






Local prey shortages drive foraging costs and breeding success in a declining seabird, the Atlantic puffin

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Abstract

1. As more and more species face anthropogenic threats, understanding the causes of population declines in vulnerable taxa is essential. However, long-term datasets, ideal to identify lasting or indirect effects on fitness measures such as those caused by environmental factors, are not always available.
2. Here we use a single year but multi-population approach on populations with contrasting demographic trends to identify possible drivers and mechanisms of seabird population changes in the north-east Atlantic, using the Atlantic puffin, a declining species, as a model system.
3. We combine miniature GPS trackers with camera traps and DNA metabarcoding techniques on four populations across the puffins' main breeding range to provide the most comprehensive study of the species' foraging ecology to date.
4. We find that puffins use a dual foraging tactic combining short and long foraging trips in all four populations, but declining populations in southern Iceland and north-west Norway have much greater foraging ranges, which require more (costly) flight, as well as lower chick-provisioning frequencies, and a more diverse but likely less energy-dense diet, than stable populations in northern Iceland and Wales.
5. Together, our findings suggest that the poor productivity of declining puffin populations in the north-east Atlantic is driven by breeding adults being forced to forage far from the colony, presumably because of low prey availability near colonies, possibly amplified by intraspecific competition. Our results provide valuable information for the conservation of this and other important North-Atlantic species and highlight the potential of multi-population approaches to answer important questions about the ecological drivers of population trends.

KEYWORDS

biologging, diet, DNA metabarcoding, dual foraging, foraging ecology, intraspecific competition, population decline, seabirds

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1 | INTRODUCTION

Biodiversity is experiencing its highest rate of extinction to date in the Anthropocene, driven by overexploitation, land use change, pollution, invasive species and disease (Maxwell et al., 2016), with extinction risks caused by climate change predicted to accelerate (Urban, 2015). More than ever, understanding the causes of species declines is essential to inform conservation, design mitigation measures and prepare for further declines. Despite impacts on marine biodiversity, declines in marine species have been less well documented (Polidoro et al., 2008). With the risk of marine species loss predicted to increase (McCauley et al., 2015), filling this knowledge gap is becoming critical.

Seabirds are top marine predators and valuable indicators of ocean health (Einoder, 2009), but are declining worldwide and are now among the most threatened birds on Earth (Dias et al., 2019). They face numerous threats, from invasive species and nesting habitat loss on land, to overfishing, bycatch and climate change at sea (Dias et al., 2019). However, the causes of declines of many seabirds remain poorly understood, especially when these are not directly observable threats such as predation by invasive species, but instead indirectly affect breeding performance or survival. Some declines may be driven by reduced prey availability, caused by climate change—for example, through changes in sea temperature, pH, salinity and trophic phenology—or/and by fisheries activity (Grémillet & Boulinier, 2009; Grémillet et al., 2018). Furthermore, while some populations have been the subject of detailed long-term studies, the mechanisms leading to the declines of many others often remain unclear. This applies particularly to species difficult to study because of their inaccessibility and/or sensitivity to disturbance, which leads to poor knowledge of their foraging ecology and a lack of longitudinal studies long enough to encompass periods of both stable and declining population trends. Exploring possible causes of declines is however essential for scientists to uncover and quantify key relationships between environmental factors and demographic parameters, to better inform conservation decisions both locally and at a larger scale, and predict future populations trends and prepare for these scenarios. We use a multi-population approach incorporating contrasting population trends as a complementary approach to long-term studies of single populations to identify the causes of population declines.

In this study, we use the Atlantic puffin *Fratercula arctica* (hereafter puffin) to investigate seabird declines in the North Atlantic. Puffins are a good model species because they are one of the most abundant North Atlantic seabirds (~20 million individuals, Harris & Wanless, 2011), and because their diet (mainly *Ammodytidae* and *Clupeidae* fish) and breeding range (northern France to the high Arctic, with a stronghold in Iceland and Norway) overlap with many other North Atlantic seabirds, making our results applicable to a wide range of other important diving species (e.g. other auks) in the region. Our study also provides an important test of whether expected relationships between environmental conditions and demographic parameters usually tested in more traditional models (e.g.

Frederiksen et al., 2004) hold in widely distributed but harder-to-work-with species. Puffins have been declining for decades, especially in the central part of their range, and are now classified globally as 'Vulnerable' and 'Endangered' in Europe (IUCN, 2019). For example, the Røst archipelago's breeding population in Norway—formerly the world's largest puffin concentration—decreased by 81% from 1.41 million pairs to 274,000 pairs between 1979 and 2019, and productivity has remained poor since the late 1960s, including total breeding failure between 2007 and 2015. These trends are locally mirrored by many other seabird species (Anker-Nilssen et al., 2020). In the Westman Islands in Iceland, currently the world's largest puffin aggregation with ~530,500 breeding pairs, the geometric mean population growth rate between 2007 and 2019 of 0.953 strongly reflects a poor productivity (Hansen, 2019).

However, large gaps in our knowledge of seabird foraging ecology limit our understanding of the mechanisms leading to such declines. Recent evidence suggests that during the non-breeding season, intraspecific competition, migration distance and wintering habitat quality affect subsequent breeding performance at a population level (Fayet et al., 2017), but these reasons alone cannot explain the dramatically low breeding performance of some populations. Low prey availability during breeding is an important driver of low productivity in seabirds (Cury et al., 2011) and is likely to be responsible for poor breeding performance in several puffin populations (Durant et al., 2003). Here we aim to explore this relationship further to uncover mechanisms by which prey availability may affect breeding performance. If preferred prey is scarce near the colony, birds may have to switch to less nutritious prey. Alternatively, if there is suitable prey for chick provisioning away from the colony, adults may extend their foraging distance, or combine both and employ a dual foraging tactic (Weimerskirch et al., 2003). Prey availability may also affect foraging temporally (Welcker et al., 2009) while the effect of low prey abundance may be exacerbated by intraspecific competition at larger colonies, also forcing birds to increase foraging distance (Ashmole, 1963). Additionally, the phenology of prey occurrence may also affect breeding performance. If prey availability is poor from the start of breeding, adults may be in poor body condition and delay or skip breeding, or abandon their egg. If prey availability declines later during breeding, breeders may endure to hatch the egg but struggle to feed their chick. Over time, each scenario would lead to population declines, with few new individuals recruited into the population (Halpern et al., 2005) while adult survival could also decrease due to higher breeding costs (Erikstad et al., 1998).

Observations at one declining puffin colony indicate chick mortality there is high (Anker-Nilssen & Aarvak, 2006), and sightings of birds feeding far offshore suggest a lack of prey near the colony (Anker-Nilssen & Lorentsen, 1990). In this study, we therefore test the hypothesis that low food availability during chick rearing is the main driver of poor puffin breeding performance in the central part of their range and forces birds to forage beyond sustainable distances. To do so, we compare the foraging ecology of chick-rearing puffins at four colonies across the north-east Atlantic with contrasting trends in population growth and breeding success, ranging from a growing population with

high breeding success to a fast-declining population with low breeding success. We use state-of-the-art miniature GPS technology to track for the first time the movements of chick-rearing puffins from Iceland, Norway and Wales, including the world's two largest populations. We analyse the birds' at-sea behaviour to determine feeding locations and flight time—by far the most energy-demanding behaviour in auks (Elliott et al., 2013), and measure foraging effort using a novel method based on missed underwater GPS fixes. We use novel DNA metabarcoding techniques on faecal samples to investigate the poorly known adult diet and compare adult and chick diet within and between populations. Additionally, we measure chick-provisioning frequencies with nest-based camera traps. We combine and compare these metrics across populations to provide the most comprehensive study of puffin foraging ecology to date and new insight into the mechanisms leading to poor breeding success, and ultimately population declines, of puffins in the north-east Atlantic.

2 | MATERIALS AND METHODS

The study was carried out in June–July 2018 on Skomer, Wales (51°44'N, 5°19'W), Heimaey, Westman Islands, Iceland (63°25'N, 20°16'W), Grimsey, Iceland (66°32'N, 18°00'W), and Hernyken, Røst, Norway (67°26'N, 11°52'E).

All work was conducted with approval from the University of Oxford's AWERB, British Trust for Ornithology, Natural Resources Wales, Skomer Island Advisory Committee, Norwegian Animal Research Authority (FOTS ID: 16067), Norwegian Environment Agency and Icelandic Institute of Natural History. Puffins are sensitive to handling and previous tracking attempts with back-mounted loggers led to interruptions in chick-provisioning and nest desertion (Harris et al., 2012; Symons & Diamond, 2019). To minimise disturbance, we used the lightest possible GPS loggers weighing <1.1% of the birds' body mass, including remote-download devices not requiring recapture. Bird handling was minimised to <10 min. The birds' reaction to the devices was tested in Wales in 2017 by tagging and monitoring the behaviour of four birds. All birds continued to feed their chicks, which later fledged; therefore, we expanded the study in 2018. We used cameras to monitor behaviour at the nest and detect any potential reaction to tagging.

2.1 | GPS tracking

Chick-rearing birds were caught at their nest by hand or with purse-nets (in Norway 8 birds carrying fish were caught in a mistnet). Based on size and plumage development of tagged birds' chicks (or, in Norway, on monitoring accessible nests), chicks were 10- to 20-day old during tracking. Birds were weighed, ringed and fitted with a GPS logger attached with two strips of marine cloth tape (Tesa 4651) to their back feathers. Loggers were PathTrack Nanofix GPS loggers, either archival (Wales: 2.3–3.3 g, 0.6%–0.9% body mass) or remote-download (Norway and Iceland: 4 g, 0.8%–0.9% body mass), recording position every 5 min. Two birds in Wales were tagged with TechnoSmart Axy-Trek integrated GPS + dive loggers (6 g, 1.1% body mass) also on a 5-min interval and recording depth (1 Hz) to validate our behavioural classification (see below). Five small breast feathers were collected for DNA sexing. Birds were then released in their burrow (Wales, Iceland) or outside (Norway). Birds with archival tags were recaptured at their nest 4–10 days after tagging, while a base station on the colony downloaded data from remote-download tags. In total, we tagged 55 birds and recovered data from 34 (62%). In southern Iceland, only two birds produced data; others either did not return before the tag died or did not stay long enough on the colony for the base station to download data. Camera trap footage suggests this was a colony-wide behaviour not restricted to tagged birds (details in Supporting Information).

2.2 | Spatial analysis

Spatial data processing and analysis were performed in MatLab (R2017b, MathWorks) and R (3.6.0, R Core Team, 2019). Trips <2 km away from the colony were excluded, as so close to the colony puffins are likely to be on land or rafting on the water and not foraging, although the occasional dive may occur (A. L. Fayet, pers. obs.). Trip duration and distance were calculated as the time spent and distance covered between the last location before leaving the 2 km radius around the colony and the first subsequent location within the same radius. Our dataset included 280 foraging trips, with 1–33 trips per bird (Table 1). Duration, total distance, maximum distance from the colony, departure and arrival times were calculated for each trip. As the distribution of trip distances showed a

TABLE 1 Population trends and tracking data collected from each colony

Colony	Colony size (no. of pairs) (in 2018–2019)	Population trend	Tracking period	Birds tagged	No. and sex of birds yielding data	Trips collected (containing flight)	Mean no. of trips per bird [range]
Wales	24,108	+125% since 2004	12–25 June 2018	20	12 (4F, 8 M)	94 (69)	5.8 [1–18]
Southern Iceland	530,500	–46% since 2007	18–22 July 2018	11	2 (2F, 0 M)	4 (4)	2 [1–3]
Northern Iceland	71,220	+25% since 2011	10–16 July 2018	12	12 (8F, 4 M)	148 (86)	17.5 [4–33]
Norway	274,000	–81% since 1979	4–10 July 2018	12	8 (3F, 5 M)	34 (30)	10.2 [1–15]
			Total	55	34	280 (189)	11.9

combination of short and long trips at each colony (Figure S1), we split trips into 'short' and 'long', determining the threshold for each colony by minimising the sum of variances of each group (Welcker et al., 2009). We quantified individual route fidelity by calculating the average nearest neighbour distance of each trip to all other trips within a population, and compared within- to between-individuals values (Fayet, Freeman, Shoji, Boyle, et al., 2016). As trip length affects nearest neighbour distance, we compared trips of similar length only (short vs. short, and long vs. long, as defined above).

2.3 | Behavioural analysis

Mean ground speed was calculated for each location. Based on the bimodal distribution of speed (Figure S2), we selected a 2.7 m/s threshold separating flight from on/in-water behaviour, similar to 2.5 m/s found by Guilford et al. (2008) in shearwaters. Based on this threshold, we split each trip into 'flight bouts' and 'wet bouts', which did not contain flight and were therefore spent on/in the water (drifting, swimming, diving). In all, 91 trips (93% within 5 km of the colony) did not include flight and likely represented rafting near the colony (although a small amount of foraging may still have occurred during those trips), so were excluded from further analysis (details in Supporting Information).

Chick-rearing puffins dive >400 times and spend ~4.5 hr underwater each day (Shoji, Elliott, et al., 2015), where GPS fixes cannot be obtained. We therefore developed a new method using missing at-sea GPS fixes as proxies for diving behaviour (validation with diving data in Supporting Information). To exclude underground nest visits and possible device failure being classified as diving, we ignored periods where >2 fixes were missed—that is, more than 18 min passed without a fix (details in Supporting Information). Locations of missing fixes were interpolated using piecewise cubic Hermite polynomials, and the total number of missed fixes per trip was used as a proxy for foraging effort. We calculated the birds' daily activity budgets, using the speed threshold described above to determine time in flight and on/in the water, and measured time at the colony from the GPS data (details in Supporting Information).

2.4 | Diet analysis

Faeces excreted during bird handling were collected opportunistically. Additional samples were collected by catching other chick-rearing adults and chicks at the nest and holding them briefly above a clean metal cup. In Norway and southern Iceland where most nests were too deep, fresh samples were collected off rocks when birds were observed defecating while taking off. Samples were poured from the cup or scraped with a single-use spatula into a plastic micro-centrifuge tube filled with RNAlater (Invitrogen), then frozen at -18°C until processed. Field-blanks were collected from rocks and the metal cup to monitor for contamination from surfaces. In total, 167 samples were collected. Samples of whole fish ($n = 15$) dropped by chick-feeding adults and representing the main prey species

observed at each colony were collected for validation of species in the analysis of faecal samples.

For brevity, the following is a short description of laboratory and sequencing protocols (full protocol in Supporting Information). DNA was extracted separately from the faecal material and from the fish samples. The latter were combined to create a mock community which we ran alongside the faecal samples.

Fish 12S rRNA gene sequences were amplified in a two-step PCR, using MiFish primers (Miya et al., 2015) in the first step, then adding unique dual indexes in the second step. Sequencing was performed on an Illumina HiSeq 2500 and demultiplexed reads were imported into Qiime2 v2019.4 (Bolyen et al., 2019). Primers at the 3' and 5' end were trimmed using the cutadapt plugin (Martin, 2011) and reads were merged and denoised using DADA2 (Callahan et al., 2016). Taxonomy was assigned with an iterative blast method using a custom script (link in Supporting Information) and a custom database including all vertebrate 12S and mitochondrial sequences, excluding primates, downloaded from GenBank on 15/12/2017. We re-sequenced samples with <3,000 prey reads to ensure we had captured the entire diversity of each sample, and rarefied our final feature table to a depth of 1,500 reads per sample. A genus- or family-level assignment was made if a percent identity was <97% or if there were multiple species with percent identity >97% co-occurring in the North Atlantic (e.g. we grouped herring *Clupea harengus* and sprat *Sprattus sprattus* into the *Clupeinae* sub-family; those identified in Norway are herring and those in Wales sprat).

To identify invertebrate prey taxa, we amplified the V7 region of the 18S gene using universal metazoan primers (McInnes et al., 2017) in a similar protocol. However, these primers amplified a large amount of avian sequences (i.e. from puffins themselves) so we were not able to identify invertebrate prey items successfully without sequencing the samples to a higher depth, which was beyond the scope of this study.

Out of 167 samples, we had sufficient read depth to estimate the diets of 68 birds (sample sizes on Figure 3; in Norway 8 samples from 2017 were pooled with the 2018 samples as their content and breeding success were similar to 2018). As the relationship between read abundances and the relative amount of each species in an individual's diet can be biased by many factors (Deagle et al., 2018), the data are presented as the frequency of occurrence of prey species in the population diet, which despite the lack of prey abundance data, still allows us to make inferences about the importance of specific prey species for each puffin population.

2.5 | Video analysis

Motion-activated cameras (Browning Recon Force Extreme) were deployed near tagged birds' nests and programmed to record a 10s video when detecting movements during the tracking period in northern Iceland ($n = 12$), Wales ($n = 11$), southern Iceland ($n = 11$) and Norway ($n = 4$ as the precise location of most nests was unknown). Videos were analysed manually to record the frequency of

chick-provisioning visits of tagged birds and their partners. In total, we analysed 203 days of nest activity and identified 275 visits, 210 of which could be confirmed as feeding visits. Feeding frequency was calculated as the number of chick-provisioning visits at a nest per day (in southern Iceland where few nests had >1 feeding visit recorded, we also included the time between the first recorded visit and the time of tagging, when an adult bird was last seen in the nest). When possible, the number of prey items was counted ($n = 76$, in Wales and northern Iceland only). Comparisons of feeding frequency between tagged and untagged birds and between sexes, and of number and size of prey items, were performed on northern Iceland and Wales data only, because of low samples sizes elsewhere (for Norway, we report data collected separately on 20 prey loads from mistnets).

2.6 | Breeding success

At each colony, breeding success was measured from 53 to 138 marked burrows examined at least twice by hand or using an infrared video probe, first during incubation and again later in the nestling season. Breeding success was calculated as the proportion of active nests which successfully raised a chick.

2.7 | Statistical methods

In R, we used linear models (LM) and linear mixed models (LMM, LME4 package, with bird ID as a random effect) to test for differences in

spatial and behavioural metrics between populations, for data averaged per bird and per trip, respectively. When necessary, response variables were transformed to meet assumptions of normality and homoscedasticity (details in Supporting Information). Sex was controlled for in all models; for brevity we only report instances where sex differences were detected. For LMMs, significance levels were obtained by comparing the full models to null models (without the fixed effect of interest) with a likelihood ratio test. Because of the small sample size, GPS data from southern Iceland were not included in the analyses but only used for qualitative comparisons. Means are indicated \pm SE throughout.

3 | RESULTS

Breeding success differed between colonies ($\chi^2_3 = 41.6$, $p < 0.001$). It was highest in northern Iceland (70%, $n = 53$), followed by Wales (62%, $n = 138$), southern Iceland (41%, $n = 98$) and Norway (20%, $n = 60$).

3.1 | Foraging trips

The foraging distributions of each population are illustrated in Figure 1 (see Figure S3 for foraging locations only), all trips metrics are in Table 2. At all colonies, birds took a combination of short trips 5–14 km away from the colony, and longer trips further afield, indicative of a dual foraging tactic. Trip range differed between colonies

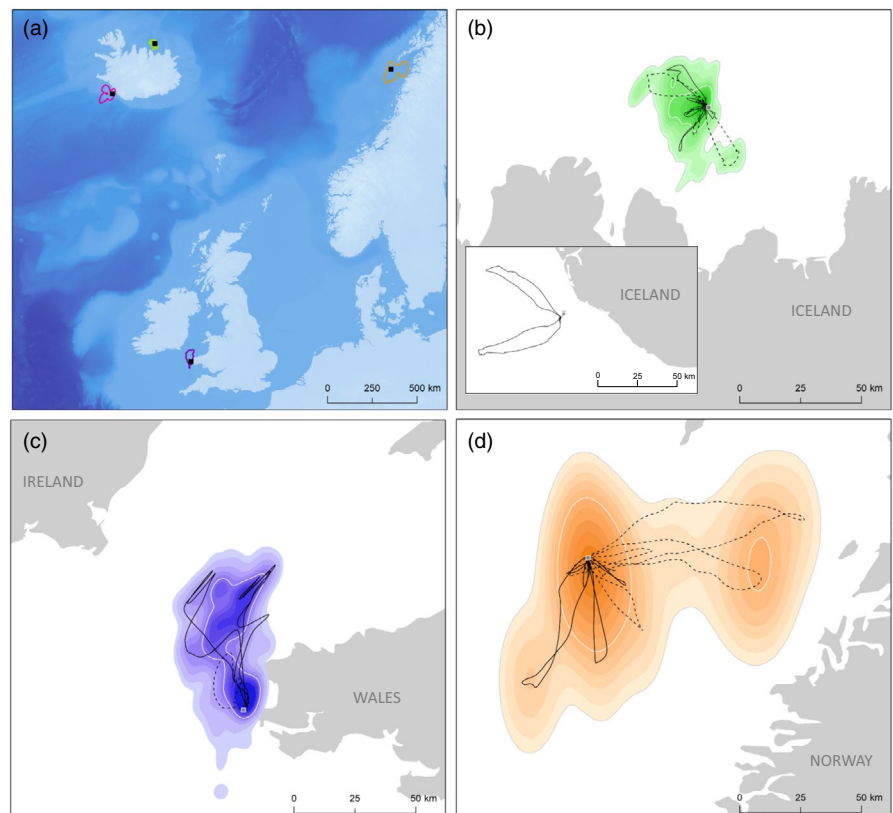


FIGURE 1 Puffin foraging distributions on four colonies in the north-east Atlantic. (a) 95% density kernels of colonies. (b–d) Density kernels (10%–95% occupancy, from dark to light) with core foraging areas (50% occupancy) in white and example tracks from two birds for northern Iceland (b), with tracks for southern Iceland in the insert, Wales (c) and Norway (d)

		N Iceland	Wales	S Iceland	Norway
Breeding success (%)		70	62	41	20
Feeding frequency (visits/day)		4.2 ± 0.9	1.4 ± 0.2	1.0 ± 0.4	0.9 ± 0.4
Trip range (km)	Short	6.6 ± 0.4	12.3 ± 1.4	5.3 ± 1.2	13.8 ± 1.9
	Long	21.7 ± 1.1	52.0 ± 1.8	60.4 ± 1.5	74.0 ± 6.4
Trip duration (hr)	Short	4.3 ± 0.5	4.1 ± 0.7	4.3 ± 0.5	3.8 ± 0.8
	Long	13.3 ± 1.5	20.4 ± 2.5	15.1 ± 6.2	15.6 ± 1.8
Proportion of long trips (%)		30.1 ± 4.8	51.0 ± 8.5	33.3 ± 33.3	7.4 ± 3.5
Number of trips per day	Short	1.3 ± 0.2	0.9 ± 0.2	3.6 ± 2.7	2.6 ± 0.7
	Long	0.6 ± 0.1	0.6 ± 0.1	0.2 ± 0.2	0.2 ± 0.1
Time in flight per trip (min)	Short	12.9 ± 1.0	28.3 ± 4.4	9.3 ± 3.4	28.9 ± 4.9
	Long	30.3 ± 3.5	85.9 ± 5.6	124.3 ± 22.8	115.9 ± 23.2
Daily time in flight (hr)		0.4 ± 0.1	1.4 ± 0.2	1.8 ± 1.2	1.0 ± 0.4
Daily time sitting on water/diving (hr)		16.8 ± 0.8	17.1 ± 1.0	22.2 ± 1.2	15.3 ± 2.8
Daily time on/near colony (hr)		6.8 ± 0.8	5.5 ± 1.0	<0.1	7.7 ± 2.8
Number of fly bouts per trip	Short	2.6 ± 0.2	2.9 ± 0.3	n/a	2.8 ± 0.2
	Long	4.1 ± 0.8	5.4 ± 0.6	5.0 ± 0.0	6.5 ± 1.2
Foraging effort (AU)	Short	3.5 ± 0.5	4.1 ± 0.6	5.0 ± 5.0	3.8 ± 1.1
	Long	10.3 ± 1.4	14.1 ± 1.9	22.0 ± 6.0	20.23 ± 3.5
Nearest neighbour distance within/between birds (short trips, km)	Within	3.0 ± 0.2	6.0 ± 1.0	n/a	6.6 ± 0.8
	Between	3.3 ± 0.1	7.9 ± 0.3		5.9 ± 0.3
Nearest neighbour distance within/between birds (long trips, km)	Within	11.1 ± 1.0	11.2 ± 1.3	n/a	17.0 ± 0.6
	Between	10.6 ± 0.3	10.5 ± 0.3		39.6 ± 6.6

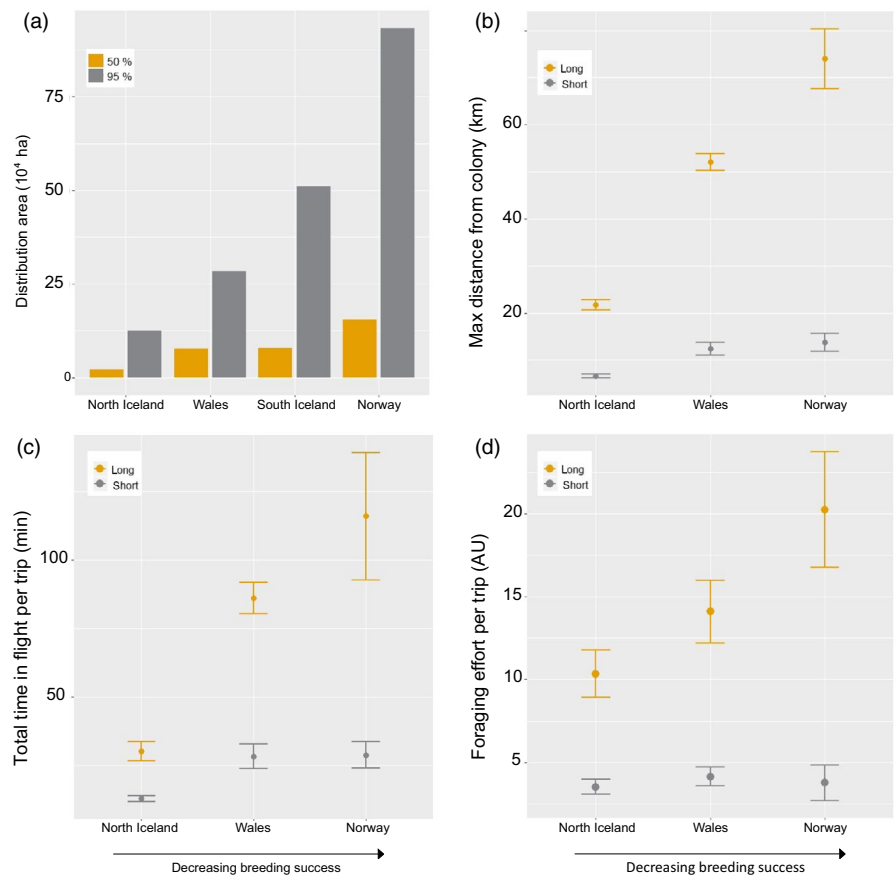
TABLE 2 Metrics from each population (mean ± SE). Grey values for southern Iceland relate to small sample sizes excluded from analyses but presented here for comparison

for short trips (LMM, $\chi^2_2 = 14.66$, $p < 0.001$, $R^2 = 0.34$) and even more so for long trips ($\chi^2_2 = 68.12$, $p < 0.001$, $R^2 = 0.84$; Figure 2; Figure S4), for example, birds in Norway went approximately twice as far as those in northern Iceland on short trips, and three times as far on long trips. Importantly, trip range for both short and long trips increased as breeding success decreased: Norway had the lowest success and longest trips, Wales had intermediate breeding success and trip range while northern Iceland had the highest breeding success and shortest trips. This was reflected in the populations' at-sea distribution and core distribution (95% and 50% occupancy kernels, respectively), which increased with decreasing breeding success (Figure 2a). Trip duration differed between colonies on long but not short trips (short: LMM, $\chi^2_2 = 0.1$, $p = 0.948$, $R^2 = 0.11$; long: $\chi^2_2 = 7.2$, $p = 0.027$, $R^2 = 0.68$). Welsh birds took long trips ~5 hr longer, presumably forced by darkness to stop until dawn (78% of long trips in Wales included ≥ 1 night away) while other colonies experienced almost continuous daylight. However, after controlling for trip range (included as a covariate), trip duration differed between colonies on short but not long trips (short: LMM, $\chi^2_2 = 8.5$, $p < 0.014$, $R^2 = 0.38$; long: $\chi^2_2 = 4.1$, $p = 0.128$, $R^2 = 0.76$), suggesting that trip duration on

those trips differed independently of distance, perhaps because of behavioural differences. The proportion of long trips differed between colonies and was especially high in Wales, perhaps for the same reason (LM, $F_{2,27} = 9.7$, $p < 0.001$, $R^2 = 0.43$). Birds did not show route fidelity between multiple foraging trips at any colony, that is, repeated trips from an individual were not more similar than trips from different birds (LMM, $\chi^2_1 = 1.32$, $p = 0.261$).

These differences in trip length were reflected in the birds' at-sea behaviour. Time in flight was strongly correlated with trip range (LMM, $\chi^2_1 = 89.1$, $p < 0.001$, $R^2 = 0.57$); therefore, flight time per trip differed between colonies (Figure 2c, LMM, $\chi^2_2 = 21.9$, $p < 0.001$, $R^2 = 0.33$). Most flight occurred in a few sustained bouts (short trips: 2.7 ± 0.1 bouts; long trips: 4.9 ± 0.4 bouts) suggesting that birds flew out to a feeding area, then spent most of the time sitting on the water and diving in a 'tidal-drift' tactic (Bennison et al., 2019), rather than engaging in area-restricted search (this is also visible from the tracks, Figure S5). Across all colonies, foraging effort was consistently higher on long trips than on short trips, but there were no differences between colonies (LMM, short vs. long: $\chi^2_1 = 61.8$, $p < 0.001$, $R^2 = 0.48$; colony: $\chi^2_2 = 2.7$, $p = 0.253$; $R^2 = 0.48$), although

FIGURE 2 (a) Size of foraging areas for all colonies, for the full (grey) and core (yellow) distributions. (b–d) Metrics for short (grey) and long (yellow) trips, including maximum trip range (b), flight time per trip (c) and foraging effort (d). Colonies are ordered by decreasing breeding success



it seemed to increase on long trips from northern Iceland to Norway (Table 2; Figure 2d).

3.2 | At-colony behaviour

Chick feeding frequency (from both mates together) differed between colonies (LMM, $\chi^2_3 = 14.7$, $p = 0.002$). Visits were most frequent in northern Iceland (4.2 ± 0.9 visits/day), followed by Wales (1.4 ± 0.2 visits/day), southern Iceland (1.0 ± 0.4 visits/day) and Norway (0.9 ± 0.4 visits/day). The difference between northern Iceland and Wales held true even when only considering Welsh visits during the same day (as Welsh birds stopped feeding at night while Icelandic birds did not, LMM, $\chi^2_1 = 7.4$, $p = 0.006$). Camera traps did not record any abnormal behaviour from tagged birds (none were seen trying to pull their tag off). After release into their nests, tagged birds remained underground for a few hours then seemed to resume normal activities including chick provisioning (Figure S6). Tagged birds fed their chick slightly less frequently than untagged birds (untagged: 4.7 ± 1.0 hr between visits vs. 6.1 ± 1.4 hr for tagged) but the difference was not statistically significant (LMM, $\chi^2_1 = 2.4$, $p = 0.119$). There was no detectable difference between sexes (males: 6.3 ± 1.5 hr between visits, females: 4.3 ± 0.8 hr, LMM, $\chi^2_1 = 0.3$, $p = 0.574$). Number of prey items per load differed between colonies (LM, $F_{2,93} = 45.3$, $p < 0.001$): on average, birds in Norway brought back 15.9 ± 1.4 ($n = 20$) prey items

per visit, versus 9.5 ± 0.3 ($n = 55$) in northern Iceland and 5.5 ± 0.4 ($n = 21$) in Wales. Prey were also largest in Wales (see Supporting Information; Figure S7).

3.3 | Diet

Out of 8.86 million sequences retrieved from the faecal samples, 4.74 million passed our filters and were assigned as fish sequences. Diet differed greatly between colonies (Figure 3; Table S1). Prey diversity was lowest in Wales (3 species) and highest in northern Iceland (11 species). Only sandeels were present in all populations, albeit at very different frequencies (14%–100%). On all colonies, adult and chick diets overlapped. There were consistently more species in adults' diet (except Wales where both contained three species) but this could be due to fewer chick samples. In Wales, adults and chicks fed on sandeel *Ammodytidae*, haddock *Melanogrammus aeglefinus* and sprat, with sandeel present in 94% of samples. In southern Iceland, nine species were recorded in adult samples, with sandeel and capelin *Mallotus villosus* the most common (present in 82% of samples). In Norway, 10 species were recorded. In adult diets, herring were the most common prey (86%), followed by Atlantic cod *Gadus morhua*. All chick samples in Norway contained haddock, with cod as second most common prey. In northern Iceland, the most common prey in both adult and chick diet were sandeels (adult: 85%, chick: 100%), then cod. Another finding of note includes the first published record

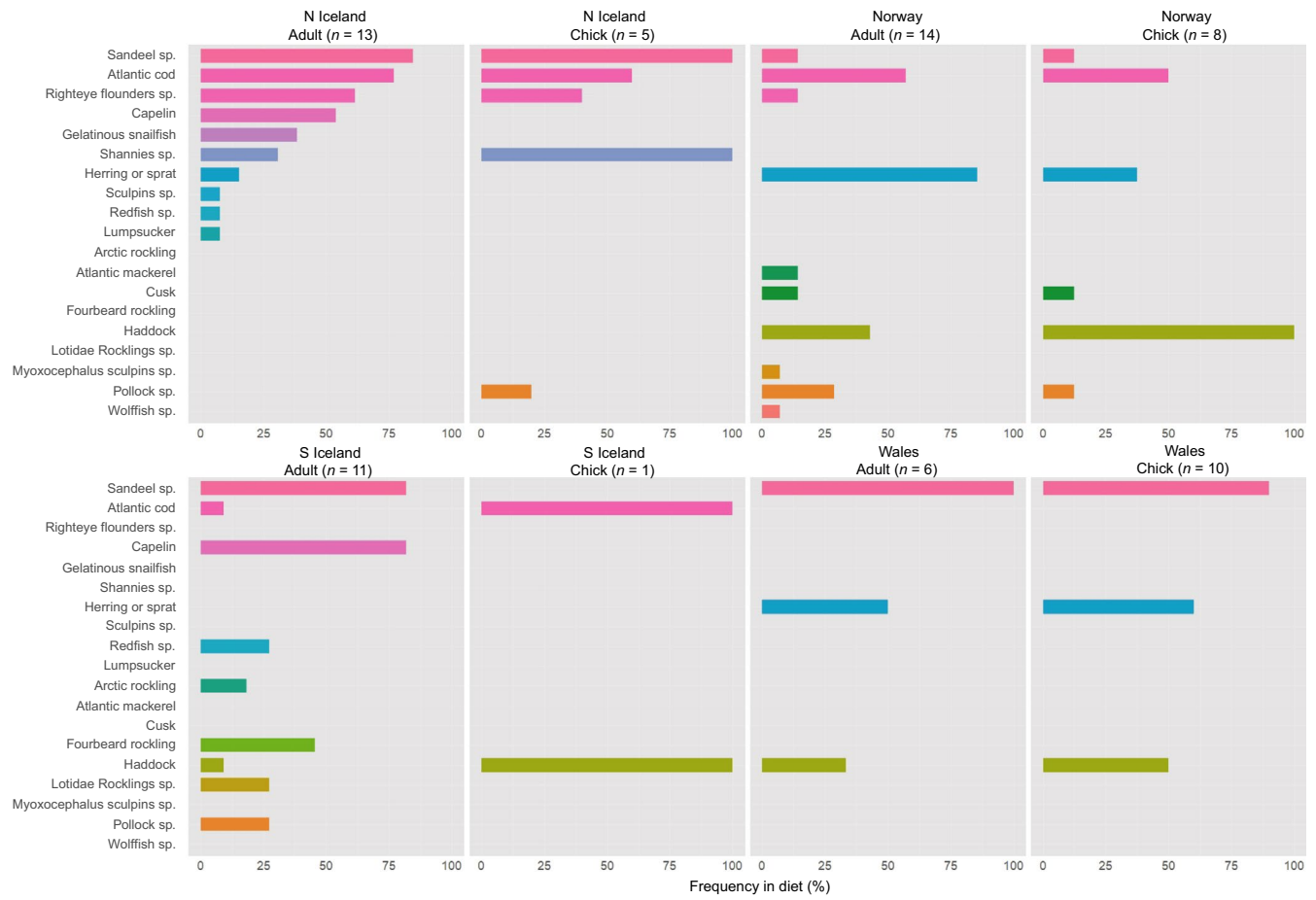


FIGURE 3 Fish prey frequency of occurrence in adult and chick puffin diet on each colony

of Arctic rockling *Gaidropsarus argentatus* and the first snailfish identified to species level in puffin diet.

4 | DISCUSSION

Our study provides unprecedented insight into the foraging ecology of breeding puffins across their range and reveals important foraging areas for puffins at major breeding grounds, essential information to inform conservation. Additionally, our multi-population approach allows us to gain insight into potential mechanisms driving low breeding success in puffins which contributed to population declines and the species to become endangered in Europe. These results have broad implications for other sympatric seabirds feeding on similar prey and highlight the value of multi-population studies.

Our key finding was that feeding distance was directly reflected in population breeding performance. Although we could not test the relationship statistically at the population level, the pattern in increasing foraging distance and other associated metrics (foraging range, foraging area, time in flight and foraging effort) clearly matched the decreasing breeding success of each population. Flight costs are extremely high in auks (Elliott et al., 2013) so flight has a key impact on energy expenditure. Consistent with this, studies

suggest that chick-rearing puffins usually feed within 25 km of the colony (Bennison et al., 2019; Harris et al., 2012). However, in our study, puffins fed near the colony but also much further, and used a dual foraging mode combining short and long trips, with the negative relationship between trip range and breeding success holding for both types of trips. Welsh birds took more long trips than others, mostly overnight, presumably because they would not fly back at night while other colonies experienced almost constant daylight. Dual foraging in auks has been observed in some studies (Evans et al., 2013; Welcker et al., 2009) but not others (Regular et al., 2013), with mixed results in puffins (Bennison et al., 2019; Harris et al., 2012). As such, it may differ between species and populations, or may be more plastic, perhaps driven by resource availability near the colony (Storey et al., 2020). Dual foraging has been suggested as a tactic to cope with low local resource availability (Granadeiro et al., 1998) but this is not always the case (Welcker et al., 2009). Our results suggest that dual foraging in our study was not a response to low prey availability locally, but instead that birds adapted their dual foraging strategy to local conditions, with birds at colonies with poor productivity extending both short and long trips. Interestingly, we found no evidence that individuals returned to the same foraging locations multiple times. Fidelity to foraging areas is common in seabirds, but evidence in auks is scarce (Ceia &

Ramos, 2015; Regular et al., 2013) and our study confirms this trend. This apparent lack of site fidelity regardless of foraging range and prey availability suggests that puffins may rely on other factors than their own experience to locate prey patches—perhaps information from the colony (Ward & Zahavi, 1973) or aggregations of birds at sea (Thiebault et al., 2014)—and that their prey distributions may be unpredictable. As puffins are notoriously sensitive to back-mounted tracking devices (Harris et al., 2012; Symons & Diamond, 2019), it is also important to note that our tagged birds seemed to behave normally and feed their chick comparably to untagged partners (albeit slightly less frequently). This is likely due to using very light tags, which is encouraging for future tracking of sensitive species.

In central-place foraging theory, foraging distance (or travel time) plays a key role on a trip's net energy gain, and ultimately on fitness (Houston & McNamara, 1985). Accordingly, negative relationships between foraging distance and breeding success have been reported in multiple central-place foraging species (Boersma & Rebstock, 2009; Chivers et al., 2012; Lorentsen et al., 2019), and our results support this. Increased foraging range can result in reduced breeding success through lower chick-provisioning frequency (Houston et al., 1996). Our finding of lower chick-feeding frequencies associated with longer trips supports this, indicating that low breeding success in northern puffin colonies is mediated by an increased foraging range during breeding. Reduced energy intake reduces chick growth and survival (Øyan & Anker-Nilssen, 1996); indeed in Norway, where puffins fed furthest and breeding success was lowest, 2018 fledglings were extremely underweight (175.6 ± 9.1 g, $n = 10$, ~40% lighter than in good years) and highly unlikely to survive (Anker-Nilssen & Aarvak, 2006). Over time, this can cause low recruitment and eventually a decline of the breeding population (Halpern et al., 2005), consistent with the 81% population decrease observed at our Norwegian colony in the last 40 years (Anker-Nilssen et al., 2020).

Increased foraging distances may also affect breeding success through reducing adult condition. Foraging further came at a cost for our study birds, which spent more time in flight; given the extremely high flight costs of auks this likely considerably impacted their daily energy expenditure. These increased breeding costs can have negative carry-over effects on future breeding performance (Fayet, Freeman, Shoji, Kirk, et al., 2016), increase the likelihood to skip breeding (Shoji, Aris-Brosou, et al., 2015) or lead parents to prioritise survival and abandon breeding (Erikstad et al., 2009; Wernham & Bryant, 1998). However, other studies have shown that despite having to forage further in certain conditions, auks can maintain breeding success through behavioural plasticity (Gulka et al., 2020) even while maintaining condition (Grémillet et al., 2012). Therefore, the lower breeding success associated with longer feeding distances in our study suggests that the efforts required to maintain chick-provisioning under the conditions near some colonies exceeded the puffins' ability or willingness to adjust their foraging behaviour. In other words, the conditions near our southern Iceland and Norwegian colonies were simply too poor for the birds to compensate.

Our diet analysis highlighted stark inter-colony differences in prey. Under habitual conditions, puffins feed chicks a low-variety diet dominated by forage fish species, especially lipid-rich sandeels in Britain and southern Iceland and capelin in northern Iceland, whereas leaner herring dominates in north-western Norway (Harris & Wanless, 2011). Our analysis shows that sandeel dominated chicks' diet in Wales and northern Iceland, and herring was common in Norway, but other species also occurred, especially at the latter two colonies. Adult diet is poorly known outside the west-Atlantic (Bowser et al., 2013); we therefore provide the first detailed insight into adult diet across the north-east Atlantic, while confirming Bowser et al.'s (2013) finding that adult and chick vertebrate diets are similar. Such information is of great importance for understanding key interactions between puffins and their prey, considering that the adults themselves likely consume 80%–90% of the energy they take out of the system during chick-provisioning (Anker-Nilssen & Øyan, 1995). Based on the size-dependent energy density of these species (Anker-Nilssen & Øyan, 1995) and our observations of differences in the number of prey items per load and prey size, it is likely that puffin diet in Iceland and Norway was substantially less nutritious than in Wales. Unfortunately, we could not identify invertebrate prey, which are unlikely to form a large component of chick diet but may form a larger component of adult diets (Bowser et al., 2013). In future, using arthropod- and cephalopod-specific primer sets to amplify invertebrate DNA or avian blocking primers could allow researchers to characterise invertebrates in diet, although secondary consumption complicates interpretation.

The link between fish availability and breeding success is well known in seabirds, including puffins (Cury et al., 2011; Durant et al., 2003). However, the low breeding success we observed is not simply caused by a general decrease in prey abundance near breeding grounds, which could lead to a switch to alternative prey without affecting foraging distance, as observed in other auks (Gulka et al., 2020; Ito et al., 2009). Instead, our results indicate that it is due to a combination of low prey availability near the colony, forcing birds to feed further, and a lack of suitable prey within the extended foraging range, as evidenced by birds' higher foraging effort on longer trips, prey load composition in northern colonies (two to three times more and smaller items than in Wales), and by our diet analyses. This combination of factors is known to have major effects on chick growth and survival in other species (Wanless et al., 2005). Besides puffins, forage fish like sandeel, sprat, herring and capelin dominate the diet of many common seabird species in the north-east Atlantic, including razorbills *Alca torda*, common guillemots *Uria aalge*, black-legged kittiwakes *Rissa tridactyla*, common and Arctic terns *Sterna hirundo* and *S. paradisaea* (Barrett, 2002; Christensen-Dalsgaard et al., 2018; Furness & Tasker, 2000; Lilliendahl & Solmundsson, 1997). As such, our findings have implications beyond puffins. Many of these seabird species are declining in the north-east Atlantic (Frederiksen, 2010), and the major effects caused by lack of prey on puffin foraging distance, chick provisioning and breeding success we report at some colonies are likely impacting these species in similar ways. We are not aware of comparable

multi-population studies across a similar geographical range in these other species, hence we encourage this avenue of research.

Drivers of prey shortages around declining colonies in Norway and southern Iceland are likely a complex interaction of multiple location-dependent drivers. In western Norway, the Norwegian spring-spawning herring stock, which collapsed in the 1960s—likely intensified by overfishing—then recovered in the 1980s, has not produced a strong year class after 2004, with poor productivity and serious population declines recorded in puffins, kittiwakes and other offshore-feeding seabirds (Anker-Nilssen et al., 2020). This is likely due to large-scale changes in sea temperature and currents, which affect herring growth, survival, drift patterns and retention time from the spawning grounds to puffin colonies further north (Sandvik et al., 2016). Similar bottom-up factors affecting sandeel growth, abundance and timing may be taking place in southern Iceland, most likely caused by changes in sea temperature, driven by the Atlantic Multidecadal Oscillation and amplified by global warming (Moore et al. 2017). This is supported by our observations of much smaller 0-group sandeels in Iceland (especially south) than Wales and reports of low breeding success in other sandeel-feeding seabirds (Vigfusdottir et al., 2013).

Importantly, the devastating effects of these environmental changes on seabird prey availability may also be amplified by intraspecific competition at larger colonies. Our two colonies with the greatest foraging range are also the world's largest two puffin colonies, much larger than our Wales and northern Iceland colonies. Even under 'normal' prey conditions, higher intraspecific competition near those colonies may lead to prey becoming quickly depleted, forcing birds to switch to less profitable prey and/or feed further afield. Conversely in northern Iceland, despite smaller prey than Wales, low competition may allow birds to feed nearby and compensate for less nutritious prey with more frequent provisioning. This 'halo' of poor foraging conditions near large colonies, predicted by Ashmole (1963), has received empirical support (Lewis et al., 2001), including in auks (Elliott et al., 2009). Under Ashmole's halo hypothesis, increased intraspecific competition when prey availability declines may lead to a larger, faster-growing halo, causing birds to increase their foraging distance even more. Disentangling the effects of intraspecific competition and decline in food availability would require repeat studies during breeding, with intraspecific competition intensifying over time as prey depletion increases while monitoring prey quality and feeding frequency. Ashmole's halo effect may act as a regulator of seabird population numbers (Jovani et al., 2016). Our results, combined with the continued population declines observed in Norway and southern Iceland, suggest that these populations, because of widespread declines in prey availability, may now be above their maximum size and currently unsustainable. Evidence also suggests birds from these larger colonies migrate further and winter in less productive waters, which may reduce body condition for subsequent breeding (Fayet et al., 2017). However, despite unsuitable conditions for breeding, high breeding philopatry could prevent birds from settling on other colonies with more abundant prey. As these large populations in the north-east Atlantic represent

a substantial part of the global puffin population and their breeding areas are also important for many other seabird species, these results present serious cause for concern for seabird conservation in Europe.

Although conducted in a single year, our multi-population approach including colonies with contrasting population trends allowed us to reveal the effects of differences in resource availability on foraging ecology and breeding success, and to highlight the possible effects of intraspecific competition on these processes. These questions can be challenging to address with single-population studies, as it requires repeated measures covering a sufficiently long period of time to encompass periods with differing population trends and prey availability. Such studies exist; in fact, long-term demographic studies have provided important insights into seabird population dynamics and the response of populations to environmental change (e.g. Croxall et al., 2002; Frederiksen et al., 2004). However, because of the high investment in time and cost required, they are limited in number and often avoid species or populations which are harder to access, and/or more difficult to work with. Shorter multi-population studies can therefore play an important role to fill this gap, by providing a broader comparative perspective to complement the more detailed but narrowly focused long-term studies (although they also have limitations, such as greater susceptibility to bias from short-term variation in prey availability that deviates from long-term patterns). Furthermore, multi-population approaches are essential to investigate demographic responses in space, including the consideration of key parameters such as adult survival, recruitment or dispersal (Frederiksen et al., 2005; Grémillat & Boulinier, 2009), and are therefore an important tool for the study of population dynamics and life-history evolution. Finally, while species- or family-specific approaches have been recommended to determine the appropriate scale of protected areas near breeding grounds (Oppel et al., 2018), our findings highlight the need to also consider inter-population differences, and therefore the relevance of multi-population approaches to conservation.

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AUTHORS' CONTRIBUTIONS

A.L.F. designed the study; A.L.F., M.S., T.A.-N. and E.S.H. collected the data; A.L.F. and G.V.C. analysed the data; A.L.F. led the writing of the paper with contributions from all authors.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.z08kprbx> (Fayet et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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