

No relationship between feeding rate and breeding success in Atlantic puffins breeding in the Faroe Islands

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Abstract

Here we investigate the possible link between feeding rates and poor breeding success in an Atlantic puffin (*Fratercula arctica*) colony on the island Skúvoy in the Faroe Islands. We compare two years of field observations from an early period, 1992 (N = 26) and 1993 (N = 47), with two years of video footage from inside the burrows from 2018 (N = 9) and 2019 (N = 13). 1993 had good breeding success, whereas it was relatively poor in the other three years. Average feedings per day varied between 7.3 (in 1992) and 9.5 (in 2018). Feeding frequency did not differ significantly between early and late years or between good and poorer years. However, the breeding season was shorter in the good year and because of this, chicks were fed fewer times in that year than in the poorer years. Our results suggest the amount or quality of food brought to chicks by parents per feeding event were more important in determining breeding success than number of feedings.

Keywords Atlantic puffins, feeding rates, Faroe Islands

Introduction

The Atlantic puffin *Fratercula arctica* is one of the most abundant seabirds in the North Atlantic. The Faroe Islands are found in the central part of their range, naturally making these islands an important breeding area for puffins with several hundred thousand breeding pairs (Harris & Wanless, 2011). Knowledge on the Faroese puffins is limited (Olsen et al. 2025) and rapid declines throughout its breeding range, including the Faroe Islands where the population was likely five times larger 100 years ago (Harris & Wanless, 2011), make it particularly important to study the reason for the decline (Olsen et al. 2025). Monitoring through standardised surveys of the breeding population of puffins in the Faroe Islands has not been carried out. In 1987 the population was estimated at 550,000 pairs (\pm

75%, Grimmet & Jones, 1989) and population assessments have shown decrease since (Olsen et al. 2000, Hammer et al. 2014). 400,000 pairs were estimated in 2009 (Harris & Wanless, 2011), 200,000 - 300,000 pairs in 2015 (Jensen & Sørensen, 2015), and most recently, 150,000 – 250,000 pairs in 2022 (Olofsson & Sørensen, 2022). The global puffin population is projected to decline even further by 50-79% over the next three generations (40 years; BirdLife International, 2021).

In the late 1980s, several dead puffin chicks were found in the colonies (Gaard et al. 2002) and the number of attending puffins was very low. The situation improved in 1993 (Merkel and Nielsen 1997, Gaard et al. 2002) and the number of adults attending the colony reached a maximum in 1998–2001 when about 100,000 puffins were hunted each of these years. But in 2003 there was again a drastic decline in the number of puffins attending the colonies (Olsen 2004, Olsen & Jensen, unpublished) and the traditional hunting was given up in most places and has not been revived (Olsen et al. 2025).

Since the late 1980s, the Faroe Islands has reported fluctuating breeding performance annually in the Faroese puffins with on average, delayed breeding start, prolonged chick-rearing periods, and greater seasonal fluctuations in fish species and the number of fish they are observed to bring back from the sea (Olsen et al. 1996; Jensen, 2021), suggesting a change in the feeding ecology affecting the length of the chick-rearing period and the overall breeding success. Very similar changes have been reported from Machias Seal Island in Canada (Major et al. 2021, Diamond 2021). Long-term food shortage is noted to compromise breeding success (Cury et al. 2011) and changing sea temperatures and the quality of fish has been shown to influence breeding success and adult survival of auks (Durant et al. 2003; Fluhr et al. 2017). We hypothesise that a change in feeding ecology, likely a shortage of prey, has led to the decline of puffins in the Faroes and that the food shortage could in turn lead to fewer feedings.

Here, we use both direct field observations and video surveillance to study the food provisioning of puffin chicks in the Faroe Islands during the period in which the population has declined. The data cover the period from hatching to fledging for four years: two early years based on field observations (1992 and 1993) and two late years based on video recordings (2018 and 2019), all from the same colony on the small island of Skúvoy. The four years included one reportedly good breeding year (1993; high numbers of adults attending the colony, high breeding success) and three years with relatively poor breeding (1992, 2018 and 2019; low numbers attending, low breeding success) (Merkel and Nielsen 1997, Gaard et al. 2002, Olsen 2004, Olsen & Jensen unpublished, Olsen et al. 2025). *A priori*, we expected that feeding frequencies would be higher in good breeding years compared to poor ones, based on the assumption that food shortage would increase foraging distance, as observed for other central-place foraging species (Houston & McNamara 1985, Boersma & Rebstock 2009; Chivers et al. 2012, Lorentsen et al. 2019). Alternatively, if the flexibility of feeding frequency is somehow limited or unaffected by food availability, we expected the length of the breeding season to be shorter in years with good breeding performance and vice versa (Barrett & Rikardsen 1992; Durant et al. 2006; Anker-Nilssen et al. 2024). Here, we quantify feeding frequencies

across the breeding season for the four years considered. We aim to investigate if there is a general change in feeding frequency between early and late years and highlight differences in the feeding ecology between years of reported good and poor breeding.

Methods and materials

The study was performed in a small colony, Byrgisbakki, on the island Skúvoy in the Faroe Islands (61°47'N 6°49'W) (Figure 1).

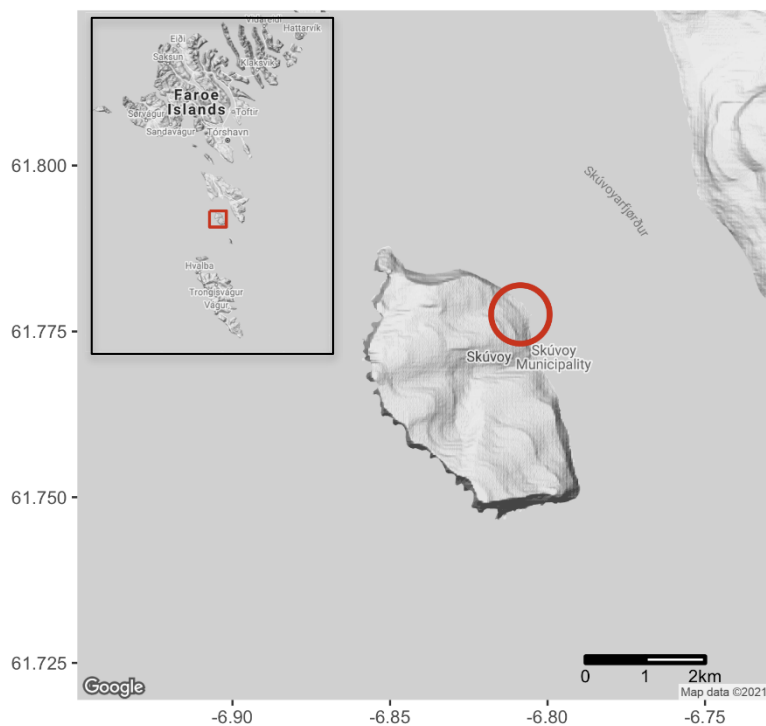


Figure 1. Map showing the study site, Byrgisbakki puffin colony, on the small island of Skúvoy. Insert shows the Faroe Islands and the location of Skúvoy within.

Sampling in 1992 and 1993

In 1992 and 1993, Merkel & Nielsen (1997) completed direct dawn-to-dusk observations of puffin chick provisioning from a hide in the colony. Observations were performed on individually marked active nests, 73 in 1992 and 90 in 1993. In 1992, observations were performed every other day between 9 July and 9 September; in 1993, every other day from 27 June to 17 July and every fourth day from 17 July to 26 August. Surveillances resulted in 32 days of observations in 1992 with a total number of 2,359 feedings, and 20 days of observations in 1993 with a total number of 1,856 feedings.

Chick age was estimated in two different ways these two years. In 1992, starting age was estimated from wing length (Merkel & Nielsen 1997), and in 1993, the chick was estimated to be 1 day old when it received the first load of fish. Age of fledging was determined from the last observed feeding

or the last time the chick was seen in the burrow during weighing. Chicks were weighed every second day in 1992 and every fourth day in 1993.

Sampling in 2018 and 2019

Fifteen artificial, natural-looking puffin burrows, were video monitored from the inside with infrared cameras throughout the breeding period. Each artificial burrow was equipped with a camera connected to a computer placed in the same hide used for direct observations in 1992 and 1993. Video material from the 2018 and 2019 breeding seasons were analysed and divided between two observers. Observers noted every feeding event that occurred on the video recordings during these two breeding years, using Geovision Digital Surveillance System ViewLogEx (v. 8.5.9.0) set on speed modes from x32 to slow motion as appropriate. In 2018 and 2019, feeding events were characterised using the same method applied in 1992 and 1993. A feeding event is defined as an adult puffin returning to the burrow with fish in its bill. When a feeding event was detected the best photo of the bill load was saved using the option to stop, rewind and replay in slow motion, or frame by frame, resulting in a data subset of 6,481 still pictures. The subset was used for further analysis of feeding events.

Out of 15 burrows monitored annually by video, technical limitations and natural circumstances (e.g., unhatched eggs) resulted in six burrows being fully monitored in 2018 and eleven in 2019. In total, 17 camera deployments were included in this study, yielding 254 full days of footage in 2018 and 529 in 2019.

The time of egg laying is defined as the first day an egg was spotted in the burrow, and the time of hatching is defined as the first day a chick was spotted in the burrow. The chick was observed until it fledged or died. Fledging was defined as a chick having left the burrow for a continuous 72 hours. Death was concluded when the chick had been immobile for at least one full day.

During video recordings, occasional minor technical issues occurred resulting in brief periods of unrecorded footage, which could not be reviewed. Camera lenses were cleaned approximately once per week; however, lenses sometimes became soiled, particularly following chick feedings, potentially causing a few feeding events to go undetected.

Data analysis

Feeding frequencies

In 1992 and 1993, field observations were not conducted daily. To account for missed feeding events on days without observations, we estimated the total sum of feedings by multiplying the average daily number of feedings (derived from the observed days) by the estimated age at fledging. Chicks with unknown fledging dates were excluded from the analysis. We incorporated the estimated total

sum of feedings from 1992 and 1993 into the analysis: 3,813 events recorded from 25 active nests in 1992 and 4,436 events from 47 active nests in 1993.

In 2018 and 2019, continuous 24-hour video monitoring of the artificial burrows ensured complete observation coverage; thus, all feeding events from active nests were included, totalling 2,263 events from 8 nests in 2018 and 4,218 events from 11 nests in 2019 (Table 1). Two chicks - one from 2018 and one from 2019 - were excluded from the analysis due to a large proportion of the feeding events occurring outside of the camera view.

Table 1. General summary of breeding season success for Atlantic Puffins (*Fratercula arctica*) nesting at Skúvoy in 1992, 1993, 2018, and 2019.

	Number of burrows with egg	Number of burrows with chick	Hatch success (%)	Number of chicks fledged	Breeding success (%)
1992	26	25	96	17	65
1993	47	47	100	45	96
2018	9	8 (6*)	89	6	86
2019	13	11	85	10	77

*Due to camera malfunction, we were only able to follow 6 burrows with chicks throughout the entire breeding season and thus these two burrows were excluded from calculation of breeding success.

In total, 14,730 feeding events were retained for analysis.

We tested for differences between timing of hatch dates and fledging dates, respectively, between early and late periods using t-tests (performed in MS Excel). Assumptions of normality were assessed by visually inspecting plots of data which revealed no obvious departures from normality. All other data analyses were performed using R Statistical Software (v.4.0.5 R Core Team 2021). We tested whether the average feeding rate and the total number of feedings differed between years and between chick status (fledged vs. died) using ANOVA and Tukey Honest Significant Differences.

Results

In 1992, the hatching success was 96 % (N = 26), 100 % (N = 47) in 1993, 89 % (N = 9) in 2018, and 85 % (N = 13) in 2019 (Table 1). The mean dates (\pm S.D.) for egg hatching in 1992 and 1993 were 6 July (\pm 8.35 days) and 7 July (\pm 7.37 days), respectively, and in 2018 and 2019 2 July (\pm 2.14 days) and 29 June (\pm 4.13 days), respectively. The season started significantly earlier in the later period, 2018 and 2019 ($P < 0.001$, t-test of early versus late period; $N_1 = 72$, $N_2 = 18$ nests). Mean incubation time was 39 days (\pm 0.90 days) in 2018 and 40 days (\pm 1.21 days) in 2019 (egg laying dates not known for 1992 and 1993).

In 1992, the fledging success was 68 % (N = 25), 96% (N = 47) in 1993, 100 % (N = 6) in 2018, and 91 % (N = 10) in 2019 (Table 2). Mean fledging date (\pm S.D.) ranged from 11 August in 1993 to 20 August in 1992 and 2018. Interannual variation in fledging date was highest in 1992 (\pm 10.90 days) and 1993 (\pm 9.13 days), whereas variation was lower in 2018 (\pm 4.70 days) and intermediate in 2019 (\pm 6.35 days). Breeding success in 1992 was 65 %, 96 % in 1993, 86 % in 2018, and 77 % in 2019 (Table 1).

Table 2. Summary of feeding frequencies and fledging success (hatched chick surviving until fledging) for Atlantic Puffins (*Fratercula arctica*) nesting at Skúvoy in 1992, 1993, 2018, and 2019.

Year	N	Sum of feedings	Mean feeding rate \pm SD	Median feeding rate (min. –max.)	Fledging success (%)	Mean fledging age
1992	25	3813	7.29 \pm 6.21	6 (0–27)	68	45
1993	47	4436	7.62 \pm 4.41	7 (0–22)	96	36
2018	8 (6*)	2263	9.47 \pm 5.42	9 (0–25)	100	47
2019	11	4218	8.45 \pm 5.79	7 (0–25)	91	50

*Only 6 of 8 burrows were followed throughout the entire breeding season.

The maximum recorded feeding frequency per day in each of the four sampled years ranged between 22–27; in all four years chicks experienced days with no feedings (Table 2; Figure 2). The highest mean feeding (\pm S.D.) frequency occurred in 2018 (9.47 \pm 5.42 feeds d⁻¹) and the lowest in 1992 (7.29 \pm 6.21 feeds d⁻¹; Table 2). A one-way ANOVA showed no significant difference in average feeds d⁻¹ between years ($F_{3,83} = 1.92$; $P = 0.132$; Figure 3) but showed a significant difference in average feeds d⁻¹ between chicks that fledged and died ($F_{1,85} = 6.161$; $P = 0.015$; Figure 3). The average feeding rate was lower for chicks that died (5.97 \pm 2.11 feeds d⁻¹) compared with chicks that successfully fledged (7.85 \pm 2.36 feeds d⁻¹).

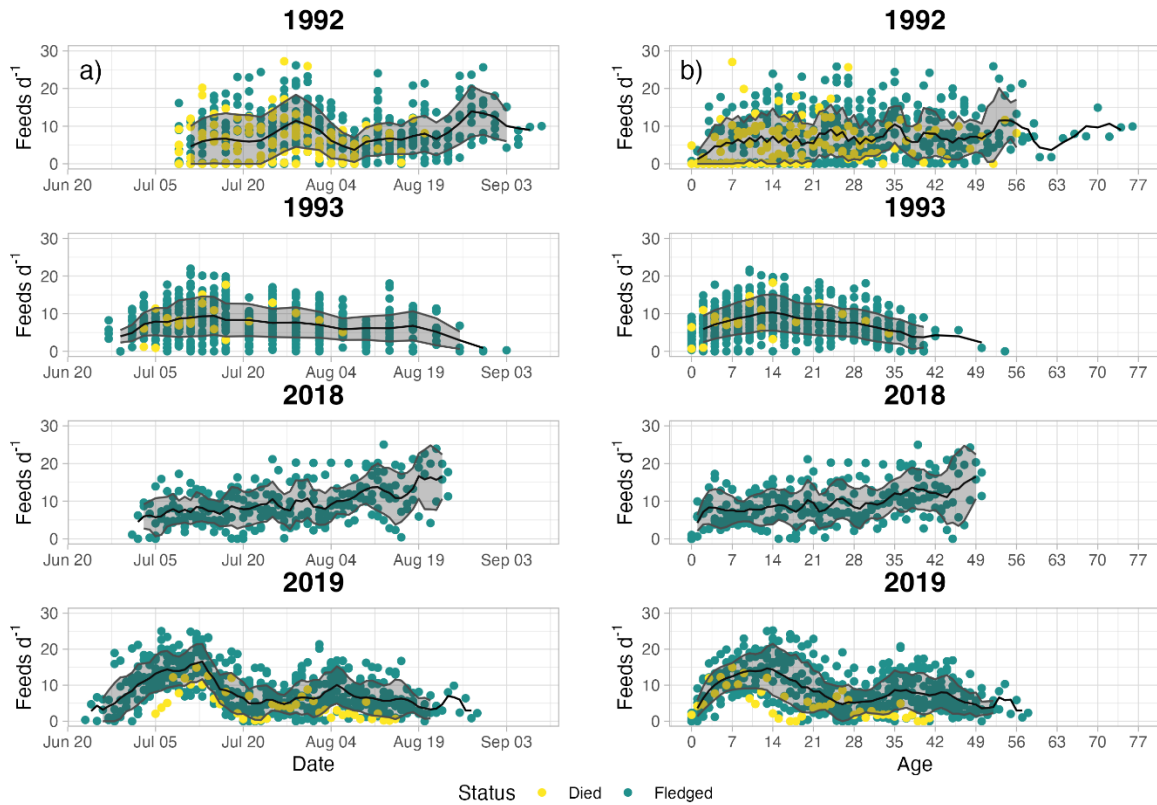


Figure 2. Running means (black line) of feeding frequency \pm *SD* for all individual Atlantic Puffins (*Fratercula arctica*) chicks monitored at Skúvoy in 1992, 1993, 2018, and 2019 **a)** according to date, and **b)** according to chick age in days. Each dot represents a chick and the number of feedings it received. Chicks that survived to fledging are represented by a green dot whereas chicks that died are represented by a yellow dot.

A two-way ANOVA showed significant difference between the total number of feedings between years ($F_{3,82} = 12.26$; $P < 0.001$) and chicks that fledged or died ($F_{1,82} = 15.37$; $P < 0.001$; Figure 3). Subsequent post-hoc pairwise comparisons on total number of feedings between years, showed that in 1993 the chicks received a significantly lower number of feedings compared to 1992, 2018 and 2019 (all $P_{\text{adj}} \leq 0.01$), whereas 1992, 2018 and 2019 were not significantly different from one another (all $P_{\text{adj}} > 0.35$) (Figure 3).

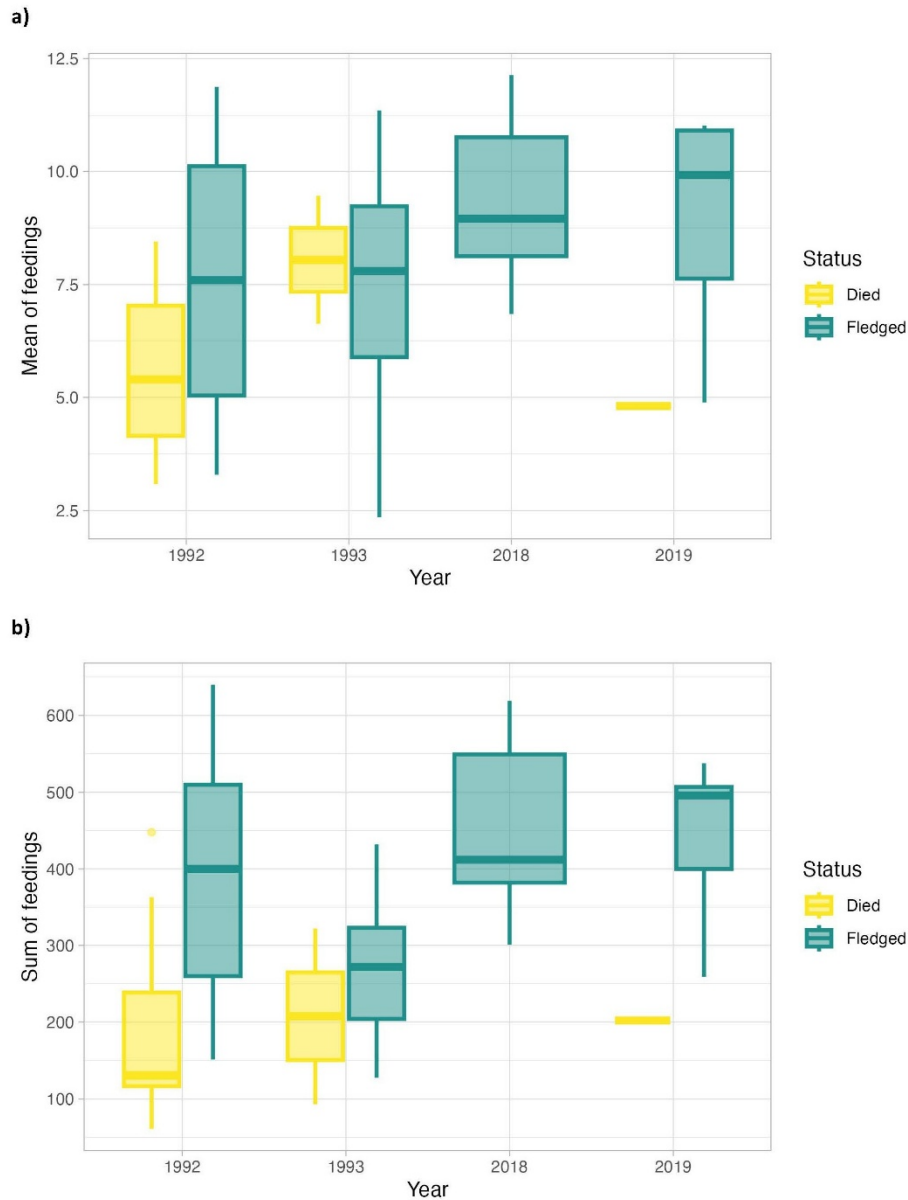


Figure 4. Boxplot showing how **a)** sum of feedings and **b)** mean of feedings are distributed in 1992, 1993, 2018 and 2019. The median is presented by a bold horizontal line in the middle of the boxes with the 1st and 3rd quartiles, whiskers show the minimum and maximum of feeding sum and dots show outliers of total number of feedings of Atlantic Puffins (*Fratercula arctica*) nesting at Skúvoy in 1992, 1993, 2018, and 2019. Yellow boxes denote chicks that died and green those that survived to fledge.

A two-way ANOVA showed a significant difference in the age at fledging between years ($F_{3,80} = 30.52$; $P < 0.001$; Figure S1), as well as significantly lower age at death than age at fledging ($F_{1,80} = 26.24$; $P < 0.001$; Figure S1). The subsequent post-hoc pairwise comparisons between age at fledging and year, showed that the chicks fledged significantly earlier in 1993 compared to 1992, 2018 and 2019 (all $P_{adj} < 0.001$), whereas 1992, 2018 and 2019 were not significantly different from one another (all $P_{adj} >$

0.8) (Figure S1). In the poorer breeding years, age at fledging ranged between 45–50 days whereas it was 36 days in 1993 (the good year).

Feeding frequencies over the course of the breeding season varied among years (Figure 4). There was high variability in feeding frequencies in 1992, 2018 and 2019, whereas feeding frequency appeared relatively constant in 1993 (Figure 4a) but sample size was also higher this year. In all years there seemed to be an increase in provisioning in the beginning, but the duration of the increase was variable between the years (Figure 4b).

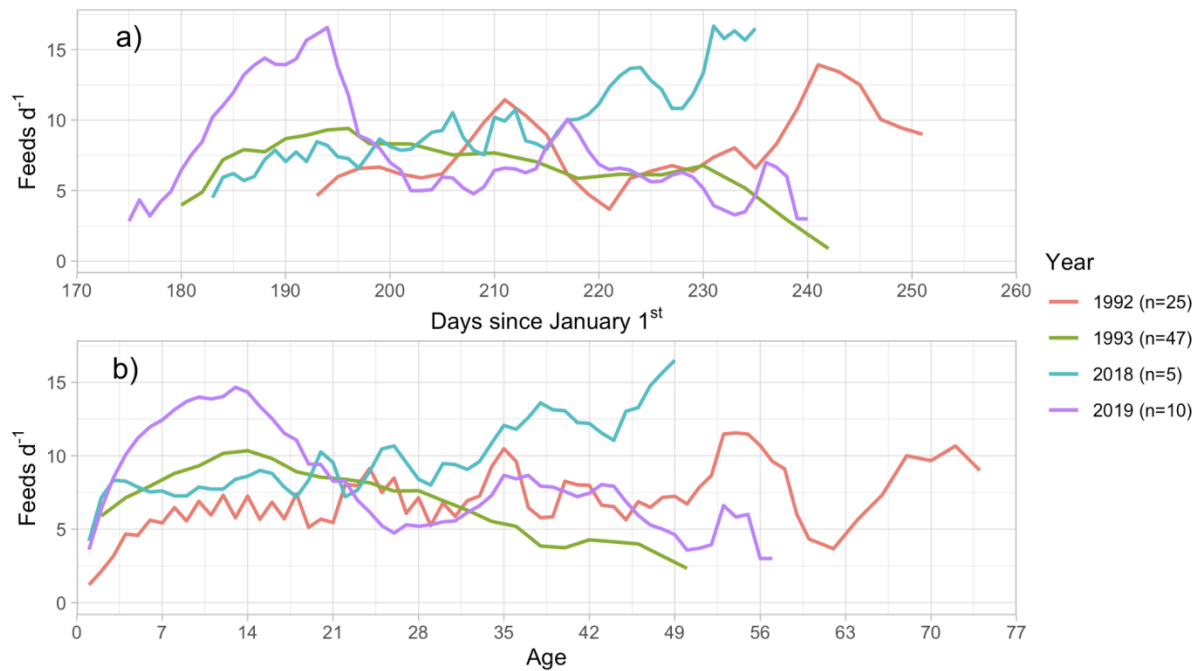


Figure 4. Running means (3 days) of feeding frequency per nest for Atlantic Puffins (*Fratercula arctica*) nesting at Skúvoy in 1992, 1993, 2018, and 2019 against **a)** days since 1 January, and **b)** age of the chicks in days.

Discussion

Our study aimed to provide insight into the feeding rates of puffin chicks in the Faroe Islands and how these relate to reported variation in breeding performance (good or poor, also reflected in the breeding success observed in this study) across years. However, we observed no difference in mean daily feeding frequency among the four study years, even though 1993 was a good breeding year and 1992, 2018 and 2019 were relatively poorer, which shows that a good breeding season does not necessarily coincide with a high feeding frequency. Instead, chicks in the good year received fewer total feedings because the chick-rearing period was markedly shorter, whereas poor years were characterised by longer chick-rearing periods and consequently higher cumulative numbers of feeds. Most chicks in our three relatively poor years nevertheless fledged, in contrast to the very poorest years in the Faroes, when chick production can fail almost completely (Olsen et al. 2025), indicating

that the study years examined here likely span a range from very good to intermediate breeding conditions.

Our results indicate that feeding frequency alone is not sufficient for predicting breeding success once it exceeds a minimum threshold. On Skúvoy, chicks that died had lower mean feeding rates than fledged chicks, indicating that sustained under-provisioning can be fatal. Based on several study species and ecosystems, Cury et al. (2011) identified a threshold in prey abundance - approximately one third of the maximum prey biomass observed in long-term studies - below which seabirds exhibit consistently reduced and more variable productivity. On Skúvoy, the system appeared to operate largely above this threshold during our study years, given the high or moderate high proportion of chicks surviving to fledging, although this is not always the case (Olsen et al. 2025).

Other studies of Atlantic puffins indicate that chick provisioning rates indeed can covary with breeding success, but the relationship is context-dependent and can vary in direction. Fayet et al. (2021) compared feeding rates across several puffin colonies in the Northeast Atlantic during a single year and found that lower feeding rates were associated with poor breeding performance, primarily because birds were forced to forage farther from the colony, presumably due to low prey availability near the colonies. From the Isle of May, Harris and Wanless (2011) reported a change in the opposite direction. From the mid-1900s to 2010, puffin chicks were fed more frequently, yet breeding performance declined, alongside more diverse but smaller prey loads and a longer chick-rearing period. Atlantic puffin populations in the Western Atlantic have been reported as more stable (Wilhelm et al. 2015), but since around 2005, breeding success has also been declining on Machias Seal Island in Canada, related to poor feeding conditions associated with a shift in prey regime (Major et al. 2021, Diamond 2021); however, it is unclear how these changes affected provisioning rate. Long-term studies of puffins in Norway have documented substantial population declines (e.g. Anker-Nilssen et al. 2020), with inter-annual variation in herring availability near the colony identified as a key factor underlying poor breeding performance (Anker-Nilssen, 1992; Durant et al. 2003). In some cases, this also involved an evident decrease in food provisioning of chicks due to a change in direction and distance travelled to the feeding grounds (Anker-Nilssen and Lorentsen 1990). Farther north in Norway, at Hornøya, a long-term (1989–2013) decrease in the size of fish delivered to puffin chicks was observed; however, because this was accompanied by a parallel increase in the number of fish per food load, chick growth rates remained largely unchanged (Barrett 2015). Although feeding rates were not reported in this study, the Hornøya case illustrates how feeding rates may remain relatively constant despite marked changes in the available prey source.

The above examples clearly show that feeding frequency alone is an incomplete predictor, as it interacts with prey quality, prey load size, chick-rearing duration, and potentially other factors. It may be useful if breeding performance is fatal or close to fatal, but this was not the case in our study period. To better describe the role of feeding in chick production on Skúvoy, species specific prey delivery rates and quantities would be required.

Conclusion

Our study shows that puffin chick feeding rates in the Faroe Islands do not directly predict annual breeding success. High breeding success was associated with shorter chick-rearing periods rather than higher daily feeding frequencies, whereas poorer years involved longer rearing periods and higher cumulative feedings. Chicks receiving consistently low provisioning were unlikely to fledge, indicating that sustained under-provisioning can be fatal. Comparisons with other studies show that provisioning rates may covary with breeding success under certain conditions but rarely function as a sole indicator, as prey availability, prey quality, and foraging effort often complicate this relationship. Future studies incorporating quantitative data on prey composition, food load size, and prey availability are needed to better understand chick production in Faroese puffins.

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Data Availability

Data are available from the Zenodo data repository: <https://doi.org/10.5281/zenodo.19512641> (Aagard *et al.* 2026).

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