BEHAVIORAL RESPONSE OF ATLANTIC PUFFINS *FRATERCULA ARCTICA* TO MARINE HEATWAVES IN THE GULF OF MAINE, USA: A WEBCAM STUDY

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ABSTRACT

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We observed a family of Atlantic Puffins *Fratercula arctica* in a burrow on Seal Island National Wildlife Refuge in the Gulf of Maine, USA, during the 2017–2020 and 2022 breeding seasons. The burrow was equipped with a high-resolution web camera, which allowed 24-hour daily observations. We investigated the impacts of elevated sea surface temperature (SST) and marine heatwaves (MHWs), which are linked to low food availability, on chick provisioning and burrow attendance. In 2017, 2019, 2020, and 2022, the female was the primary provisioner, providing twice as many feedings as the male, and the male was the primary burrow guardian, spending twice as much time at the burrow as the female. Using generalized linear models to estimate relationships between SST, feeding rates, and burrow attendance, we found that higher SST was associated with lower feeding rates and burrow attendance. These impacts were amplified in 2018 amid a prolonged MHW. The puffins struggled to find food consistently, leading to lower provisioning rates, smaller bill-loads of mostly low-quality prey, and a visibly under-nourished chick. This prompted the male to trade his burrow-guarding role for additional chick provisioning, and the chick fledged after 69 days, 28 days longer than is typical. This study is the first to demonstrate that Atlantic Puffins can modify their usual parenting roles in response to prey availability, deferring migration and extending chick-rearing by as many as four weeks. We also observed modification in chick behavior amid a high-intensity MHW in 2022, during which the chick was frequently provisioned with American Butterfish *Peprilus triacanthus*, a deep-bodied fish that is not easily swallowed. The chick consistently consumed butterfish piecemeal, pulling off and swallowing small pieces, until the remaining portion was small enough to be swallowed. This was an effective strategy and a behavior that has not previously been reported.

Key words: Atlantic Puffins, marine heatwaves, parenting roles, plasticity, chick behavior

INTRODUCTION

Marine heatwaves (MHWs) are episodes of anomalously high sea surface temperature (SST) that last for extended periods of time (Hobday et al., 2016). They occur globally (Smale et al., 2019), often superimposed on already-warming oceans (Merchant et al., 2025). The impacts on marine ecosystems are varied (Venegas et al., 2023) and include coral bleaching (Le Nohaïc et al., 2017), altered plankton communities (Arteaga & Rousseaux, 2023), movement of taxa into or out of affected areas (Lonhart et al., 2019), and mortality of upper trophic-level predators such as seabirds (Piatt et al., 2020). Smale et al. (2019) found that while sessile taxa, such as corals, were more adversely affected than mobile taxa that could move to more suitable environments, the impact on seabirds was second only to corals. Alcids are among the most susceptible seabirds (Woehler & Hobday, 2024) because as central place foragers (Orians & Pearson, 1979), they are geographically constrained to prey patches close to the colony. Some seabirds, such as Procellariiformes (tubenoses), fare better because their greater flight efficiency allows them to search more expansive areas for prey, while the higher energetic costs of alcid flights limit their foraging range (Cushing et al., 2024).

The northwestern Atlantic Ocean, which includes the Gulf of Maine, has emerged as a hotspot for MHWs in recent years, with a strong warming trend, long-duration MHWs, and a high number of annual heatwave days (Marin et al., 2021). The Gulf of Maine marine ecosystem had intermittently experienced MHWs of short duration in past decades, but since 2010, they have become more prevalent and more intense (Gulf of Maine Research Institute, 2024). Severe, long-duration MHWs dominated 2012, impacting commercial fisheries (Mills et al., 2013; Pershing et al., 2015) and exacerbating species redistribution that was already in progress in response to ocean warming (Nye et al., 2009, 2011). The post-2010 warming trend was attributed to incursion of warm water associated with the Gulf Stream, at depth (Balch et al., 2022; Record et al., 2024; Seidov et al., 2021).

Atlantic Puffins *Fratercula arctica* are among the colonial seabirds nesting on islands in the Gulf of Maine during spring-summer. Chick-rearing requires a steady supply of good-quality prey to meet the energetic needs of the chick (Scopel et al., 2019). MHWs that impact the species' foraging grounds in winter-spring (prior to breeding), may alter the food web (Gomes et al., 2024), potentially reducing prey availability for puffins during chick-rearing (Piatt et al., 2024; Staudinger et al., 2019). MHWs in spring-summer may cause preferred prey to move out of the puffins' usual foraging grounds to seek cooler waters (Kleisner et al., 2017; Mills et al., 2024). The highest

MHW intensities typically occur in the summer (Sen Gupta et al., 2020), coinciding with chick-rearing and, therefore, amplifying the detrimental impacts on seabirds and their chicks (Ramírez et al., 2016).

Changes in fish availability may require seabirds to modify provisioning behavior, possibly with negative consequences for adults and chicks. Longer foraging trips (Fayet et al., 2021; Osborne et al., 2020) or deeper dives (Symons & Diamond, 2022) to find suitable prey require greater energy expenditure that could cause adult body condition to deteriorate (Cushing et al., 2024; Grilli et al., 2018). Breeding success and fledgling body condition may also be compromised (Fayet et al., 2021; Lescure et al., 2023). However, puffins are generalist predators that can mitigate shortage of preferred prey by feeding chicks a broader range of taxa, including those of lower quality (Kress et al., 2016; Scopel et al., 2019). They may also counter the effects of lower quality prey with a higher rate of chick provisioning (Eilertsen et al., 2008; Schrimpf et al., 2012).

In this study, we used a webcam to observe the behavior of a family of Atlantic Puffins in a burrow on Seal Island National Wildlife Refuge in the Gulf of Maine. We collected data from a single burrow over several years, during which there were periods of anomalously high SST and frequent MHWs. We examined breeding behavior and sex-specific roles of the parents, as well as chick behavior, under the prevailing environmental conditions. While our observations may be echoed elsewhere in the colony, this study may not be representative of the entire colony.

METHODS

Study site

Seal Island National Wildlife Refuge in the Gulf of Maine (Maine, USA: 43°53′23″N, 068°44′02″W; Fig. 1) is a 26-hectare (0.26 km^2) island managed by the US Fish and Wildlife Service in cooperation with the National Audubon Society. In 2024, 672 active puffin burrows were confirmed on the island (Jackson, 2024). Our study burrow was equipped with a 24-hour high-resolution infrared webcam, installed and operated by the philanthropic organization explore (online portal available at explore.org), in partnership with Audubon's Project Puffin/Seabird Institute. During the breeding season, a research team from Audubon is present on the island.

Background

The study burrow had been monitored for several years, and in 2017, a new pair occupied and bred in the burrow. The female was sexed by DNA at Cornell University, and the male was identified by leg bands as "Willie," who was banded as an adult in 2002. Puffins raise a single chick each season, and this pair reared chicks in 2017 and 2018. Willie returned in 2019 with a new partner, together rearing chicks in 2019–2022 (Table 1).

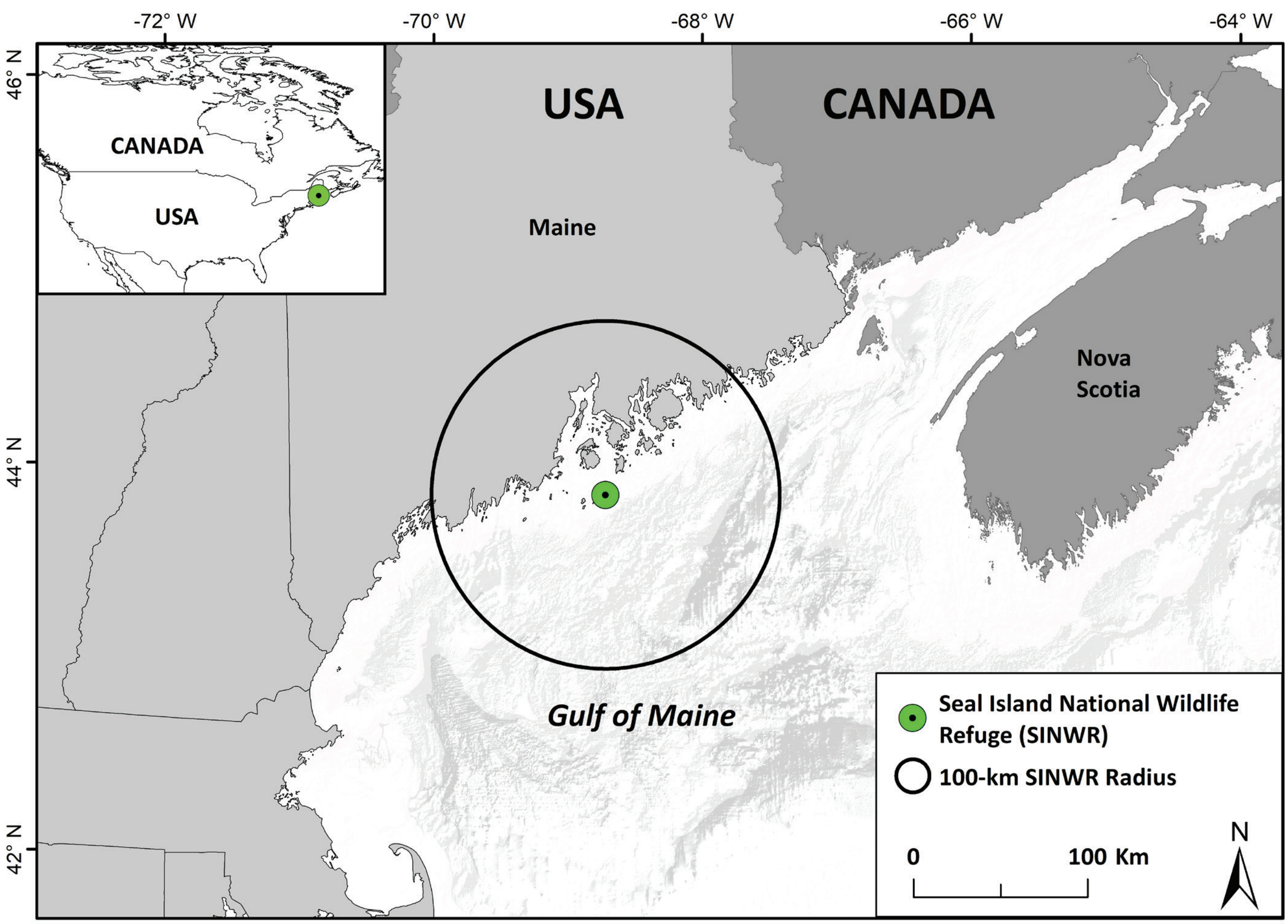

Fig. 1. Location of Seal Island, Maine, USA, showing a 100-km radius around the island.

TABLE 1
Parameters of Atlantic Puffin *Fratercula arctica* chick development at Seal Island, Maine, USA, 2017–2020 and 2022

Year	2017	2018	2019	2020	2022
Egg-laying date	05/20 [a]	05/15	05/14	05/08 [a]	05/15
Hatch date	06/30	06/24	06/26	06/18	06/25
Fledge date	08/10	09/01	08/08	07/28	08/10
Fledging age (d)	41	69	43	40	46
Banding date	07/30	08/28 [b]	07/29	07/24	07/26
Age on banding day (d)	30	65	33	36	31
Weight at banding (g) [c]	344	349	310	326	268
Wing chord at banding (mm)	111	137	116	124	105
Growth rate (g/d) [d]	11.47	5.37	9.39	9.06	8.65
Weight wing index (g/mm) [e]	3.10	2.55	2.67	2.63	2.55
Average annual SSTA (°C) [f]	–0.12	1.40	–0.61	1.34	1.72

[a] Egg-laying was not observed, but it was inferred as 41 days prior to the hatch date.
[b] Last assessment date. The stated measurements were taken on this day. Banding date was 08 August, and the chick weighed 150 g.
[c] Weight and wing chord measurements were provided by Audubon's Project Puffin/Seabird Institute.
[d] Growth rate = weight at banding/age (g/d)
[e] Weight wing index = weight at banding/wing chord (g/mm)
[f] SSTA = Sea Surface Temperature Anomaly

Data

Burrow variables

We collected data by real-time remote viewing via the burrow cam. We acquired data for five seasons, 2017–2020 and 2022, during the nestling period, i.e. from hatch (when the chick emerged from the egg) to fledge (when the chick departed the burrow). We documented the dates and times of daily feedings (DF), the number of daily feedings, species of prey and number of each species where possible, identity of the provisioning parent, and daily burrow attendance (BA). The latter was defined as the total number of hours that each parent attended the burrow each day. If a parent was out of view for a few minutes, but regularly in and out of the burrow, with nesting material for example, those out-of-view minutes were included in BA.

When the chicks were about five weeks old, the research team fitted them with leg bands for identification and resighting purposes. Morphometric measurements were taken simultaneously, and we derived metrics of chick body condition from these data. Growth rate was defined as chick weight/age (g/d), and weight wing index was defined as chick weight/wing chord measurement (g/mm). Table 1 presents measurements taken at the time of banding, except those for the 2018 chick, which are the final of five chick assessments.

Sea surface temperature anomaly (SSTA)

All data analyses were carried out using the R statistical software (v.4.4.1; R Core Team, 2024), unless otherwise stated. We retrieved daily SST from the NOAA Optimum Interpolation Sea Surface Temperature dataset, version 2.1 (OISST.V2.1; Huang et al., 2020) for the Gulf of Maine between 42°N–45°N and 66°W–71°W, for the period 01 January 1982 to 15 October 2022. The "heatwaveR" package (Schlegel & Smit, 2018) was used to extract and process the gridded data, which were then mapped with ArcGIS v10.7 (Environmental Systems Research Institute, 2023). We performed analyses using the daily SST within 100 km of Seal Island rather than the entire Gulf of Maine because puffins typically forage within this range (Fayet et al., 2021; Harris et al., 2012), which, therefore, represents the area of greatest influence. Daily SST at grid points within the 100-km radius were averaged to provide a single daily value for statistical analyses.

A 30-year daily mean SST was calculated using daily averages from 01 January 1982 to 31 December 2011, to represent a multi-decade baseline temperature climatology. For the study years, the daily SST anomaly (SSTA) was calculated as the difference between the OISST.V2.1 value for each day and the 30-year climatological mean for the corresponding month-day.

Marine heatwave (MHW)

A commonly accepted definition of an MHW is an event during which the daily average SST exceeds the 90th percentile of a 30-year climatological mean, for at least five consecutive days (Hobday et al., 2016). We extracted MHWs from the gridded OISST.V2.1 data within 100 km of Seal Island, using the "heatwaveR" package (Schlegel & Smit, 2018). A key metric of an MHW is the intensity or magnitude of the SSTA. We categorized MHWs as Moderate, Strong, Severe, or Extreme, based on intensity criteria described by Hobday et al. (2018). The methodology is described in Appendix 1 (available on the website), along with MHW plots for the full study years. Within these categories, moderate events have the least impact, strong and severe events can cause significant damage, and extreme events cause widespread, lasting damage.

Statistical analysis

In 2018, the web camera experienced overnight outages during a severe MHW (Fig. 2B). The outages persisted from 23 July to 12 August and occurred at various times between 21h00 and 09h00 Eastern Daylight Time (EDT) the following day, resulting in early-morning data gaps. We explored several options for aggregating all data for analysis, given the 2018 outages. The study spanned 239 days over the five years, and we removed days with camera outages, days when the chick hatched, and days when the chick fledged before feedings. We prepared three datasets to assess the best-performing model: Option 1 - all years with all cam outage days removed (n = 212); Option 2 - all years truncated to 09h00 to 21h00 daily, which would eliminate 2018 data gaps (n = 232); Option 3 - four years excluding 2018 (n = 165). We constructed generalized linear models (GLMs) with response variables Total BA (Gaussian model) and Total DF (Poisson model) for each

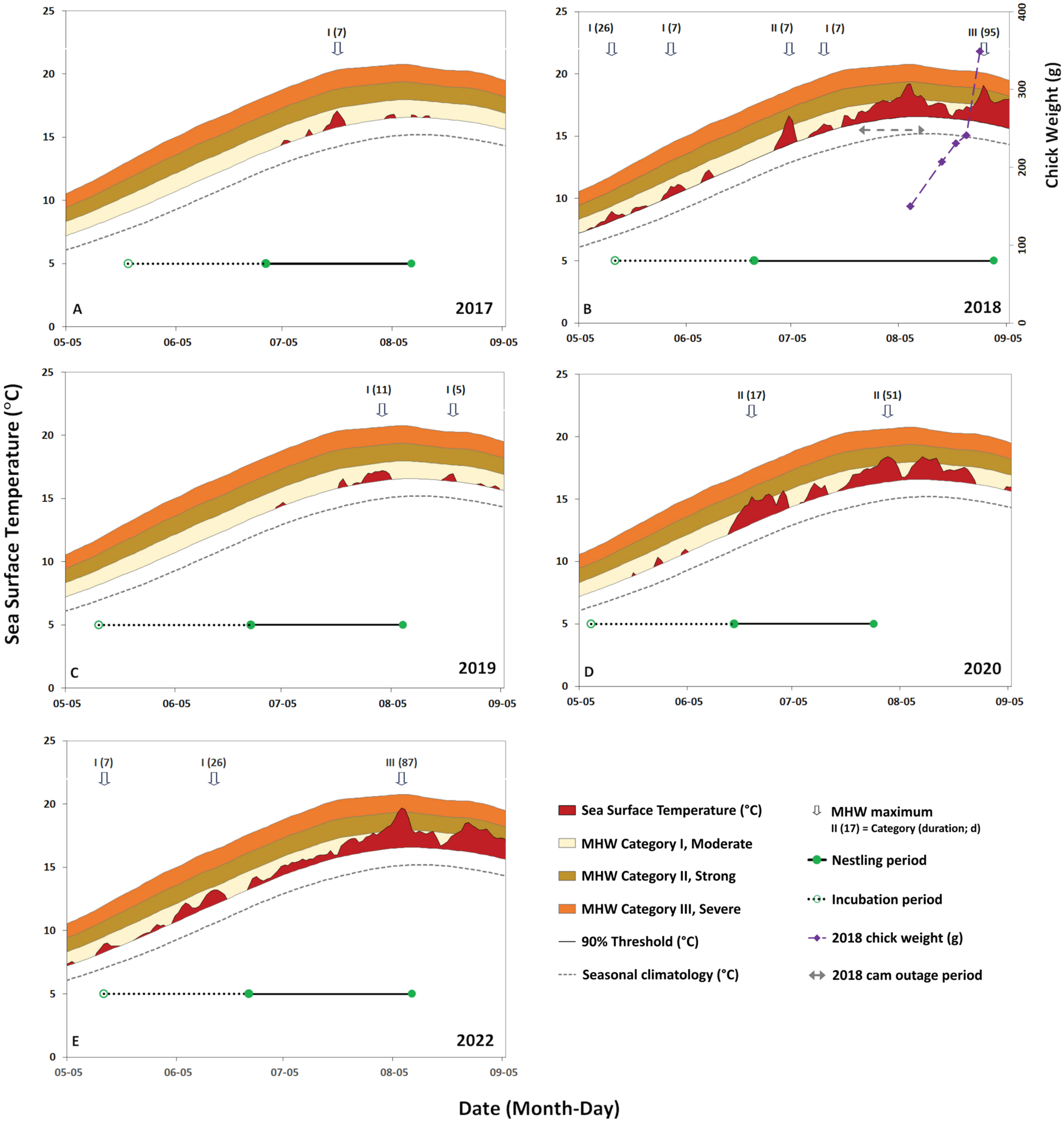

Fig. 2. Marine heatwaves (MHW) within 100 km of Seal Island, Maine, USA, during the breeding seasons in 2017–2020 and 2022. Categories ranging from I (Moderate) to III (Severe) are displayed along with duration (d) at the point of maximum intensity. Atlantic Puffin *Fratercula arctica* incubation and nestling periods are indicated by horizontal lines spanning the appropriate dates. The additional line plot on panel B shows chick weight (g) measured between 08 August–28 August 2018, and the additional horizontal line spans the period of overnight webcam outages. The temperature climatology is based on the 30-year period from 1982–2011.

option, as described in the next section. We assessed the best model fits based on Akaike Information Criterion (AIC) scores (Akaike, 1998), normality and homoscedasticity in the residuals, as well as R-squared and chi-square model fits. For Options 1, 2, and 3, respective AIC scores for Total BA models were 1474, 1314, and 1109; scores for Total DF models were 990, 1013, and 737. When the lowest AIC scores and other metrics of fit were taken into consideration, Option 3 provided the best models.

We therefore proceeded with two datasets: one for 2017, 2019, 2020, and 2022 combined, which we have designated the Normal Years; and another for 2018.

Generalized linear models – Normal Years

We constructed GLM regression models to explore the association between SSTA, DF, and BA. All models were checked for collinearity, and residuals were checked for homoscedasticity and normality. Models were tested at the 95% level of significance.

Three GLM Poisson (log link) models were created for DF using response variables Female DF, Male DF, and Total DF, each with explanatory variables SSTA (°C), Male BA (h), Female BA (h), and chick's Age (d). Age was treated as a categorical variable, since there was a mid-season peak for feedings in some years. We created three age categories: Age Season-Start for the first seven days, Age Season-End for the last seven days, and Age Season-Mid for all days in between. We chose Age Season-Start as the base-level reference category against which other age categories would be compared.

Datasets for Female DF, Male DF, and Total DF exhibited mild under-dispersion (mean, variance = 4.4, 3.0; 2.0, 1.9; 6.5, 6.1, respectively). We compared the standard GLM Poisson regression (log link) to two models designed to address mild violations of equi-dispersion: the Quasi-Poisson regression (log link), and the Poisson regression with robust standard error estimates from the R package "Sandwich" (Zeileis, 2006). Results from both were very similar, and we opted for the latter. Chi-square goodness-of-fit tests were used to check model fits. The results were back-transformed to indicate the relative change in DF with a unit increase in each explanatory variable.

Three GLM Gaussian models were created for BA using response variables Female BA (h), Male BA (h), and Total BA (h), each with explanatory variables SSTA (°C), Male DF, Female DF, and chick's Age (d). Other GLM regression models were tested, but none improved the model fits.

Non-parametric tests – 2018

A long-duration, multi-peak MHW occurred during the 2018 nestling period, peaking first on 08 August before abating for several days (Fig. 2B). This event was associated with a marked reduction in both daily feedings and burrow attendance, and an extended chick-rearing period (69 days instead of the expected 38–44 days) in addition to the aforementioned overnight webcam outages and data gaps. For analysis, we will refer to this phase of the MHW as MHW Phase 1 (MHW1). To eliminate the overnight data gaps and achieve the most robust analyses across the full season, we prepared a subset of the data truncated to 09h00–21h00 EDT (Subset 1). This subset produced poor GLM fits, and we used Kruskal-Wallis non-parametric tests to compare male and female DF and BA across three periods: pre-MHW1 (25 June–22 July, n = 28), MHW1 (24 July–12 August, n = 20), and post-MHW1 (13 August–31 August, n = 19). There was a missing day on 23 July due to extended outages. We conducted post-hoc analyses with Pairwise Wilcox Rank Sum Tests to identify statistically significant differences among pairs in the MHW1 periods.

We further explored the data with similar analyses of a second data subset (Subset 2), which included 24-hour observations for the pre-MHW1 (n = 28) and post-MHW1 (n = 19) periods, excluding the MHW1 period with the data gaps.

The puffling and the butterfish

The American Butterfish *Peprilus triacanthus* is a warm-water species that has become more prevalent in the Gulf of Maine in recent years (Adams, 2022). It is a high-lipid fish (Budge et al., 2002), but it is deep-bodied and generally too wide for young puffin chicks (pufflings) to swallow whole, so it may be rejected (Ainley & Boekelheide, 1990). Because it is difficult to consume, significant amounts in the diet could lead to low growth rates or even starvation (Kress et al., 2016; Smith & Craig, 2023).

In 2022, moderate to severe MHWs spanned the nestling period (Fig. 2E), and butterfish was often provisioned. We observed the puffling consuming butterfish in a piecemeal fashion, pulling off and swallowing small pieces, thus reducing the fish to a size sufficiently small to be swallowed. This highly unusual behavior has not previously been reported. We describe the eating process.

To determine the food conditions under which the chick demonstrated such atypical behavior, we quantified the biomass of delivered prey, as described in Appendix 1. While butterfish was provisioned throughout the season, there was a marked increase during the latter weeks, as the MHW intensified to severe levels. We compared biomass during the Moderate phase of the MHW (MMHW, 25 June–27 July) to the Strong/Severe phase (SMHW, 28 July–09 August), when butterfish provisioning increased.

RESULTS

Chicks' body condition

Chick growth rates ranged from 5.37 g/d in 2018 to 11.47 g/d in 2017 (Table 1). Weight wing indices ranged from 2.55 g/mm in 2018 and 2022 to 3.10 g/mm in 2017. Fledging age was 40–46 days (median 42 days) in normal years and 69 days in 2018.

MHWs

MHW plots are presented for the breeding seasons (Fig. 2) and for the calendar years (Appendix 1).

In 2017, a winter event was carried over from 2016, and there were no spring events. The nestling period was free of MHWs except for a moderate event that lasted seven days (Fig. 2A).

In winter 2018, a 33-day event reached a maximum intensity of 2.2 °C; 33% of these days were classified as strong. This was followed by moderate events in the spring. Post-hatch, a seven-day event (43% of days classified as strong) spiked at 3.8 °C, when the chick was 10 days old (Fig. 2B). This was followed by a multi-peak, 95-day event that strengthened and subsided several times. The first peak reached intensity of 4.1 °C (strong category) when the chick was 45 days old, subsided significantly before strengthening to a maximum intensity of 4.4 °C (severe category), when the chick was 66 days old. Over the duration of this event, 1% and 37% of days were classified as severe and strong, respectively. This event extended into the post-fledge period, with further periods of abatement and intensification.

In 2019, there were no events in the winter or spring, but a moderate event lasting 11 days reached 2.2 °C during the nestling period (Fig. 2C).

Events in 2020 emerged throughout the year, with moderate events in winter and spring, prior to hatch (Fig. 2D). Two strong events dominated the nestling period. The first was a 17-day event with 53% of days classified as strong and a maximum intensity of 3.6 °C when the chick was five days old. The second was a 51-day event with 22% of days classified as strong and a maximum intensity of 3.5 °C four days post-fledge.

MHWs were pervasive in 2022, with five moderate events in the winter and spring, prior to hatch (Fig. 2E). An 87-day event spanned the nestling period, with 3% and 33% of days in the severe and strong categories, respectively. This event reached a maximum intensity of 4.6 °C when the chick was 43 days old, three days prior to fledge.

Normal Years – daily feedings and SSTA

In normal years, the female was the primary provisioner, delivering approximately two-thirds of all observed feedings (Table 2). The highest rate of provisioning occurred in 2019, and the lowest in 2022. Daily feedings ranged from 1–13 per day, with lower rates typically after hatch and before fledge (Fig. 3A–3D). The SSTA line plots reflect persistent high temperatures in 2020 and 2022. Overall, the average annual SSTA for the study years ranged from −0.61 °C in 2019 to 1.72 °C in 2022 (Table 1).

Statistical analyses

We present results of GLM models as forest plots, with the regression coefficient of each explanatory variable represented as a point on a line that spans the 95% confidence interval (Fig. 4). In models for DF (Column 1), points greater than one reflect a positive association with DF, and vice versa. Both Female DF and Total DF show a negative association with SSTA (i.e., a decrease in feedings with rising SSTA), though neither was statistically significant (p = .088 and .078, respectively). Male DF shows a small, non-significant negative association (p = .779) with SSTA.

The models also provided insight into provisioning efforts as the chicks aged, with an increase in Female DF in the Season-Mid ($p < .001$) and Season-End (p = .045) periods compared to Season-Start. Male DF increased during Season-Mid (p = .165) and decreased during Season-End (p = .543), but neither change was statistically significant.

Normal Years – burrow attendance and SSTA

In normal years, the male was the primary guardian of the chick and burrow, typically spending twice as much time as the female at the burrow (Table 2). The distribution of Total BA across each season was variable, but it was usually highest at the start of each season (Fig. 3A–3D) and sometimes exceeded 24 hours because both parents attended the burrow simultaneously, most often in the week after hatch. Average BA was highest in 2017 and lowest in 2022.

Statistical analyses

In forest plots for BA (Fig. 4, Column 2), regression coefficient points greater than zero reflect a positive association with BA, and vice versa. Both Female BA and Total BA decreased significantly with rising SSTA ($p < .001$ and p = .004, respectively). Male BA showed no significant association with SSTA (p = .737).

TABLE 2
Descriptive statistics for daily feedings and burrow attendance by the observed Atlantic Puffins *Fratercula arctica* at Seal Island, Maine, USA, in Normal Years (2017, 2019, 2020, and 2022)

		Daily Feedings, (Total, Mean ± SD[a])				
Year	***N*[b]**	**Female**	**Male**	**Unidentified**	**Total**	**Female/Male (%)**
2017	41	179, 4.4 ± 2.1	79, 1.9 ± 1.2	7, 1.0 ± 0.6	265, 6.5 ± 2.8	67/30
2019	42	212, 4.9 ± 1.7	100, 2.3 ± 1.5	4, 0.1 ± 0.3	316, 7.3 ± 2.7	67/32
2020	38	165, 4.2 ± 1.8	88, 2.3 ± 1.4	0, 0.0 ± 0	253, 6.5 ± 2.5	65/35
2022	44	175, 4.0 ± 1.2	70, 1.6 ± 1.3	0, 0.0 ± 0	245, 5.6 ± 1.8	71/29
		Burrow Attendance (h), (Total hours, Mean ± SD[a])				
Year	***N*[b]**	**Male**	**Female**	**Unidentified**	**Total Hours**	**Male/Female (%)**
2017	41	587, 14.3 ± 4.4	396, 9.6 ± 4.0	-	983, 24.0 ± 7.1	60/40
2019	42	613, 13.9 ± 3.8	254, 5.8 ± 4.2	-	867, 19.7 ± 6.2	71/29
2020	38	579, 14.8 ± 4.6	184, 4.7 ± 4.1	-	763, 19.6 ± 7.1	76/24
2022	44	525, 11.7 ± 6.2	260, 5.8 ± 4.8	-	785, 17.4 ± 9.6	67/33

[a] Standard deviation
[b] Number of study days

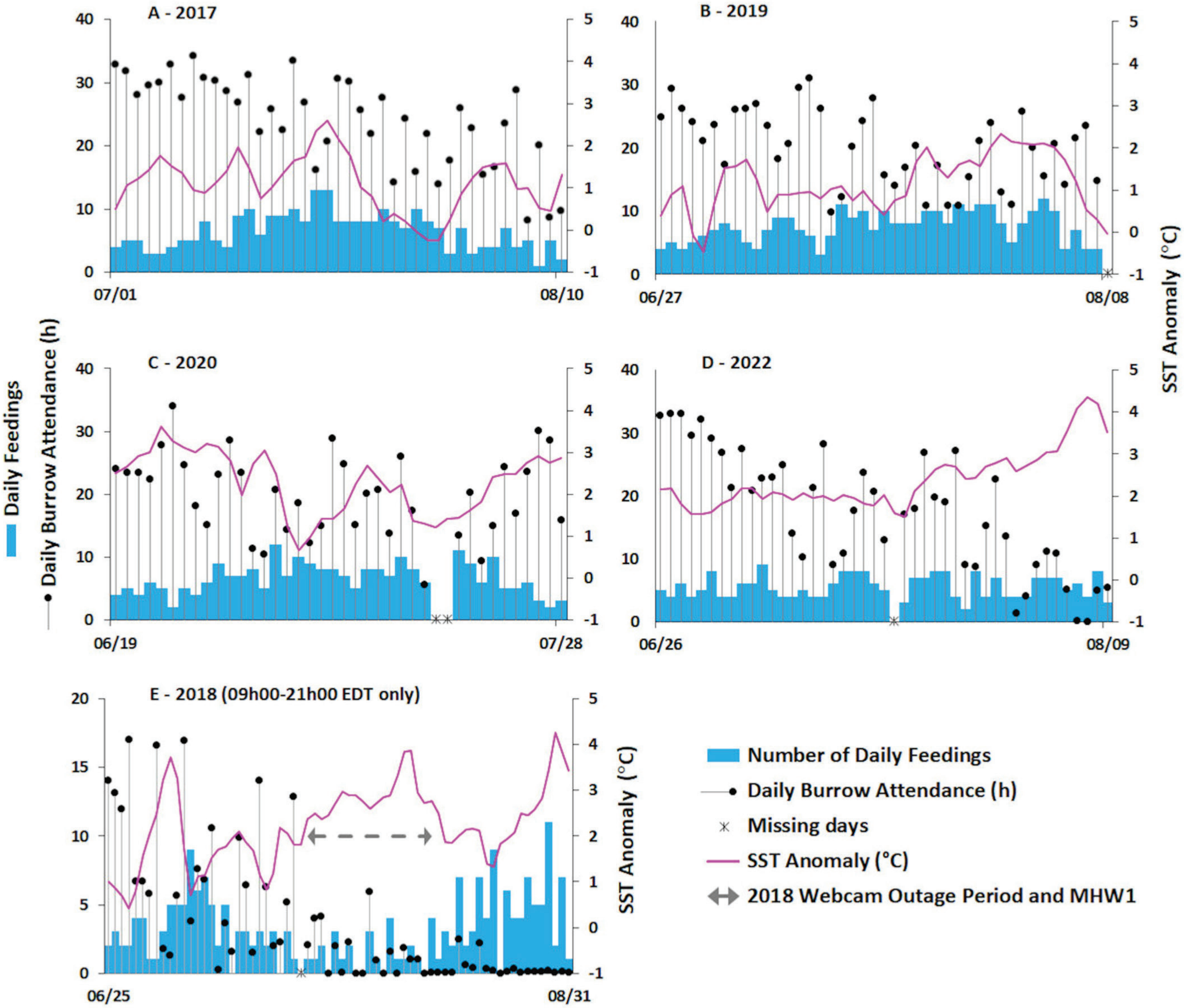

Fig. 3. Distribution of daily feedings and daily burrow attendance during the Atlantic Puffin *Fratercula arctica* nestling period in normal chick-rearing years: A - 2017, B - 2019, C - 2020, D - 2022. Panel E shows 2018 data truncated to 09h00 to 21h00 EDT. SST = sea surface temperature; MHW1 = marine heatwave, phase 1; EDT = Eastern Daylight Time

The models show that BA varied with the chick's age. Female BA decreased during Season-Mid (p < .001) and Season-End (p < .001), compared to Season-Start. Hence, the female logged most of her burrow attendance at the start of the season during the brooding period, and less time as the chicks matured and food demands increased. Male BA decreased in the Season-Mid (p = .147) and Season-End (p = .005) periods, but only the latter was significant. This suggests that the male decreased BA primarily at the end of the season, with impending fledge.

2018

Subset 1, 09h00–21h00 EDT, full season

The season started normally, with the female delivering roughly two-thirds of all feedings (Table 3), but provisioning declined sharply during MHW1 (Fig. 3E). Despite the cam outages, we know that feedings were scarce at this time because of the poor chick condition, weighing just 150 g at 45 days old (Fig. 2B). During the post-MHW1 period, feedings rebounded as the heatwave briefly abated, and the female averaged 2.1 daily feedings, which was similar to her pre-MHW1 average of 2.2. The male averaged 1.9 daily feedings, a rate comparable to that of the female, and almost double his pre-MHW1 average of 1.0. We were unable to identify the parent for 13 feedings during the post-MHW1 period, as the chick sometimes obscured the camera view while receiving a hurriedly delivered feeding at the burrow entrance. It is noteworthy that even if the 13 feedings were assigned to the female, the primary provisioner, the male will still have almost doubled his pre-MHW1 provisioning rate.

Kruskal-Wallis tests indicated statistically significant differences among the three MHW1 periods for Total DF (χ^2 = 18.6, df = 2, p < .001), Female DF (χ^2 = 14.1, df = 2, p < .001), and Male DF (χ^2 = 11.8, df = 2, p < .001). Post-hoc analyses for Female DF in

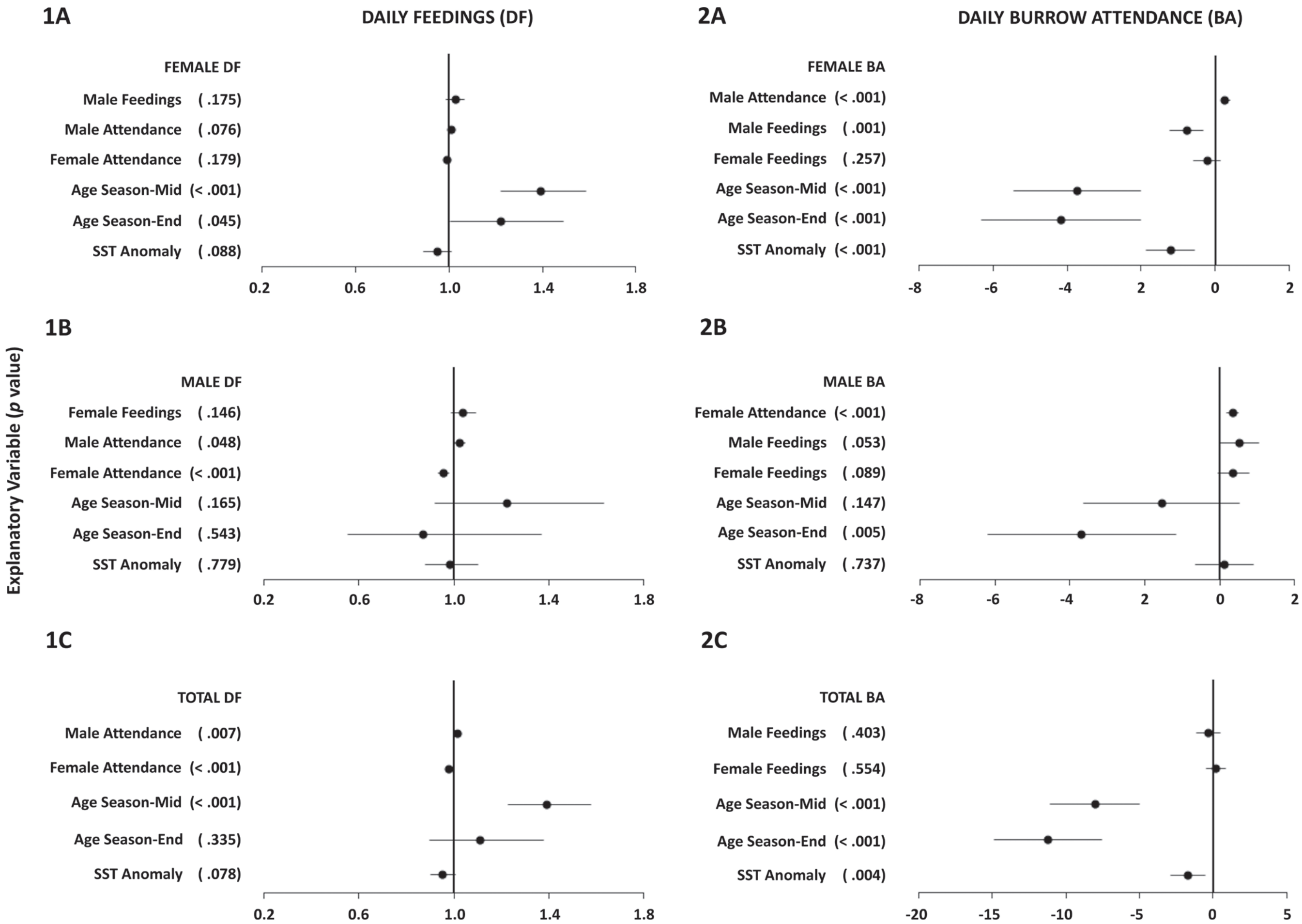

Fig. 4. Forest plots for generalized linear models (GLMs), with regression coefficients (points) and 95% confidence intervals (lines). Each plot represents a model (n = 165), with the response and explanatory variables (p value) indicated. Column 1: Daily Feedings (DF); 1A - Female DF, 1B - Male DF, 1C - Total DF. Deviance Goodness of Fit: χ^2 p value > .05 for all models. Coefficients > 1 indicate a positive association. Column 2: Daily Burrow Attendance (BA); 2A - Female BA, 2B - Male BA, 2C - Total BA. Model R^2 values are 0.37, 0.22, 0.26, respectively. Coefficients > 0 indicate a positive association. Reference level for Age is Age-Season-Start. Units: Burrow Attendance (h), Age (chick's age; d), SST Anomaly (sea surface temperature anomaly; °C).

the pre-MHW1 to MHW1, MHW1 to post-MHW1, and pre-MHW1 to post-MHW1 periods yielded p values of .002, .003, and .672, respectively. For the same periods, Male DF yielded respective p values of .046, .007, and .046, while Total DF yielded p values of .002, < .001, and .080. Hence, post-MHW1 rates were statistically distinct from pre-MHW1 rates for Male DF but not for Female DF and Total DF.

Male and Female BA were significantly reduced during MHW1 and further reduced post-MHW1 (Fig. 3E), as both parents spent time foraging for the chick and themselves. For example, Total BA fell by 97% in the post-MHW1 period, compared to the pre-MHW1 period (Table 3).

Kruskal-Wallis tests indicated statistically significant differences among the MHW1 periods for Total BA (χ^2 = 35.9, df = 2, p < .001), Female BA (χ^2 = 22.6, df = 2, p < .001), and Male BA (χ^2 = 32.7, df = 2, p < .001). Post-hoc analyses show that BA decreases were significant for Male, Female, and Total BA (p < .001) from pre-MHW1 to MHW1 and from pre- to post-MHW1, but changes from MHW1 to post-MHW1 were not significant (p = .350, .361, and .580, respectively), since BA remained consistently low in both periods.

Subset 2, 24-hour pre- and post-MHW1

Female DF pre- and post-MHW1 averaged 3.3 and 3.1, respectively (essentially unchanged), while Male DF averaged 2.0 and 3.4, respectively (a marked increase; Table 3). Kruskal-Wallis tests indicated that the increase in Male DF was statistically significant (χ^2 = 4.9, df = 1, p = .027), but changes in Female DF (χ^2 = 0.5, df = 1, p = .480) and Total DF (χ^2 = 3.7, df = 1, p = .054) were not significant.

We could not identify the parent for 22 feedings in the post-MHW1 period, as explained for Subset 1. Notably, if these feedings were all assigned to the female, her post-MHW1 average DF would increase to 4.2. We know that in normal years, Male and Female DF averaged 2.0 and 4.4, respectively (Table 2). Hence, Female DF of 4.2 post-MHW1 would not be unusual, but Male DF of 3.4 is atypical.

Male, Female, and Total BA were distinctly lower during the post-MHW1 period (Table 3). Kruskal-Wallis tests showed statistically

TABLE 3
Descriptive statistics for daily feedings and burrow attendance by the observed Atlantic Puffins *Fratercula arctica* at Seal Island, Maine, USA, during an extended marine heatwave in 2018[a]

Subset 1: 09h00–21h00 EDT, before, during and after MHW1[b]			
	Pre-MHW1 (*n* = 28)	**MHW1 (*n* = 20)**	**Post-MHW1 (*n* = 19)**
Daily Feedings			
Male	29, 1.0 ± 0.9	11, 0.6 ± 0.9	37, 1.9 ± 1.6
Female	62, 2.2 ± 1.5	17, 0.9 ± 1.2	39, 2.1 ± 1.4
Unidentified Parent	0, 0 ± 0	0, 0 ± 0	13, 0.7 ± 0.8
Total	91, 3.3 ± 2.1	28, 1.4 ± 1.3	89, 4.7 ± 2.8
Burrow Attendance			
Male (h)	114, 4.1 ± 3.4	17, 0.8 ± 1.6	5, 0.3 ± 0.6
Female (h)	98, 3.5 ± 2.8	10, 0.5 ± 0.8	2, 0.1 ± 0.3
Total (h)	212, 7.6 ± 5.2	27, 1.3 ± 1.7	7, 0.4 ± 0.7
Subset 2: 24-hour data before and after MHW1[b]			
	Pre-MHW1 (*n* = 28)	**MHW1**	**Post-MHW1 (*n* = 19)**
Daily Feedings			
Male	55, 2.0 ± 0.9	-	64, 3.4 ± 2.3
Female	91, 3.3 ± 1.6	-	58, 3.1 ± 2.0
Unidentified Parent	2, 0.1 ± 0.4	-	22, 1.2 ± 1.1
Total	148, 5.3 ± 2.1	-	144, 7.6 ± 4.4
Burrow Attendance			
Male (h)	364, 13 ± 4.1	-	13, 0.7 ± 1.4
Female (h)	207, 7.4 ± 4.3	-	2, 0.1 ± 0.30
Total (h)	571, 20.4 ± 7.3	-	15, 0.8 ± 1.5
Sea Surface Temperature Anomaly (°C): Mean ± Standard deviation			
SSTA	1.7 ± 0.8	2.8 ± 0.5	2.4 ± 0.8

[a] Values are given as (Total, Mean ± Standard deviation), unless otherwise specified.
[b] A long-duration, multi-peak marine heatwave (MHW) occurred during the 2018 nestling period. The first peak occurred on 08 August before abating for several days. We refer to this phase as MHW Phase 1 (MHW1) for our analysis, and we divided the nestling period as follows: Pre-MHW1 (25 June–22 July), MHW1 (24 July–12 August), post-MHW1 (13 August–31 August).

significant changes: Male BA (χ^2 = 33.0, *df* = 1, $p < .001$), Female BA (χ^2 = 29.8, *df* = 1, $p < .001$), and Total BA (χ^2 = 33.0, *df* = 1, $p < .001$).

The key result from both data subsets is that Male DF increased significantly during the post-MHW1 period, to a rate comparable to that of the female, while Male BA was severely curtailed. This is significant as it is contrary to the male's normal pattern of behavior. Instead, he traded his burrow-guarding role for increased chick provisioning, in response to the food scarcity and poor chick condition associated with the MHW.

The puffling and the butterfish – 2022

The most common prey of 2022 were hake, assumed to be White Hake *Urophycis tenuis* (Kress et al., 2016), Sandlance *Ammodytes* spp., Atlantic Saury *Scomberesox saurus*, Haddock *Melanogrammus aeglefinus*, and American Butterfish. Less common taxa, combined in the "other" group, included Rough Scad *Trachurus lathami*, American Monkfish *Lophius americanus*, squid (assumed to be Shortfin Squid *Illex illecebrosus*), larval fish, and unidentified species.

In the moderate MHW period, the most abundant prey were hake (66%), haddock (13%), and sandlance (12%), with butterfish, saury, and other species contributing < 5% each. Sandlance contributed most to the biomass (41%), supplemented by saury (17%), butterfish (14%), haddock (13%), hake (11%), and other species (4%). In the strong/severe MHW period, the most abundant prey were hake (41%); butterfish (24%); saury, sandlance, and haddock combined (7%); and other species (28%). The latter group included squid (8%) and larval fish (5%), which increased in number as the MHW intensified. Biomass was dominated by butterfish (57%), followed by saury (21%), sandlance (3%), and all others (19%).

Faced with a steady supply of butterfish as the MHW strengthened (2.8/d in the SMHW period compared to 0.8/d in the MMHW period), the chick seemingly discovered or devised a strategy to consume them piecemeal. While small butterfish were swallowed whole, we observed the chick pulling off and swallowing small pieces from larger butterfish on several occasions, whittling them down to a size sufficiently small to be swallowed.

The chick was 12 days old when we observed the first instance of such behavior. At first, the chick instinctively tried to swallow the whole medium-sized fish (about two adult bill lengths), a process that involves considerable head-shaking, which batters the fish somewhat, and in this case, the fish fell to the floor with the operculum (gill cover) slightly lifted. The chick picked up the fish by the operculum, which pulled away from the body, exposing the gills and flesh underneath. The chick began to pull pieces from the gills and guts and swallow them, occasionally stopping to try swallowing the whole fish, then returning to pulling small pieces from the body. After about 40 minutes, approximately one-third of the fish had been consumed, including the head, gills and guts. At that point, the chick took a break, received more palatable meals for the rest of the day, and did not return to the partially consumed fish on that day.

Henceforth, this was the normal process for consuming larger butterfish, using the operculum as an access point to the guts and soft flesh that the chick could grasp in its beak, dislodge and swallow. It is a time-consuming process, and the chick would usually take a break after 30–40 minutes. In the MMHW period, larger butterfish were reduced to about half size before being abandoned for the day, as more easily consumed fish were delivered. The first butterfish that was completely consumed in this fashion was a large, whole fish delivered to the 27-day-old chick. The chick doggedly picked apart the fish, swallowing the posterior end almost 2.25 hours later, interrupted by intervening meals and a 70-minute break. During the SMHW period, this became a regular occurrence, and the chick became more proficient. In Appendix 2 (available on the website), we provide a short video clip of the 36-day-old chick pulling small morsels from a large butterfish, which was consumed within 70 minutes.

DISCUSSION

We examined the breeding behavior of Atlantic Puffins that occupied a burrow on Seal Island National Wildlife Refuge in 2017–2020 and 2022. We investigated sex-specific parental roles of chick provisioning and burrow-guarding, as well as chick behavior, and associations with SST and MHWs in the Gulf of Maine. While this study is not intended to represent colony-wide behavior, it offers the advantage of observing the same individuals over multiple seasons, under different environmental conditions.

Sex-specific roles

We show that in normal years, the female was the primary provisioner, delivering two-thirds of all feedings, while the male was the primary protector, accounting for two-thirds of burrow attendance. It is notable that both female partners (2017–2018 and 2019–2022) exhibited the same behavior. Other studies have shown similar feeding rates by females and colony attendance by males (Anker-Nilssen et al., 2024; Creelman & Storey, 1991; Wernham, 1993). Both parents sometimes attended the burrow together, particularly in the early days following hatch, when the chick had not yet attained homeothermy and required brooding, and when food demands were not yet high. Throughout the seasons, the male assumed the overnight guard shift most often, while the female returned to sea, presumably to be ready for early-morning feedings. However, the female or both parents may overnight with the chick, particularly under good food conditions.

MHWs

All seasons experienced MHWs, but long-duration events that peaked in the strong to severe categories dominated the nestling periods of 2018, 2020, and 2022. These adversely impacted provisioning and the chicks' body condition. At a glance, body condition metrics of growth rate and weight wing index bear a relationship to the severity of heatwaves, with the highest metrics associated with low-intensity, short-duration, moderate events (2017, 2019) and the lowest metrics associated with long-duration events that strengthened to severe levels with intensities greater than 4 °C (2018, 2022). These metrics are broadly reflected in the productivity (average number of chicks fledged per nest) of the Seal Island colony in the study years, with values of 0.89, 0.60, 0.85, 0.76, 0.79 in 2017–2020 and 2022, respectively (Gulf of Maine Seabird Working Group [GOMSWG], 2024). We also note that the extended fledging period of 69 days in 2018 was echoed at the colony level, with some chicks fledging at 60 days or older (GOMSWG, 2024). Of particular note, the 2018 female did not return to this burrow in 2019, though she was seen at the colony in the days after the male had already began nesting with a new female. We speculate that she might have returned late as a consequence of extended chick-rearing and deferred migration in 2018.

Overall, the breeding seasons were not strongly affected by the moderate MHWs in winter and early spring, prior to hatch.

Statistical models

Statistical models for normal years show that the female reduced daily feedings and burrow attendance as SSTA increased. This suggests less provisioning but more time foraging as SST rises. The results were not statistically significant, but the relationship between feedings and SST is nuanced, because parents will endeavor to feed their chicks even in adverse conditions. Eilertsen et al. (2008) showed that under low-quality food conditions, chicks received the same mass of food as those fed under good-quality food conditions because the parents increased their provisioning rates to compensate for the lower quality diet. The increased effort could obscure the full impact of rising SST. Metrics of prey quality, such as lipid content and mass, may help to better specify the regression models in future studies.

We did not see significant changes in male daily feedings or burrow attendance with rising SSTA in normal years, as the male continued to focus on burrow duties. The male's role in protecting the chick is vital, as prospecting puffins seeking nesting burrows could potentially harm unattended chicks.

Behavior modifications

We have shown that in 2018, a year of low food availability associated with a severe MHW, the male relinquished his typical primary guarding role in favor of significantly increased provisioning as the MHW subsided and food availability improved. This is the first study to reveal such modification in male puffin behavior in response to food shortages. This effort boosted the chick's chances of survival, allowing the chick to fledge after an extended chick-rearing period of 69 days, well beyond the typical range of 39–44 days (Harris & Wanless, 2011). In an experiment in which puffin chicks were partially supplemented with food, Fitzsimmons (2018) noted that in a poor food year, the female increased feedings when food was not being supplemented while the male did not, suggesting that the male prioritized self-maintenance over chick maintenance. The fledging ages of chicks in that study were within the expected 38–44 days, which suggests that circumstances were not extreme. It may be that in our study, with the chick already in very poor condition at 45 days (weighing just 150 g), a good run of fish presented itself when the heatwave abated, and the male seized the opportunity to sustain the chick, joining the female in provisioning. Together, they fed the chick until it fledged.

The 2022 chick also displayed modified behavior, with piecemeal consumption of butterfish provisioned during a severe MHW, pulling off and swallowing small morsels until the fish was sufficiently small to be swallowed. The chick was 12 days old when we first observed this behavior, so though it was early in its development, it was not a very young chick. This method of eating butterfish is time-consuming, and no doubt energy-demanding, but it allowed the chick to benefit from high-lipid prey in a poor food environment and to fledge after 46 days. This highly unusual behavior has not been reported previously.

CONCLUSIONS

This study reveals that puffins in this burrow experienced negative outcomes that are associated with decreased prey availability, in accord with increasing SST and high-intensity MHWs in the Gulf of Maine: reduced chick provisioning, reduced burrow attendance, poor chick body condition, longer nestling periods, and an irregular supply of suitable prey. Further, we provide new evidence of plasticity in adult and chick behaviors, as they respond to adverse food conditions associated with MHWs: 1) the male parent traded his burrow-guarding role for additional chick provisioning, demonstrating that at least some puffins may respond to food scarcity by changing typical roles; 2) a puffling developed a strategy to pick apart deep-bodied prey, demonstrating an unconventional solution to the increased prevalence of butterfish in the diet. This study reveals granular details of puffin life in the burrow and the behavioral response to shifting environmental conditions. Further studies will help to elucidate these behaviors in the face of a changing climate.

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