



## If it ain't broke, don't fix it: variable foraging behaviour is associated with low kittiwake reproductive success



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Repeated use of a winning foraging strategy can be profitable when individuals use memory to return to successful food patches. However, in environments where patches are unpredictable, variable foraging behaviour may be more profitable. To test this idea, we explored how individual variation in foraging trip characteristics impacts breeding success in black-legged kittiwakes, *Rissa tridactyla*, on Middleton Island, Alaska, U.S.A., during a period of highly variable environmental conditions, the largest recorded marine heatwave. As anticipated, foraging trip characteristics were highly variable, within and between years and individuals. While characteristics of foraging trips alone did not influence annual breeding success, both age and variance in those trip characteristics explained variation in breeding success. Specifically, individuals with smaller variance in foraging trip characteristics among trips were more likely to fledge a chick. There was a maximum distance threshold in foraging implying that individuals searched within a restricted area, increasing foraging time rather than distance when searching was not profitable, and providing additional support for the idea that kittiwakes are most successful when foraging in known areas rather than exploring new areas. The Pacific Decadal Oscillation, which is associated with large scale shifts between cold and warm ocean climate and ecosystem regimes in the region, impacted breeding success but did not change foraging behaviour. However, mean breeding success decreased as mean time spent resting and in area-restricted search (intensive search) on foraging trips during incubation increased. Based on nearly a decade of data, we conclude that smaller variability in behaviour, even during challenging foraging conditions, enhances breeding success. As climate change and marine heatwaves continue to increase in intensity, individuals more variable in foraging behaviour may be unable to compensate.

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Individuals, populations and species vary in their movement patterns due to both extrinsic and intrinsic factors (Hayes & Jenkins, 1997; Hertel et al., 2020; Shaw, 2020; Zimmer et al., 2011). For example, climate can alter the distribution or amount of prey throughout the environment (Damien & Tougeron, 2019; Osborne et al., 2020; Ropert-Coudert et al., 2009; Suryan et al., 2021). Additionally, intrinsic factors, such as age and reproductive status, can lead to variation in movement patterns and distribution (Cunningham et al., 2017; Graf et al., 2016; Le Vaillant et al., 2012; Votier et al., 2017; Wakefield et al., 2015). However, an intriguing portion of variation in movement behaviour is inherent to the

individual, resulting in some individuals being more variable in how they move across time and context (Hertel et al., 2020, 2021; Irons, 1998; Jakubas et al., 2018; Woo et al., 2008).

Foraging movement is a particularly critical subset of animal movement because successful foraging is essential for animals to acquire resources from the environment to allocate to survival and reproductive fitness components (Haave-Audet et al., 2022; Patrick & Weimerskirch, 2014a, 2014b; Ritchie, 1990). Several types of individual foraging specialization have been shown in foraging movement, such as dietary specialization, spatial fidelity and repeatability of dive depth (DeSantis et al., 2022; Harris et al., 2020; Masello et al., 2013; Patrick et al., 2014; Tinker et al., 2007; Woo et al., 2008), making repeatability in foraging a trait with potentially strong links to individual variation in fitness. For example, within-year foraging site fidelity was associated with higher

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reproductive success in albatrosses, *Thalassarche melanophris*, possibly because those individuals that mastered a single tactic were more proficient foragers than those that switched tactics (Patrick & Weimerskirch, 2017). In other cases, individual specialization may not be associated with lifetime fitness because the benefits of one strategy may only occur in some years depending on the predictability or abundance of prey (reviewed by Woo et al., 2008). Furthermore, repeatability in foraging behaviour may only be present, or consequential, during years with low food availability (Laskowski et al., 2021; Trevail et al., 2021). For example, adult penguins with more repeatable foraging behaviour had higher growth rates during a year of poor environmental conditions when prey availability was low (Trainsnel & Pichegru, 2019).

In marine environments, food resources often follow a heterogeneous or 'patchy' distribution (Bertrand, Bêty, et al., 2021; Bertrand, Strøm, et al., 2021; Davoren et al., 2003). If these patches are predictable and constant through time, consistency in foraging behaviour is more likely to confer fitness advantages than when patches shift or disappear. For marine predators that breed on land while foraging at sea, such as seabirds, shifts in prey distribution caused by changes in environmental conditions increase the effort needed to find food, which can negatively impact reproductive success in long-lived species (Fromant et al., 2021; Osborne et al., 2020). Thus, some degree of behavioural flexibility is likely necessary to cope with extreme events. However, it is unclear whether repeatability in foraging behaviour continues to confer benefits when individuals face extreme shifts in environmental conditions.

Here, we examine foraging behaviour and breeding success of black-legged kittiwakes, *Rissa tridactyla* (hereafter 'kittiwakes') before, during and after an extreme marine heatwave to see whether individual behaviour changed during this time of major environmental change, and if those responses impacted breeding success. Among seabirds, kittiwakes are especially sensitive to changes in the distribution of prey in the water column, as they are primarily surface feeders and can only plunge dive to depths of about 1 m (Hatch et al., 1993; Maunder & Threlfall, 1972). We used a study population breeding on Middleton Island, Alaska, in which sharp fluctuations in breeding success have been linked to a large-scale climate oscillation (Pacific Decadal Oscillation, PDO); productivity tends to increase during cool climate phases but decline in warm phases (Hatch, 2013). The current study ran from 2012 to 2020, starting during a cool phase with favourable breeding conditions, which was disrupted in 2014 when a marine heatwave occurred in the North Pacific Ocean ('the Blob'; Yang et al., 2019). The heatwave lasted several years and extended throughout the water column, making it the largest marine heatwave since the 1980s (Hobday et al., 2018; Suryan et al., 2021). This impacted all levels of the marine ecosystem with sharp declines in phytoplankton surface biomass, capelin, *Mallotus villosus*, and herring abundance, seabird breeding success and sea lion pups during the heatwave (Suryan et al., 2021). The warm temperatures persisted at depth after surface amelioration of the heatwave in 2016 (Suryan et al., 2021) and kittiwakes used a large foraging range both during and after the heatwave (Osborne et al., 2020). In 2019, another marine heatwave occurred in the same location in the North Pacific, although it was shorter in duration and not as pervasive (Cornwall, 2019).

We examined three predictions. First, as the core areas of the population's foraging range overlapped before, during and after the heatwave (Osborne et al., 2020), we predicted that individuals with higher foraging repeatability would have higher breeding success because the core areas represented predictable food patches. Second, we predicted that individuals foraging closer to

the colony and for shorter durations would have higher breeding success. The first and second hypotheses are not mutually exclusive and may act additively. Following Daunt et al. (2002), we predicted the presence of a maximum distance threshold where birds search longer over a restricted space rather than expanding foraging range to search farther for food. Daunt et al. (2002) suggested that the upper limit in foraging range is due to habitat features (a sandbank that is a key location for preferred prey) rather than an energetic constraint on flight, and we wished to test whether this pattern continued in a context without a clear habitat feature at a fixed distance. Third, we predicted that annual population-wide foraging range and duration would closely track sea surface temperature as a proxy for fish availability, and in turn would be associated with population average reproductive success. As kittiwakes in the North Pacific have declined at some locations (e.g. >90% at Middleton Island alone; Hatch, 2013) and the species is now listed in the Atlantic region as vulnerable (BirdLife International, 2019), understanding how intraspecific variation in behaviour is linked to reproductive success is a critical step to establish conservation measures.

## METHODS

### Reproductive Monitoring

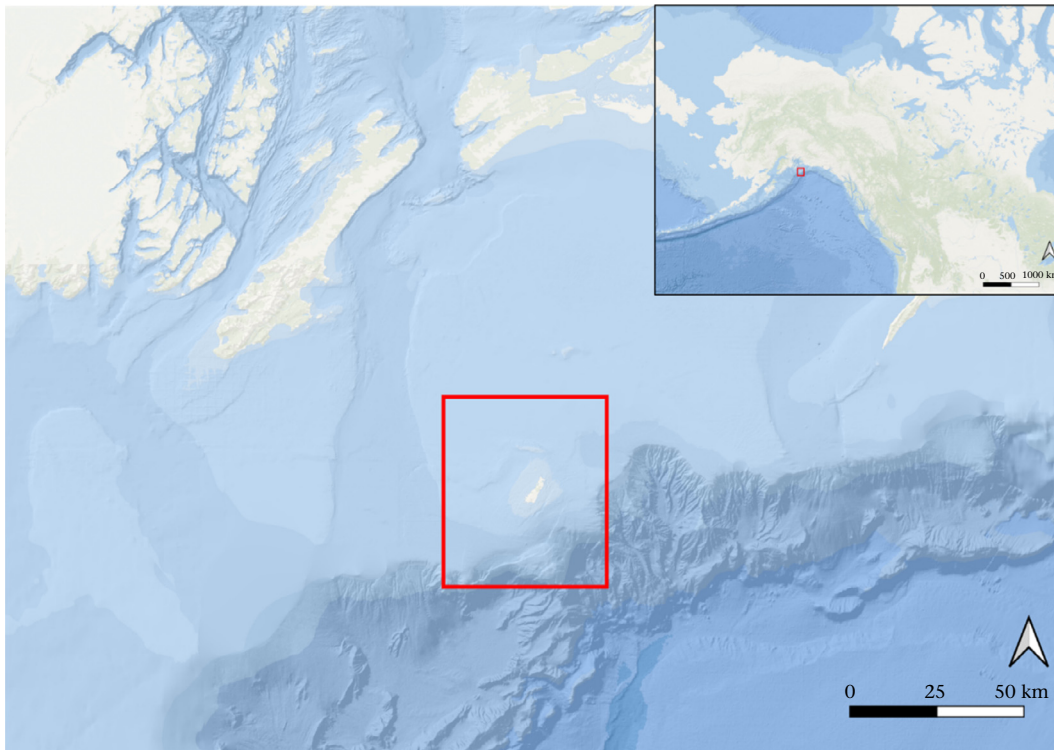
We conducted the study from 2012 to 2020 on Middleton Island, in the Gulf of Alaska (59.48°N, 146.38°W; Fig. 1). On the island, black-legged kittiwakes nest on an abandoned U.S. Airforce radar tower behind one-way mirrored glass (Gill & Hatch, 2002). To identify individual birds, adults were banded with a unique combination of colour bands. Many birds were of known age as they were banded as chicks on the tower. For those that were banded as adults, we estimated age by adding 5 years to the year banded, which is the average age first captured as an adult (Elliott, O'Reilly, et al., 2014). We monitored nests daily during May–August and any changes to nest contents (eggs laid/lost, chicks hatched/lost).

### GPS Deployments

For GPS deployments, we captured breeding adult kittiwakes at the nest using a leg hook during either incubation or chick rearing. All GPS were deployed on birds that had at least one egg or chick. During 2012, 2013 and 2015, GPS units (14 g, iGotU, Catnip Technologies, Hong Kong) were attached to the dorsal feathers using marine adhesive tape (TESA) and zip-ties. In 2016–2020, GPS accelerometers (9 g, AxyTrek, Technosmart, Rome, Italy) were attached to the central two retrices similarly using TESA tape, zip-ties and superglue. Although device effects have been observed in kittiwakes, these effects primarily impacted time spent flying and not breeding success or foraging trip metrics (Chivers et al., 2016) and so the difference in weight between the two devices likely would not impact the results of this study, especially as we primarily examine within-individual metrics. Birds were recaptured to remove the GPS unit after at least 24 h, with most retrieved within 96 h (mean  $\pm$  SD = 85  $\pm$  44 h).

### Ethical Note

All birds monitored and handled were covered under McGill Animal Care Permit 2015-7599 and U.S. Fish & Wildlife Permit 85004C. Handling was conducted by researchers with experience banding and attaching GPS units and handling time was minimized to reduce stress.



**Figure 1.** Study area for nest monitoring and GPS deployment at Middleton Island, in the Gulf of Alaska.

### Statistical Analysis

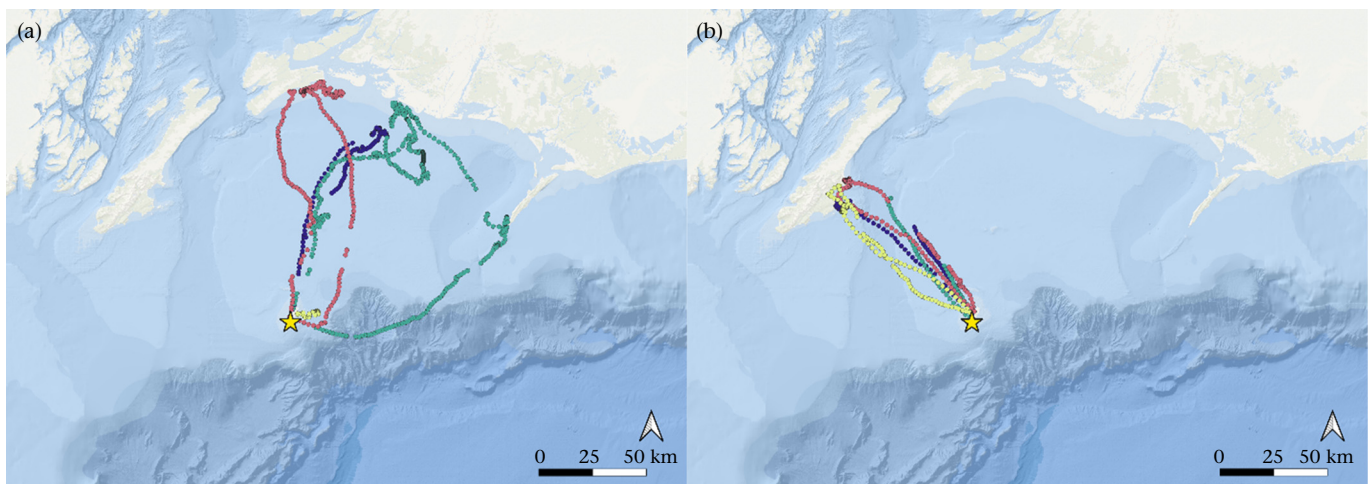
#### Foraging trip characteristics

We completed all statistical analyses in R (version 4.0.3, [R Core Team, 2020](#)). Foraging trips were defined as departures from the colony lasting more than 30 min. These trips were then subset to include only complete foraging trips where the kittiwake travelled at least 5 km from the colony to exclude loafing around the island ([Fig. 2](#)). From those, we calculated foraging trip characteristics: maximum distance from the colony (km), duration of foraging trip (h) and total distance travelled (km). To classify foraging behaviour into transit flight (flying between locations), area-restricted search (reduced speed, high turning, increased time in one area) and

resting on the water, we used a Residence in Space and Time ([Torres et al., 2017](#); radius = 1.116081; threshold = 0). The radius was calculated using mean ground speed of black-legged kittiwakes described for this population of kittiwakes ([Elliott, Chivers, et al., 2014](#)) and the GPS sampling interval. We then defined foraging patches as consecutive points classified as area-restricted search to calculate the number of foraging patches for each foraging trip.

#### Principal component analysis of foraging trips

We used a rotated principal component analysis (PCA) to avoid issues of multiple comparison by collapsing foraging trip characteristics into one or two dimensions. The PCA included maximum distance, duration, total distance, number of foraging patches and



**Figure 2.** (a, b) Example movement data from two birds that were GPS-tracked on the same dates during chick rearing in 2018. The two individuals exhibited different foraging patterns and locations, one more variable (a) and one more consistent (b). The yellow star indicates the Middleton Island kittiwake colony, where GPS devices were deployed. Each individual foraging trip is coloured differently.

the standard deviations of maximum distance, duration and total distance, which were all standardized prior to inclusion. To include the standard deviations of variables, we removed deployments where there was only one foraging trip and removed outliers with a maximum distance of  $\geq 150$  km or duration  $\geq 70$  h (incubation: 78 individuals, 86 deployments, 205 foraging trips; chick rearing: 135 individuals, 155 deployments, 699 foraging trips).

#### *Foraging trip characteristics and fledging success*

To test for effects of foraging trip characteristics on fledging success, we fitted generalized linear mixed models (GLMM) with a binomial link using lme4 (Bates et al., 2015). We tested whether age affected fledging success (defined as fledging at least one chick or not) by examining a general linear mixed model for fledging success separated by breeding phase during time of deployment, using age as a fixed effect and random intercepts of bird identity (ID) and year (known-age birds tracked during incubation: 75 individuals; 82 deployments; 197 foraging trips; known-age birds tracked during chick rearing: 128 individuals; 146 deployments; 659 foraging trips). The data set with birds of known and assigned age was then used for all GLMM with age as a fixed effect. We then modelled fledging success in response to fixed effects of PC1 and PC2 (representing all foraging trip characteristics) and age with random intercepts of bird ID and year. Using the same methods, we then separately tested for fixed effects of maximum distance and trip duration because they were loaded slightly differently along the PC2 axis. We tested for significance using *F* values and *t* values (and associated *P* values) provided by lme4. We determined significance for the variables using *P* values. To determine the impact of year as a random effect, we then ran all models without year, performed an ANOVA on the two models (with and without year) and report the Akaike's information criterion (AIC) scores.

To further test whether repeatability in foraging behaviour is associated with fledging success, we separated the data into groups based on the breeding phase during which the bird was tracked (incubation or chick rearing) and whether or not they fledged chick(s). For each group, we then ran generalized linear models (GLM) to test the relationship between the foraging trip characteristics of the first and second foraging trip for each deployment with the number of days between each trip as a covariate.

To test for a maximum distance threshold, we used the package 'segmented' (Muggeo, 2003) to analyse linear models for maximum distance in response to duration for each year in this study. This package updates linear models with segmented relationships and then uses score statistic tests to determine whether there is evidence of at least one breakpoint in the model where the slope changes.

We obtained PDO index values (NOAA, ERDDAP, <https://coastwatch.pfeg.noaa.gov/erddap/info/index.html>) and calculated average PDO index during the breeding season (May–August) for each year. We used simple linear regressions to test for an association between PDO and average population level breeding success, as well as PDO and average population level foraging behaviour.

#### *Activity budgets and fledging success*

To test whether time spent in area-restricted search (a proxy for active foraging effort) influenced fledging success across individuals, we modelled fledging success in response to time spent in area-restricted search as the fixed effect, and year and bird ID as random intercepts. To test for a population level relationship between mean time spent in each behaviour (flying, area-restricted search, resting) and mean breeding success for the colony, we used linear models on mean time spent in each behaviour and the

mean number of chicks fledged per year for birds tracked during incubation and chick rearing separately.

## RESULTS

We obtained GPS data with at least two foraging trips for each deployment from 86 deployments during incubation and 155 deployments during chick rearing (78 individuals tracked during incubation, 135 individuals tracked during chick rearing, 9 individuals tracked during both incubation and chick rearing in 2018) between 2012 and 2020 (Table 1). This included 904 foraging trips, 856 of which were for birds of known age. For birds tracked during incubation, the mean ( $\pm$  SD) maximum distance from the colony for a trip was  $59.5 \pm 41.2$  km, total distance travelled was  $214.1 \pm 152.4$  km, duration of trip was  $14.7 \pm 10.8$  h and number of foraging patches was  $14.4 \pm 9.6$ . For birds tracked during chick rearing, the mean ( $\pm$  SD) maximum distance from the colony for a trip was  $50.6 \pm 36.4$  km, total distance travelled was  $142.2 \pm 107.2$  km, duration of trip was  $7.6 \pm 6.8$  h and number of foraging patches was  $8.8 \pm 6.1$ .

#### *Principal Component Analysis*

For birds tracked during incubation, PC1 (rotated principal component 1) accounted for 50% of the variation and most closely represented the foraging trip characteristics, which were loaded in the same direction (Table 2, Fig. 3). PC2 accounted for 37% of the variation and most closely represented the standard deviations, with all standard deviations of foraging trip characteristics loading positively. For birds tracked during chick rearing, PC1 accounted for 47% of the variation and PC2 accounted for 35% of the variation.

#### *Foraging trip characteristics and fledging success*

Age had a significant effect on fledging success in all models; that is, fledging success decreased with age ('senescence') but only for birds tracked during incubation; very young and very old birds had low hatching success and the absence of variation in age-related quality may explain why no relationship occurred during chick rearing. Of all the foraging trip characteristics we analysed, only the standard deviation of total distance and PC2 (which included the standard deviation of all trip characteristics) were significantly associated with fledging success (Table 3, Fig. 4). Thus, while the foraging trip characteristics alone did not impact fledging success, variation in the foraging trip characteristics did. Additionally, all models with year had a lower AIC score than models without year, demonstrating that year was an important random effect (Table 4).

For all three foraging trip characteristics (duration, maximum distance, total distance), there was a significant relationship

**Table 1**

Number of kittiwake GPS deployments each year and breeding phase, with the number of foraging trips within those deployments shown in parentheses

Year	Incubation	Chick rearing	Total
2012	0	4 (9)	4 (9)
2013	30 (67)	38 (193)	68 (260)
2015	0	3 (8)	3 (8)
2016	0	8 (34)	8 (34)
2017	14 (32)	34 (142)	48 (174)
2018	18 (53)	40 (224)	58 (277)
2019	20 (41)	25 (74)	45 (115)
2020	4 (12)	3 (15)	7 (27)
Total	86 (205)	155 (699)	241 (904)

Each deployment within a year represents one individual except in 2018, where GPS units for nine individuals were deployed during both incubation and chick rearing.

**Table 2**  
Rotated principal component analysis of foraging trip characteristics

	Incubation		Chick rearing	
	PC1	PC2	PC1	PC2
<b>Proportion of variance</b>	0.50	0.37	0.47	0.35
<b>Loadings</b>				
Maximum distance	0.90	0.02	0.89	0.05
Duration	0.93	0.13	0.88	0.22
Total distance	0.97	0.06	0.96	0.10
Number of patches	0.90	0.06	0.84	0.05
SD maximum distance	-0.08	0.90	-0.06	0.89
SD duration	0.15	0.90	0.25	0.83
SD total distance	0.11	0.96	0.13	0.96

Proportion of variance explained for each principal component and the loadings for each foraging trip characteristic, including maximum distance, duration, total distance, number of patches and the standard deviation of maximum distance, duration and total distance. For birds tracked during incubation ( $N = 78$  individuals, 205 foraging trips), PC1 explained 50% of the variation, with all foraging trip characteristics having similar loadings, and PC2 explained 37% of variation, with all standard deviations of foraging trip characteristics having similar loadings. For birds tracked during chick rearing ( $N = 135$  individuals, 699 foraging trips), PC1 explained 47% of the variation and PC2 explained 35% of the variation.

between the first and second trip characteristics for kittiwakes that successfully fledged chicks, regardless of the breeding phase during which they were tracked (Table 5, Fig. 5). For birds tracked during incubation, there was no significant relationship between trip 1 and 2 for any of the foraging trip characteristics for birds that did not successfully fledge a chick. However, there was a significant relationship between the maximum distance of trip 1 and 2 for birds tracked during chick rearing that did not fledge a chick (Table 5). In short, although there was still some success for birds with more variable foraging trips, kittiwakes with less variable foraging behaviour during incubation and chick rearing achieved higher fledging success.

*Maximum distance and duration*

A segmented line better represented the relationship between trip duration and maximum distance for all study years ( $P < 0.05$ ). As trip duration increased, maximum distance increased up to

about 8 h trip duration; after the breakpoint, the slope decreased (Fig. 6). The relationship varied slightly between years, with a mean ( $\pm$  SD) breakpoint of  $7.89 \pm 3.57$  h. The lowest breakpoint occurred at 3.633 h in 2012, and the highest breakpoint occurred at 13.860 h in 2016.

*PDO, fledging success and foraging trip characteristics*

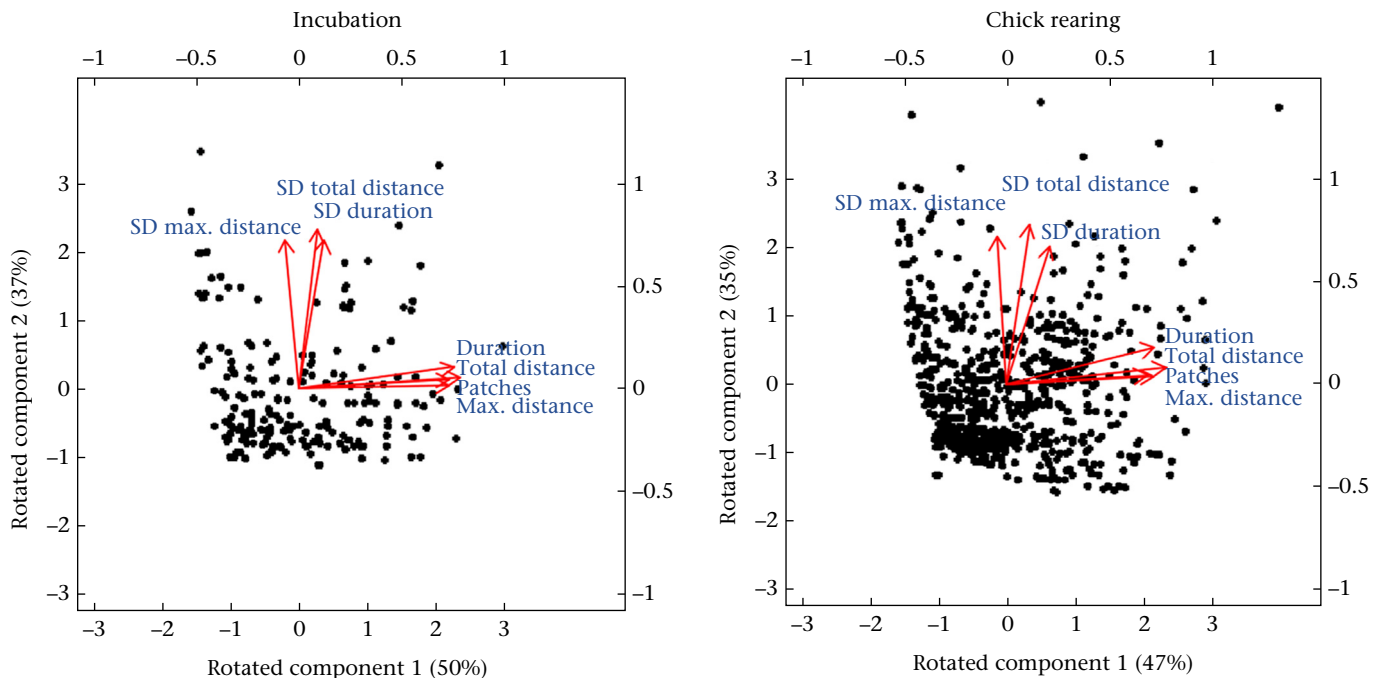
At the population level, we found a strong negative relationship between mean PDO index during the breeding season and the mean number of chicks fledged per nest (Fig. 7). However, none of the foraging trip characteristics or standard deviations of foraging trip characteristics were related to PDO (Table 6).

*Time allocation and fledging success*

The 2 years where marine heatwaves started coincided with the highest time spent in area-restricted search during chick rearing. However, time spent in area-restricted search had no significant impact on fledging success among kittiwakes tagged during incubation ( $z = 0.027$ ,  $N = 78$  individuals, 205 foraging trips,  $P = 0.97$ ) or chick rearing ( $z = -1.21$ ,  $N = 135$  individuals, 699 foraging trips,  $P = 0.22$ ). Overall, on average, fewer chicks fledged during years when kittiwakes spent more time resting on water during incubation ( $t_3 = -3.44$ ,  $P < 0.05$ ) and when kittiwakes spent more time in area-restricted search during incubation ( $t_3 = -12.57$ ,  $P < 0.01$ ; Table 7, Fig. 8).

**DISCUSSION**

Contrary to our predictions, fledging success was not associated with absolute foraging distance or duration, but rather with the individual's age and the variability of foraging parameters as represented by PC2. Kittiwakes with higher fledging success were less variable in their foraging behaviour during incubation and chick rearing, relative to unsuccessful breeders (Fig. 5). Although maximum foraging distance increased with trip duration, there was a threshold beyond which maximum distance plateaued (Fig. 6). This implies that unsuccessful individuals must find a profitable foraging patch within the fixed annual colony foraging area rather

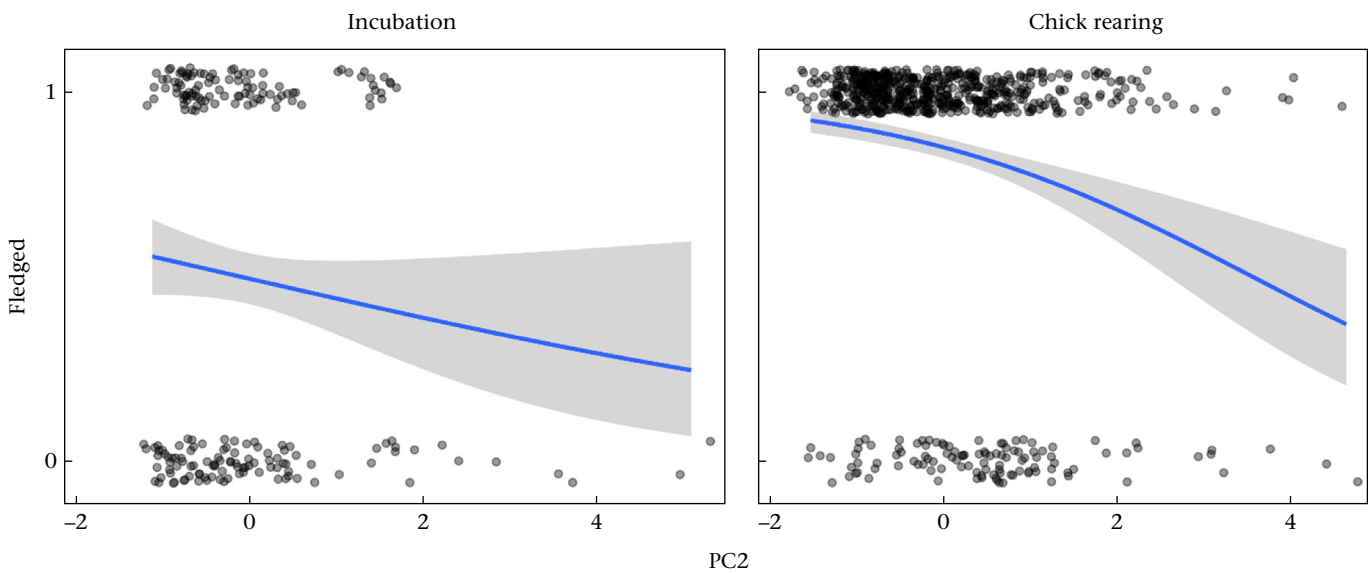


**Figure 3.** A rotated PCA of foraging trip characteristics and the standard deviation (SD) of foraging trip characteristics for birds tracked during incubation and chick rearing.

**Table 3**  
Associations between fledging success (FS), age and foraging behaviour of black-legged kittiwakes at Middleton Island, separated by the breeding phase during which the birds were tracked (incubation:  $N = 75$  individuals, 197 foraging trips; chick rearing:  $N = 128$  individuals, 659 foraging trips)

	Model	Variable	Estimate	SE	z	P
Incubation	FS ~ Age+(1 band)+(1 year)	Age (scaled)	13.29	3.54	3.74	<b>&lt;0.001</b>
		Max distance (scaled)	0.12	1.27	0.09	0.92
	FS ~ Max distance + Age+(1 band)+(1 year)	Age (scaled)	13.31	3.81	3.49	<b>&lt;0.001</b>
		PC1	0.12	0.94	0.13	0.89
	FS ~ PC2+ Age+(1 band)+(1 year)	Age (scaled)	13.32	3.60	3.68	<b>&lt;0.001</b>
		PC2	-8.01	2.64	-3.03	<b>&lt;0.01</b>
Chick rearing	FS ~ Age+(1 band)+(1 year)	Age (scaled)	20.28	4.07	4.94	<b>&lt;0.0001</b>
		Age (scaled)	-0.05	1.01	-0.05	0.96
	FS ~ Max distance + Age+(1 band)+(1 year)	Max distance (scaled)	-0.30	0.32	-0.93	0.35
		Age (scaled)	-0.11	1.05	-0.10	0.91
	FS ~ PC1+ Age+(1 band)+(1 year)	PC1	-0.20	0.29	-0.71	0.47
		Age (scaled)	-0.08	1.04	-0.08	0.93
	FS ~ PC2+ Age+(1 band)+(1 year)	PC2	-13.00	3.00	-4.33	<b>&lt;0.0001</b>
		Age (scaled)	4.89	4.47	1.09	0.27

In all models, bird ID and year were included as random intercepts. Significant  $P$  values are shown in bold.



**Figure 4.** Association between foraging trip characteristics (PC2) and fledging success (whether or not the bird fledged at least one chick) during incubation and chick rearing. Vertical jitter added to show point density. Blue line represents a GLM and shading represents the 95% confidence interval.

than extending their foraging trip, providing additional support for the idea that kittiwakes are most successful when foraging in known areas rather than when exploring new areas. Population level breeding success was higher when PDO index was more

**Table 4**  
AIC scores from ANOVAs of all models with and without year as a random effect

	Model	AIC
Incubation	FS ~ Age+(1 band)+(1 year)	121.77
	FS ~ Age+(1 band)	164.92
	FS ~ Max distance + Age+(1 band)+(1 year)	123.76
	FS ~ Max distance + Age+(1 band)	157.69
	FS ~ PC1+ Age+(1 band)+(1 year)	123.75
	FS ~ PC1+ Age+(1 band)	156.37
	FS ~ PC2+ Age+(1 band)+(1 year)	120.39
	FS ~ PC2+ Age+(1 band)	159.80
Chick rearing	FS ~ Age+(1 band)+(1 year)	193.73
	FS ~ Age+(1 band)	198.53
	FS ~ Max distance + Age+(1 band)+(1 year)	194.84
	FS ~ Max distance + Age+(1 band)	200.47
	FS ~ PC1+ Age+(1 band)+(1 year)	195.19
	FS ~ PC1+ Age+(1 band)	200.53
	FS ~ PC2+ Age+(1 band)+(1 year)	155.18
	FS ~ PC2+ Age+(1 band)	175.66

All models with year included had lower scores than models without year.

negative (i.e. cooler climate) during the breeding season, but PDO index was not linked to the mean of any foraging trip characteristics or the mean standard deviations of foraging trip characteristics (Table 6). When broken down by behaviour, mean time spent resting and in area-restricted search on foraging trips during incubation were associated with colony level breeding success (Fig. 8).

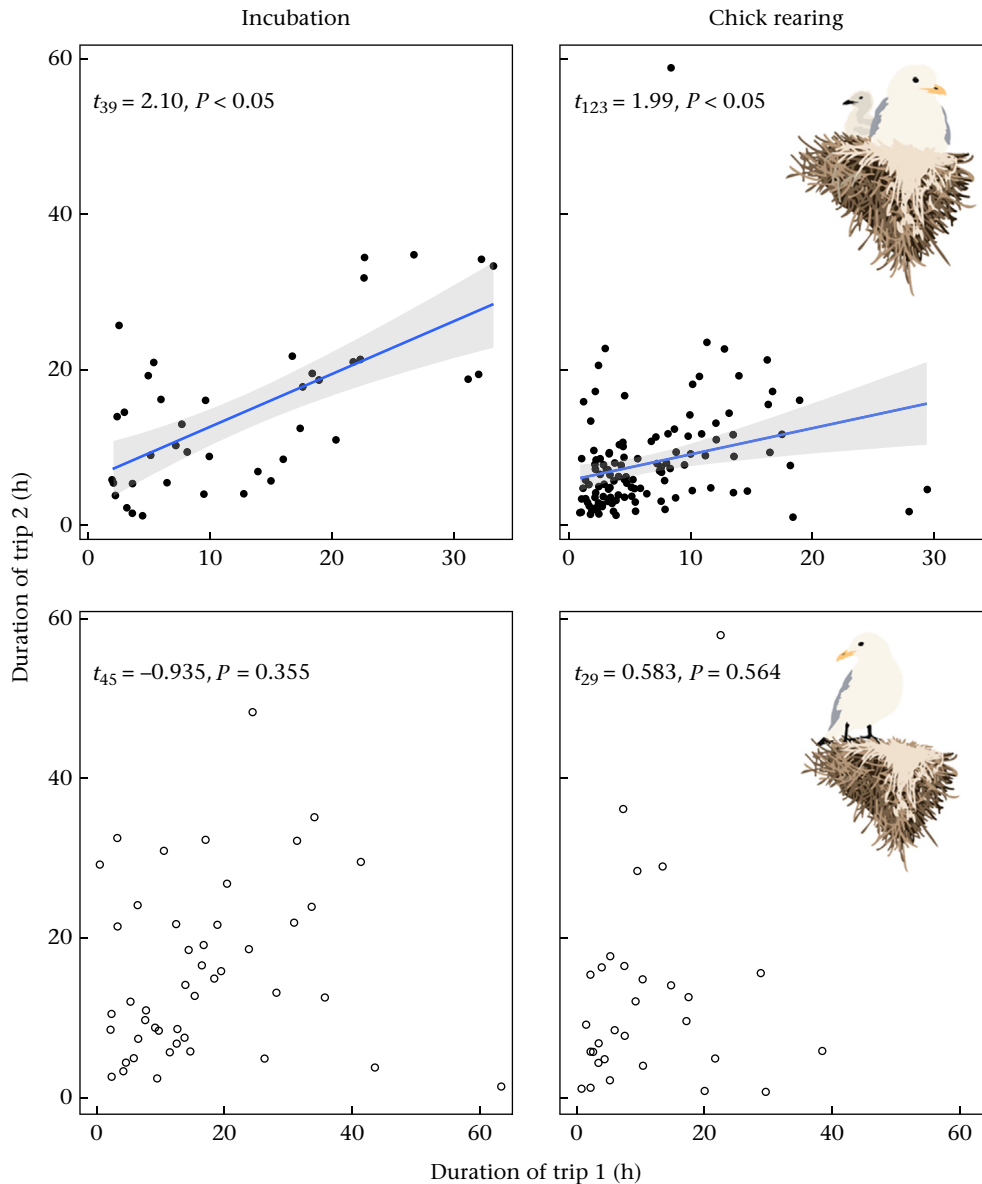
Kittiwake foraging trip distance was highly variable among years, with some individuals flying hundreds of kilometres to forage in poor years (Fig. 9) (results presented in Osborne et al., 2020). Indeed, foraging trips were short in both distance and duration during the cool, pre-heatwave years (2012–2013) but then were much longer in the subsequent years, implying that ecosystem impacts persisted even after the heatwave dissipated in 2016 (Osborne et al., 2020). These lagged effects suggest that if patchy habitats (such as marine environments) are disturbed by habitat destruction or environmental changes, the full impact on long-lived species may operate over longer timescales than for short-lived species (Kuussaari et al., 2009; Robertson et al., 2021). Changes in a number of environmental variables, including warmer temperatures, wind mixing and stratification, have been found to influence reproductive success in the years following an

**Table 5**

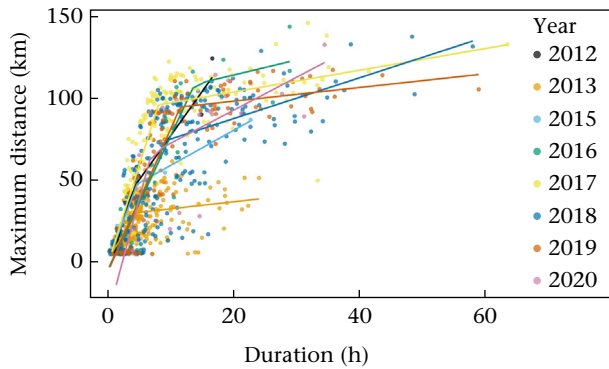
Results of generalized linear models analysing the relationship between foraging trip characteristics of the first and second foraging trip (model structure: foraging trip characteristic of trip 1 – foraging trip characteristic of trip 2 + number of days between trips) for each individual deployment separated by phase and fledging success (incubation:  $N = 86$  deployments; chick rearing: 155 deployments)

Foraging characteristic	Breeding phase during deployment	Successfully fledged $\geq 1$ chick	df	Estimate	SE	$t$	$P$
Duration	Incubation	Yes	39	0.393	0.186	2.10	<b>&lt;0.05</b>
Duration	Incubation	No	45	-0.139	0.149	-0.935	0.355
Duration	Chick rearing	Yes	123	0.248	0.124	1.99	<b>&lt;0.05</b>
Duration	Chick rearing	No	29	0.224	0.385	0.583	0.564
Maximum distance	Incubation	Yes	39	0.736	0.182	4.04	<b>&lt;0.001</b>
Maximum distance	Incubation	No	45	0.308	0.166	1.85	0.071
Maximum distance	Chick rearing	Yes	123	0.550	0.084	6.57	<b>&lt;0.0001</b>
Maximum distance	Chick rearing	No	29	0.667	0.208	3.20	<b>&lt;0.05</b>
Total distance	Incubation	Yes	39	0.649	0.159	4.05	<b>&lt;0.001</b>
Total distance	Incubation	No	45	-0.122	0.151	-0.812	0.421
Total distance	Chick rearing	Yes	123	0.488	0.100	4.84	<b>&lt;0.0001</b>
Total distance	Chick rearing	No	29	0.309	0.276	1.12	0.272

For each foraging characteristic, there was a significant relationship between the two foraging trips for kittiwakes that successfully fledged a chick. The relationship between trip 1 and 2 was not significant for kittiwakes that failed to fledge a chick during incubation. For birds tracked during chick rearing, there was also a significant relationship between the first two foraging trips for birds that did not successfully fledge a chick when looking at maximum distance. Significant  $P$  values are shown in bold.



**Figure 5.** Correlations between duration of the first foraging trip compared to the second foraging trip for birds tracked during incubation and chick rearing.



**Figure 6.** Relationship between maximum distance and trip duration for each year of the study ( $N = 904$  foraging trips).

environmental change (Zador et al., 2013). The delayed return to pre-heatwave kittiwake foraging behaviour may be due to the impact of the heatwave working its way up through trophic levels via bottom–up effects. This is supported by evidence that primary prey species of the kittiwake population, such as Pacific sand lance, *Ammodytes personatus*, and capelin, decreased in availability during the heatwave and had still not recovered 5 years after the initial onset (Suryan et al., 2021).

Regardless of whether they foraged near or far, kittiwakes that were less variable in their foraging behaviour during both incubation and chick rearing were more likely to fledge a chick, implying that birds that found a successful strategy were able to continue to use that strategy while other individuals appeared to switch tactics searching for success. Evidence of a win–stay–lose–shift strategy has been found in at least one other species of seabird where individuals were more likely to return to a foraging location if the previous trip was successful (Bonnet-Lebrun et al., 2021). Although individuals may be more likely to return to successful locations if the prey location is predictable (Bicca-Marques, 2005). Indeed, other studies have found that individual repeatability in foraging behaviour can vary between years (Camprasse et al., 2017; Ceia et al., 2014; Patrick et al., 2021) and, in one case, found higher repeatability in trip

**Table 6**

Results of linear models exploring the relationship between Pacific Decadal Oscillation and both mean number of chicks fledged and averaged foraging trip characteristics for the GPS-tracked kittiwakes

~ Pacific Decadal Oscillation	Estimate	SE	<i>t</i>	<i>P</i>
<b>Mean chicks fledged (<i>df</i> = 15)</b>	–0.17	0.08	–2.15	<b>&lt;0.05</b>
<b>Foraging trip characteristics (<i>df</i> = 6)</b>				
Duration	0.71	1.22	0.58	0.57
Maximum distance	3.08	7.06	0.43	0.67
Total distance	1.13	18.16	0.06	0.95
SD duration	0.69	0.50	1.37	0.21
SD maximum distance	1.83	2.65	0.69	0.51
SD total distance	5.37	7.83	0.68	0.51

Pacific Decadal Oscillation index during the breeding season (May–August) explained the mean number of chicks fledged. There were no significant relationships between the means of any foraging trip characteristics or mean standard deviations of any foraging trip characteristic and Pacific Decadal Oscillation ( $N = 8$  years). Significant *P* values are shown in bold.

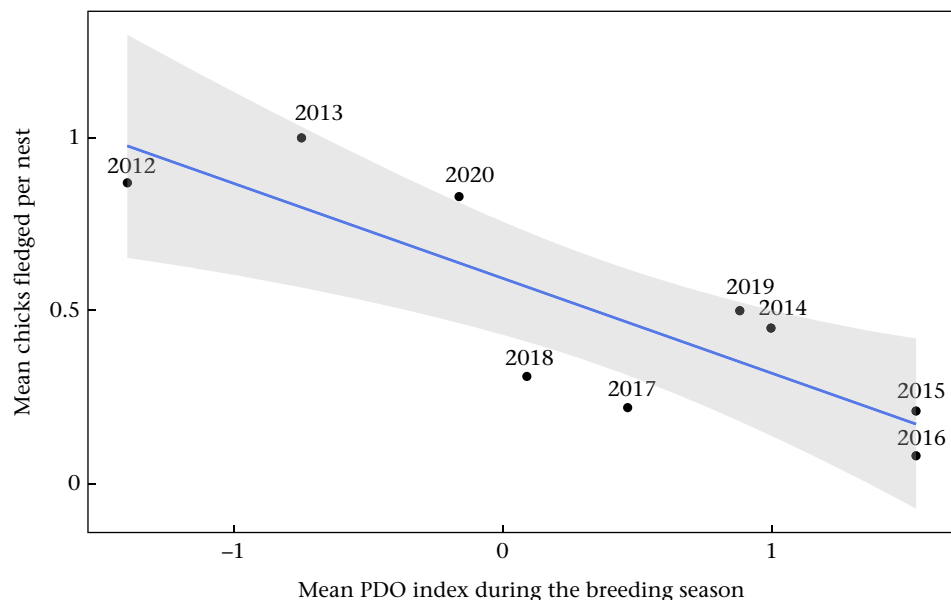
**Table 7**

Relationship between mean time spent in each behaviour while away from the colony on foraging trips and mean chicks fledged per year for black-legged kittiwakes tracked during incubation and chick rearing (incubation:  $N = 5$  years; chick rearing:  $N = 8$  years)

	Estimate	SE	<i>t</i>	<i>P</i>
<b>Incubation (<i>df</i> = 3)</b>				
Transit flight	–0.15	0.07	–2.23	0.11
Rest	–0.12	0.03	–3.44	<b>&lt;0.05</b>
Area-restricted search	–0.17	0.01	–12.57	<b>&lt;0.01</b>
<b>Chick rearing (<i>df</i> = 6)</b>				
Transit flight	–0.17	0.08	–1.98	0.09
Rest	–0.10	0.13	–0.77	0.46
Area-restricted search	0.10	0.14	0.70	0.50

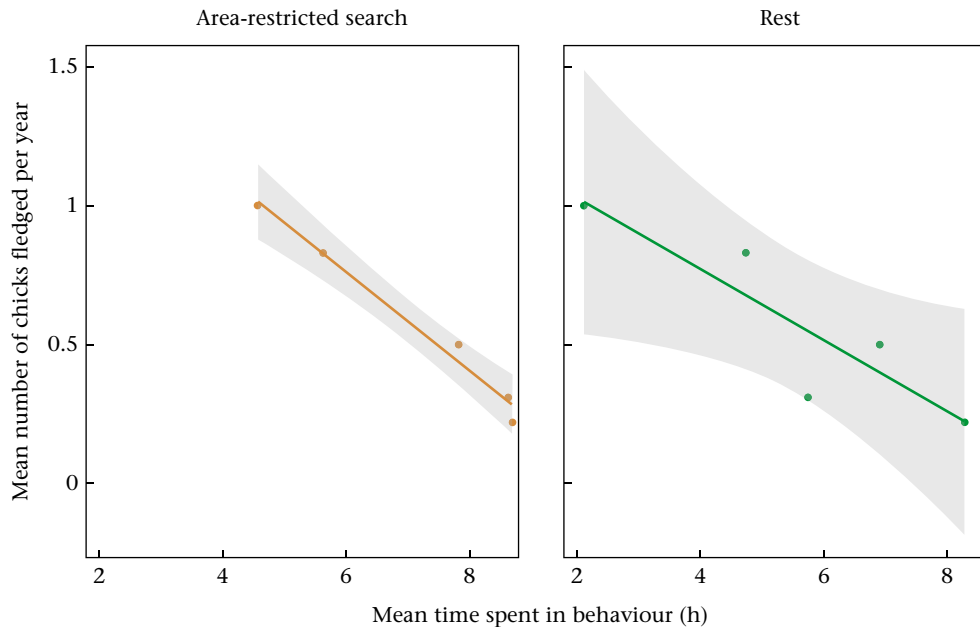
Significant *P* values are shown in bold.

duration and straightness during years with less profitable environmental conditions (Traisnel & Pichegru, 2019). Individuals that are less variable in their behaviour exploit one (or a few) known successful foraging patches and are better able to find prey for their chicks. This is supported by previous findings that foraging site fidelity increases reproductive success (Patrick & Weimerskirch,



**Figure 7.** Relationship between mean Pacific Decadal Oscillation (PDO) index during the breeding season (May–August) and mean number of chicks fledged per nest ( $N = 9$  years).





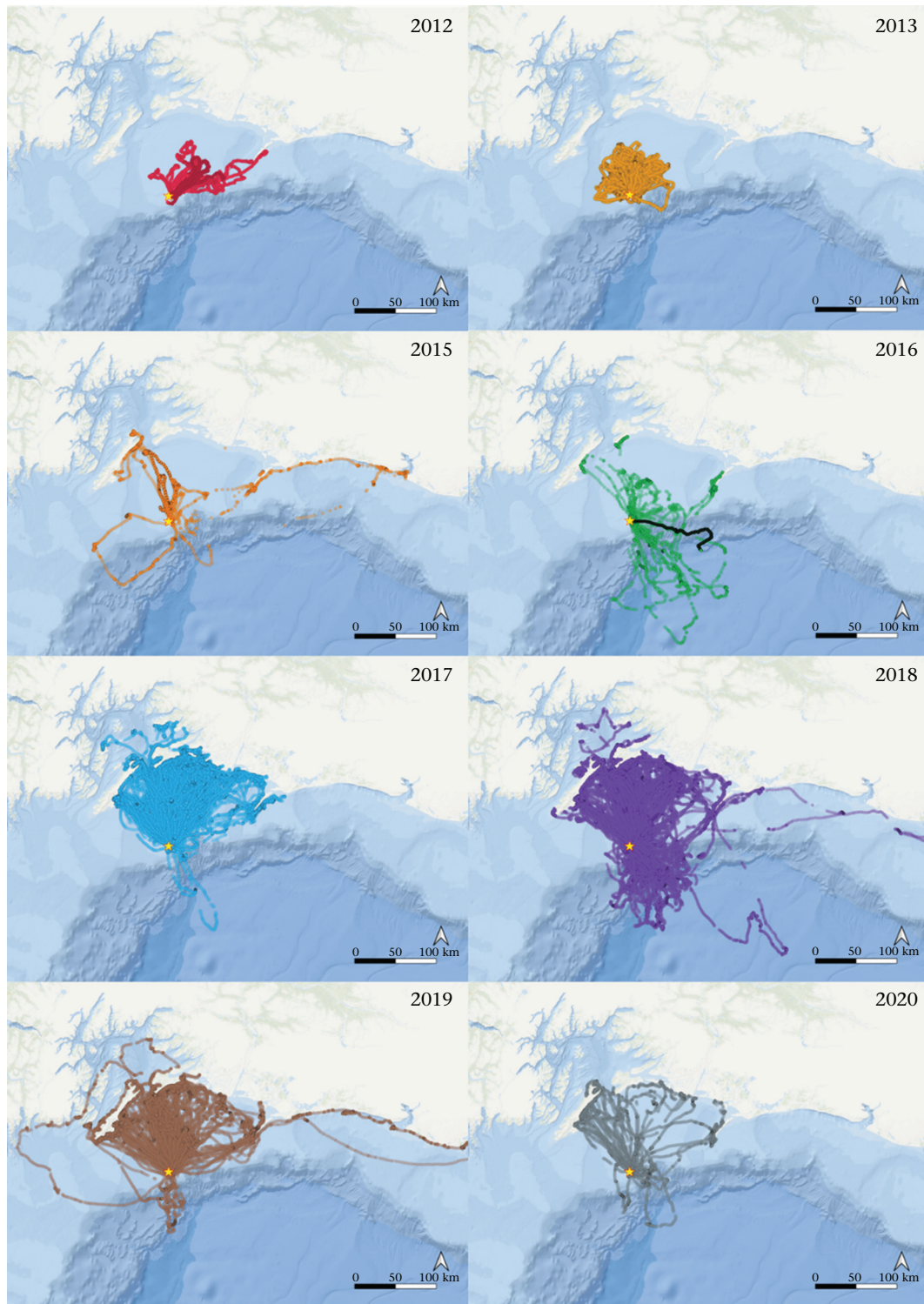
**Figure 8.** Relationship between mean number of chicks fledged and mean time spent in area-restricted search and resting on foraging trips during incubation.

2017). In another study, during positive PDO phases (associated with cooler waters in the area of study), individuals with lower site fidelity performed well, but in neutral PDO years, they performed worse than their more repeatable counterparts, which had more stable mass gain (Abrahms et al., 2018). Long-term foraging site fidelity to predictable and profitable locations (especially in marine environments) may provide an advantage over an individual's entire life span, even if some years are less profitable than others (Arthur et al., 2015; Bradshaw et al., 2004). This may be an important influence on foraging strategy for long-lived species such as seabirds. We assume that low variation in foraging behaviour in our study indicates fidelity to a foraging location; however, foraging location fidelity was not measured in this study and may not necessarily be the case for all individuals with low variability. There is also evidence that, for some species, repeatability in foraging behaviour, regardless of the location of those foraging sites, results higher foraging success (Speakman et al., 2021).

While some individuals travelled exceptionally far, there appears to be a maximum distance threshold for kittiwakes on Middleton Island. Every year, maximum distance increased with duration until around 8 h, after which the increase in maximum distance slowed. In northern gannets, *Morus bassanus*, the maximum distance/duration threshold was linear for much longer but similarly plateaued after 60 h (Hamer et al., 2000, 2007). In an Atlantic kittiwake population, travelling flight duration in kittiwakes reached an asymptote after 6.5 h and did not increase any further (Daunt et al., 2002). This threshold seems to exist in every year during and after the heatwave. There was also a threshold in 2012 and 2013, prior to the heatwave, although this threshold was much lower than years during and post-heatwave. This suggests there may be a greater benefit to foraging more intensively over a restricted area rather than expanding foraging range. Alternatively, variation in these thresholds among populations may be linked to the local oceanographic features; the breakpoint thresholds for the Middleton Island kittiwakes coincide with the distance to mainland coast. Middleton Island kittiwakes may also encounter higher competition with other kittiwake and seabird colonies if they forage beyond that point. However, we suspect that the threshold may have to do with familiarity of the area and presence of some

persistent and predictable core foraging areas (Bracis et al., 2015; Osborne et al., 2020). Indeed, it has been suggested that kittiwakes learn and can recall where and when to forage, which would contribute to a preference for local areas (Irons, 1998) and may explain why in each year we see a maximum distance plateau. Kittiwakes are not alone in this phenomenon; urban gulls have been observed to adapt their foraging to human schedules, visiting schools during lunch breaks and waste centres as they open (Spelt et al., 2021). This may also contribute to the benefits of repeatability in behaviour: once a profitable foraging location is found, it may be better to return to that area rather than expend energy to travel to locations with unknown profitability.

A large-scale climate oscillation, PDO, coincided with a decline in breeding success but had no correlation with foraging parameters. Contrary to our predictions, none of the mean foraging trip characteristics or the mean standard deviations of foraging trip characteristics were strongly influenced by PDO (Table 6). Even though PDO index was lower in 2020, foraging behaviour did not return to what it was pre-heatwave, possibly due to lagged ecosystem recovery from the 2019 heatwave (Amaya et al., 2020). Rather than foraging parameters, breeding success may be responding to changes in diet and prey quality. In little auks, *Alle alle*, sea surface temperature was not associated with changes in foraging behaviour, but it was negatively correlated with the number of prey items brought back to the nest and with fledging probability (Hovinen et al., 2014). While capelin, the main forage fish species kittiwakes relied on pre-heatwave, returned to near-mean levels in 2019, the frequency of occurrence in kittiwake diet was still far lower than what it was before the heatwave (Arimitsu et al., 2021). Another common species in kittiwake diets, Pacific sand lance, decreased in nutritional value during the years of the heatwave (von Biela et al., 2019). The slightly higher increase in time spent in area-restricted search suggests that while PDO may have been returning to pre-heatwave levels, foraging conditions and prey abundance may not return as quickly. Indeed, all trophic levels were observed to have long-term impacts for several years after the onset of the heatwave (Suryan et al., 2021). This indicates that the current Gulf of Alaska ecosystem may lack the resilience needed to endure future marine heatwaves (Frölicher et al., 2018).



**Figure 9.** All foraging trip data from 2012 to 2020, with the onset of the heatwave in 2015–2016. Each colour represents 1 year, with overlapping tracks shown in the colour scale.

Time spent during area-restricted search was highest during the first years of the heatwaves (2015 and 2019), implying that the kittiwakes needed to search more for food during those years. While this did not significantly influence breeding success when analysed at the individual level, on a population level, there was a significant relationship between mean time spent in area-restricted search on foraging trips during incubation and mean number of chicks fledged that year. While kittiwakes in this colony did

increase their foraging range during and after the heatwave (Osborne et al., 2020), our study demonstrates that the kittiwakes also increased foraging effort by spending more time in core areas rather than continuing to fly further to compensate for reduced prey availability. Breeding success was lower during years when kittiwakes spent more time resting and in area-restricted search on a foraging trip during incubation. We conjecture that, in poor years, birds spent more time searching for food and were therefore in

poorer condition, which reduced their incubation performance and ultimately their hatching success.

In this study, we found that individuals with less variable foraging behaviour during incubation and chick rearing were more likely to fledge a chick. We propose that variability in foraging behaviour may reflect differences in personality, with subsequent effects on individuals' ability to acquire resources and on individual quality (Laskowski et al., 2021). In our study system, personality was associated with reproductive success, with chicks of bolder pairs surviving longer than chicks from shy pairs (Collins et al., 2019). Other studies have found that personality influences repeatability in foraging behaviour with bolder individuals being more consistent in foraging behaviour than shy individuals (Harris et al., 2020; Krüger et al., 2019). These bolder individuals may be more willing to compete for productive foraging patches they consistently visit, leaving shy individuals to search for novel food patches to avoid competition (Krüger et al., 2019). Stress response and some measures of boldness were associated with age in kittiwakes, with younger birds being shy, middle-aged birds being bolder and older birds being shy as well (Elliott, O'Reilly, et al., 2014). If it is indeed the case that boldness is a plastic trait that varies with age, this could be one explanation for how age impacts reproductive success.

Variability in foraging behaviour was more important to reproductive success than absolute foraging behaviour. The mechanisms underlying individual variation in foraging repeatability remain unclear, but personality could be a factor. Future studies should focus on where birds less variable in their behaviour are foraging, as this might also inform how those birds have better breeding success. Marine heatwaves have increased in both frequency and duration over the past century and this trend is predicted to continue (Oliver et al., 2018, 2019). Heatwaves can have detrimental impacts on marine predators through bottom-up trophic web disruptions, evidenced by the impact of the 2014–2016 heatwave (Arimitsu et al., 2021). While we found that less variable individuals may have an advantage in years of poor environmental conditions, the extent of their resilience may be put to the test under longer-lasting climate change impacts.

## Author Contributions

**J.S., K.E. and M.G.:** Conceptualization and Methodology. **J.S., K.E., S.W. and S.H.:** Data collection and curation, **J.S.:** Formal analysis, Writing - Original draft, Visualization. **K.E., M.G., S.W. and S.H.:** Writing - Review and editing.

## Data Availability

Data are available upon request.

## Declaration of Interest

None.

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