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Population trends of marine versus terrestrial bird species on Skúgvoy, Faroe Islands, 1961–2023

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ABSTRACT

Capsule: Long-term breeding bird censuses on the Faroese Island of Skúgvoy showed differing trends of declining seabird populations and more stable terrestrial birds.

Aim: To examine the population trends from 1961 to 2023 using periodic breeding bird censuses on Skúgvoy, in the Faroe Islands, encompassing most terrestrial and marine species.

Methods: Skúgvoy is the only Faroese Island with periodic bird censuses, conducted since 1961 at approximately 20-year intervals, with a new census in 2023. Inland birds were counted by mapping breeding territories, with colonial seabirds counted individually on cliff ledges from the sea surface. These historical censuses provided a long-term quantitative assessment of species' population dynamics and exploration of potential causes of observed declines, especially among seabirds.

Results: Seabird populations have not only declined drastically since the previous comprehensive census in 2001 but have also experienced acceleration in the scale of decline. In contrast, terrestrial species have exhibited only minor fluctuations.

Conclusion: The differing trends between seabirds and inland birds suggest that the declines are likely driven by regional-scale processes, such as reduced food availability for pelagic seabirds, rather than local-scale processes operating within the island system.

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North Atlantic seabirds have experienced historically high declines, particularly in the UK and the continental north-east Atlantic (Fauchald *et al.* 2015, Wauchope *et al.* 2017, JNCC 2021b, Burnell *et al.* 2023). However, information on bird populations on more isolated islands in the North Atlantic is more limited. The Faroe Islands have large concentrations of breeding seabirds of the order Charadriiformes, particularly Black-legged Kittiwake *Rissa tridactyla* (hereafter Kittiwake), skuas (Stercorariidae) and auks (Alcidae) (Bayes *et al.* 1964, Joensen 1966, Dyck & Meltofte 1975, Bloch 1981). Moreover, the Faroe Islands, at just 1400 km² in area, have previously supported over 175,000 pairs of Common Guillemot *Uria aalge*, recognized as one of the largest breeding concentrations in the north-east Atlantic (Tuck 1960, Dyck & Meltofte 1975). These seabirds often breed in close proximity to inland birds, largely exposed to the same local conditions over time. Despite the Faroe Islands' large concentrations of seabirds, few studies have assessed their population trends over extended periods of time.

Skúgvoy is unique among the Faroe Islands for its bird censuses, which have been conducted approximately every 20 years since 1961 (Joensen 1963, Bloch 1981, Olsen 2003). Historically, Skúgvoy supported the largest concentrations of Common Guillemots in the Faroe Islands, with 140,000 pairs reported by Dyck & Meltofte (1975). In 2012, Skúgvoy was designated as a Ramsar site, partly due to its large seabird colonies. Large colonies of Northern Fulmar *Fulmarus glacialis* (hereafter Fulmar) and Kittiwake breed along the tall western coastline, while the island's southern grassy slopes house a large colony of Atlantic Puffin *Fratercula arctica* (hereafter Puffin), previously estimated to be 40,000 pairs (Grimmett & Jones 1989). The inland wet tundra habitats are breeding sites for the majority of Faroese shorebirds. Even the small wader species, such as the Purple Sandpiper *Calidris maritima* and Dunlin *C. alpina*, both rare breeders on the Faroe Islands, have maintained breeding pairs since the first census.

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This broad representation of marine birds and waders, monitored for more than half a century, provides a foundation for comparing population trends of species with distinct foraging and breeding ecologies. For example, declining populations within locally unchanged conditions could indicate regional-scale impacts, such as decreased survival rates of birds during the non-breeding season or decreased pelagic food availability for seabirds.

Apart from the broad representation of breeding birds, the small island of Skúgvoy constitutes a standardized model system for comparing species population trends. The island is free from rats, mice and cats (Jensen & Olsen 2020), which otherwise put critical pressure on insular birds (Dias *et al.* 2019, Jensen & Olsen 2020). Moreover, land use has largely been unaltered throughout the survey period, as evidenced from historical maps (e.g. Joensen 1963). Besides Sheep *Ovis aries* grazing, the outfield area surrounding the island's village, and the infield, are largely unaffected by human activity. The island's human population has declined over the past 20 years, from approximately 80 to 18 permanent residents, with several houses used as vacation homes and not occupied year-round. In conjunction with the depopulation, the hunting pressure on most seabirds has declined due to increasingly restrictive local regulations and decreased economic value. Local hunting of terrestrial birds is minimal, although some persecution of Great Skuas *Stercorarius skua* does occur (Olsen 2003, Hammer 2017). In this case, aggravating regional-scale pressures, such as changes in climate, resource exploitation and decreased survival during the non-breeding season, could explain why some species groups are more prone to decline than others.

Here, we present a standardized comparison between the population trends of marine versus terrestrial species breeding within close geographic proximity on Skúgvoy. We utilize the historical census data for the island's breeding birds since 1961 and contribute a new complete census from 2023. With data collected over this long period, we discuss possible explanations for the population trends of marine versus terrestrial species.

The foundation for this study began with Anders Holm Joensen's bird census of Skúgvoy's breeding birds in the summer of 1961 (Joensen 1963) and a nationwide census of breeding inland birds in the Faroe Islands in 1981 (Bloch 1981), with data provided by the Natural History Museum in Tórshavn. These two censuses were synthesized in a count in 2001 (Olsen 2003), revealing trends in bird

populations at approximately 20-year intervals. Overall, the terrestrial birds showed idiosyncratic population trends up to 2001, whereas the seabirds have consistently declined since the first census period. It has remained an open question as to whether this decline has persisted at a similar rate or accelerated further.

Methods

Study area

The size of Skúgvoy is 9.7 km² and it can roughly be classified into the areas covering the village, infield and outfield (see Supplementary Figure S1). The village consists of small, closely situated houses with narrow streets. Some houses remain uninhabited, while others are abandoned, serving as habitats for Rock Doves *Columba livia* and Eurasian Wrens *Troglodytes troglodytes* (hereafter Wren). The infield consists of lush green meadows covering 1.1 km², where grass is cultivated for Sheep and enclosed by wire fences or stone walls (See Supplementary Figure S1). This area is rich in flowers, including characteristic species such as Meadow Buttercup *Ranunculus acris*, Marsh Marigold *Caltha palustris*, Heath Spotted Orchid *Dactylorhiza maculata* and the rare Northern Marsh-orchid *Dactylorhiza purpurella*. The remaining and largest area on the island is the outfield, which features lower vegetation, fewer flowers and protruding rocky outcrops compared to the infield. In the north-west part of the outfield there are swampy mires with Common Cotton-grass *Eriophorum angustifolium* and Marsh Marigold. Purple Sandpipers and Dunlins occur here, along with characteristic birds of the outfield, such as the European Golden Plover *Pluvialis apricaria* (hereafter Golden Plover), Great Skua and Arctic Skua *Stercorarius parasiticus*.

The island's elevation gradually increases towards the west-south-west, reaching its maximum of 393 m at Point Knúkur. The vertical bird cliffs are exclusively located on the island's western side (See Supplementary Figure S1). Common Guillemots and Razorbills *Alca torda* nest along these steep cliffs, which descend to a height of 130 m at Høvdin, the island's northernmost bird cliff (see Supplementary Figure S2 for an overview of individual cliff sections). The Høvdin cliff faces towards the island and is the only location on Skúgvoy where the cliff is visible from land. Hence, annual counts of Common Guillemots have been conducted here since 1972 (Olsen 2010a). Along the southern coast, the steep cliff sides give way to grass-covered slopes. Here, Skúgvoy's largest colony of Puffins occurs,

together with the island's only colony of Manx Shearwaters *Puffinus puffinus*. The area around the settlement features the island's lowest cliffs.

The island is grazed by 700–800 Sheep, giving a density of 0.7–0.8 Sheep per hectare. In comparison, the density of Sheep in the Shetland Islands of Scotland is 1–4 (Scottish Government RESAS, April 2017). Considering this low Sheep density on Skúgvoy, it is unlikely that grazing constitutes a threat to the burrow-nesting seabirds. Nevertheless, the grazing pressure influences the vegetation composition in the outfield, as a distinctive flora is found in gullies inaccessible to Sheep. However, grazing could have a negative impact on the inland-breeding waders, as their legs can become entangled in shed wool (Hammer *et al.* 2014).

Inland bird surveys

In 2023, we used the same counting methods from the 2001 census (Olsen 2003), where the island was divided into nine sections to lay out survey transects and ease field navigation (see Supplementary Figure S3). These sections were delineated based on the island's transverse Sheep fences. All birds in the infield and outfield were counted along line transects spaced 100–150 m apart. All breeding bird territories were precisely mapped so that the spatial location of territories could be compared with the previous census. When two birds were seen together, they were considered a pair and counted as one territory. For Common Snipe *Gallinago gallinago*, we recorded all calling and displaying males as breeding pairs. Eurasian Oystercatchers *Haematopus ostralegus* (hereafter Oystercatcher), Golden Plovers and Eurasian Whimbrels *Numenius phaeopus* (hereafter Whimbrel) vocalized loudly when observers approached their nesting sites; Whimbrels, in particular, often feigned an injured wing to lure the observer away from the nest. Breeding Great Skuas and Arctic Skuas aggressively defended their territories, sometimes flying directly at the observer and almost making physical contact. The colony-nesting inland birds, such as skuas and Arctic Terns *Sterna paradisaea*, were counted from a high point outside the colony, the count repeated several times to ascertain the maximum number of birds. The largest pond in the centre of the islands aggregates non-breeding Great Skuas, which were deliberately not recorded in the census.

Rock Pipits *Anthus petrosus*, Meadow Pipits *A. pratensis* and Northern Wheatears *Oenanthe oenanthe* (hereafter Wheatear) were recorded as

breeding territories. Meadow Pipits occur predominately in the infield, whereas Rock Pipits are more widely distributed. Common Starlings *Sturnus vulgaris* (hereafter Starling) were assessed based on large flocks of juveniles moving around the island. To obtain the number of breeding pairs, we divided the total number of juveniles by four, which approximates the average number of chicks per clutch (Collins & de Vos 1966, Crossner 1977). House Sparrows *Passer domesticus* breed only around the settlement. The number of breeding pairs was estimated by counting the number of males. European Storm Petrels *Hydrobates pelagicus* were not counted due to the time-consuming and near-impossible task of locating their nests hidden in old stone walls scattered across the island. European Storm Petrels were seen and heard along stone walls north of the village late in the evening.

Surveys of bird colonies

In 2023, we counted all colony-nesting seabirds from a boat over three days of sailing. The west coast, spanning 7.4 km, was divided into 44 smaller delineated segments (see Supplementary Figure S2). This numbering system originated from the original complete survey of Common Guillemots in Dyck & Møltøfte (1975). Thus the number of breeding pairs on each cliff face was directly comparable with the previous census, assuming similar limitations and sampling biases. Moreover, all cliff faces were photographed from the boat using a Canon full-frame R5 camera with an RF 100–500 mm lens, taking 20–50 pictures of each cliff face, which were merged into a single image using Photoshop software. We used these images to count the Common Guillemots and Kittiwakes, which nest exposed on the vertical cliffs.

Unlike Common Guillemots, the Kittiwakes do not nest in rows on the cliff ledges, and, therefore, all breeding pairs could be counted from the photographed cliff faces. Each individual Fulmar observed sitting along the western coastline was recorded as a breeding site; sometimes the birds were quite concealed in the vegetation, but their white heads were still visible to be recorded. Numbers of breeding pairs on the eastern coast were extrapolated based on the inland field observations.

Estimating population sizes

The Common Guillemots often stood in multiple rows on each cliff ledge, not all of which were visible from the sea surface. To estimate the proportion of

Common Guillemots on ledges that could not be seen from the sea, we calibrated the counted number with observations from the island's northernmost bird cliff (Høvdin, cliff no. 3, Supplementary Figures S1 and S2), which is the only one of the island's cliffs that could be counted directly from the land looking down at the cliff face. We photographed the Høvdin bird cliff from above on 4 July 2023 at 15:00 local time, counting 1615 Common Guillemots, and again on 11 July at 8:00 when we counted 1508 individuals. We selected these two time periods to explore variations in Common Guillemot occurrence on the cliffs between dates and the time of day. We used the average number of individuals counted from land (viewed top-down) to calibrate the number of individuals counted from the boat (images available in Olsen *et al.* 2024). Thenceforth, we multiplied the total number of Common Guillemots counted from the boat (41,690 individuals) by a factor of 1.36, resulting in approximately 56,700 individuals. To estimate the number of actively breeding birds, we multiplied by a factor of 0.67, which is believed to correspond to the ratio between breeding and non-breeding birds used in previous studies (Dyck & Meltofte 1975, Tschanz 1978).

Razorbills nest hidden in crevices or burrows and were not counted directly, but were instead estimated through extrapolation. From a boat, we counted all individuals of both Razorbills and Common Guillemots on the sea surface along the west coast. The number of Common Guillemots was known from the cliff counts, and we extrapolated the estimated number of Razorbills based on the ratio of Razorbills (15) to Common Guillemots (701), giving a ratio of 1:47. To estimate the number of breeding Razorbill pairs, we applied the same ratio of 0.67 used for Common Guillemots, but acknowledging the uncertainty of this number when applied to a closely related species.

We did not attempt to census Manx Shearwaters on land, because they breed in burrows on grassy slopes and only return to the nesting sites at night. However, the Manx Shearwaters gathered in large flocks offshore in the afternoon. As in the 1961 and 2001 censuses, we counted the size of these flocks and used this number as an approximation for trends in the population size. For Puffins, we counted individuals seen next to a burrow during a boat trip around Skúgvoy. After 1 May, this number is considered to approximate the number of breeding pairs (Calvert & Robertson 2002, Burnell *et al.* 2023).

The survey day was chosen when there appeared to be a 'landing day' (mass arrival on land) for the

Puffins, assessed by an extraordinarily large number of individuals seen flocking around the southern colony. A few sections of the colony were not directly visible from the boat and, for these, we extrapolated the number of individuals based on the density of birds in adjacent visible sections. We acknowledge this is a highly uncertain approach to estimating population size, also given that a few slopes of the colony were not visible from the boat. Therefore, the numbers should be interpreted as a 'best guess' estimate.

For Black Guillemot *Cepphus grylle* and European Shag *Gulosus aristotelis* (hereafter Shag), all adult individuals were counted on a boat trip around the island. Solitary birds were considered a breeding pair, as it was assumed that the other bird was at the nest. If there were two birds close together they were counted as a pair. Black Guillemot individuals observed more than 300 m from the coast were assumed to be non-breeders and were ignored (Burnell *et al.* 2023). For Common Eider *Somateria mollissima* (hereafter Eider), males and females with chicks were counted around the island.

Processing data from previous censuses

The four censuses that were conducted at 20-year intervals since 1961 included all inland birds and used similar sampling protocols (Joensen 1963, Bloch 1981, Olsen 2003). The 1981 census differs from the other three counts in that only inland birds were counted (Bloch 1981). In addition to the regular 20-year counts, sporadic local censuses of inland birds were conducted in 1992 (Højgaard 1995) and 2010 (Olsen 2010b). Our survey protocol for Common Guillemots in 2023 followed the survey from 1972, with the west coast similarly divided into 40 cliff sections (Dyck & Meltofte 1975). Four new cliff sections that held breeding birds had appeared since the first census, along the southern coast of the island, and these were assigned new identification numbers (41–44). In 1987, the Common Guillemot population was counted again and estimated to 75,000–90,000 pairs (Grimmett & Jones 1989). No comprehensive seabird counts were conducted on Skúgvoy between 1987 and 2023, except for the Høvdin cliff face, which can be surveyed from land. Based on previous census counts, it has been estimated that Høvdin comprise 4–5% of the island's total population of Common Guillemots. In 2001, the Common Guillemot numbers on Høvdin were apparently similar to 1987 (Olsen 2010a), and so the 2001 total population was again assessed at 75,000–90,000 breeding pairs (Olsen 2003).

Interviews of knowledgeable locals

Semi-structured interviews of approximately one hour duration were conducted with five of the island's permanent residents. We asked these interviewees whether they wished to remain anonymous, and also their age, how many years they had lived on Skúgvoy, their knowledge of the importance of birds to the local community, levels of exploitation and the population trends of six seabirds: Puffin, Manx Shearwater, Storm Petrel, Common Guillemot, Fulmar and Kittiwake. Furthermore, we requested information about the intensity of fishing and if the Ramsar site designation for Skúgvoy made a difference, in their opinion. The people were selected based on their experience and willingness to share information with our team (see the Supplementary Information for additional methodological details regarding the interviews).

Analysis

We partitioned the species into four groups according to their breeding biology and foraging niches. The marine group (A) comprised all pelagic birds, including coastal species exclusively dependent on marine food resources; most are coastal breeders, except the Arctic Skua that breeds inland but kleptoparasitizes seabirds (predominately Kittiwakes, Arctic Terns and auks) for the largest proportion of their diet (Løvenskiold 1964, de Korte 1972, Furness 1978). The group of waders (B) all feed and breed on the open grassland. The Great Skua and three large gull species form a separate group (C) with opportunistic foraging strategies, relying on both marine and terrestrial food resources. All of the group C species have inland breeding territories, except for the Great Black-backed Gull *Larus marinus*, which nests close to the seabird colonies. Lastly, the passerine birds (group D) have distinct life-history traits (see Figure 1 for species assigned to each group). In the statistical analyses we excluded the Eider, as it is ecologically different from the other seabirds by feeding almost exclusively on molluscs inshore, compared to the other seabirds that feed on fish. We also excluded Rock Dove and Arctic Tern due to data deficiencies.

To determine changes in the species population trends, we first scaled the population size (i.e. the number of breeding pairs, individuals or territories) according to the number counted in the initial census year (representing 100%). Meadow Pipits were

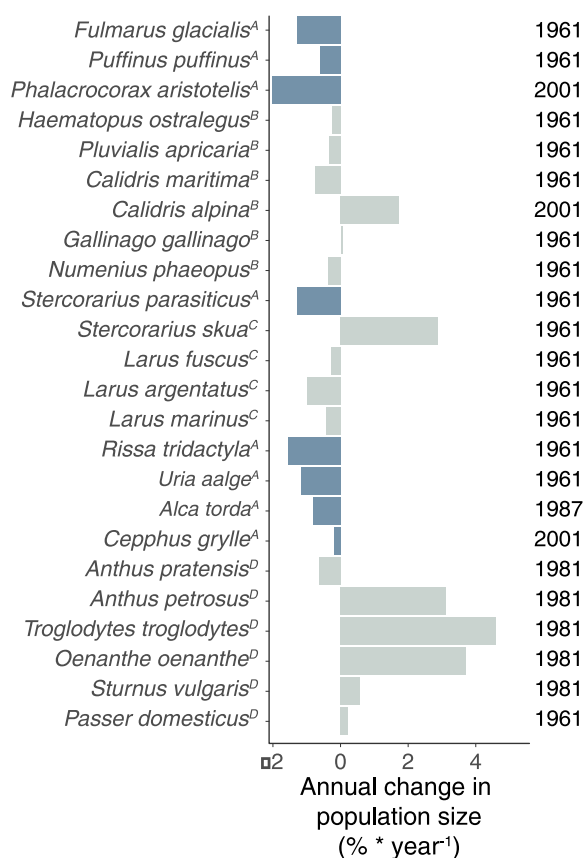


Figure 1. Annual percentage change in the number of breeding pairs of species censused between 1961 and 2023. The trends in population sizes are slope coefficients from linear models regressing the number of breeding pairs against the census year. The annotated years correspond to the first census year that entered the analysis, where at least five breeding pairs were counted. Superscripts next to the species names correspond to their ecological guild class: Marine (A), Waders (B), Large Gulls and Great Skua (C) and Passerines (P).

recorded in 2001 with only a single breeding pair, and to avoid vastly overestimating its population trend we excluded the species from analyses of the contemporary census period. For the other species, we then regressed the population size (breeding pairs, individuals or territories) against the census year using a linear model. From these regression models, we extracted the slope coefficients corresponding to the annual percentage change in population size. We compared the annual percentage change in the breeding populations of species belonging to the four groups using a Kruskal-Wallis test, followed by Wilcoxon one-sample tests, asking if the population trend of a focal group differed significantly from zero. The *P*-values from these post-hoc tests were adjusted using the false discovery rate. All statistical analyses were conducted in R.

Results

Population trends from bird censuses

We found significant differences in the population trends of birds with a distinct breeding biology and foraging niches between 1961 and 2023 (Figure 2A, $H = 12.45$, $P = 0.006$). The marine species (group A) stood out as the only group showing significant declines since the first census in 1961 ($P_{\text{adjusted}} = 0.031$). This rate of decline was not consistent throughout the period but accelerated from $-0.89\% \pm 0.39$ SE during 1961–2001 to $-2.65\% \pm 0.20$ SE in the last two decades (2001–2023; Figure 2B). The marine species showing the greatest declines since 2001 were the Fulmar, Kittiwake and Arctic Skua, which declined by 89%, 87% and 84% respectively. Skúgvoy has previously comprised the Faroe Islands' largest colonies of Common Guillemots, which was a decisive argument for the island's categorization as a Ramsar site. However, this species also experienced an accelerating decline, from -1.48% annually between 1961 and 2001 to -3.96% annually since 2001. As a part of this study, we generated high-resolution images of each Common Guillemot cliff, numbered 1–44, as a resource for future comparative studies (Olsen *et al.* 2024; see Supplementary Figure S2 for geographical references).

The accelerating decline in Skúgvoy's marine birds was not found in the other ecological groups. The Black Guillemot is the only pelagic seabird with a small but stable population. Eiders also maintained a stable population (-0.31% annually between 1981 and 2001), although this species was considered ecologically distinct from the other pelagic seabirds. The abundance of Arctic Terns was highly variable between census years, the species being absent from the island between 1992 and 2001 but re-establishing a colony of 45–50 pairs after the 2010 census. Due to this unpredictable variability in the population size, the Arctic Tern's long-term population trend remained unassessed.

The group consisting of the Great Skua and three large gull species (group C) also declined from 1961 to 2001. However, this trend reversed over the subsequent 20 years. The three gulls generally had few breeding pairs, which could explain their large demographic changes between census years. Great Skuas maintained the most stable population and this grew rapidly from 65 pairs in 2001 (Olsen 2003) to 145 pairs in 2010 (Olsen 2010b), stabilizing at that approximate level (150–200 pairs) over the following decade (Hammer 2017; Olsen B. unpublished).

The six wader species (group B) showed the most stable population trend. However, the fluctuations

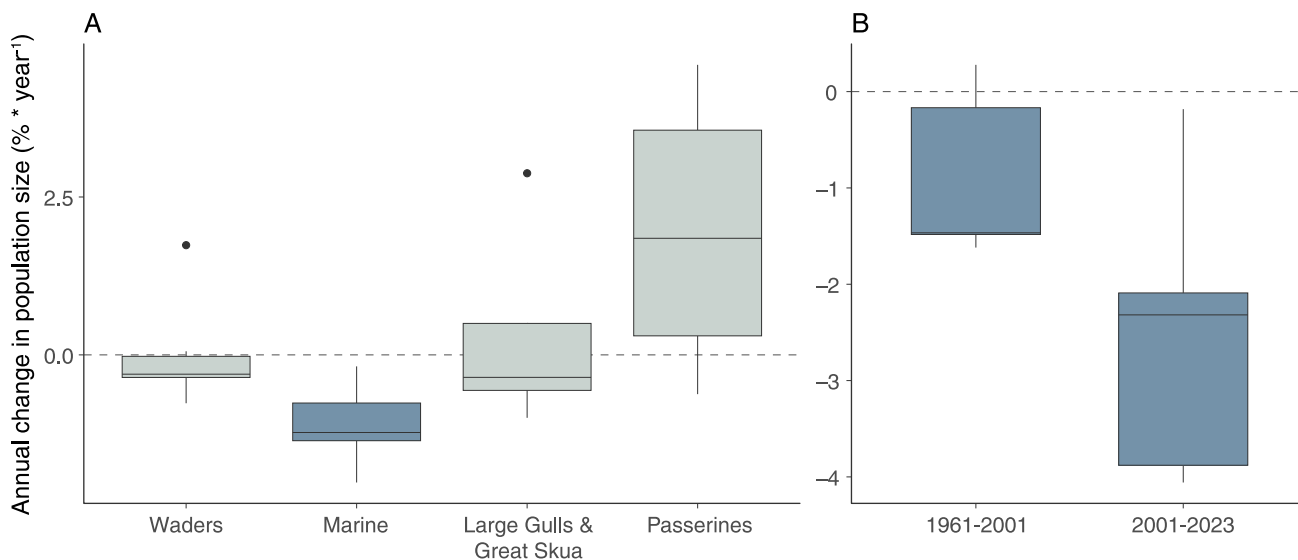


Figure 2. Annual percentage change in the number of breeding pairs, summarized for each ecological group between 1961 and 2023 (A). The trends in population sizes are slope coefficients from linear models regressing the number of breeding pairs against the census year. The ecological groups comprise six species of inland waders ('waders'), nine species of obligate piscivores and marine omnivores of coastal breeding habitats ('marine'), three large gull species plus the Great Skua ('separate group') and five songbirds ('passerines'). The marine species have declined since 1961, which has accelerated since the previous seabird census in 2001 (B). The box borders mark the interquartile range (quartiles 1–3); horizontal lines inside the boxes are medians; vertical lines mark $\pm 1.5 \times \text{IQR}$; circles mark data outliers.

between census years were substantial. Oystercatchers have increased from 34 to 51 pairs since 1961, although the population was 115–240 pairs in 1981–1992. Similarly, the population of Whimbrels remained stable, with approximately 40 pairs in 1961 and 47 pairs in 2023, although the territories changed positions, concentrating on localities where Great Skuas were absent. Other waders, such as Common Snipe and the two small *Calidris* waders, maintained stable populations since 2001; this was perhaps surprising for the sandpipers given their few breeding pairs. These species were primarily associated with mire vegetation at the Gráumýra locality (see Supplementary Figure S1).

The passerine species were challenging to count reliably, and their populations fluctuated drastically between census years. Historical censuses showed a marked increase from 1961 to 2001, but this had stabilized from 2001–2023.

Interviews

The importance of seabird-catching and egg-collecting for the local economy and livelihoods was recollected by interviewees as being essential in the 1930–1970s (reported from parents, grandparents and personal memories), whereafter the importance decreased to be of no real significance today (see Supplementary Information for a full summary of the interviews). It was reported that in the 1930s one barrel of Puffins and a similar barrel of salted Common Guillemots was almost essential for islanders' survival over winter, and a barrel of salted Puffins was a significant contribution to winter survival up to the 1960s. Today, bird catches are locally regulated, but the limited catching of Manx Shearwaters, for example, has some recreational value, although there is no essential economic or survival need to catch seabirds at the present time.

Interviewees reported that population trends of the six seabirds had undergone drastic declines, since the 1960s for Puffins and with the Common Guillemot population halving several times, with the crash beginning in the 1950s. The opinions for Manx Shearwaters were contradictory, with two interviewees reporting large declines but two others reporting stable populations. Information for Fulmars and Kittiwakes was inconclusive, and there were no reports for the European Storm Petrel's population trend. Interviewees reported that fishing had increased markedly, with vessels becoming larger and fishing now taking place year-round, in contrast to earlier decades. Moreover, it was reported that fish stocks were observed to have decreased.

Discussion

Since 1961, the population trend of breeding birds on Skúgvoy has varied substantially between inland and marine species. Our results showed minor fluctuations in the populations of inland-breeding birds (Figure 2A). In contrast, the entire group of marine birds, except the small population of Black Guillemots, has declined since the first census year. This decline has not slowed, but rather accelerated since the previous seabird census in 2001 (Figure 2B), particularly among the abundant colony-breeding species, like the Fulmar, Kittiwake, Common Guillemot and Razorbill (Figure 1). This comparison of species with different foraging ecology pointed to a lack of oceanic food availability and reduced survival during the non-breeding season as the best possible explanation for Skúgvoy's declining seabird populations.

The decline in seabirds on Skúgvoy coincides with other studies from the North Atlantic. Surveys from Great Britain and Ireland show similar declines in 11 of 21 seabird species (Mitchell *et al.* 2020, Burnell *et al.* 2023). The Shetland Islands closely resemble the Faroe Islands in vegetation, landscape and climate, and also have some of Britain's largest seabird colonies. Here, since 2020, populations of Fulmar, Common Guillemot and Razorbill have declined by 20%, 55% and 66% respectively (1.2%, 4.4% and 5.5% annually). However, in the southern parts of Great Britain the Razorbill population has apparently increased (Burnell *et al.* 2023). Kittiwakes have experienced the most severe decline in Great Britain, by 80% since 2000 (8.5% annually).

In contrast to Skúgvoy, Shetland's Black Guillemot population has declined by 26% since 2000 (2.6% annually), but shows idiosyncratic population trends on other British islands (Burnell *et al.* 2023). Shetland therefore replicates the pattern of declining seabirds found on Skúgvoy, indicating that the population trends are not caused by local-scale processes, but rather regional processes associated with the conditions in the surrounding ocean.

We acknowledge the caveats associated with comparing historical population estimates obtained from different methodologies. In our analyses, this caveat mostly applies to the Common Guillemot. Despite this, the species population trend follows the general pattern observed for colonial seabirds at Skúgvoy and other regions of the North Atlantic.

Skúgvoy's land use has remained almost unchanged since the first bird census in 1961, and according to our interviews with the residents, local-scale pressures (such as hunting and exploitation of seabirds) have decreased

considerably, and completely ceased for several species. Therefore, we find it unlikely that a direct effect of land use and habitat change or exploitation on the island has caused distinct demographic patterns for marine and terrestrial birds. Instead, the drastic decline of seabirds may result from a regional-scale decrease in food, i.e. prey fish, in the marine environment.

The literature discusses many possible causes for the decline of seabirds in the North Atlantic (Olsen 2003, JNCC 2016, Mitchell *et al.* 2020, JNCC 2021a, Burnell *et al.* 2023, Jensen 2023). Notably, climate change and fishing-related pressures are highlighted as two main explanations for reductions in oceanic resource availability (Planque *et al.* 2010, Niiranen *et al.* 2013, Burnell *et al.* 2023). Studies in the north-east Atlantic indicate that increases in sea temperature reduce productivity at lower trophic levels (Beaugrand *et al.* 2008, Reygondeau & Beaugrand 2011, Frederiksen *et al.* 2013). In particular, marine copepods play a fundamental role in the marine food web, maintaining the fish populations that seabirds depend upon (Hamer *et al.* 1993, Rindorf *et al.* 2000, Daunt *et al.* 2008, Frederiksen *et al.* 2013, Carroll *et al.* 2017). Notably, the bottom-up relationship between ocean currents and primary productivity impacts the recruitment of sand-eels (*Ammodytes* spp.), which several seabirds have in their diet (Jacobsen *et al.* 2019, Burnell *et al.* 2023).

The relationship between commercial fish species and seabird abundance is well described for the Faroe Shelf ecosystem (Gaard *et al.* 2002, Hátún *et al.* 2017). By contrast, the implications of fishing-related pressures on seabird survival and reproduction can be difficult to measure at the population level. Seabird bycatch is listed as a major global threat to seabirds, particularly albatrosses, large petrels, shearwaters and penguins (Dias *et al.* 2019). There are no gillnet fisheries permitted in Faroe waters above 380 m depth (Kunngerðarblað 2019 A), although there may have been some rare exploratory exceptions in shallow gillnet fisheries for lumpfish (Cyclopteridae). By contrast, bycatch by longline fishing is frequently recorded as affecting surface-feeding seabirds, particularly Fulmars (~9500 individuals killed per year around the Faroe Islands; Havstovan 2022). The main pressure from bycatch happens during the non-breeding season. A recent study quantified seabird bycatch in the north-east Atlantic, which was most pronounced for Common Guillemots and Fulmars (respectively >27,000 and >22,000 birds killed per year; Ramírez *et al.* 2024).

Overexploitation is another fishing-related pressure on North Atlantic seabirds. Even if seabirds do not

directly exploit the targeted fish species, overfishing could still induce cascading effects on the configuration of the food webs (Planque *et al.* 2010, Niiranen *et al.* 2013). The sand-eel fishery is a special case in being directly associated with the reduced breeding success of Kittiwakes (Daunt *et al.* 2008, Dunn 2021, Searle *et al.* 2023). Consequently, a long campaign led by the Royal Society for the Protection of Birds recently resulted in the permanent end of the sand-eel fishery in English and Scottish waters (Searle *et al.* 2023, Marine Directorate Communications 2024). However, the negative ecological impact of sand-eel fisheries on seabirds in the North Sea and around Shetland has presumably not been an important driver in the Faroes, where there is no industrial sand-eel fishery (Eliassen *et al.* 2011).

This study did not aim to disentangle the climate versus exploitation pressures. However, given the broad range of foraging niches among the declining seabirds (i.e. pelagic and surface feeders), we find it unlikely that the seabirds' decline on Skúgvoy is solely explained by one single factor. Climate change likely elevates the pressures that the fishing industry already impose, resulting in accelerated declines of colonial-breeding seabirds.

Local industrialization and legislative changes in the fishing industry could have other effects on food availability, for instance, by reductions in the amount of fish waste discarded at sea. This human-facilitated resource is believed to have caused an artificially high food availability for surface-foraging seabirds (Burg *et al.* 2003), with Fulmars (Danielsen *et al.* 2010), Great Skuas (Hammer 2017) and gulls collecting discards behind fishing vessels, or at least acquiring fish that would otherwise be unavailable to them. Thus it is possible that the historical population increases observed in Fulmars may return to a more natural level (Burnell *et al.* 2023).

Decreased food availability might have a greater impact on surface-feeding seabirds than diving seabirds, with the former being more constrained in their access to prey (Furness & Tasker 2000, Wanless *et al.* 2007). This idea coincides with the pronounced declines observed in Kittiwakes, Fulmars and Manx Shearwaters (Figure 1). The only other seabird showing a similar decline was the Arctic Skua, which specializes as a kleptoparasite during the breeding season, primarily targeting Kittiwakes, auks and Arctic Terns (Furness 1978, Andersson & Götmark 1980). A similar devastating decline of Arctic Skuas has been observed on Shetland, which holds the largest population in Great Britain. Here, the Arctic Skua has declined by 74% since 2000, which, as on Skúgvoy,

could be attributed to the lack of food following the declines of its main hosts, particularly Kittiwakes and auks (Meek *et al.* 1994, Perkins *et al.* 2018).

A large outbreak of Highly Pathogenic Avian Influenza between 2021 and 2022 greatly impacted several seabird species in Great Britain and the Faroe Islands, particularly Great Skuas (Camphuysen *et al.* 2022). Seemingly, the same disease had a minimal effect on the Arctic Skua population (no cases from Shetland and only one case from the Faroe Islands, Burnell *et al.* 2023, WOAH 2023). These results coincide with the idea of bottom-up pressures on food availability influencing the Arctic Skua's decline in Great Britain and at Skúgvoy (Perkins *et al.* 2018).

Nevertheless, the seabirds experiencing the most significant declines on Skúgvoy were subject to the most lenient hunting regulations in the Faroe Islands, with no regulation on Fulmars, Great Skuas, Arctic Skuas or Kittiwakes. The absence of hunting restrictions on these species is concerning, particularly as their declines on Skúgvoy have accelerated since 2001. Historically, Skuas are seen by local people as nuisance birds, and Fulmars have been considered as 'intruders', negatively impacting Puffins and guillemots. Persecution of Great Skuas has also been recorded in Scotland, particularly Shetland (Mitchell *et al.* 2004, Burnell *et al.* 2023). However, the Faroe Islands is one of the few, if not the only, area in the North Atlantic where killing of Great Skuas remains unregulated. This local pressure may drastically affect the Great Skua population between census periods (Hammer 2017). Although the hunting pressure has likely decreased significantly (Ólavur á Skipagøtu pers.

commun.), the hunting regulations for these species should be reassessed based on a precautionary principle, in view of the accelerating decline of populations.

Processes influencing population dynamics in colony-breeding seabirds are expected to differ from those affecting terrestrial breeders. Colonial seabirds distribute themselves across different strata on the cliffs, rarely competing interspecifically for nesting sites (Sørensen & Bloch 1990). Conversely, competitive exclusion between land-breeding species is a process that can greatly influence the population dynamics of inland-breeding birds. Maps of bird breeding territories show a geographical segregation between Skúgvoy's two skua species (Figure 3). The Great Skua has steadily increased since 1961, after being persecuted to near extinction on Skúgvoy in 1902 (Hammer 2017). Great Skuas spread even further since 2001 and now occupy areas that previously hosted Arctic Skuas. This result coincides with a study from Scotland that showed Arctic Skua productivity correlating negatively with the density of Great Skuas (Meek *et al.* 1994, Perkins *et al.* 2018). Thus the pattern observed at Skúgvoy could suggest that Great Skuas have depredated and competitively excluded Arctic Skuas (Meek *et al.* 1994, Phillips *et al.* 1998, Jones *et al.* 2008, Dawson *et al.* 2011, Hammer 2017, Perkins *et al.* 2018).

The larger species of waders (Whimbrel and Oystercatcher) were also associated with areas where Great Skuas were absent. However, the smaller and more cryptic waders (Common Snipe, Dunlin and Purple Sandpiper) seemed unaffected by the presence

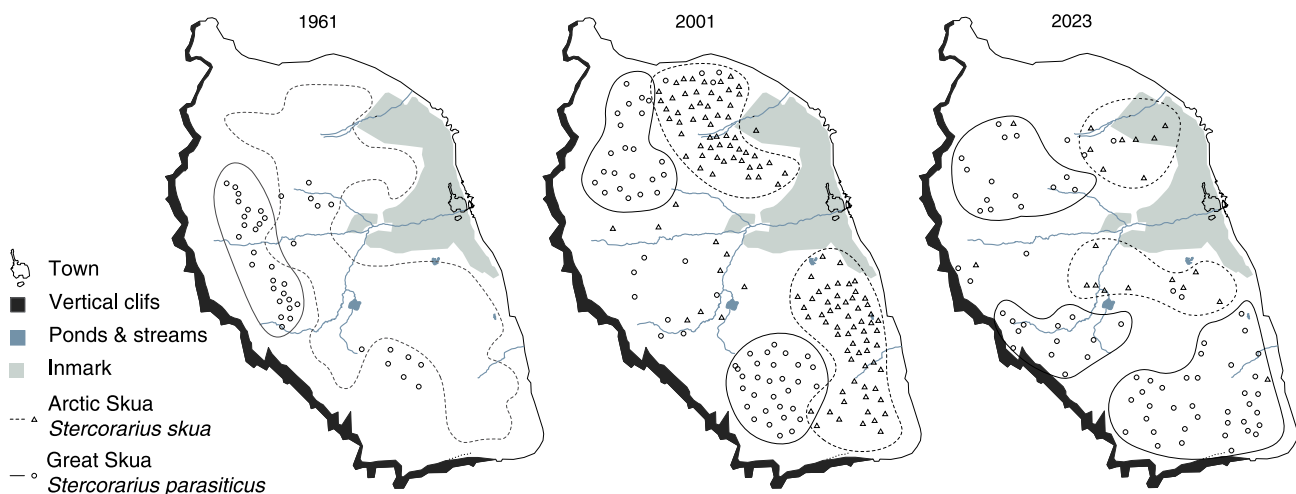


Figure 3. Broad habitat areas on Skúgvoy and long-term spatial segregation between two species of inland-breeding birds. Map from 1961 showing the original representation of Arctic Skua territories (circles) in relation to the breeding area of Great Skuas (dashed line, individual territories not shown). Solid black lines mark areas with high concentrations of Arctic Skuas. Maps from the 2001 and 2023 census years additionally show the individual territories of Great Skuas.

of Great Skuas. These top-down effects on terrestrial species are expected to continue, as the legal persecution of Great Skuas was reinstated in 1974 and occurs periodically, most recently in 2021 (Hammer 2017, Schreven & Hammer 2020).

Dunlins and Purple Sandpipers had only a few breeding pairs on Skúgvoy during the 2023 census and are generally scarce in the Faroe Islands. Therefore, it was surprising to rediscover nearly identical nesting territories recorded in 2001, despite the impacts of demographic stochasticity and potential threats during migration. Acknowledging the caveats associated with interpreting the small number of individuals, the continued presence of these small waders could result from a high degree of site fidelity and the successful return of their offspring to the same breeding grounds. Notably, the southern Dunlin subspecies, *C. a. schinzii*, is of international conservation concern. This subspecies has declined in European Russia and other countries surrounding the Baltic Sea, possibly due to land use changes or inbreeding (Blomqvist *et al.* 2010, Mischenko 2020). However, counts during

migration show moderate stability of this taxon within the East Atlantic Flyway, and they remain common breeders in Iceland (Nagy & Langendoen 2020). Thus we speculate that negligible changes in land use explain the persistence of *schinzii* ssp. Dunlins in the northwestern corner of its distribution.

Population trends for the remaining waders on Skúgvoy follow the general patterns in the East Atlantic Flyway (Nagy & Langendoen 2020), with declines of Oystercatchers and Golden Plovers over the past 20 years. These patterns indicate that the demographic variation between Skúgvoy's shorebirds could have regional-scale explanations associated with survival during overwintering and migration.

While the historical accounts of Skúgvoy's breeding birds contribute valuable information, direct comparisons of the different census periods have noticeable caveats. The earliest literature focused more on the larger species than the small passerines. Hence, it is unlikely that the passerine populations have increased dramatically since the first census year. Direct comparison with the 2001 census (led by IO)

Table 1. Overview of the number of breeding pairs of each species in 1961–2023. The 1961, 2001 and 2023 censuses include terrestrial and marine birds. The 1981, 1992 and 2010 censuses include only terrestrial birds. The 1972 and 1987 censuses focused on seabirds.

Species	Unit	1961	1972	1981	1987	1992	2001	2010	2023
<i>Fulmarus glacialis</i>	Pairs	30,000					28,000		3000
<i>Puffinus puffinus</i>	Individuals	8–10,000*					10,000*		4900*
<i>Hydrobates pelagicus</i>									
<i>Gulosus aristotelis</i>	Pairs						40–50		20–30
<i>Somateria mollissima</i>	Pairs			35		22	24	0	30
<i>Haematopus ostralegus</i>	Territories	34		115		240	92	78	51
<i>Pluvialis apricaria</i>	Territories	32–34		41		51	58	21	30
<i>Calidris maritima</i>	Territories	5–10		3		2	4	1	4
<i>Calidris alpina</i>	Territories	0		1		0	8	0	10
<i>Gallinago gallinago</i>	Territories	60–80		37		36	75	41	65
<i>Numenius phaeopus</i>	Territories	39–41		41		68	35	12	47
<i>Phalaropus lobatus</i>	Territories	0		0		0	0	0	1
<i>Stercorarius parasiticus</i>	Territories	280–300		102		121	128	55	20
<i>Stercorarius skua</i>	Territories	40–45		23		63	65	145	71
<i>Larus canus</i>	Territories	0		1		0	2	0	2
<i>Larus fuscus</i>	Territories	20		9			18	4	17
<i>Larus argentatus</i>	Territories	50–100		7		14	12	16	14
<i>Larus marinus</i>	Territories	10–20		3		9	8	5	9
<i>Rissa tridactyla</i>	Pairs	100,000					35,500		4552
<i>Sterna paradisaea</i>	Pairs	20–30		312		68	0–2	0	45–50
<i>Uria aalge</i>	Pairs	184,000	142,000		75–90,000		75–90,000**		38,000
<i>Alca torda</i>	Pairs				1300				810
<i>Cepphus grylle</i>	Pairs						50–75		50–70
<i>Fratercula arctica</i>	Pairs								25–30,000
<i>Columba livia</i>	Pairs	20		3		7	10	7	10
<i>Anthus pratensis</i>	Territories			7		20	1	5	10
<i>Anthus petrosus</i>	Territories			51		82	117	88	118
<i>Troglodytes troglodytes</i>	Territories			6		25	17	0	19
<i>Oenanthe oenanthe</i>	Territories			42		47	82	62	110
<i>Turdus merula</i>	Pairs	0		0		4	2		1
<i>Corvus corone</i>	Pairs			4			3		8
<i>Corvus corax</i>	Pairs	4		2		0	2		1–2
<i>Sturnus vulgaris</i>	Pairs			>200			>250		>250
<i>Passer domesticus</i>	Pairs	10–15		>10			25	0	15–20

* Total number of individuals counted at sea in flocks gathering during the evening.

** Estimated numbers from the Høvdin cliff face, equivalent to the 1987 census.

showed negligible changes in the passerine populations. Hence, we speculate that their apparent increase results from sampling bias.

Conclusion

This study contributes to the growing literature with historical accounts of all breeding birds within a small and confined geographic area, providing insights into population trends among species with a different foraging and breeding ecology. All birds on Skúgvoy breed within close proximity and are subject to the same regional changes in environmental and climatic conditions over time. The significant decline in seabirds compared to the island's terrestrial birds could suggest reduced oceanic food availability as the best possible explanation, and the causes most likely to be regional-scale pressures, such as climate change and commercial fishing. Fishery bycatch may constitute an added top-down pressure on certain Faroese seabirds, predominately during the non-breeding season.

The historical censuses of all bird species leave behind valuable data for continued studies of trends in the bird's food resources and population dynamics. Our census contributes to Skúgvoy's history of regular bird surveys, spanning over 60 years. We encourage maintaining such periodic surveys, as they are the main resource for mitigating the shifting baseline syndrome (Pauly 1995) concerning seabird abundance.

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Data availability statement

Data from current and previous censuses are provided in Table 1. High-resolution images of the Common Guillemot cliffs numbered 1–44 are provided in Olsen *et al.* (2024). See Supplementary Figure S2.

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