorded chick body mass and wing length to obtain an estimate of chick mass relative to age in 2023, as in some previous seasons (Birkhead 1976; Hatchwell 1988).

In 2024, we continued to monitor the population, recording numbers, timing of breeding, breeding success, chick diet, off-duty parental attendance and sightings of ringed individuals as a preliminary estimate of adult mortality since 2023. We were unable to record chick body mass in 2024 as the threat of a further HPAI outbreak (see below) meant that no ringing – and therefore no biometric data collection from chicks or adults – was undertaken.

Guillemot

Klaus Nigge

4. Colour-ringed Common Guillemot, Skomer, Pembrokeshire, July 2023.

Results

Timing of breeding

The median laying date in 2023 was 12th May (n = 133 sites), which was relatively late compared with the previous four years (2nd May in 2019 and 2020, 4th May in 2021 and 2nd May in 2022). The median laying date has advanced by over two weeks since the start of data collection in the 1970s, albeit with some year-on-year variation including some ‘late’ years (e.g. 11th May 2018; see Birkhead & Montgomerie 2023). In 2024, the median laying date was 8th May (n = 120 sites).

Breeding success

In 2023, breeding success was measured at 0.81 chicks/pair (n = 133 pairs), which was similar to breeding success in all recent years since 2000, excluding 2021, when storms during the breeding season reduced breeding success to 0.64 chicks/pair (Birkhead 2023). In 2023, only one out of 18 pairs (6%) that lost their first egg laid a replacement, a lower proportion than in 2018 (25%), 2019 (82%), 2020 (50%), 2021 (31%), 2022 (44%) and 2024 (57%) (unpublished data). In 2023, a small number of dead chicks were observed on our study plots and, at the time, their deaths were attributed to the recent extremely hot and extremely wet weather. In 2024, breeding success was 0.68 (n = 120 pairs), which was lower than in 2023 and most recent years.

Off-duty attendance

The index of parental effort in 2023 was 1.03, showing that off-duty partners spent very little time at the colony during chick rearing. This contrasts with 2024 (1.32) and earlier years for which equivalent data are available (1.31 Birkhead (1976) and 1.18 Hatchwell (1988)) and is consistent with there being a shortage of food in 2023 (see Wanless *et al.* 2023) and by our chick growth data (below). In addition, the k value in 2024 at one study site was 0.63, which is similar to the value of years on Skomer in the early 1970s (0.67; Birkhead 1976), but strikingly different from the situation on the Isle May during a period of food shortage and population decline when both k values and the index of parental effort were close to 1.0 (Harris *et al.* 2015; Wanless *et al.* 2023). No estimate of the k value on Skomer was made in 2023.

Amos Common Guillemot Uria aalge study colony

Klaus Nigge

5. The Amos Common Guillemot *Uria aalge* study colony on Skomer, Pembrokeshire, in (a) late June 2023 and (b) late June 2024. In both photographs, the density of birds is similar because of compensatory recruitment (see text), despite the substantial bird-flu mortality after the end of the 2023 breeding season. During the mid-incubation period in 2024, the density on the Amos was noticeably lower than in late June, suggesting that immature Guillemots continued to recruit onto the breeding ledges throughout the 2024 season.

Guillemot colony

Molly Brown

Sightings of ringed birds

Fig. 1 shows the cumulative total of individually marked birds (each counted only once per year) seen at the main study plot ('The Amos') each year between 2019 and 2024. Trajectories for the years 2019–23 were broadly similar, but sightings in 2024 (a total of 650 different individuals) were 20–30% lower and were probably a reflection of mortality caused by HPAI in 2023. Sightings provide a useful proxy for adult survival, which can be calculated, using CMR methodology, after just one or two further years of data to allow for birds missed in one year and resighted in another (White & Burnham 1999). It is possible that the lower rate of sightings in 2024 could be the result of birds not visiting the colony because of some carry-over effect of HPAI in 2023, but we will be able to check this only in 2025–26.

Fig. 1

Fig. 1. Cumulative number of sightings of individually colour-ringed Common Guillemots *Uria aalge* on the Amos study site on Skomer. The total number of birds seen in 2024, the year after the bird flu outbreak on the island, was much lower than in the previous five breeding seasons.

However, the exceptional number of ringing recoveries in 2023 concerning birds found dead indicates a much higher than normal mortality, rather than birds simply not visiting the colony. Specifically, between 16th July and 8th August 2023, we received reports of five of our colour-marked birds being found dead (a sixth bird, which probably also died during this period, was found long dead in February 2024). The combined total number of Skomer-ringed birds recovered dead in July and August between 1988 and 2020 was just ten, with no more than two of these coming from any given year (fig. 2). The scarcity of Guillemot ringing recoveries at this time of year has been documented at other colonies (Harris *et al*. 1997; Wernham *et al*. 2002). In other words, the number of recoveries of Skomer-ringed birds in July/August 2023 was 16 times greater than the average in previous years. The recoveries included one chick recovered 28 days after ringing, with the rest being adult birds aged between four and 30 years old.

Fig. 2

Fig. 2. Mean number of ringing recoveries per month of Common Guillemots ringed on Skomer in the 32 years between 1988 and 2020 and found dead as adults (total = 137 recoveries). The exceptionally high number of recoveries between 16th July and 8th August 2023 is indicated by the red square.

Additionally, an unringed adult Guillemot was observed dead and being eaten by a Great Black-backed Gull *Larus marinus* in the sea beneath the Amos colony on 1st July 2023. To see a dead adult Guillemot at the colony during the breeding season is extremely unusual.

In 2024, an adult Guillemot that had been ringed on Skomer in 2006 was found dead in north Cornwall, 150 km to the south, on 15th June. As mentioned above, ringing recoveries of Guillemots during the breeding season are unusual and this bird may have been the victim of another HPAI outbreak. This was further supported by observations through June 2024 –as chicks began hatching, a minimum of six were seen dead on the breeding ledges and, on 27th June 2024, an adult Guillemot was seen dead in the sea beneath the breeding colony. We therefore decided not to conduct any ringing, which prevented us from collecting data on chick or adult body mass. There was no subsequent evidence for an HPAI outbreak on Skomer – or, for that matter, at any other colony in the UK (BTO data; Dawn Balmer pers. comm.) – but a cautious approach nonetheless seemed most appropriate.

ringed Guillemot

Dan Parkinson

6. An 11-year-old adult Common Guillemot, ringed as a chick on Skomer in 2012 and found dead on 23rd July 2023 at Newgale, Pembrokeshire. It was most likely a victim of HPAI.

Chick diet

In both 2023 and 2024, the majority of fish fed to Guillemot chicks were clupeids (84% in 2023; 85.4% in 2024), with much smaller numbers of gadids (10.7%; 5.3%), sandeels (3.7%; 6.6%) and other species (1.6%; 2.7%). However, there was an indication of unusual prey species being fed to chicks in 2023, with the 'other species' including Atlantic Mackerel *Scombrus scombrus*, which had not been recorded previously during the 50 years of study. Fish specimens obtained from Guillemots during ringing showed that some fish that had been recorded as clupeids in visual assessments were in fact Atlantic Mackerel and Atlantic Herring *Clupea harengus*. Collected specimens, however, confirmed that the majority of clupeids were, as in previous years, European Sprats *Sprattus sprattus* (Riordan & Birkhead 2018).

Chick growth

Guillemot chicks with a wing length of 60 mm are old enough to leave the colony (Hatchwell 1988). From regression models (e.g. fig. 3), the mean mass of chicks at this age was 240 g in 1975, 206 g in 1985, 213 g in 1986, 220 g in 1987 and just 166 g in 2023. Therefore, the mean mass of chicks in 2023 was some 25% lower than in earlier years, presumably because of a food shortage.

Fig. 3

Fig. 3. Body mass vs wing length (as an index of age), for Common Guillemot chicks measured at ringing on Skomer in 2023 and 1986. Note log scale on both axes and that chicks in 2023 were extremely underweight (see text).

In addition, the median fledging age of chicks in 2023 was 24 days (range 18–29 days, n = 108), whereas in 2021 and 2022 it was 21 days (which is typical; e.g. Hatchwell 1988). No values for chick growth were obtained in 2024, although the median fledging age of 19 days (n = 79) is consistent with normal or slightly better than normal growth.

Adult body mass

The mean body mass of 51 breeding adult Guillemots on the Amos on 1st July 2023 was 820.0 g (±48.6 SD, range 730–930 g) and did not differ significantly from the combined average body mass of 838.5 g for adults weighed during the chick-rearing period in 1986 and 1987 (± 57.9 SD, range 714–928, n = 17; Hatchwell 1988) (t = 1.15, 66 df, P>0.05).

Census counts

In 2023, counts of individual Guillemots at study plots averaged 356.2 birds, while the whole island count was 29,141, both down on the 2022 counts of 389 and 31,790 respectively (Newman *et al.* 2023; unpublished data). This 8% decrease was in contrast to the expected ~5% rise had the population continued its trajectory of increase (table 1). In 2024, the whole island count was 29,491 individuals, an apparent slight increase on the 2023 value, although the combined counts at four study plots counted on ten occasions in 2024 had a mean value of 333.9 individuals, 6.3% lower than in 2023.

Compensatory recruitment

In 2023, 20 out of 137 birds (14.6%) in our breeding study plots were breeding for the first time, with a mean age of 7.30 years (± 1.17 SD, n = 20). In 2024, 30 of 120 birds (25%) on our plot were first-time breeders, with a mean age of 6.18 years (± 1.49 SD, n = 30). Both effects – the higher proportion of first-time breeders and the reduction in their age – were statistically significant ($p<0.01$) between years. In other words, following the HPAI mortality in late 2023, the population in 2024 contained a greater proportion of recruits that were also younger than in the year before. In addition, and as expected, the breeding success of first-time breeders was relatively low in both 2023 (0.29 chicks/pair) and 2024 (0.47 chicks/pair) compared with the overall breeding success of around 0.80 chicks/pair on Skomer (see above) and at sites elsewhere (Harris *et al.* 2016).

Discussion

In the 40 years of intensive Guillemot monitoring on Skomer, 2023 was the most unusual breeding season, resulting from an unprecedented food shortage followed by an outbreak of HPAI that killed a large number of birds.

The 2023 Guillemot breeding season on Skomer was late compared with recent years. There are two possible causes of this late breeding. The first of these is 'Storm Noa', which hit the UK on 12th April 2023 and was reported to be 'the most significant April wind storm to affect England and Wales since April 2013' (https://bit.ly/49pr4RO). It is well established that storm conditions and heavy seas can compromise the ability of Guillemots to find sufficient food (Underwood & Stowe 1984; Morley *et al*. 2016), and this storm, which coincided with the period when female Guillemots would normally be starting to form their egg (i.e. approximately two or three weeks before laying (Birkhead & del Nevo 1987; Hatchwell & Pellatt 1990)), may have resulted in later laying than in recent years.

However, a more likely cause of late breeding in 2023 is that sea temperatures around the UK coast were higher than in any previous year on record (https://bit.ly/3Bd3Bq6). Fish populations can be negatively affected by sudden rises in sea temperatures with knock-on negative effects on Guillemots – as occurred during a 'marine heatwave' in 2014–16 on the west coast of North America (Piatt *et al*. 2020).

High sea temperatures in the vicinity of Skomer in 2023 may have affected the abundance or availability of small fish that comprise the Guillemots' diet.

However, there was no evidence that other seabird species breeding on Skomer or the neighbouring island of Skokholm were similarly affected in 2023 (G. Eagle & R. Brown pers. comm.; M. Wood pers. comm), although these other species are monitored less rigorously than the Guillemots on Skomer.

These two environmental events – Storm Noa, and unprecedented sea temperatures and associated food shortage –make assessing the effects of the subsequent HPAI outbreak in 2023 more complex than it would otherwise be.

Changes in the status of a population are usually assessed through census counts. On Skomer, two types of counts have been made each year: whole island counts (since the 1960s) and study plot counts (since 1973) (see Birkhead & Montgomerie 2023) Both censuses showed that numbers were 8% lower in 2023 than they were in 2022. In 2024, the whole island count was similar to that in 2023 and the study plot counts were 6.3% lower than in 2023, suggesting overall only a small reduction in numbers between 2023 and 2024 and hence only a small impact of HPAI on the Guillemot population.

However, there are two reasons why it is not possible to use these census counts *directly* to assess the extent of HPAI mortality on Skomer's Guillemots. Firstly, a comparison between 2023 and 2024 is confounded by the low level of off-duty partner attendance in 2023, which superficially suggested a reduction in the size of the population when, in fact, no reduction had occurred.

The interpretation of census counts of individual Guillemots relies on the assumption that the ratio between the number of breeding pairs and the number of individuals on the same ledges (k values), or the attendance of off-duty partners, is constant between years. This was not the case on Skomer in 2023 and, as Harris *et al*. (2015) showed, this was also often not the case at the Isle of May where, in contrast to Skomer, Guillemot food availability has varied dramatically between years (see Wanless *et al.* 2023).

Secondly, it is established that in the year(s) immediately following a major mortality event in animal populations, such as those caused by culling, acute oil pollution or acute food shortage, census counts are often higher than expected from the observed mortality. This is because of compensatory recruitment, with premature movement of individuals from the non-breeding population into the breeding population – a phenomenon that has been recorded in whales, ungulates and fish, as well as birds (Coulson *et al*. 1982; Boyce *et al*. 1999; Votier *et al*. 2008). In the case of Guillemots, non-breeding birds, generally aged 3–5 years old, congregate in 'clubs' on tidal rocks near breeding colonies during the breeding season, while older birds spend more time on the breeding ledges and breed for the first time at around five to seven years old (Birkhead 1976; Birkhead & Hudson 1977; Hatchwell 1988).

By inflating numbers on the breeding areas counted in censuses (as in 2024; see table 1), compensatory recruitment can mask and reduce the perceived amount of damage inflicted on a population caused by severe environmental and/or anthropogenic events (Tremlett *et al*. 2024). Moreover, unusually high mortality followed by compensatory recruitment can have complex knock-on effects for a population. In a study of gulls, for example, a cull of adult birds followed by compensatory recruitment resulted not only in a reduction of the age at recruitment and first breeding but also body size, egg size and colony fidelity (Coulson *et al*. 1982). A study of Bighorn Sheep *Ovis canadensis* showed that mortality mediated by trophy hunting resulted in inexperienced, sometimes lower-quality individuals breeding in place of more experienced individuals that had been shot (e.g. Coltman *et al.* 2003).

table 1

Sightings of ringed Guillemots in 2024 suggested that 20–30% of the Skomer population died as a result of the 2023 HPAI outbreak (fig. 1). However, it is possible to obtain an independent estimate of the numbers killed in the 2023 HPAI outbreak using existing knowledge of the Skomer Guillemot population trajectory (see Birkhead & Montgomerie 2023), together with a careful interpretation of the 2022 and 2024 census counts.

Since 1980, the Skomer Guillemot population has increased at about 5% per annum. Assuming that it would have continued to do this after 2022 (a reasonable assumption given that the population was still well below the 1930s carrying capacity of 100,000 individuals (Birkhead 2016)), the population in 2024 would have been substantially larger than that recorded (table 1). However, because recruitment was 10% greater in 2024 than in 2023 (see above), the 2024 population counts are around 10% higher than they would otherwise have been. Together, these values suggest that the mortality due to HPAI was 17–30% (table 1), very similar to the estimate derived from the sightings of individually marked birds (fig. 1).

The most reliable estimate of the magnitude of the damage caused by the HPAI outbreak is, however, the mortality rate calculated from the resightings of individually marked birds. Because of the need to account for birds missed in one year and seen in a later year the data enabling us to make these calculations for the adult Guillemot population on Skomer will not be available until 2026. It will take even longer to detect any effect on recruitment into the breeding population because of the progressive return of immatures to the breeding colony over several years (Birkhead 2023).

Since the 2023 HPAI outbreak occurred late in the Guillemot breeding season and mainly after the birds had left the colony, there was little direct evidence of the epidemic at other, less closely monitored colonies. It is difficult therefore to assess the total mortality across the entire Welsh region or, indeed, elsewhere in the UK. An added complexity is that bird flu outbreaks seemed to occur patchily, both within and between colonies. We noticed in July 2023, for example, that areas of Skomer that had held breeding Guillemots the year before were completely devoid of birds. On Skokholm, this same 'patchiness' was apparent, with one colony (North Gulley, where a dead adult had been seen in July 2023) noticeably depleted in 2024 while Guillemot numbers at others were either unchanged or had increased (see https://skokholm.blogspot.com/2024/06/following-yesterdays-glorious-weather.html, G. Eagle & R. Brown pers. comm.).

As we predicted, Guillemot breeding success in 2024 was lower than in most previous years, for two reasons. Firstly, success depends upon high-density breeding to provide protection to eggs and chicks from gulls and corvids. It was evident both on Skomer and at other colonies (e.g. Skokholm, see above) that, in the early part of the 2024 breeding season, density was reduced following the 2023 HPAI outbreak. The relationship between breeding density and breeding success in Guillemots is a form of positive density dependence, also referred to as the Allee effect, and is typical of Guillemots (Birkhead 1977; Hatchwell 1991). Secondly, Guillemots breeding for the first time have lower success than older birds and, in 2024, the proportion of birds breeding for the first time was higher than in the previous year.

David Lack, the twentieth-century authority of population regulation in birds, identified three density-dependent factors that regulate the size of bird populations – (i) food shortage; (ii) predation; and (iii) disease –with food the most important of these (Lack 1954, 1966). He also recognised that these three factors may interact with each other in complex ways. Such interaction is exemplified in the present study.

First, food. The sustained 40-year increase in the size of the Skomer Guillemot population since 1980 is likely to have been facilitated by food availability. In contrast, the acute shortage of food during the 2023 breeding season resulted in an increase in parental effort during chick rearing and a reduction in chick body mass on leaving the colony, both of which may result in reduced survival and a reduction in population size (see Wanless *et al.* 2023).

Second, disease. As is evident from the present study, the outbreak of avian influenza in 2023 resulted in a substantial increase in adult mortality, although its true effect on population size is masked by several confounding factors (see above). Guillemots typically breed at high density, a feature that almost certainly facilitated the transmission of HPAI within colonies and may well have been far worse had the outbreak occurred earlier in the breeding season.

And third, predation. The decrease in the 2024 breeding population size following the HPAI outbreak in 2023 resulted in a reduction in breeding density that made Guillemots more susceptible to egg and chick predation by gulls and corvids and, while breeding success has a much less powerful effect on population size than the survival of adult and immature birds (Meade *et al*. 2012), it nonetheless has some effect on population change.

In conclusion, our estimates suggest that 20–30% of the Guillemot population may have died as a result of bird flu in 2023 – equivalent to putting back numbers by five years in the long-term population increase. This loss was not reflected in the 2024 census counts, however, because of compensatory recruitment – an earlier-than-normal influx of birds from the non-breeding population onto the breeding ledges –creating the impression that the damage caused by bird flu was much less than it actually was.

Fig. 4

Fig. 4. A summary of events affecting the Guillemot population on Skomer Island, Pembrokeshire, in 2023 and their consequences in 2024.

Because Guillemots typically do not breed until they are seven years old, there is always a population of non-breeding birds, and it is from this non-breeding population that the new recruits come.

The status of a bird population is usually assessed from census counts. However, it is not widely recognised that the interpretation of census counts depends on several assumptions, notably here that the ratio of individual Guillemots (the usual count unit) to breeding pairs is the same between years, and that levels of mortality and recruitment are fairly constant between years. Neither assumption was true in the years during and after the bird flu outbreak.

The reduced colony attendance by off-duty birds in 2023, owing to food shortage before the outbreak, resulted in census counts that were lower than during the previous year and lower than predicted from the decades-long trajectory of population increase. The 2023 census counts therefore provided an inappropriate point of comparison for counts made in 2024 when off-duty parent attendance was normal.

Although superficially reassuring, compensatory recruitment comes with at least two potential costs. First, as studies of other species have shown, it allows individuals to breed that under normal circumstances would be unable to acquire breeding status because they are of low quality (e.g. Coltman *et al.* 2003). Second, this in turn may result in fewer potential recruits in subsequent years and lower, or even negative population growth. This would be the case if compensatory recruitment in 2024 left only a small population of non-breeding individuals. On the other hand, if the remaining non-breeding population is large, compensatory recruitment will probably make little difference to subsequent population change. Population modelling, together with census counts of both the breeding population and the non-breeding population present in clubs (see above) will be needed to assess the consequences of the 2023 bird flu outbreak and 2024 compensatory recruitment seen in the Skomer population of breeding Guillemots.

This study emphasises the value of scientifically rigorous long-term monitoring not only for interpreting events in 2023 and 2024, but also for assessing future changes in the Skomer Guillemot population and seabird populations elsewhere.

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