Consequences of individual variation in foraging behaviour in black-legged kittiwakes (*Rissa tridactyla*)

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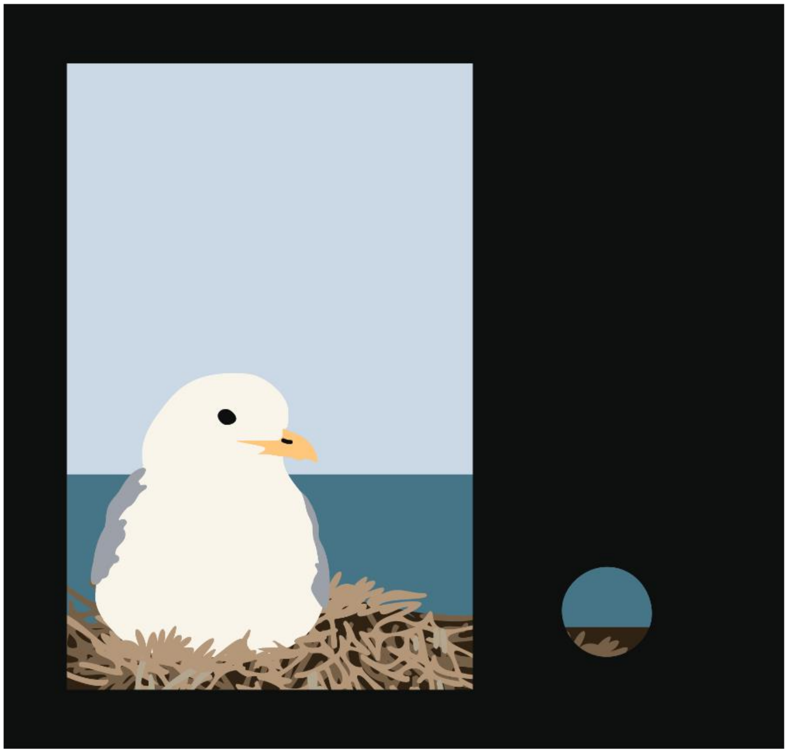

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ABSTRACT

Climate change is an imminent threat to biodiversity worldwide, but especially at high latitudes. In particular, marine heatwaves are increasing in frequency, with one of the largest on record occurring in the north Pacific in 2014-15. To understand the resilience of wildlife to climate change, we need to understand the importance and implications of foraging specialization. This is especially true for surface-feeding seabirds that do not have the capacity to modulate depth in the water column. In this thesis, I first complete a literature review examining climate change and its links to seabird foraging specialization, and then use GPS tracking to analyze the influence of specialization on productivity of a surface-foraging seabird. As central place foragers, seabirds must leave to forage and return to the nest during the breeding season. Changes in seabird productivity or population sizes may indicate changes in the marine environment. Marine heatwaves can have dramatic impacts on the marine ecosystem, with bottom-up effects on seabirds. Specialization in foraging behaviour may be beneficial as some individuals consistently return to reliable prey patches. This may become less advantageous, though, in highly variable environments. To explore this idea, I tested how individual variation in foraging trip characteristics impacted breeding success in black-legged kittiwakes (*Rissa tridactyla*) on Middleton Island, Alaska before, during, and after an intense marine heatwave. Foraging trip characteristics were highly variable between individuals and years. Though none of the foraging trip characteristics alone influenced reproductive success, age and consistency in behaviour between foraging trips did. Individuals with smaller variance between two foraging trips during incubation were more likely to fledge a chick than those with a larger variance. Additionally, there was evidence of a maximum distance threshold, suggesting that, rather than increasing foraging range in response to potentially challenging foraging conditions, kittiwakes

were increasing time spent foraging in a specific area. While Pacific Decadal Oscillation (a long-term pattern of oceanic climate variability in the Pacific) clearly impacted reproductive success, it did not influence individual foraging behaviour. In summary, individual consistency in foraging behaviour, even during poor conditions, positively influenced reproductive success. Our results suggest that individuals that are more consistent in foraging behaviour may be better able to cope as climate change progresses but these benefits may wane as events such as marine heatwaves continue to occur unpredictably.

RESUMÉ

Les changements climatiques sont une menace importante pour la biodiversité dans le monde entier, mais surtout aux hautes latitudes. En particulier, les vagues de chaleur océanique sont de plus en plus fréquentes, l'une des plus importantes jamais enregistrées ayant eu lieu dans le Pacifique Nord en 2014-15. Pour comprendre la résilience de la faune aux changements climatiques, nous devons comprendre l'importance et les implications de la spécialisation du comportement d'alimentation. Ceci est particulièrement vrai pour les oiseaux marins se nourrissant en surface qui n'ont pas la capacité de moduler leur profondeur dans la colonne d'eau. Dans cette thèse, j'effectue d'abord une revue de la littérature sur les changements climatiques et ses liens avec la spécialisation du comportement d'alimentation des oiseaux marins, puis j'utilise des données de suivi GPS pour analyser l'influence de la spécialisation sur la productivité d'un oiseau marin se nourrissant en surface. En tant qu'espèces dont le comportement d'alimentation se fait à partir d'un point central, les oiseaux marins doivent partir à la recherche de nourriture et revenir au nid pendant la saison de reproduction. Les changements dans la productivité ou la taille des populations d'oiseaux marins peuvent indiquer des changements dans l'environnement marin. Les vagues de chaleur océaniques peuvent avoir des impacts dramatiques sur l'écosystème marin, avec des effets ascendants sur les oiseaux marins. La spécialisation dans le comportement d'alimentation peut être bénéfique, car certains individus reviennent constamment vers des sites de proies fiables. Cependant, cette spécialisation peut devenir moins avantageuse dans des environnements très variables. Pour explorer cette idée, j'ai testé l'impact de la variation individuelle des caractéristiques des voyages d'alimentation sur le succès reproducteur des Mouettes tridactyles (Rissa tridactyla) sur l'île de Middleton, en Alaska, avant, pendant et après une vague de chaleur océanique intense. Les caractéristiques des voyages

d’alimentation étaient très variables entre les individus et les années. Bien qu’aucune des caractéristiques des voyages d’alimentation n’ait influencé à elle seule le succès reproducteur, l’âge et la constance dans le comportement entre les voyages d’alimentation l’ont fait. Les individus avec une plus petite variance entre deux voyages d’alimentation étaient plus susceptibles de donner naissance à un poussin que ceux avec une plus grande variance. De plus, il y avait des preuves d’un seuil de distance maximale, ce qui suggère que, plutôt que d’augmenter la distance de recherche de nourriture en réponse à des conditions de recherche potentiellement difficiles, les mouettes augmentaient le temps passé à chercher de la nourriture dans une zone spécifique. Alors que l’oscillation décennale du Pacifique (un modèle à long terme de variabilité du climat océanique dans le Pacifique) a clairement eu un impact sur le succès reproducteur, elle n’a pas influencé le comportement individuel de recherche de nourriture. En résumé, la constance individuelle dans le comportement de recherche de nourriture, même dans de mauvaises conditions, a influencé positivement le succès reproducteur. Nos résultats suggèrent que les individus qui ont un comportement plus constant en matière de quête alimentaire peuvent être mieux équipé à faire face à la progression des changements climatiques, mais ces avantages peuvent s’estomper si des événements tels que les vagues de chaleur océanique continuent à se produire de manière imprévisible.

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GENERAL INTRODUCTION

The United Nations proclaimed 2021-2030 as a Decade of Ocean Science for Sustainable Development in an effort to stop and reverse the ongoing damage to ocean health. Humans are having an impact on the ocean through overfishing (Bearzi et al. 2006; Daskalov et al. 2007), pollution (Eriksen et al. 2014), and climate change (Bates et al. 2012). This campaign aims to generate knowledge needed to face these challenges, inform policy to restore ocean health and support sustainable development goals. Two of the desired outcomes of this campaign are a healthy, resilient ocean and a predictable ocean in which we can understand and respond to changes. One of the challenges listed is to understand the impacts of current stressors on ocean ecosystems, and to develop ways to protect and restore ecosystems and biodiversity. Understanding how individual differences in behaviour impact reproductive success, especially during a period of environmental change, is one way to contribute to the knowledge of how to maintain a resilient ocean and maintain biodiversity.

Distributed across the globe in a variety of marine habitats, seabirds can be excellent indicators of ocean health. Studying seabird foraging behaviour can be one tool for understanding ocean resilience and biodiversity; in my literature review I will discuss a few reasons this is possible. There are many factors that can influence foraging behaviour. Time of year is particularly important, as some species during the breeding season become tied to a central location, such as a nest or colony, which can restrict those foraging movements. Age (Votier et al. 2017), sex (Patrick and Weimerskirch 2014b), and personality (Harris et al. 2020) can all influence individual foraging behaviour as well. Because seabirds are frequently top marine predators, changes in seabird diet (Cunningham et al. 2018) and reproductive success (Arimitsu et al. 2021) can be signals of changes in the lower trophic system. Technological advances in GPS tracking now allows researchers to use seabirds to understand forage fish distributions (Charrassin et al. 2002), and how that changes within and between seasons. This information is becoming increasingly valuable as events such as marine heatwaves increase in frequency with climate change (Oliver et al. 2019a), which can have negative impacts on fish stocks critical to the humans and marine life which rely on them (Cheung and Frölicher 2020). Black-legged kittiwakes (*Rissa tridactyla*) are a small gull species which frequently live in large colonies and primarily feed on forage fish, making them excellent indicator species as changes in diet, reproductive success, or survivorship could indicate changes in the marine environment. Middleton Island has one of the longest histories of seabird monitoring in Alaska (Rausch 1958), and also hosts a large colony of breeding black-legged kittiwakes. The colony of kittiwakes on Middleton has experienced large changes in population size over the past few decades, which is due in part to changes in prey (Hatch 2013) warranting further investigation.

The goal of this thesis is to explore individual differences in foraging behaviour in black-legged kittiwakes using biologging and to explore how these differences impact reproductive success in a changing environment. There have already been studies on the foraging behaviour of black-legged kittiwakes and their reproductive success at the population level, there has yet to be a study that connects the two at the individual level. For my study, I used eight years of GPS data from black-legged kittiwakes on Middleton Island, Alaska. These years of tracking data span pre, during, and post-marine heatwave in the Gulf of Alaska. Using these data, I tested the impact of individual variation in foraging trip characteristics (total trip distance, duration, maximum distance, and number of foraging patches) on reproductive success. I also looked at other factors including age and consistency in foraging behaviour and how those played a role in reproductive success as well.

For central place foragers, when food becomes scarce, species (and perhaps individuals within a species) must either expand their foraging range or spend more time foraging in one area. Understanding the consequences of these changes in foraging behaviour is important as climate change continues to force species to make these changes. Long term ecological research stations, such as the one on Middleton Island are critical to begin answering some of these questions. This thesis aims to begin to fill the knowledge gap of how individual differences influence reproductive success.

LITERATURE REVIEW

In the first section of this literature review I will discuss seabird foraging ecology. Seabirds are central place foragers, which is an important constraint in their behaviour. I then explain some of the factors influencing foraging behaviour including sex, age, and personality. Next, I summarize how seabird foraging, diet, and reproductive success can be used as bioindicators of the health of the greater marine environment. This is particularly important, as climate change and events such as marine heatwaves disrupt food webs. I will describe both regime shifts and marine heatwaves, their differences, and how they both have negative impacts on all trophic levels, including seabirds. Black-legged kittiwakes are one species of seabird which have been impacted by marine heatwaves and changes in prey availability. I will discuss black-legged kittiwake life history, and some of the challenges the species is currently facing. Middleton Island, located in the Gulf of Alaska, hosts a large colony of black-legged kittiwakes which has experienced a great change in population size over the past few decades. The unique research station on Middleton has provided researchers with a greater ability to closely monitor individual birds over many years, allowing us to answer questions that would be difficult in other breeding sites, including how individual consistency in foraging behaviour impacts reproductive success.

Foraging ecology

Foraging is a critical aspect of ecology as it is essential for survival and the ability to reproduce. Seabirds are central place foragers, meaning during the breeding season they need to return to a specific location (the nest) to feed their chicks. This puts additional pressure on foraging, as the birds are constrained in how far they go or how long they forage because they must return to the nest. Increased time spent foraging during chick rearing can negatively impact reproductive success (Boersma and Rebstock 2009). One of the reasons for this is that it can make the nest vulnerable to predators (Hunt Jr. 1972). This can be mediated by both adults taking turns attending the nest (Roberts and Hatch 1993), but this may be more difficult to balance during years of environmental stress when foraging efforts have to increase, and in many cases both parents must leave the offspring unattended at the nest to meet their growing nutritional needs.

Meeting the nutritional needs of seabird offspring requires biparental care, which means that each sex may have different foraging behaviour. One of the causes of this may be sexual dimorphism. While for most seabird species the differences between male and females are only slight, for species where there are notable size differences this may influence foraging behaviour (Lewis et al. 2005). Sex can also influence consistency in foraging behaviour, in one species of seabird females were consistent in their foraging behaviour, where males switched from foraging at sea to foraging in rice field habitats during the weekends when fishery discards were not available (García-Tarrasón et al. 2015). Indeed sexual niche segregation and specialization may be beneficial for reproductive success (Patrick and Weimerskirch 2014b).

Age can also influence foraging behaviour. Older breeding birds can have higher foraging site fidelity and are more consistent in the routes they take than younger birds (Votier et al. 2017). This could be the result of learning over time (Riotte-Lambert and Weimerskirch 2013; Wakefield et al. 2015) as memory has been identified to be an important factor for some seabirds (Irons 1998). Another study looking at two albatross species found that foraging capabilities improved with age until around 26, after which there was evidence for senescence with older birds taking longer foraging trips (Frankish, Manica, and Phillips 2020).

Although some of the variation in foraging behaviour is associated with sex and age, there is also considerable variation that is not explained by either parameter. Although many seabirds are considered generalists, there is growing evidence for individual specializations which may help to further reduce niche overlap and competition and could benefit reproductive success (Woo et al. 2008; Ceia and Ramos 2015). Individual specializations can be prey-based, with some individuals within a typically generalist species specializing on only one or a few prey types (Masello et al. 2013). Some of these specializations are place-based, with some individuals being highly consistent in their foraging locations both within and between years (Wakefield et al. 2015). One study found that while some individuals were more specialized in habitat selection than location, it was site fidelity that influenced reproductive success regardless of age (Patrick and Weimerskirch 2017). In a diving bird, there has been evidence of individual consistency in dive depths in a colony where all birds that were tracked were found to forage in the same vicinity (Kotzerka, Hatch, and Garthe 2011) which may be another way to reduce competition.

One possible cause for these differences in consistency in behaviour is personality. Personality can be defined as consistent individual differences in behaviour over time and in different contexts. Boldness, one type of personality trait, has been found to be both repeatable (Collins et al. 2019) and heritable in seabirds (Patrick, Charmantier, and Weimerskirch 2013)**.** Seabird foraging behaviour has been linked to differences in boldness with bolder individuals foraging closer to the nest and being more consistent in foraging locations than shyer individuals (Patrick and Weimerskirch 2014; Harris et al. 2020). Though the reason for this correlation is still unknown, one theory is that bold individuals may be more willing to compete for closer optimal foraging locations than shyer individuals (Krüger et al. 2019). Furthermore, sex and personality were found to influence reproductive success depending on environmental conditions (Patrick and Weimerskirch 2014b).

Seabirds as bioindicators

A bioindicator is an organism whose life history traits (such as density, survivorship, reproductive success etc.) can be studied and used as a proxy for the health of the ecosystem they inhabit. Bioindicators may provide early warning signals of changes in the environment, and in some cases, even identify the cause. Seabirds have been identified as being excellent bioindicators, as they are spread throughout the globe, many are conspicuous which makes for easier observational studies, and they are typically at or near the apex of the marine food web. They require different types of habitats for breeding (land) and foraging (ocean). Changes in survivorship or reproductive success for seabirds may indicate changes in their breeding or foraging habitats.

Seabirds have been used to track forage fish populations for decades (Cairns 1988; Hatch and Sanger 1992; Velarde and Vieyra 1994; Piatt et al. 2007; Brisson-Curadeau et al. 2017; Sydeman et al. 2022). During the breeding season, adult seabirds leave to forage and return to the nest to provision food for their chicks. When the adults return to land, they provide researchers with opportunities to study diet based on what the birds are bringing back for their chicks, and can provide insight into the forage fish available in the area. One study used GPS loggers and diet sampling to test the use of rhinoceros auklet (*Cerorhinca monocerata*) chick diet as a method to understand forage fish populations in the Gulf of Alaska and found that the auklets were returning to the nest with sand lance in areas where trawlers had previously not found any (Cunningham et al. 2018). This suggests that auklets may be able to provide more fine-scale resolution of abundance and distribution than previous methods. Another study found correlations between pollock cohort strength and the proportion of pollock in puffin diets, suggesting that puffins may also serve as bioindicators of the distribution and abundance of an important commercial fishery species and can provide important information for fishery management (Hatch and Sanger 1992; Sydeman et al. 2022). In addition to studying diet to gain information on forage fish abundance, other studies have found that reproductive success (Hatch 2013; Arimitsu et al. 2021), chick growth rates (Suryan et al. 2002), stress hormone levels (Kitaysky et al. 2006), and survivorship (Paredes et al. 2014) can all be indicators of food stress and poor foraging conditions.

Traditional methods of sampling oceanographic conditions can be cost prohibitive and difficult to replicate. New technological advances have opened up the opportunity to gain oceanographic information from seabird diets and movement. Stable isotope analysis has created opportunities to use seabirds as indicators of toxins in lower trophic levels (Elliott and Elliott 2013). GPS devices can provide information on locations birds are foraging, which may give insight into their patchy prey distribution (Schneider and Piatt 1986). Temperature and depth loggers attached to seabirds provide information on differences in temperature at associated depths along the water column (Daunt et al. 2003). Diving seabirds are particularly useful for these types of studies, as they can frequently dive over 100 meters (Croll et al. 1992), penguins can even dive over 450 meters (Kooyman and Kooyman 1995). This has answered questions about why some areas are more productive than others using data gained from seabird foraging effort (Charrassin et al. 2002). Another study used tracking data to find that seabirds began breeding during a time of low prey availability, but prey availability increased over the breeding season, peaking during the time of chick fledging, suggesting that seabirds may be able to adjust breeding times so that optimal oceanographic and prey conditions occur when it is most important (Passuni et al. 2016). Using seabirds as tools to understand foraging behaviour and oceanographic conditions is critical, as changes in the marine environment can negatively influence forage fish abundance, resulting in breeding failure for seabirds (Frederiksen, Mavor, and Wanless 2007; Arimitsu et al. 2021).

Regime shifts and marine heatwaves

Regime shifts are dramatic shifts from cool to warm conditions (or the reverse) and are thought to be driven by changes in prey, coastal development, and climate change (Parsons and Lear 2001; Beaugrand et al. 2002; Rocha et al. 2015). These regime shifts are often characterized by sudden changes from one regime to the other, are low-frequency events occurring on large spatial scales, and impact multiple trophic levels (Lees et al. 2006). Regime shifts have been noted across the globe, and have impacted numerous seabird populations (Cury and Shannon 2004; Durant et al. 2004; Flint 2013; Passuni et al. 2018). Though some species may benefit from increases in temperature from climate change, there are more which are experiencing negative impacts from these changes (Descamps et al. 2017).

Lower sea surface temperature during the breeding season is associated with higher breeding success, especially for non-diving seabirds such as kittiwakes (Carroll et al. 2015). Some species even opt to skip breeding altogether in years of higher sea surface temperature

(Cubaynes et al. 2011). Increases in sea surface temperature have also been found to cause a decrease in foraging success and chick growth both within and among seasons (Peck et al. 2004). This means that not only does prey availability change annually, but there may be daily fluctuations as well. Though one study suggests that pursuit-diving birds and pinnipeds may be restricted in range due to water temperature not because of lack of prey in warm water, but rather ectothermic prey may be able to take advantage of higher temperatures making it more difficult for seabirds and pinnipeds to capture (Cairns, Gaston, and Huettmann 2008). The rate of warming may actually be more important than the warming itself, with sharper increases in temperature coinciding with sharper declines in seabird populations (Descamps et al. 2017).

Marine heatwaves differ from (but may be influenced by) climate change and regime shifts, and are defined as "discrete prolonged anomalously warm water events in a particular location" (Hobday et al. 2018a). A study on the marine heatwave frequency from 1925 to 2016 discovered that both frequency and duration of marine heatwaves has increased over time, with the number of marine heatwave days increasing 54% globally (Oliver et al. 2018). One model analyzing the future of marine heatwaves predicts a continued upward trend through the 21st century due to anthropogenic impacts (Oliver et al. 2019a).

Marine heatwaves have profound impacts on the marine ecosystem, which we are only beginning to understand. Intense marine heatwaves can exacerbate issues caused by climate change such as coral bleaching, causing mass bleaching events even in heat-tolerant corals (Le Nohaïc et al. 2017; Klein et al. 2022). Marine heatwaves can also cause shifts in distributions of fish stocks and decrease biomass faster and more dramatically than typical in regime shifts (Cheung and Frölicher 2020). First detected in 2013, one of the largest and most persistent marine heatwaves occurred in the North Pacific and lasted through 2016. During the heatwave there were widespread breeding failures for multiple species of seabirds as well as a mass mortality event of common murres (Piatt et al. 2020). While the cause of death for most of these birds was determined to be starvation likely due to lack of prey availability (Jones et al. 2018; Piatt et al. 2020), other factors may also be in play. Along with marine heatwaves, over the past few decades frequency and intensity of harmful algal blooms have also increased (Gobler et al. 2017). The heatwave in the North Pacific created conditions favorable for the growth of *Alexandrium catenella* which produces the neurotoxin called saxitoxin (Vandersea et al. 2018). In specimens tested, saxitoxin was detected in both individuals that died, and healthy individuals, with the highest concentrations detected in the liver of murres that died during the event (Van Hemert et al. 2020) suggesting that this neurotoxin may have exacerbated already challenging foraging conditions. Since the 2014 die-off, there have been other die-offs of various sizes and impacting different species almost every year in Alaska. Testing of carcasses found once again that saxitoxin was present in 60% of all individuals tested (Van Hemert et al. 2020), and while starvation still appears to be the main cause of death, further studies need to be done to explore how the neurotoxin is impacting the birds antemortem. In addition to the breeding failures and mass mortality events, higher levels of a hormone associated with nutritional stress were found in one species of zooplanktivorous seabird, whereas a more generalist seabird was found to have relatively stable hormone levels suggesting that generalists may be slightly buffered from these warming events (Tate et al. 2021).

Black-legged kittiwake life history

Black-legged kittiwakes (hereafter referred to as “kittiwakes”) are a small, pelagic gull in the Laridae family that live in the arctic and subarctic regions of the Atlantic and Pacific. Kittiwakes primarily nest on coastal cliffs but will also opportunistically use human-made structures (Gill and Hatch 2002) in colonies of a few individuals to thousands. The global population is estimated to be around 14,600,000 -15,700,000 (Wetlands International 2016).

Kittiwakes have an average life span of 13 years but can live into their early 20’s (Hatch, Roberts, and Fadely 1993). Kittiwakes also have high mate retention and high nest site fidelity (Fairweather and Coulson 1995), making them excellent candidates for long-term studies as the same individuals will return to the same colony year after year. While many bird species are socially monogamous there are few that are sexually monogamous, often resulting in extra-pair offspring (Griffith, Owens, and Thuman 2002). Even though they often breed in large colonies where extra-pair copulation opportunities would be easily accessible, the black-legged kittiwake is one of few species that is sexually monogamous with very rare extra-pair copulation attempts (Helfenstein et al. 2004). It is suggested that this certainty in paternity may influence a more equal effort of male and females in raising chicks (Xia 1992; Coulson and Johnson 1993). This equal effort by both parents makes kittiwakes even better candidate species to study behaviour as sex should be less likely to be the cause of individual differences.

Black-legged kittiwakes will typically lay one to two eggs, with three egg clutches only occasionally being recorded (Maunder and Threlfall 1972). In nests with two chicks, facultative siblicide often occurs with the first chick to hatch generally having faster growth rates and being more aggressive towards the second chick to hatch (Braun and Hunt 1983). This appears to be influenced by environmental conditions with higher rates of aggression occurring during years where food availability is lower (White et al. 2010). Productivity may vary based on population, with Pacific populations having generally lower productivity but higher survivorship compared to those in the Atlantic (Hatch, Roberts, and Fadely 1993).

The diet of black-legged kittiwakes primarily consists of forage fish such as capelin, herring, and sand lance, but they will also eat small crustaceans such as euphausiids (Barrett 2007). Contrary to other closely related gull species, kittiwakes do not often utilize fishery discards (Camphuysen et al. 1995; Harris and Wanless 1997). While they do occasionally forage solitarily, kittiwakes frequently forage in flocks. Those foraging in flocks have been found to have a higher chance of success than those foraging individually (Bayer 1983). Kittiwakes are surface feeders and plunge divers (Drury 1978, Bayer 1983) meaning they typically feed on fish at the surface of the water and can only dive around a meter into the water making them especially sensitive to changes in the distribution of prey in the water column (Furness and Tasker 2000).

Though it is one of the most abundant gulls, kittiwakes were recently listed as a vulnerable species. In 2017 the International Union for Conservation of Nature (IUCN) changed the designation for black-legged kittiwakes from least-concern to vulnerable, citing global population declines (IUCN 2018). Some of the challenges kittiwakes are facing include competition with fisheries (Frederiksen et al. 2004), pollution (including oil spills) (Goyert et al. 2017), and climate change (Carroll et al. 2015). The largest factor contributing to the decline appears to be food availability. Adult kittiwakes nesting in a colony in a food-poor area were found to have a greater decrease in body condition over the breeding season compared to adults in colonies in food-rich areas (Kitaysky, Wingfield, and Piatt 1999). Declines in food supply have also been found to be linked to both increases in the stress hormone corticosterone, and in turn declines in productivity (Kitaysky, Piatt, and Wingfield 2007; Buck, O'Reilly, and Kildaw 2007). In the North Sea, where black-legged kittiwake populations have declined over 50% since the 1990's, warmer winters and the presence of a sandeel fishery were found to negatively impact breeding success and adult survival (Frederiksen et al. 2004). While fisheries may have some impact on food availability, there is more evidence for environmental changes being the cause. In both the southeastern Bering Sea and Gulf of Alaska, increases in sea surface temperature were associated with a decrease in the presence of capelin and other fatty fish in black-legged kittiwake diets as well as a decrease in reproductive success (Hunt, Decker, and Kitaysky 1996; Arimitsu et al. 2021). When there was a switch from warm to cool conditions, capelin increased in availability and kittiwakes responded with a notable increase in number of chicks fledged per nest (Hatch 2013). Having a lipid-rich diet is important, as diets low in lipids cause slower growth, increases in stress hormones, and impacts learning capabilities of chicks (Kitaysky et al. 2006). To deal with changes in prey availability, kittiwakes respond by increasing foraging effort, which may lead to increases in adult mortality (Paredes et al. 2014). Part of this increase in foraging effort may be from changing prey selection, resulting in longer foraging trips, and in turn slower chick growth and reduced chick survival (Suryan et al. 2002).

Middleton Island as an opportunity to study kittiwakes

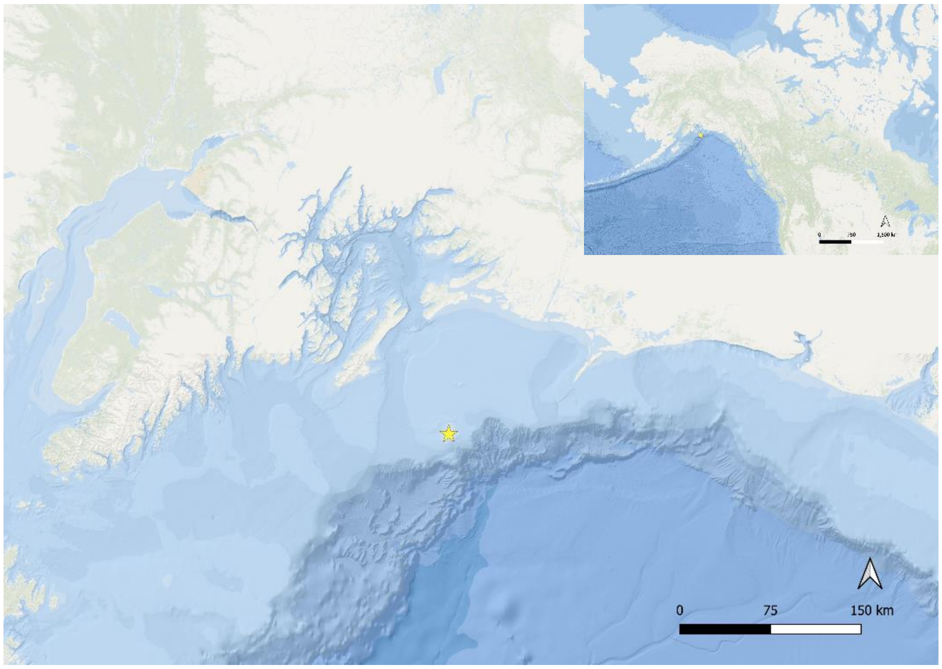

Figure 1. Middleton Island (starred) is located in the Gulf of Alaska.

Middleton is an approximately 2200-acre island located 120km south of Cordova, Alaska in the Gulf of Alaska and has a unique history (Figure 1). An Air Force base was constructed in 1958 during the Cold War and was decommissioned in 1963. In 1964 a large earthquake raised the island 3.7m. It has one of the longest histories of seabird monitoring in Alaska. The first bird survey was conducted in 1956 (Rausch 1958) and more frequent surveys led by USFWS began after 1974. Since 1981 kittiwakes have been studied every year on Middleton (Gill and Hatch 2002). In 1986 the first pair of black-legged kittiwakes were discovered nesting on the abandoned radar towers, increasing to 1200 pairs in 1997 (Gill and Hatch 2002). By 1994 enough kittiwakes were nesting on the tower that researchers decided to repurpose the radar tower to more closely study the birds nesting on it by installing more platforms for the birds to nest on and installing one-way windows in front of each nest (Figure 2). Since then, the tower has been used every year to monitor the population and explore questions that would otherwise be difficult to answer given black-legged kittiwakes usual cliff-nesting locations.

Figure 2. A radar tower on Middleton Island has been repurposed with one-way glass to study nesting black-legged kittiwakes and pelagic cormorants.

Since the 1970s many kittiwake colonies in Alaska (including Middleton) experienced chronic breeding failure, with almost half of the colonies studied failing entirely (Hatch et. al. 1993). A previous study on Middleton had discovered signs of food stress during this time of breeding failure (Roberts and Hatch 1993). In most cases, there are a number of confounding factors that could lead to breeding failure and it would be difficult to point to prey availability alone as the cause of reduced productivity. However, the unique design of the tower on

Middleton provided an opportunity to try to answer this question. Beginning in 1996, a subset of the kittiwake pairs nesting on the tower were supplementally fed during the breeding season to determine if food availability was what was limiting reproductive success (Gill and Hatch 2002). The results of this study found that supplementally fed pairs fledged twice to three times as many chicks per nest compared to unfed birds (Gill and Hatch 2002) showing that food availability was indeed negatively impacting reproductive success of kittiwakes on Middleton. This supplemental feeding experiment has continued every year since, and is now one of the longest ongoing studies on Middleton as a way to monitor annual forage fish conditions as when forage fish conditions are good, there is less of an impact of supplemental feeding on reproductive success than in years where forage conditions are poor (Lanctot et al. 2003). Other studies have built on this ongoing experiment. One of those studies found that supplementally fed adults reduced their daily energy expenditure, suggesting that in addition to reproductive success food availability may influence parental effort (Jodice et al. 2011). Another found that supplementally fed birds had decreased stress hormones, helping to validate the connection between food availability and nutritional stress (Kitaysky et al. 2010).

Changes in prey abundance in the diet of kittiwakes on Middleton in the early 2000s and 2008-2011 suggested that there may have been a potential regime shift from the warm conditions that began in 1977, influencing the population declines, to cooler conditions (Hatch 2013). This was predicted to indicate a shift to favorable conditions for kittiwakes for the following 20-30 years (Hatch 2013), but then the major marine heatwave occurred in the North Pacific which lasted through 2016 (Hobday et al. 2018b). This had dramatic impacts on the whole Gulf of Alaska including changes in prey availability and reproductive success for kittiwakes on

Middleton, which persisted even after the end of the heatwave (Arimitsu et al. 2021; Suryan et al. 2021).

The miniaturization of biologgers, permitting examination of foraging behaviour directly, created an additional component to understand the impact of food shortages on kittiwakes at Middleton. Indeed, the tower on Middleton lends itself well to conducting studies on foraging behaviour. Advances in GPS technology have allowed devices to now be small enough for most birds, which provides an opportunity to gain even greater insight on foraging behaviour (López-López 2016). However, many devices still require two captures, one to deploy and another to retrieve the unit. Capturing birds can be very challenging. With their usual cliff-nesting proclivities, capturing kittiwakes once let alone twice can be difficult. The one-way glass in the tower allows researchers to get close enough to the birds to be able to easily identify each bird (based on colour bands) and capture them more easily than if they were on a cliff. The first GPS deployments to occur on kittiwakes occurred on Middleton in 2007, and found that foraging behaviour was highly variable between individuals (Kotzerka, Garthe, and Hatch 2010). Since then, other studies have incorporated the use of accelerometers to answer questions on physiology, the impact of wind on foraging, and how heatwaves impact foraging behaviour (Table 1).

Table 1. A summary of published studies using GPS on black-legged kittiwakes on Middleton Island

Title	Year	Reference
GPS tracking devices reveal foraging strategies of black-legged kittiwakes	2010	Kotzerka, Garthe, and Hatch 2010
Windscapes shape seabird instantaneous energy costs but adult behavior buffers impact on offspring	2014	Elliott et al. 2014
Accelerometry reveals an impact of short-term tagging on seabird activity budgets	2016	Chivers, Hatch, and Elliott 2016
A comparison of techniques for classifying behavior from accelerometers for two species of seabird	2019	Patterson et al. 2019
Coping with the commute: behavioural responses to wind conditions in a foraging seabird	2020	Collins et al. 2020
Breeding seabirds increase foraging range in response to an extreme marine heatwave	2020	Osborne et al. 2020
Accelerometry predictions muscle ultrastructure and flight capabilities in a wild bird	2020	Lalla et al. 2020
Increased summer food supply decreases non-breeding movement in black-legged kittiwakes	2020	Whelan et al. 2020
The effects of food supply on reproductive hormones and timing of reproduction in an income-breeding seabird	2021	Whelan et al. 2021
Resting costs too: the relative importance of active and resting energy expenditure in a sub-arctic seabird	2022	Tremblay et al. 2022

In contrast to the highly variable nature of foraging in kittiwakes (Kotzerka et al. 2007), other studies on Middleton have found that both nesting rhinoceros auklets and pelagic cormorants (*Phalacrocorax pelagicus*) exhibited individualized foraging site fidelity (Kotzerka, Hatch, and Garthe 2011; Cunningham et al. 2018). However, most of the studies conducted thus far on kittiwakes have looked at the behaviour of all birds, rather than focusing on the behaviour of individuals. My thesis will be building on the findings from the first study on kittiwakes

(Kotzerka, Garthe, and Hatch 2010) and the results of the analysis on foraging behaviour during the marine heatwave (Osborne et al. 2020) to look at how individual variation in foraging behaviour impacts reproductive success using GPS data collected before, during, and after the 2013-2016 marine heatwave.

Chapter 1: Winners stay and losers shift: repeatability in foraging behaviour predicts reproductive success

Note on this chapter

This chapter corresponds to a manuscript in which I am first author to be submitted to the journal of Animal Behaviour. This manuscript has been written in collaboration with Kyle Elliott, Mélanie Guigueno, and Shannon Whelan from McGill University and Scott Hatch from the Institute for Seabird Research and Conservation.

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ABSTRACT

Consistent 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, such consistency in foraging behaviour may be less 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, 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 consistency in those trip characteristics explained variation in breeding success. Individuals with smaller variance in foraging trip characteristics among trips, and thus higher consistency in foraging behaviour during incubation, 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, as mean time spent resting (in incubation) and flying (in chick rearing) increased during a foraging trip, breeding success decreased. Based on nearly a decade of data, we conclude that consistency in behaviour, even during challenging foraging conditions, enhances breeding success. As climate change and marine heatwaves continue to increase in intensity, individuals less consistent in foraging behaviour may be unable to compensate.

Keywords:

Biologging, GPS tracking, Individual variation, Movement behaviour, Predictability, Seabirds

INTRODUCTION

Individuals, populations, and species vary in their movement patterns due to both extrinsic and intrinsic factors (Hayes and Jenkins 1997; Zimmer et al. 2011; Hertel et al. 2020; Shaw 2020). For example, climate can alter the distribution or amount of prey throughout the environment (Ropert-Coudert et al. 2009; Damien and Tougeron 2019; Osborne et al. 2020; Suryan et al. 2021). Alternatively, intrinsic factors, such as age and reproductive status, can lead to variation in movement patterns and distribution (Le Vaillant et al. 2012; Wakefield et al. 2015; Graf et al. 2016; Cunningham et al. 2017; Votier et al. 2017). However, an intriguing portion of variation in movement behaviour is inherent to the individual, resulting in consistent individual differences in movement that persist across time and context (Irons 1998; Woo et al. 2008; Jakubas et al. 2018; Hertel et al. 2020; 2021).

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 (Ritchie 1990; Patrick and Weimerskirch 2014a; 2014b; Haave-Audet et al. 2022). Several types of individual foraging specialization or consistency have been shown in foraging movement, such as dietary specialization, spatial fidelity and repeatability of dive depth (Tinker et al. 2007; Woo et al. 2008; Masello et al. 2013; Patrick et al. 2014; Harris et al. 2020; DeSantis et al. 2022), making consistency in foraging a trait with potentially strong links to individual variation in fitness. For example, within-year foraging site fidelity was associated with higher reproductive success in albatrosses, possibly because those individuals that mastered a single tactic were more proficient foragers than those that switched tactics (Patrick and 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, consistency in foraging behaviour may only be present, or consequential, during years with low food availability (Trevail et al. 2021; Laskowski et al. 2021). For example, adult penguins with more consistent foraging behaviour had higher growth rates during a year of poor environmental conditions when prey availability was low (Traisnel and Pichegru 2019).

In marine environments, food resources often follow a heterogeneous or “patchy” distribution (Davoren et al. 2003; Bertrand et al. 2021a; 2021b). 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 (Osborne et al. 2020; Fromant et al. 2021). Thus, some degree of behavioural flexibility is likely necessary to cope with extreme events. However, it is unclear whether consistency 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 if 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 one meter (Maunder and Threlfall 1972; Hatch et al. 1993). 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); breeding output tends to increase during cool climate phases but decline in warm phases (Hatch 2013). The current study ran from 2012-2020, 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 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 the 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).

As the core areas of the population’s foraging range overlapped before, during, and after the heatwave (Osborne et al. 2020), we hypothesized that individuals with higher foraging consistency would have higher breeding success because the core areas represented predictable food patches. We also hypothesized that changes in foraging behaviour at the individual and population level would be linked to breeding success. Specifically, we predicted that individuals foraging closer to the colony and for shorter durations would have higher breeding success. 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. We also predicted that annual population-wide foraging range and duration would closely track sea surface temperature as a proxy for fish availability, and that 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 (IUCN 2022), 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 until 2020 on Middleton Island, in the Gulf of Alaska (59.48ºN, 146.38ºW; Figure 3). On the island, black-legged kittiwakes nest on an abandoned US Airforce radar tower behind one-way mirrored glass (Gill and 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 five years to the year banded, which is the average age first captured as an adult (Elliott et al. 2014). We monitored nests daily from May-August and any changes to nest contents (eggs laid/lost, chicks hatched/lost).

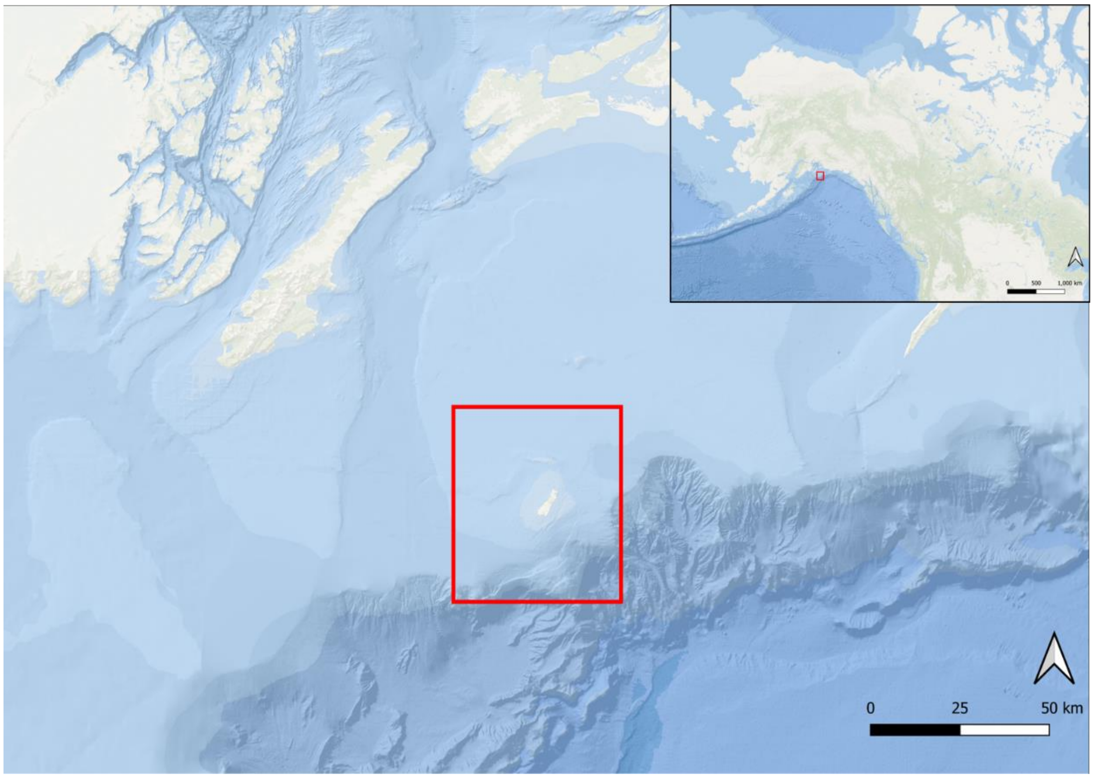

Figure 3. Study area for nest monitoring and GPS deployment was Middleton Island, located in the Gulf of Alaska.

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 a 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. Birds were recaptured to remove the GPS unit after at least 24 h, with most retrieved within 96 h (mean ± standard deviation: 85 ± 44 h).

Ethical note

All birds monitored and handled were covered under McGill Animal Care Permit 2015-7599 and US Fish & Wildlife Permit 85004C.

Statistical Analysis

Foraging trip characteristics

We completed all statistical analyses in R (version 4.0.3, R Core Development Team 2020). Foraging trips were defined as departures from the colony extending farther than 1 km and lasting more than 30 minutes. 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. From those, we calculated foraging trip characteristics: maximum distance from the colony (km), duration of foraging trip (h), and total distance traveled (km). To classify foraging behaviour into transit flight, area-restricted search, and rest we used a Residence in Space and Time (Torres et al. 2017; radius = 1.116081; threshold = 0). We then defined foraging patches as consecutive points classified as area-restricted search to calculate the number of foraging patches for each foraging trip.

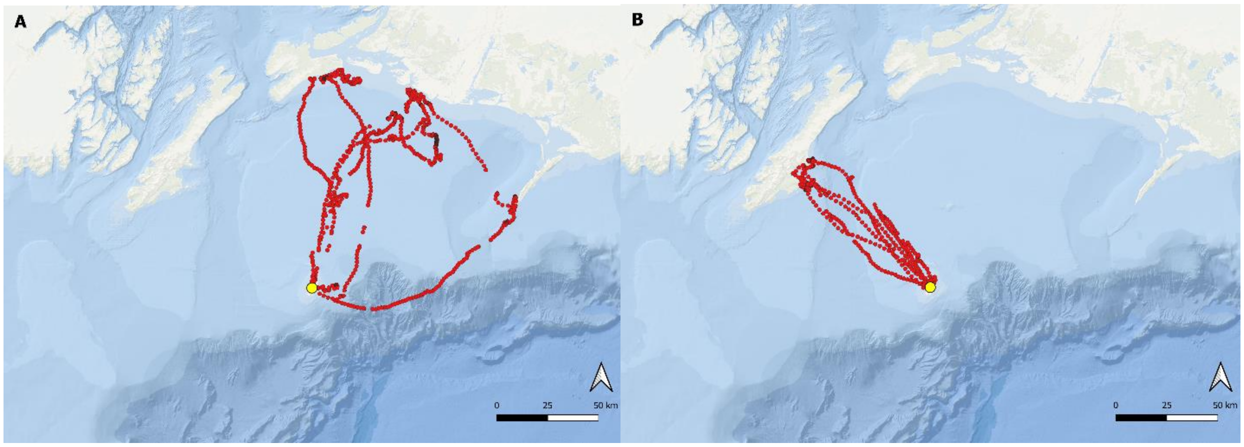

Figure 4. Example movement data from two birds GPS-tracked on the same dates during chick rearing in 2018. The two individuals exhibit different foraging patterns and locations. Yellow point indicates the Middleton Island kittiwake colony, where GPS devices were deployed.

Principal component analysis of foraging trips

We used a principal component analysis (PCA) to determine if there were correlations among foraging trip characteristics including maximum distance, duration, total distance, number of foraging patches and the standard deviations of maximum distance, duration, and total distance (Figure 5). To include the standard deviations of variables, we removed deployments where there was only one foraging trip and used this reduced dataset (n = 243 deployments, 913 foraging trips) for all subsequent analyses. Transformations of the data yielded non-normal distributions and so the data were not transformed. PC1 accounted for 61.3% of the variation and all of the foraging trip characteristics were correlated in the same direction (Table 2). PC2 accounted for 25.1% of the variation with all of the foraging trip characteristics loaded positively and all of the standard deviations loaded negatively.

Table 2. Principal component analysis of foraging trip characteristics for the subset of data in which each deployment had more than one foraging trip. 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. PC1 explained 61% of the variation with all of the characteristics having similar loadings.

	PC1	**PC2**	**PC3**
Proportion of variance	0.613	0.251	0.062
Loadings			
Maximum distance	0.370	0.339	0.603
Duration	0.427	0.175	-0.413
Total distance	0.423	0.329	0.163
Number of patches	0.396	0.300	-0.255
Standard deviation of maximum distance	0.273	-0.545	0.455
Standard deviation of duration	0.370	-0.375	-0.408
Standard deviation of total distance	0.365	-0.468	-

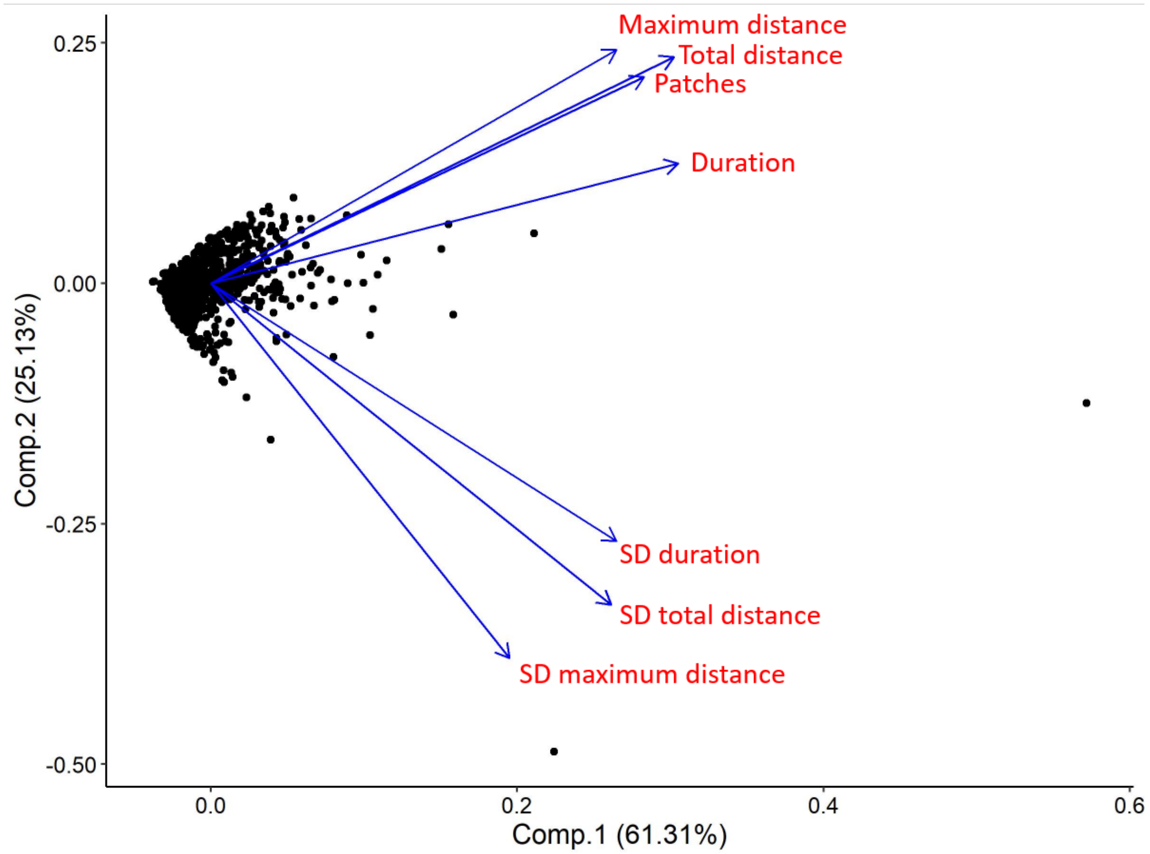

Figure 5. PCA of foraging trip characteristics and standard deviation (SD) of foraging trip characteristics. The PCA shows that all characteristics are correlated in the same direction on the PC1 axis. On the PC2 axis, all of the foraging trip characteristics are correlated in the positive direction and all of the standard deviations are correlated in the negative direction.

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 for an effect of age on fledging success (defined as fledging at least one chick or not) using fixed effects of age, breeding phase, (incubation or chick rearing) and their two-way interaction, and random intercepts of bird ID and year (known age: N = 229 deployments; 863

foraging trips). The dataset with birds of known and assigned age was then used for all models with age as a fixed effect. We then modeled fledging success in response to fixed effects of PC1 (representing all foraging trip characteristics), age, breeding phase, and two-way interactions with age and breeding phase, 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 correlated with PC2 in opposite directions. We determined significance for the variables using p values.

To further test whether consistency in foraging behaviour is associated with fledging success, we subset the data for individuals that made at least two foraging trips within a deployment. We separated those 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 used a Pearson correlation analysis to test for consistency in foraging trip characteristics for the first and second foraging trips.

To test for a maximum distance threshold, we used the package *segmented* (Muggeo 2003) to analyze 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 if there is evidence of at least one break-point in the model where the slope changes.

We obtained PDO index values (NOAA, ERDDAP) and calculated average PDO index during the breeding season (May-August) for each year. We used linear models 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, we modeled 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, and resting) and mean breeding success for the colony, we used linear models on time spent in each behaviour and the mean number of chicks fledged per year for both incubation and chick rearing.

RESULTS

We obtained GPS data from 160 deployments during incubation and 183 deployments during chick rearing (343 deployments total) between 2012-2020 (Table 3). This included 1015 foraging trips, 863 of which were for birds of known age. The mean (± standard deviation) maximum distance from the colony for a trip was 52.8 (± 40.6) km, total distance traveled was 163.9 (± 142.3) km, duration of trip was 10.0 (± 13.8) h, and number of foraging patches was 10.4 (± 8.6). While there were only 23 more deployments of similar duration in chick rearing compared to incubation, there were more than double the number of foraging trips during chick-rearing.

Table 3. Number of kittiwake GPS deployments each year and breeding phase, with the number of foraging trips within those deployments recorded in parentheses.

	2012	2013	2015	2016	2017	2018	2019	2020	Total
Incubation	0	70 (107)	0	0	23 (41)	24 (59)	35 (57)	8 (16)	160 (280)
Chick Rearing	9 (14)	39 (196)	7 (12)	8 (35)	44 (152)	42 (228)	31 (83)	3 (15)	183 (735)
Total	9 (14)	109 (303)	7 (12)	8 (35)	67 (193)	66 (287)	66 (140)	11 (31)	343 (1015)

Foraging trip characteristics and fledging success

The interaction between age and breeding phase had a significant impact on fledging success in all models. That is, fledging success decreased with age ('senescence') but only during incubation. Of all the foraging trip characteristics we analyzed, only PC1, which included the standard deviation of all trip characteristics, was significantly associated with fledging success (Table 4, Figure 6). Thus, while the foraging trip characteristics alone did not impact fledging success, variation in the foraging trip characteristics did.

Table 4. Associations between fledging success (FS), age, breeding phase, and foraging behaviour for black-legged kittiwakes at Middleton Island. In all models, bird ID and year were included as random intercepts.

Model	Variables	Estimate	Std. Error	*z*	*P*
FS ~ Age*Phase	Age (scaled)	-0.73	1.49	-0.49	0.62
	Phase	-34.7	4.34	-7.97	<0.0001
	Age (scaled)*Phase	9.15	2.40	3.80	<0.001
FS ~ Duration*Phase + Age*Phase	Duration	-0.07	0.067	-1.06	0.29
	Age (scaled)	-0.98	1.80	-0.54	0.59
	Phase	-29.9	5.15	-5.81	<0.0001
	Duration*Phase	-0.10	0.13	-0.78	0.44
	Age (scaled)*Phase	7.47	2.64	2.83	<0.01
FS ~ Max distance*Phase + Age*Phase	Max distance (scaled)	-0.47	0.35	-1.39	0.17
	Age (scaled)	-0.81	1.53	-0.50	0.61
	Phase	-31.1	4.78	-6.13	<0.0001
	Max distance (scaled)*Phase	-0.76	1.14	-0.59	0.56
	Age (scaled)*Phase	7.43	2.44	3.07	<0.01
FS ~ PC1*Phase+ Age*Phase	PC1	-1.36	0.34	-4.02	<0.0001
	Age (scaled)	-1.75	2.31	-0.76	0.45
	Phase	-31.8	7.02	-4.60	<0.0001
	PC1*Phase	0.76	0.79	0.96	0.34
	Age (scaled)*Phase	8.56	3.42	2.53	<0.05

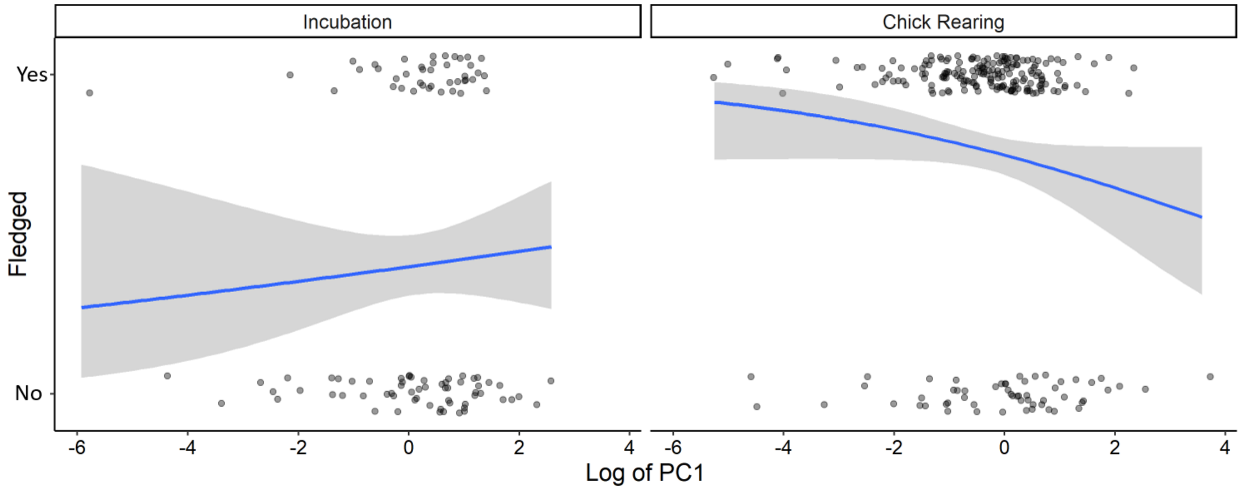

Figure 6. The association between foraging trip characteristics (PC1) and fledging success (whether or not the bird fledged at least one chick) differed between breeding phases of foraging trip characteristics. During incubation, there was a weak association between PC1 values and fledging success; during chick rearing, higher PC1 values associated with further foraging distances and durations were associated with lower fledging success. The log of PC1 was used to better visualize the data. Vertical jitter added to show point density.

For all three foraging trip characteristics (duration, maximum distance, and total distance) the first and second trip characteristics were significantly positively correlated among kittiwakes that successfully fledged chicks, regardless of breeding phase (Figure 7). There were no significant correlations between trip duration and total distance for the first and second trips for birds that did not successfully fledge a chick during incubation. However, there was a significant correlation between maximum distance during incubation and chick rearing and total distance during chick rearing for those which did not successfully fledge a chick (Table 5). These correlations were strongest for birds during incubation which successfully fledged a chick. In short, though there is still some success for birds with more variable foraging trips, kittiwakes with consistent foraging behaviour during incubation achieved higher fledging success.

Table 5. Correlation analysis between the first and second foraging trip for each individual separated by phase and fledging success. For each foraging characteristic, the two trips during incubation were significantly correlated for kittiwakes that were successful in fledging a chick. The correlations were not significant for kittiwakes that failed to fledge a chick during incubation, with the exception of maximum distance, but maximum and total distance for trip one and two were still significantly correlated for those which failed to fledge a chick during chick rearing.

	DF	*t*	*P*	r
Duration				
Incubation + Fledged	38	4.98	<0.0001	0.628
Incubation + Failed	44	0.986	0.330	0.150
Chick rearing + Fledged	122	3.26	<0.01	0.283
Chick rearing + Failed	28	1.63	0.115	0.293
Maximum distance				
Incubation + Fledged	38	6.18	<0.0001	0.708
Incubation + Failed	44	3.43	<0.01	0.460
Chick rearing + Fledged	123	7.05	<0.0001	0.536
Chick rearing + Failed	28	3.90	<0.001	0.593
Total distance				
Incubation + Fledged	38	5.59	<0.0001	0.672
Incubation + Failed	44	1.19	0.241	0.176
Chick rearing + Fledged	123	5.44	<0.0001	0.440
Chick rearing + Failed	28	2.90	<0.01	0.480

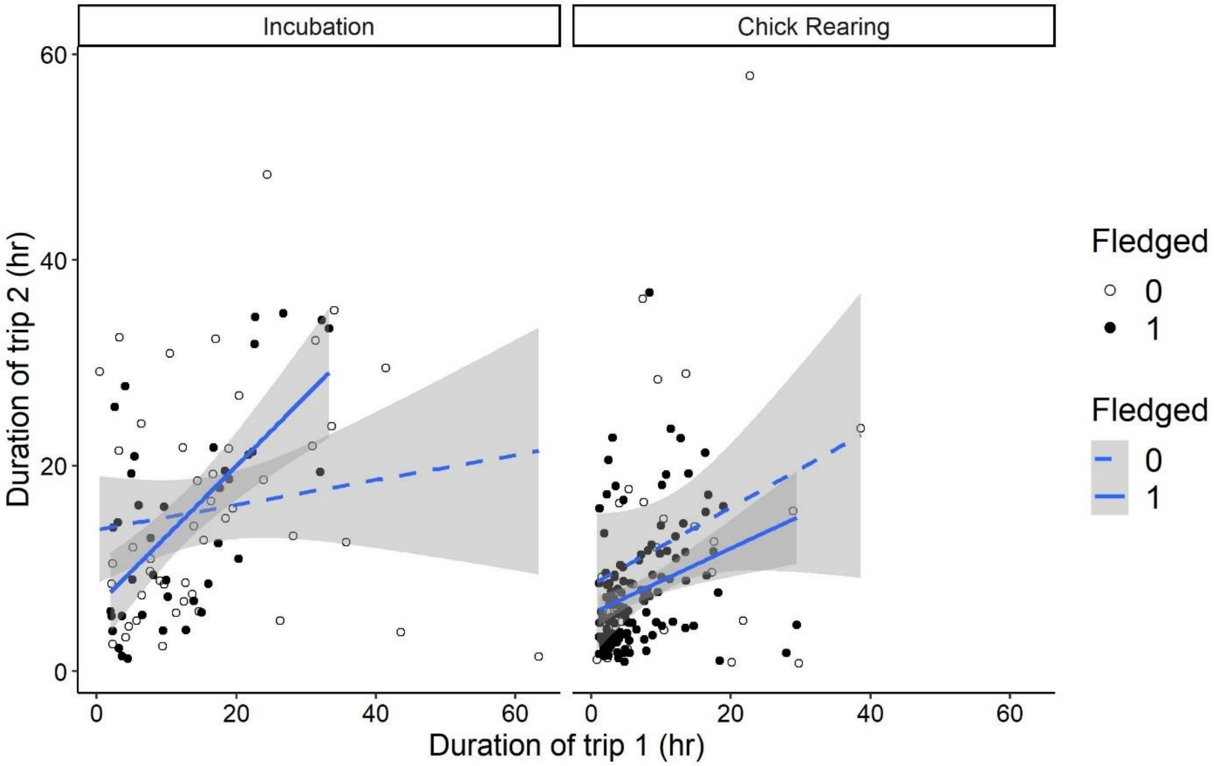

Figure 7. Correlations between duration of the first foraging trip compared to the second during incubation and chick rearing. The relationship between trip one and two were significantly correlated during incubation for birds which successfully fledged a chick (solid line in left panel: $r_{38} = 0.628$, $P < 0.0001$). During chick rearing the correlation was also significant for those which successfully fledged a chick, but this relationship was weaker (solid line in right panel: $r_{122} = 0.283$, $P < 0.01$). Filled circles represent birds which fledged at least one chick and open circles are for birds whose nest failed.

Maximum distance and duration

A segmented line better represented the relationship between trip duration and maximum distance for all study years ($P < 0.05$) except for 2012 ($P = 0.2$). As trip duration increased, maximum distance increased up to about 10 h trip duration; after the breakpoint, the slope decreased (Figure 8). The relationship varied slightly between years with the mean breakpoint at 8.6 h ± 4.8 (mean ± standard deviation). The lowest breakpoint occurred at 4.7 h in 2015 and the highest breakpoint occurred at 18.0 h in 2016.

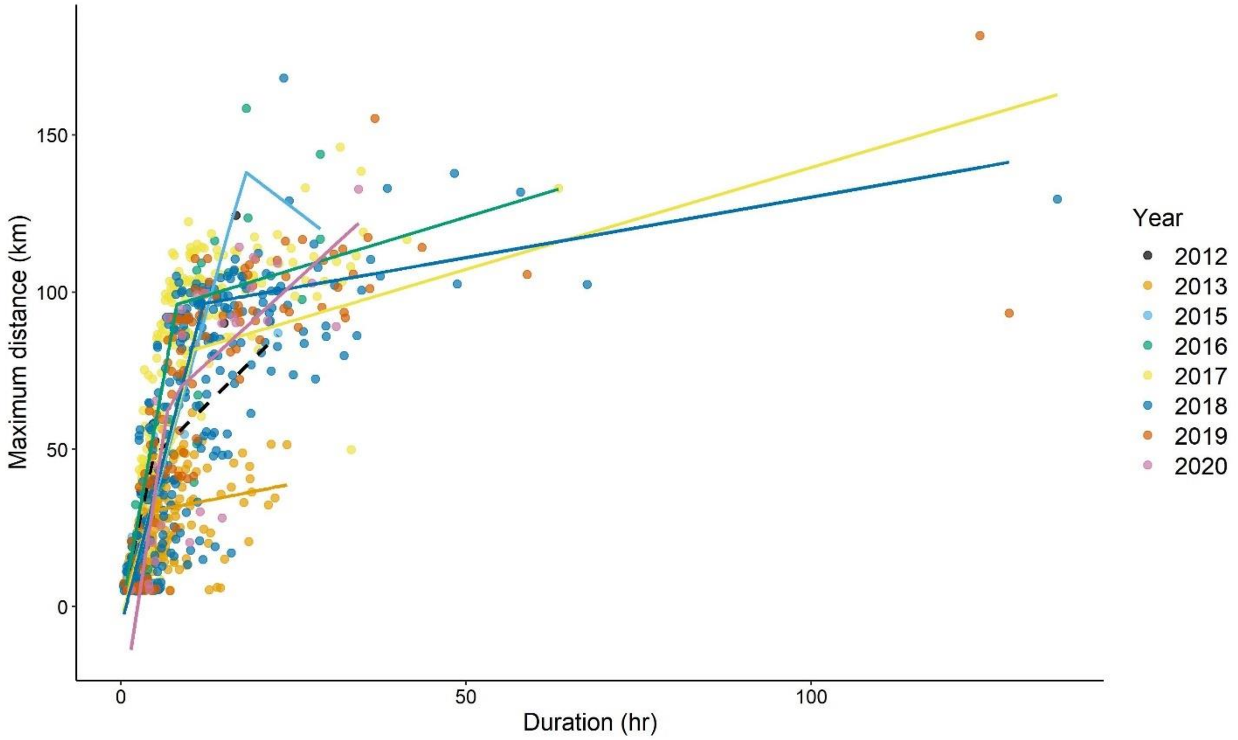

Figure 6. Multiple segmented linear models, rather than single linear models, best explained the relationship between trip duration and maximum distance in every year ($P < 0.05$) except for 2012 ($P = 0.2$). Trip duration increased with maximum distance, but at around 8 h, on average, that increase dropped.

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 (Figure 9). However, PDO was not related to any of the foraging trip characteristics or standard deviations of foraging trip characteristics (Table 6).

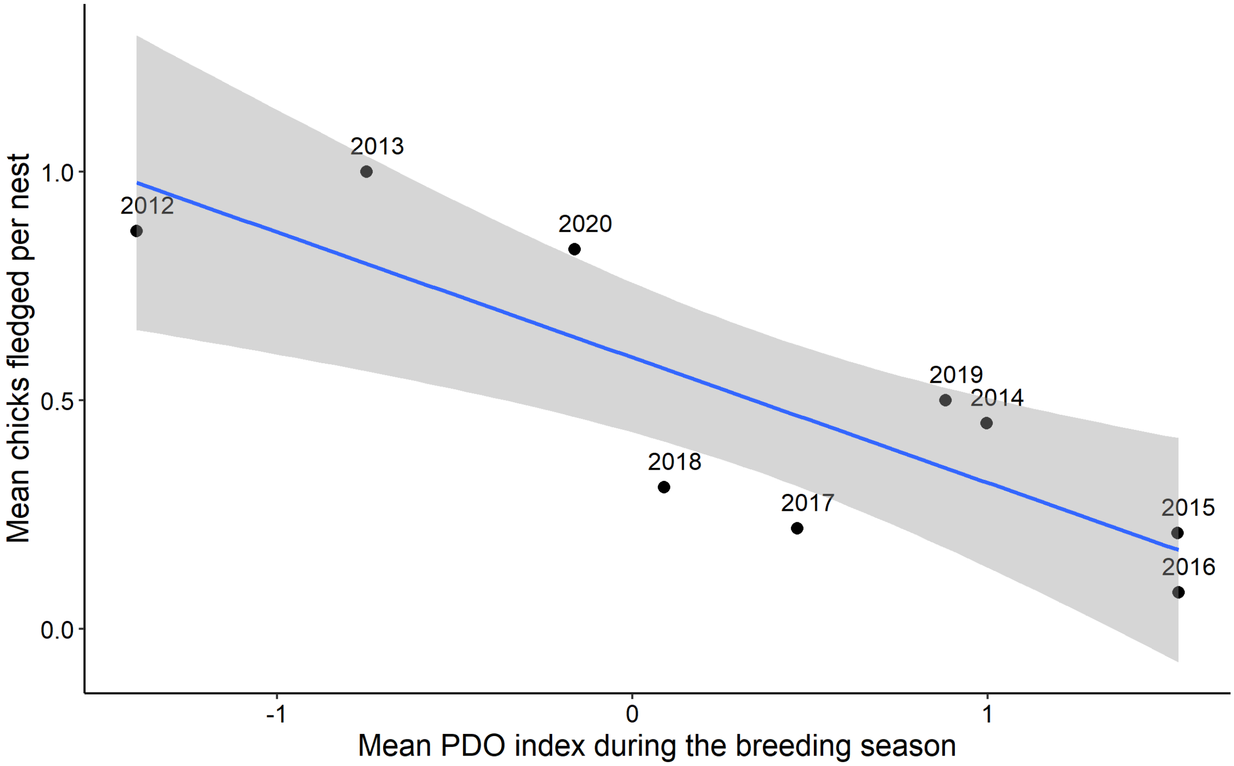

Figure 9. There was a significant negative relationship between mean PDO index during the breeding season (May-August) and the mean number of chicks fledged per nest ($t_{15} = -2.15$, $P < 0.05$).

Table 6. Results of a correlation analysis between PDO and both mean number of chicks fledged and averaged foraging trip characteristics for the GPS-tracked kittiwakes. PDO index during the breeding season (May-August) was significantly correlated with mean number of chicks fledged, but not correlated with foraging trip characteristics.

~PDO	Estimate	SE	*t*	*P*
Mean Chicks Fledged (DF = 15)	-0.17	0.08	-2.15	<0.05
Foraging trip characteristics (DF = 6)				
Duration	1.08	1.54	0.702	0.51
Maximum distance	3.99	7.24	0.553	0.60
Total distance	4.37	19.4	0.225	0.83
SD Duration	1.20	1.08	1.11	0.31
SD Maximum distance	2.70	2.78	0.971	0.37
SD Total distance	9.01	9.65	0.934	0.386

Time allocation and fledging success

The two 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 ($z = -0.22$, $P = 0.82$) or chick rearing ($z = -1.42$, $P = 0.16$). Overall, we found that, on average, fewer chicks fledged during years when kittiwakes spent more time resting on water during incubation ($t_3 = -8.24$, $P < 0.01$) and when kittiwakes spent more time in transit flight during chick rearing ($t_6 = -2.50$, $P < 0.05$) (Table 7, Figure 10).

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 during incubation and chick-rearing.

	Estimate	SE	*t*	*P*
Incubation (DF = 3)				
Transit flight	-0.11	0.13	-2.52	0.09
Rest	-0.08	0.01	-8.24	<0.01
Area-restricted search	-0.08	0.04	-2.09	0.13
Chick rearing (DF = 6)				
Transit flight	-0.10	0.4	-2.50	<0.05
Rest	-0.02	0.03	-0.81	0.45
Area-restricted search	-0.01	0.03	-0.50	0.63

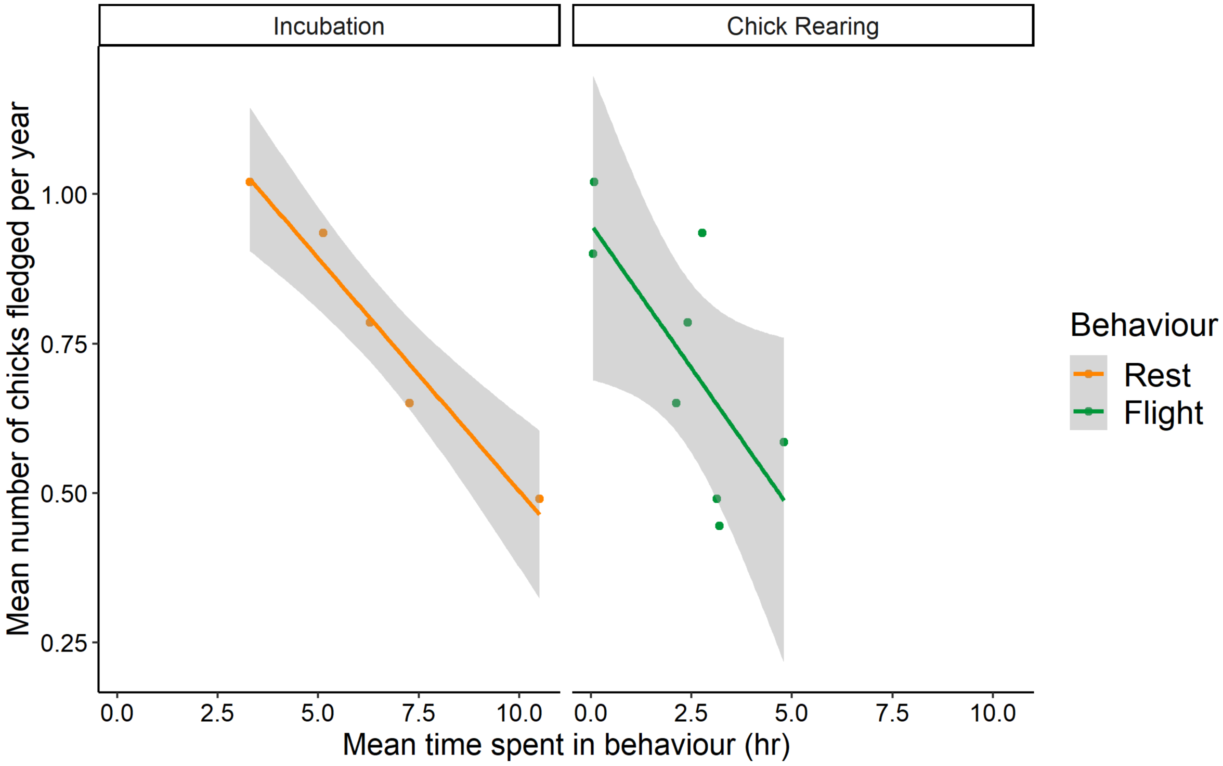

Figure 10. Fewer chicks fledged during years when kittiwakes spent more time resting on water during incubation, and when kittiwakes spent more time in transit flight during chick rearing.

DISCUSSION

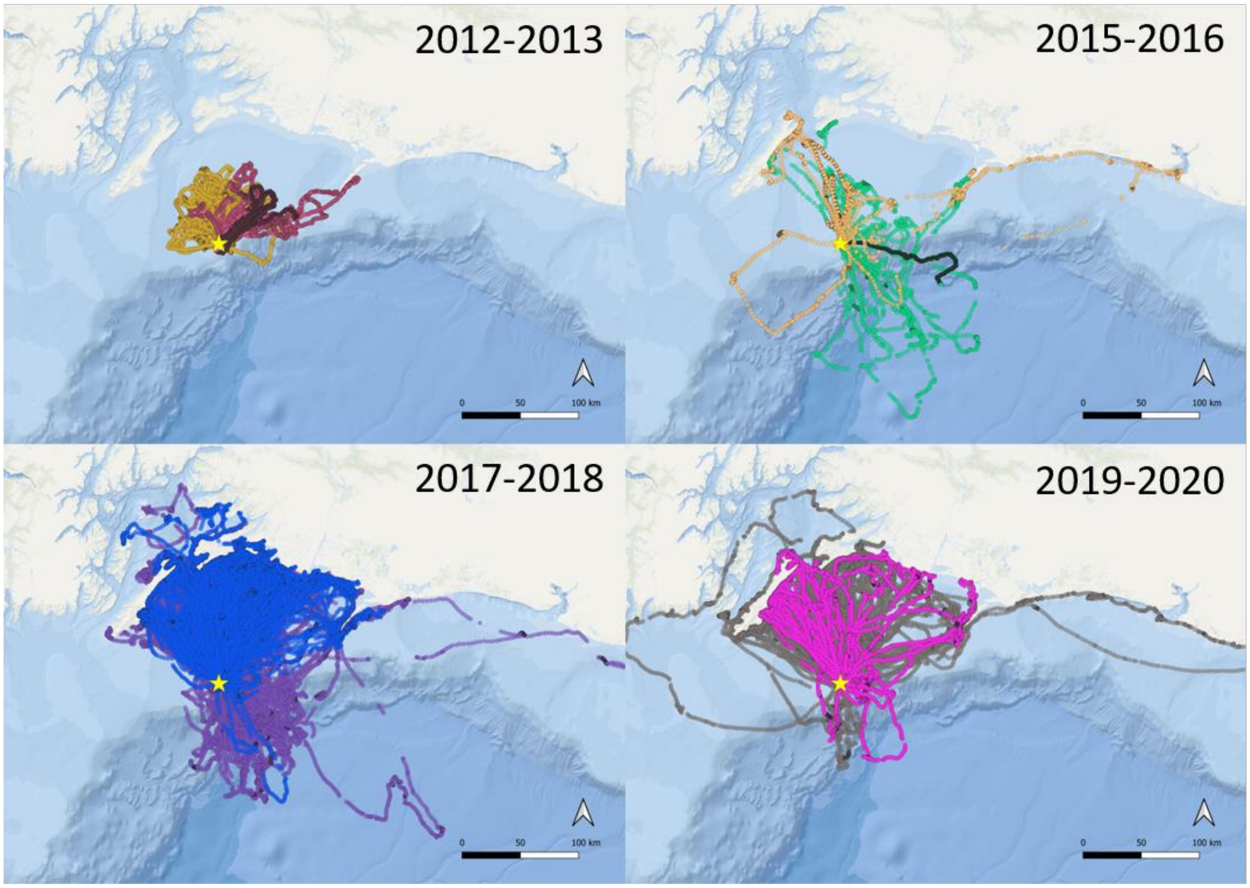

Figure 11. All foraging trip data from 2012-2020. Foraging range expanded after the onset of the heatwave (2015-2016) and these ranges persisted even after the heatwave ended. Each colour represents one year, with overlapping tracks shown in the colour scale.

Contrary to our predictions, breeding success was not associated with any absolute foraging parameter, but rather with the individual's age and the variability of foraging parameters as represented by PC1. Kittiwakes with higher breeding success were more consistent in their foraging behaviour during incubation, relative to unsuccessful breeders (Figure 7). Though maximum foraging distance increased with trip duration, there was a threshold beyond which maximum distance plateaued (Figure 8). This implies that unsuccessful individuals must find a profitable foraging patch within the fixed annual colony foraging area rather 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 negative (i.e. cooler climate) during the breeding season, but PDO index was not linked to any foraging trip characteristics (Table 6). When broken down by behaviour, only mean time spent resting (during incubation) and flying (during chick rearing) during foraging trips were associated with breeding success (Figure 10).

Kittiwake foraging trip length was highly variable among years, with some individuals flying hundreds of kilometers to forage in poor years (Figure 11). 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 the environmental change (Zador et al. 2013). The delayed return to baseline 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 sand lance and capelin, decreased in availability during the heatwave and had still not recovered five years after the initial onset (Suryan et al. 2021).

Regardless of whether they foraged near or far, kittiwakes that were more consistent in their foraging behaviour during incubation were more likely to fledge a chick, implying that birds that found a successful strategy were able to continue to employ 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). Though 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 consistency in foraging behaviour can vary between years (Ceia et al. 2014; Camprasse et al. 2017) and in one case found higher consistency in trip duration and straightness during years with less profitable environmental conditions (Traisnel and Pichegru 2019). Individuals that are more consistent in their behaviour exploit one (or a few) known successful foraging patches and are better able to consistently find prey for their chicks. This is supported by previous findings that consistency in foraging site fidelity increased reproductive success (Patrick and Weimerskirch 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 performed worse than their more consistent 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 lifespan, even if some years are less profitable than others (Bradshaw et al. 2004; Arthur et al. 2015). This may be an important influence on foraging strategy for long lived species such as seabirds. Though there is also evidence that, for some species, consistency in foraging behaviour regardless of 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 eight hours, 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 hours (Hamer et al. 2000; 2007). In an Atlantic kittiwake population, traveling flight duration in kittiwakes reached an asymptote after 6.5 hours 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 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 foraged 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 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 centers as they open (Spelt et al. 2021). This may also contribute to the benefits of consistency 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 foraging trip characteristics were strongly influenced by PDO (Table 6). Even though PDO index was lower in 2020, foraging behaviour did not return to pre-heatwave baselines, 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, however it was negatively correlated with the number of prey items brought back to the nest and 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 (*Ammodytes personatus*), 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 be returning 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).

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, however this did not significantly influence breeding success. 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 continue to fly further to compensate for reduced prey availability. However, these behaviours did not have a clear or direct impact on breeding success. Breeding success was lower during years when kittiwakes spent more time resting during a foraging trip (incubation) and more time in transit flight during a foraging trip (chick rearing), but the underlying mechanisms are unclear.

In this study, we found that individuals with more consistent foraging behaviour during incubation were more likely to fledge a chick. We propose that consistency in foraging behaviour may reflect differences in personality, with subsequent effects on individuals' ability to acquire resources and 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 shyer pairs (Collins et al. 2019). Other studies have found that personality influences consistency in foraging behaviour with bolder individuals being more consistent in foraging behaviour than shyer individuals (Krüger et al. 2019; Harris et al. 2020). These bolder individuals may be more willing to compete for productive foraging patches they consistently visit, leaving shyer 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 shyer, middle-aged birds being bolder, and then older birds being shy as well (Elliott 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 impacted reproductive success.

Consistency in foraging behaviour was more important to reproductive success than absolute foraging behaviour. The mechanisms underlying individual variation in foraging consistency remain unclear, but personality could be a factor. Future studies should focus on where birds more consistent 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 that 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 more consistent 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.

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GENERAL DISCUSSION

In this thesis I found that those individual kittiwakes that were more consistent in their foraging behaviour were more likely to fledge a chick, and that maximum distance plateaued rather than increased with foraging duration. This suggests that it is more profitable to return to and search a known location than to search randomly or expand the foraging range. Though this thesis focused mostly on one colony in the Pacific, kittiwakes are declining throughout their range (Descamps et al. 2017), with Atlantic populations struggling with similar issues of prey depletion (Frederiksen et al. 2004) and ocean warming (Sandvik et al. 2014). Oceanic prey are often already patchily distributed, and if climate change and marine heatwaves are making prey even more unpredictable, then perhaps some birds are losing their reliable patches and are being forced to expend more energy foraging in unknown areas with fewer or less nutritious prey. This means that marine heatwaves may reduce fecundity, and, ultimately, if they occur with more frequency, will reduce population sizes. This could be the case not only for kittiwakes, but many species of seabirds which have similar behaviours. Seemingly ubiquitous gull species such as herring (*Larus argentatus*) and great black-backed gulls (*Larus marinus*) have been in decline (Mittelhauser et al. 2016) which could be due to similar issues of prey availability especially considering gulls inability to dive for prey. Nonetheless, even diving seabirds are clearly struggling to find prey during heatwaves, with several species having high rates of mortality (Piatt et al. 2020; Major et al. 2021).

The role that personality plays in foraging behaviour in this system could inform the cause of some of these individual differences. In this study, I found that consistency in foraging behaviour positively impacted reproductive success. In another study on the same system, it was discovered that chicks from bolder pairs survived longer than those where even just one of the adults was shyer (Collins et al. 2019). Bolder kittiwakes have also been found to be more consistent in their foraging behaviour than shyer individuals (Harris et al. 2020). Perhaps boldness influenced the foraging behaviour of individuals in this study, and in turn, reproductive success. In this study, age also played a role in reproductive success, though the mechanism is still unknown. Other studies have found that boldness is repeatable within individuals across years (Patrick, Charmantier, and Weimerskirch 2013; Collins et al. 2019). However, these studies were only conducted over the course of a few years, whereas many seabirds live for twenty years or more. In other species tested over many years, personality was indeed found to change over time (Suomi, Novak, and Well 1996). In kittiwakes, stress response (including some measures of personality), was associated with age, with younger birds being shyer and more reactive, middle-aged birds being bolder and more proactive, and older birds being shy as well (Elliott et al. 2014). If personality is indeed impacted by age, this could also be one explanation for how age impacts reproductive success, as reproductive success peaks in middle age in this population. While most studies on personality in seabirds have focused on boldness, aggression is another aspect of personality that would be valuable to investigate as this may impact how individuals respond to inter and intraspecific competition.

This research was only possible because of the many years of data collected on Middleton Island. Long-term ecological research stations such as the one on Middleton are critical for tracking trends and changes in populations. With continued tracking studies on Middleton, we can gain a better understanding of why birds that are more consistent are having higher success than those which have more variable foraging behaviour. Kittiwakes, like many seabirds, have a relatively long life span and knowledge gained over time is likely to play a strong role in foraging success. We can also gain considerable information on how within individual behaviour changes (or remains the same) through their lifetime and how this impacts reproductive success. Age played an unknown role in the consistency of behaviour in this study and future studies should focus on tracking individuals we have previous years of data for so we can better understand if age is directly impacting the consistency in behaviour.

The Gulf of Alaska has experienced numerous dramatic events over the last few decades. The Exxon Valdez oil spill was a catastrophic event which had immediate, dramatic, and long-term impacts on seabird populations which we still are trying to understand the extent of (Golet et al. 2002). There have also been two large marine heatwaves in the last ten years, and marine heatwaves are only predicted to increase in frequency and intensity (Oliver et al. 2019b). Continued monitoring and research is needed to understand all of the threats seabirds in the Gulf of Alaska and around the world are facing so that we can establish conservation efforts and create policies to protect and preserve their populations and diversity.

GENERAL SUMMARY AND CONCLUSION

The goal of my research was to investigate the individual differences in foraging behaviour in black-legged kittiwakes and how those differences impact reproductive success during years of high environmental variability. Reproductive success was influenced by both age and consistency in foraging behaviour, with birds that had less variation in foraging behaviour between trips during incubation being more likely to fledge a chick than birds that were more variable. There was evidence of a maximum distance threshold in each year of data we collected, with maximum distance increasing with trip duration until around eight hours. Though increasing PDO was highly correlated with decreases in nest success, there was no relationship between PDO and foraging behaviour. Time spent flying, resting, and searching for prey during foraging trips increased steadily over the study period. Area restricted search increased at a slightly higher rate during incubation, but this was not significant. Increase in mean time spent resting during a foraging trip in incubation, and flying during a foraging trip in chick rearing were both negatively correlated with mean number of chicks fledged per year.

As central place foragers with high nest-site fidelity, seabirds are tied to one location for a significant portion of the year. When conditions in those locations decline seabirds cannot simply go somewhere conditions are better. Marine heatwaves and climate change are both contributing to reduced marine biodiversity and unpredictable oceanic conditions. The Decade of Ocean Science for Sustainable Development is a call to use science to understand the widespread impacts of these events and policy to slow and reverse them. In this thesis, I found that individuals which were consistent in foraging behaviour, especially during incubation had greater reproductive success. Future studies should look at the causes of these individual differences and consistency in foraging behaviour and if and how they change over time so we can better understand if and how populations will be impacted by changing environments. If there are particular locations which are foraging hotspots, especially for multiple species, these could be identified as potential marine protection areas (Davies et al. 2021).

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