Personality, reproductive success and mate choice in a burrowing seabird

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Out of all those kinds of [birds], you've got a face with a view.

This Must Be the Place - The Talking Heads

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ABSTRACT

Animal personality, which has been shown to exist and be repeatable in virtually every taxon it has been examined in, including seabirds, is an aspect of cognition which may gain insight into how individuals respond to contrasting environmental conditions providing key information on ecosystem health. Degrading environmental conditions may decrease personality diversity in seabirds, favouring shyer individuals, while food-rich environmental conditions may favour bold individuals. The implications of a potential loss of personality diversity are still unclear within seabirds, especially since the scope of species studied and of questions asked has been limited thus far. While nearly 25% of seabird species nest in burrows, few studies have assessed the personality of burrowing seabirds. Furthermore, while behaviour traits such as boldness have been shown to directly impact reproductive success, fewer studies have examined the mechanism behind that link. In burrowing seabirds, where mate and site fidelity are confounded but often related to fitness, there is potentially a link between personality, mate choice, reproductive success and site fidelity. In this thesis, I first complete a literature review where I explore animal personality and its links to various aspects of reproduction in seabirds, then examine such questions on a burrowing seabird: the rhinoceros auklet (*Cerorhinca monocerata*). Variation in animal personality represents important life-history trade-offs, impacting reproductive success, through both individual and partner traits. Notably, bolder individuals (more willing to take risks) tend to reproduce more successfully, but at a lower survival rate cost. The higher reproductive success may lead to higher mate and site fidelity. To test these ideas, we explored the link between personality, reproduction and mate choice in the rhinoceros auklet. Auklet personality scores were repeatable across years, but there was no assortative mating with personality or association with reproductive success. However, shyer individuals were more likely to switch sites and mates. We conclude that shy

individuals may be less willing to partake in intraspecific competition for mates and sites, choosing to invest in a new match instead, but with little impact on fitness (at least in a good year). This study is one of the first to associate mate choice, reproductive success and site fidelity in a seabird. It sheds light onto how individuals employ different strategies, and how environmental conditions may affect these. Personality may shape populations through persistent environmental variations, such as climate change. Understanding such changes in an indicator taxon, here seabirds, may be crucial in flagging poor marine environmental conditions.

RÉSUMÉ

La personnalité animale, son existence ayant été démontrée dans la plupart des taxons dans laquelle elle a été examinée, incluant les oiseaux marins, est un aspect de la cognition qui élucide comment certains individus réagissent face à des conditions environnementales variables. La dégradation de ces conditions peut entraîner une perte de diversité chez la personnalité des oiseaux marins, en faveur des individus timides. Parallèlement, des environnements riches en nourriture pourraient favoriser les individus téméraires. Les implications d'une perte de diversité en personnalité chez les oiseaux marins sont peu claires, surtout étant donné que la portée d'espèces étudiées et des questions posées a été limitée jusqu'à présent. Bien que 25% des espèces d'oiseaux marins nichent dans des terriers, peu d'études ont évalué la personnalité de ces derniers. De plus, alors que des traits tels que la timidité aient été démontrés comme ayant un impact directe sur le succès reproducteur, peu d'études ont examiné les mécanismes derrière ce lien. Chez les oiseaux marins de terriers, où la fidélité de site et de partenaire sont souvent confondues toutefois reliées aux aptitudes phénotypiques, il y a potentiellement un lien entre la personnalité, le choix de partenaire, le succès reproducteur et la fidélité de nid. À travers cette thèse, je complète premièrement une revue de littérature où j'explore la personnalité animale et ses liens à différents aspects de reproductifs chez les oiseaux marins. Ensuite, j'examine ces questions chez un oiseau marin fouisseur : le macareux rhinocéros (*Cerorhinca monocerata*). La variation dans les personnalités animales représente souvent des importants compromis de cycles de vie, ayant un impact chez le succès reproducteur, à travers des traits chez les individus et les partenaires. Notamment, des individus téméraires (propices a prendre des risques) ont tendance à se reproduire avec plus de succès, mais à un coût sur leur survie. Ce succès reproducteur élevé pourrait mener à une plus grande fidélité de partenaire et de site. Pour tester de telles idées, nous avons exploré le lien entre

la personnalité, la reproduction et le choix de partenaire chez le macareux rhinocéros. Les scores de personnalité chez les macareux étaient répétables chez les individus à travers les années. Nous n'avons cependant pas observé d’accouplement par sélection basée sur la personnalité ou d’association avec le succès reproducteur. Néanmoins, les individus plus timides étaient plus propices à changer de site ou de partenaire. En conclusion, les individus timides pourraient être moins disposés à s’engager dans des compétitions intraspécifiques pour des partenaires ou des sites. À la place, ils investissaient dans un nouvel accouplement, avec un impact limité sur leur aptitude phénotypique (du moins lors d’une année favorable). Cette étude est l’une des premières à associer le succès reproducteur, le choix de partenaire et la fidélité de site chez un oiseau marin. Elle élucide comment certains individus emploient différentes stratégies, et comment les conditions environnementales pourraient les affecter. La personnalité peut façonner des populations à travers des variations environnementales persistantes, tels que les changements climatiques. Comprendre ces changements dans un taxon indicateur tels que les oiseaux marins pourrait être crucial dans le signalement de mauvaises conditions environnementales marines.

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INTRODUCTION

Seabirds are often described as sentinels of the sea, as they can provide insight into ecosystem health, fish stocks and marine pollution (Piatt et al. 2007; Elliott and Elliott 2013; Le Bohec et al. 2013). Indeed, seabirds are predators with a diverse diet, and by studying them we can gain insight into fish stocks through fluctuating prey availability, as well as broader ecosystem stability (Montevecchi 1993; Frederiksen et al. 2007; Einoder 2009; Cunningham et al. 2018). For example, Amey showed a significant relationship between the catch per unit effort of herring (*Clupea harengus*) by local fisheries and the proportion of herring in the Arctic tern's (*Sterna paradisea*) diet (Amey 2000). Seabirds are also often colonial, which makes them easy to capture and to sample, facilitating large samples sizes (Piatt et al. 2007). Finally, seabirds integrate information over space and time whereas conventional boat-based sampling only provides a snapshot of the marine environment's state (Piatt et al. 2007). For northern research, seabirds have been shown to be a valuable proxy for arctic ecosystem health (Mallory et al. 2006).

If seabirds are sentinels of the sea, then they have an alarming message. The decline of global seabirds could be up to 70% since the 1950s (Paleczny et al. 2015). Especially in the Arctic where temperatures are increasing twice the global average, northern seabird monitoring stations are as relevant as ever for tracking such changes (Screen and Simmonds 2010). Modern biologgers facilitate that task as they record the exact moment where predator meets prey and thus can provide an accurate index of catch per unit effort (CPUE) (Brisson-Curadeau et al. 2017). However, these monitoring techniques can be invasive, time consuming and harmful to seabird fitness and reproductive success (Carey 2009; Sun et al. 2020). At the Middleton Island (Alaska) seabird research station, direct handling, and the placement of tags even below 3% body mass on rhinoceros auklets (*Cerorhinca monocerata*) increased their nest abandonment (Sun et al. 2020).

It is the researchers of these long-term monitoring stations' responsibility to strive to improve their monitoring methods, not only because minimizing stress will make measurements more accurate, but also for the seabirds' well-being, and the mental well-being of local community members implicated in the projects.

As part of my master's project, I helped build a study system combining nest boxes and RFID (Radio-Frequency Identification) technology to monitor the sensitive rhinoceros auklet on Middleton Island with minimized disturbance. I then used this system to answer questions on personality and reproductive success in this subarctic burrowing auk, to understand the strategies individuals of this taxa use for navigating their rapidly warming northern oceans. Personality is a trait often overlooked which may help gain insight into how individuals are responding to these contrasting environmental conditions (Krüger et al. 2019). Notably, degrading environmental conditions may decrease personality diversity in seabirds (Jeffries et al. 2021).

My thesis aims to explore the link between personality and multiple aspects of reproduction in the rhinoceros auklet. I specifically look at boldness, an aspect of personality that represents important life-history trade-offs and which may impact reproductive success, both through individual or partner traits. For my study, I assessed the boldness of auklets nesting on Middleton Island during the 2023 and 2024 breeding seasons, linking this trait to reproductive success, mate choice and site fidelity. Understanding how personality affects reproduction and foraging in this burrowing species sheds light onto how seabirds face poor-quality years. Personality is an important element of animal behaviour and must not be overlooked when managing conservation efforts (Collins et al. 2023). The Middleton Island station is funded by GulfWatch Alaska, a legacy fund from the Exxon Valdez oil spill that "aims to provide sound scientific data and products that inform management agencies and the public of changes in the environment" of Prince William Sound and the surrounding region. By examining links between personality, site fidelity and reproductive success, I aim to provide a baseline that could be used to (i) understand changes in reproductive success of auklets over time, an important part of the GulfWatch monitoring program, and (ii) provide baseline data on variables linking personality and reproductive success so that personality, combined with the use of non-invasive RFID technology might become part of the long-term monitoring program for auklets.

LITERATURE REVIEW

In this literature review I will first define animal personality, give a brief history of the field and describe the Five-Factor Model of animal personality as proposed by Réale et al. 2007. Specifically, I will delve into boldness as an important aspect of personality with its life-history fitness trade-offs. I will then expand on the fitness consequences of personality by giving examples of the effects of personality on reproductive success. I will explore how personality can affect reproduction directly through individual traits, but also indirectly through mate choice. Specifically, I will give examples of instances where assortative mating and disassortative mating related to personality occur in various species. I will later review personality studies performed on seabirds. I perform a scoping review of the literature and summarize key findings. Next, I discuss limitations and implications of personality-oriented research in seabirds. I consider the lack of diversity in taxa and the importance of broadening the scope of the field to conservation and climate change. Finally, I will give a natural history of the rhinoceros auklet (*Cerorhinca monocerata*), a sensitive burrow nesting auk, whose personality we assess in this thesis.

Animal Personality

There is now little doubt that personality exists in animals and has ecological and evolutionary implications (Gosling and John 1999; Sih et al. 2004; Locurto 2006; Wolf et al. 2007; Griffin et al. 2015). Personality in animals is defined as "repeatable inter-individual differences in behaviour (Roche et al. 2016). Intrinsic to the individual (personality variations may be attributed up to 50% to additive genetic variation), these behaviours are consistent across time and situations (Réale et al. 2007; Dochtermann et al. 2015). While personality may vary through an individual's lifetime, repeatability is essential for it shows how important the phenotypic variation of said trait is explained by individual variation (Falconer et al. 1996). Repeatability can notably be calculated using a mixed model with individual as a random effect (Diaz-Uriarte 2002).

The field of animal personality emerged in the late 20th century, where researchers started considering individual differences in a long-term time frame (Sloan Wilson et al. 1994). While studies had been studying animal personality in the 20th century, the term was not always employed (for example, "temperament" or "behavioural syndrome" were often used). In 1999, the term was officially incorporated into behavioural ecology (Gosling and John 1999). Personality as the repeatability of traits which impact fitness and shape ecological and evolutionary outcomes became slowly recognized at the beginning of the 2000s (Whitham and Washburn 2017).

In 2007, Réale et al. published a framework for studying animal personality, suggesting that animal personality can be measured and interpreted following five main traits: boldness, aggressiveness, exploration, activity and sociability (Réale et al. 2007). While these traits may be approximated in some contexts as binary, they are continuous, meaning they exist on a spectrum and an individual can fall anywhere on it. Bellow we synthesize the tenets of the paper and provide examples of tests and studies used to measure the traits:

- The **shyness-boldness** continuum can be defined as an individual's willingness to take risks. It is quantifiable by measuring an individual's reaction to a risky situation (for example, an encounter with a predator or a human). It is typically measured with tests that record an animal's avoidance, inspection or aggression towards a threat. Such tests include human approach tests (Grace and Anderson 2014), predator presentation tests (Godin and Dugatkin 1996) and latency to move tests (e.g. bag struggle test used in Vasilieva et al. 2024) to name a few.
- The **exploration-avoidance** continuum represents an individual's reaction to a new situation. A more exploratory, or neophilic individual nay react positively to new situations, or have a propensity towards exploring new habitats, new nest sites, etc. Tests to measure this trait usually include open field tests (Powell et al. 2004), novel environment tests (Minderman et al. 2010) and novel object tests (Johnson et al. 2015). Novel object tests are often used to measure boldness, however (Blaszczyk 2017; Collins et al. 2019; Quesada et al. 2022; Sakai et al. 2024). Perhaps neophobia can be linked to boldness since a situation can be also considered risky if, for example, a new object represents a potential predator.
- The general **activity** level of an individual can also be measured, by quantifying energy expenditure and movements of an individual. Activity can be closely linked to exploration and boldness and must therefore be measured in a non-risky and non-novel environment. The metric measured is often the distance covered during a certain period of time in a closed environment. To do so, cage activity tests may be employed (Tang et al. 2002), as well as open field tests (Ramos et al. 1997; Carlson and Langkilde 2013).

- **Sociability** is defined as an individual's reaction to conspecifics, excluding aggressive behaviours. While sociable individuals will seek out the presence of conspecifics, unsociable individuals will avoid them. It can be measured through separation tests, whereby an animal will be separated from the group and their reaction to the isolation and/or the latency to rejoin the group will be examined (Faure and Mills 2014). Playback experiments and the response to them have also been used to measure sociability (Capitanio 2002; Bollinger 2019).
- Finally, **aggressiveness** represents an individual's level of agonistic behaviours towards conspecifics (not predators). A common way to test for this trait is the mirror image stimulus test (Desjardins and Fernald 2010; Balzarini et al. 2014), but playbacks and decoys may also be used to measure agonistic behaviours towards a conspecific (Amy et al. 2010; Thys et al. 2017).

It is common to find certain tests such as open field tests and novel object tests used to test different traits. In some cases, this occurs as they may be applicable to multiple ecological situations. Because the way we name traits is arbitrary, confusion does exist on whether we are testing for the same behaviour traits (Carter et al. 2012; Greggor et al. 2015; Perals et al. 2017; Yuen et al. 2017). Since many traits are correlated, it may be wiser to focus on their fitness consequences and ecological relevance, without worrying about the semantics of naming what was measured. While the five trait model is extremely helpful and has guided personality research, scientists shouldn't restrict themselves too much by it.

Out of these traits, assuredly one of the most studied is boldness. Since it is defined as an individual's willingness to take risks, for example towards a predator or a human). It not only is easy to measure but also represents important life-history trade-offs. According to Wilson et al.

“The shy-bold continuum is a fundamental axis of behavioral variation in humans and at least some other species,” (Sloan Wilson et al. 1994). Differences in boldness levels may have evolved in multiple species through different life-history strategies (Wolf et al. 2007; Bell et al. 2009). Specifically, bold individuals may have lower future expectations, deciding to engage in high risk-high reward situations. On the other hand, shyer individuals may have higher expectations and therefore put more emphasis on future fitness by avoiding risky endeavours (Wolf et al. 2007). Notably, faster growing individuals tend to be bolder than slow-growing individuals. However, being bolder comes with costs such as higher mortality rates (Stamps 2007). Risk-related traits are therefore highly relevant evolutionary characteristics of animal personality since they have a direct impact on fitness (Wolf et al. 2007). Furthermore, behaviours where growth and mortality are increased, such as boldness, are selected by some individuals which then pass such behaviours on to their offspring (Stamps 2007).

Personality and reproduction

Personality impacts fitness through reproduction in a variety of taxa (Dingemanse et al. 2004; Mutzel et al. 2013; Clermont et al. 2023). A 2008 meta-analysis by Smith and Blumstein showed that boldness, exploration and aggression all had effects on fitness (Smith and Blumstein 2008). Specifically, high risk-taking individuals have higher reproductive success but lower survival rates. Again, variation in boldness is most likely sustained through fitness trade-offs. Such a simple explanation may not be the case for all species, however. Bolder individuals may not always equate higher reproductive success. A study on bighorn sheep (*Ovis canadensis*) revealed that young, bold rams exhibited high survival rates but lower reproductive success early in life. However, older bold rams experienced greater reproductive success (Réale et al. 2009). This highlights the importance of considering age, sex, and the natural history of a species when evaluating how personality influences fitness.

Additionally, the relationship between personality and fitness may vary depending on environmental conditions such as food availability, climatic conditions, etc. (Dingemanse et al. 2004; Tremmel and Müller 2013; Goulet et al. 2016). For example, bolder Arctic foxes (*Vulpes lagopus*) have more pups than shyer individuals, but only in years of low lemming density (Clermont et al. 2023). As for individual fitness, the effects of personality on blue tit (*Cyanistes caeruleus*) survival was dependent on the masting of beeches in the habitat, meaning certain personalities were favoured in mast years (Dingemanse et al. 2004). While personality may be quite stable in an individual's life, its effects may not be, and are extremely context dependent (age, sex, environmental conditions, etc.) (Dingemanse et al. 2004; Cote et al. 2008). Personality may impact reproduction directly, such as aggressive male blue tits provisioning their chicks less and fast exploring females having higher reproductive success (Mutzel et al. 2013). However, personality can also affect reproduction indirectly through mate choice (Chira 2014).

Animals will sometimes choose a mate based on their own and/or their conspecifics' personality (Schuett et al. 2010). Certain personality extremes may be preferred by the choosy sex as an indicator of fitness, especially since they may be inheritable (Munson et al. 2020). Sometimes, certain personalities may affect the level of choosiness itself. A study on zebra finches (*Taeniopygia guttata*) found that highly exploratory females were less choosy of their mates (David and Cézilly 2011).

Notably, animals may sometimes select a mate with a similar personality (i.e. assortative mating). Assortative mating according to personality exists in many species (González-Medina et al. 2020).

A meta-analysis conducted on pair personality showed a trend of positive assortative mating within populations (Jiang et al. 2013). However, assortative mating was also negative for many cases (about 19%), showing all personality-associated mating trends may not be assortative. Assortative mating may in some cases simply be a mechanism where individuals select for a trait which will produce fitter offspring (Ariyomo and Watt 2013; Chira 2014). Nonetheless, a study on zebra finches showed that foster parents with similar personalities raised healthier chicks, regardless of the biological parent's personality (Schuett et al. 2011). This indicates that pair personality may affect reproductive success through behavioural factors.

Choosing a mate with the right personality is not just a choice of which traits to pass off to the offspring, but also a matter of compatibility. In mound-building mice (*Mus spicilegus*), for example, pairs with similar personalities reproduce earlier (Rangassamy et al. 2015). In Seychelles warblers (*Acrocephalus sechellensis*), pairs with higher differences in personality scores had higher rates of extra pair copulations (Edwards et al. 2018). Studies on pair boldness corroborate such ideas as well. Black-legged kittiwakes (*Rissa tridactyla*) with similar boldness scores were more likely to have a successful season and less likely to divorce (McCully et al. 2023).

Pair coordination, specifically, may be a product of personality compatibility in species which exercise bi-parental care through pair coordination. In eastern bluebirds (*Sialia sialis*), birds with similar aggressiveness levels and nest defense strategies had higher reproductive success (Burtka and Grindstaff 2015). Since the authors did not find any effect of individual aggressiveness on reproductive success, they strongly recommend quantifying both parents' personality in species with bi-parental care. Pair compatibility may also be important during incubation and chick rearing, where birds must carefully coordinate their switchovers and provisioning (Spoon et al. 2006).

Coordination may not always be associated with assortative pairs. In cockatiels (*Nymphicus hollandicus*), pairs with different aggressiveness levels tended to have less intrapair aggression and subsequently better incubation coordination (Fox and Millam 2014). Negative assortative mating, or disassortative mating has also been observed in various species (Both et al. 2005; Martin-Wintle et al. 2017). Mating with a dissimilar mate may be advantageous, especially in socially monogamous species. Choosing a mate with a different personality may be helpful in mitigating challenges related to alternating environmental and foraging conditions between seasons. In great tits (*Parus major*), chick survival is related to parent personality, but exactly which traits are advantageous depends on the year and the environmental condition for both males and females (Dingemanse et al. 2004). Great tits also perform disassortative mating, potentially to help respond to contrasting conditions (Dingemanse et al. 2004). Mulard et al. (2009) even suggest that assortative mating may be maladaptive, as genetic similarity led to fitness costs such as lower growth rates in black-legged kittiwake chicks (*Rissa tridactyla*).

Personality in Seabirds

While still an emerging field, an increasing number of seabird studies studying their personality have been getting published since the beginning of the 2010s (see Table 1, a compilation of all seabird personality studies our scoping review yielded). Most studies on seabird personality have so far underlined its impact on foraging strategies. For example, bolder black-legged kittiwakes tend to have more routine-like behaviours, with high site fidelity during incubation and repeatable foraging trips (Harris et al. 2020). Individual specializations are important to seabirds on an ecological, individual and population level as they often lend advantages in breeding performance and foraging (Ceia and Ramos 2015). Northern gannets (*Morus bassanus*), for example, have been shown to have clear individual, repeatable differences in scavenging tactics (Patrick et al. 2015). In general, there seems to be a trend whereby bolder individuals show less exploratory behaviours than shy individuals, through higher repeatability and shorter foraging trips. In the wandering albatross (*Diomedea exulans*), bolder males feed in shallow and closer sites to the colony compared to shyer individuals who forage in deeper and further sites from the colony (Patrick and Weimerskirch 2015). Not all seabird taxa seem to follow the trend of shy birds foraging further: bolder female African penguins (*Spheniscus demersus*) use more sinuous paths during foraging and travelled deeper than shy females (Traisnel and Pichegru 2019). A study on wandering albatross suggests that bold individuals will prioritize travel while shy individuals will prioritize search during foraging (Gillies et al. 2023). Perhaps boldness does not affect the total effort during foraging in seabirds, rather bolder individuals will focus on patches they already know regardless of risks such as competition, while shy individuals will opt to avoid risks and therefore explore new areas.

Seabirds are also no strangers to contrasting effects of personality according to environmental conditions. Shy Cory's shearwaters (*Calonectris borealis*) notably foraged further from the colony in adverse environmental conditions (Krüger et al. 2019). Bold black-browed albatross (*Thalassarche melanophris*) also tended to forage closer to the colony and shallower, but this may not always be an advantage: shyer females had higher reproductive success in low quality years (Patrick and Weimerskirch 2014). The context-dependent fitness trade-offs of personality-influenced foraging strategies are apparent here: in a good year, it may be better to be bold as repeatable trips to good patches may lead to lower energy expenditure. However, in bad years, shyer and highly exploratory individuals may prove more resourceful in finding prey. If oceanic conditions keep declining, shyer birds may slowly be advantaged leading to potential personality diversity losses (Traisnel and Pichegru 2019; Jeffries et al. 2021).

Foraging strategies not only have an impact on individual fitness, but on the offspring as well. The second most studied effect of personality in seabirds is on reproduction (see Table 1) Certain personalities may affect reproductive success through chick rearing (Patrick and Weimerskirch 2014). Notably, shy Cory shearwaters foraged further and with larger efforts, but at lower reproductive success rates compared to bolder individuals (Pereira et al. 2024). Most studies link reproductive success to foraging in personality related seabird studies. There is a study which examined anti-predator nest defense and boldness in black-tailed gulls (*Larus crassirostris*) (Kazama et al. 2012). They found that males more aggressive males with high risk defense strategies fed their chicks more frequently. Interestingly, while most pace-of-life personality literature suggest that bolder individuals breed more but at a lower survival cost: (Van de Walle et al. 2023) found that bolder wandering albatross males overall had lower lifetime reproductive success, as they spent more time as non-breeders.

Choosing a mate according to personality may be quite relevant to a taxon such as seabirds. Being sexually monomorphic, mate choice may be more based on behaviour related aspects compared to other taxa. For an organism that is long-lived, exercising biparental care and socially monogamous, finding a compatible partner is crucial. While assortative mating has been demonstrated in black-legged kittiwakes (Collins et al. 2019), it seems unclear whether it would be the most advantageous strategy for other seabird species, especially as environmental conditions become more and more unstable. For example, Traisnel and Pichegru (2019) found a weak assortative mating trend in African Penguins which did not in itself impact reproductive success. However, in years where food was less abundant, shyer individuals were more successful as they spent energy on nest defense strategies, but rather on searching for new foraging patches.

Personality also impacts reproduction in long-lived organisms which high levels of parental care such as seabirds through fidelity. Divorce occurs to 95% of bird species (Mercier et al. 2021). Mate switching occurs as a way for individuals to increase their reproductive success. Drivers of divorce often include site quality, age of pair and success during the breeding season (Wagner et al. 2022; Gousy-Leblanc et al. 2023). The individual mechanisms behind divorce, however, aren't fully understood, but seem to depend on an individual's sex, size and age (Wheelwright and Teplitsky 2017). Individual and pair personality may therefore be an actor as well. A study on wandering albatross found that shyer males had higher rates of divorce (Sun et al. 2022a). Divorce may be a strategy especially employed in low quality years: northern gannets which decide to divorce after a breeding failure due to a poor quality year have higher reproductive success in the following year (Pelletier and Guillemette 2022). Oceanic conditions seem to impact seabird's fidelity: in Monteiro's storm petrel (*Oceanodroma monteiroi*), mate and site fidelity is higher following a successful breeding season (Robert et al. 2014).

If there is little information on personality and mate retention in seabirds, there is next to nothing on site fidelity in relation to personality. While site fidelity may often be related to mate retention, pairs may sometimes decide to change nesting sites together. We must therefore consider personality and fidelity as its own process (Naves et al. 2006). One study does test for such ideas and found that bolder black-legged kittiwakes were more site faithful during incubation, but not chick rearing (Harris et al. 2020). In general, bolder kittiwakes engaged in more-routine like behaviours. Some studies also explore the link between personality and nest site choice. A study on black-headed gulls (*Larus ridibundus*) found that parents of widely spaces nests tended to be more aggressive than parents nesting in high density areas (Druzyaka et al. 2015). More aggressive parents tended to attend the nest more, and chicks of sparsely distributed nests had higher growth rates.

Table 1. Table summarizing seabird personality studies from a literature survey through Scopus and Web of Science. I used a combination of keywords "seabird*" or "*gull*" or "puffin*" or "razorbill*" or "cormorant*" or "penguin*" or "albatross*" or "pelican*" or “auk*” or “stern*” or “boobie*” or “skua*” or “petrel*” or “gannet*” or “fulmar*” or “frigatebird*” or “skimmer*” or “prion*” or “kittiwake*” or “shearwater*” and “personalit*” or “bold*” or “shy*” or “explorat*” or “*avoidance*” or “neophob*” or “temperament*” or “neophil*” or “activit*” or “sociabilit*” or “aggressive*” to scope for any studies which assessed some form of personality in seabirds.

Reference	**Study Species**	**Latin name**	**Topic / Link**	**Test**	**Metric measured**	**Mentions personality**
Kazama et al. 2012	Black-tailed gull	*Larus crassirostris*	Reproductive success, nest defense	Predator test	Aggressiveness, boldness	no
Patrick and Weimerskirch 2014	Black-browed albatross	*Thalassarche melanophris*	Foraging, reproductive success	Novel object test	Boldness	yes
Grace and Anderson 2014	Nazca boobie	*Sula granti*	Contextual plasticity	Human approach social stimulus test	Aggressiveness, boldness, sociability	yes
Grace and Anderson 2014	Nazca boobie	*Sula granti*	Stress	Novel object, social stimulus	Aggressiveness, boldness, sociability	yes

Patrick and Weimerskirch 2015	Wandering albatross	*Diomedea exulans*	Foraging, reproductive success	Novel object	Boldness	yes
Druzayaka et al. 2015	Black-headed gull	*Chroicocephalus ridibundus*	Nest site choice	Conspecific test	Aggressiveness	no
Traisnel and Pichegru 2018	African penguin	*Spheniscus demersus*	Reproductive success, mate choice	Human approach	Boldness	yes
García et al. 2019	Olrog's gull	*Larus atlanticus*	Food consumption	Novel object	Exploration	no
Morandini and Ferrer 2019	Black-browed albatross	*Thalassarche melanophris*	Nutritional condition	Novel object	Boldness	yes
Collins et al. 2019	Black-legged kittiwake	*Rissa tridactyla*	Mate choice, reproductive success	Novel object	Boldness	yes
Traisnel and Pichegru 2019	African penguin	*Spheniscus demersus*	Foraging	Human approach	Boldness	yes
Krüger et al. 2019	Cory's shearwater	*Calonectris borealis*	Foraging	Novel object	Boldness	yes
Harris et al. 2020	Black-legged kittiwake	*Rissa tridactyla*	Foraging site fidelity	Novel object	Boldness	yes
Harris et al. 2020	Black-legged kittiwake	*Rissa tridactyla*	Carryover effects	Novel object	Boldness	yes

Gatt et al. 2021	Cory’s shearwater	*Calonectris borealis*	Migration	Novel environment	Exploration	yes
Sun et al. 2022	Wandering albatross	*Diomedea exulans*	Mate choice	Human approach	Boldness	yes
Ruiz-Raya and Velando 2022	Yellow-legged gull		Parental light environment	Tonic immobility	Boldness	yes
Gillies et al. 2023	Wandering albatross	*Diomedea exulans*	Foraging	Human approach	Boldness	yes
McCully et al 2023	Black-legged kittiwake	*Rissa tridactyla*	Mate choice, reproductive success	Novel object	Boldness	yes
Walle et al. 2023	Wandering albatross	*Diomedea exulans*	Reproductive success, demography	Human approach	Boldness	yes
Pereira et al. 2024	Cory’s shearwater	*Calonectris borealis*	Foraging, reproductive success	Novel object	Boldness	yes

Understanding how personality affects life-history strategies in seabirds, which serve as indicators of ecosystem health, will help shed light onto how individuals face poor quality years (Piatt et al. 2007; Wolf and Weissing 2012; Le Bohec et al. 2013). A few studies so far indicate that due to their highly exploratory behaviour (particularly during foraging), shyer birds may be advantaged as oceanic conditions worsen (Traisnel and Pichegru 2018; Jeffries et al. 2021). However, the broader implications of a decline in personality (and therefore genetic) diversity are not fully understood or confidently denounced, as current research has so far been limited. Out of the 21 studies our literature search yielded, 14 of them were conducted on albatross and gull species (see Table 1).

Notably, I could not find any studies that directly assessed the fitness consequences of personality in auks. Burrowing auks (such as puffins) are a taxon highly sensitive and vulnerable to disturbance (Rodway et al. 1996; Gjerdrum et al. 2003; Sydeman et al. 2017; Smith et al. 2024). Burrowing animals occupy a unique niche which provide protection from environmental extremes and predators (Boggs et al. 1984). The ecological implications of personality may be quite different for a burrow nester than, say, a cliff nester. Furthermore, unravelling the mechanisms by which certain individuals are more susceptible to nest abandonment following human disturbance may help researchers and organizations of all backgrounds mitigate their anthropogenic impact when working with these sensitive species.

Another limit in the literature was the types of questions asked. Most of the studies which clearly mention personality (see “Mentions personality” column in Table 1, where I specify whether the study was classified under that category) studied the effects of personality (and almost always boldness) on foraging strategies (Patrick and Weimerskirch 2014; Patrick and Weimerskirch 2015;

Traisnel and Pichegru 2019). In addition, by far the most used test was the novel object test. Overall, the world of seabird personality studies could benefit from expanding the range of species they study, and by asking a wider variety of questions, such as the link between personality, fidelity, mate choice and reproductive success. This thesis aims to accomplish these objectives by exploring such ideas in a burrow nesting auk: the rhinoceros auklet.

Natural history of the rhinoceros auklet

The rhinoceros auklet (*Cerrorhina monocerata*) is a small auk and a relative the puffin tribe Fraterculini (Smith and Clarke 2015). Around 400 to 600g they use their stout wings for both flying and propelling themselves while diving(Gaston and Dechesne 1996). Uniformly grey during the non-breeding season, they adorn two sets of white plumes above their eyes (their eyebrows) and another along their cheeks (moustache) (Gaston and Dechesne 1996). Some old studies affirm them as having a "vicious temperament", but our own observations show they have a diversity of personalities, with some individuals being very aggressive towards an intruder and others very docile (Richardson 1961). They are long-lived with the oldest individual on record reaching 31 years of age (Hipfner et al. 2019).

While they do not own a bright large bill like their puffin relatives, they do sport unique a horn-like ornamentation earning them their name. This small white vertical horn (also known as the rhamphoteca) protrudes from their bill at the base of the culmen and regrows each breeding season (Wilkinson et al. 2019). A study by Wilkinson et al. found that the ornamentation is fluorescent under UV light (Wilkinson et al. 2019). The mechanisms behind the purpose of the fluorescence are still unknown, but they may be a sign of fitness. Notably, while there was great variation between individuals, there was no difference in the fluorescence levels between sexes.

Rhinoceros auklets are colonial burrow nesters. They are described by some as nocturnal because they visit the colony and emerge from their nests at night, possibly to avoid kleptoparasitism by gulls and other predators (Watanuki 1990). They may also be avoiding conspecific kleptoparasitism (Senzaki et al. 2014). They nest in dense vegetation and shrubs; on Middleton Island (Alaska), our study site, the colonies can be found in between salmonberry bushes (*Rubus spectabilis*) along cliff edges (Miyazaki 1996; Sun et al. 2020).

Distributed along the North Pacific, their migration distances depend on the latitude of their breeding grounds, with individuals from northern colonies travelling larger distances during migration than their southernmost counterparts (Hipfner et al. 2020). The largest known rhinoceros auklet colony is located on Teuri Island (Japan) (Watanuki and Ito 2012), but they breed throughout the North Pacific from the Channel Islands in California to the Aleutian Islands in Alaska and in Japan and the South Korean Peninsula (Sowls et al. 1980).

Rhinoceros auklets, like all auks, are considered to be socially monogamous, but not much is known on their mate choice and retention habits (Thoresen 1983). They have been shown, however, to synchronize their pre-laying foraging habits, perhaps copulating at sea (Kubo et al. 2018). Pairs will usually arrive at the colony in March and April, digging their new or pre-existing burrows (Richardson 1961). They lay a single egg from April to June onto a nest of twigs and leaves in the nest chamber of their burrow (which tends to be slightly larger than the tunnels leading to it (Richardson et al. 1961). If an egg is lost early enough in the breeding season, they may relay (Richardson et al. 1961; observational). Incubation lasts about 50 days depending on colonies, with one parent incubating the egg throughout the day and switchovers occurring every 1-3 days at night (Heath 1915; Wilson and Manuwal 1986). (On Middleton Island, switchovers occur between 23:00 and 4:00, although our automated readers have detected entrances as early as 22:00 and as late as 5:00 (pers. obs.).

Once chick rearing begins, adults stop spending time in the burrow during the day after the chick is a few days old, instead returning nightly to deliver prey items to the nest (Bertram and Kaiser 1993; Davoren and Burger 1999). The parents provision the chick until fledging for 40 to 60 days, by which time the chick will have gone from 50 g to 400 g (Richardson 1961; Harfenist and Ydenberg 1995). This nightly provisioning of whole food items is extremely helpful for the sampling of prey items by researchers, which makes up a big part of the research led on rhinoceros auklet (Davoren and Burger 1999; Cunningham et al. 2018).

Rhinoceros auklets are not highly specialized feeders, foraging on a variety for epipelagic fish species around the colony (Vermeer 1980; Kuroki et al. 2003; Lance and Thompson 2005; Beaubier 2006). Food items delivered to chicks include sand lance (*Ammodytes tobianus*) (their preferred diet), capelin (*Mallotus villosus*), herring (*Clupea harengus*), greenling (Hexagrammidae), salmon (Salmonidae) and sablefish (*Anoplopoma fimbria*) (Bertram and Kaiser 1993; Thayer et al. 2008). This "bill load" they provision consists of varied prey items they foraged during the day and carry externally in the bill (Takahashi et al. 1999; Cunningham et al. 2018). This diverse and plentiful bill load has been shown to reduce stress in checks by providing high nutritional value (Will et al. 2014; Will et al. 2015). In general, reproductive success can be highly variable between years and between individuals (Borstad et al. 2011), with environmental conditions highly affecting chick provisioning (Bertram et al. 1991). The presence of sand lance in chick diet specifically, has historically been shown to positively affect reproductive success and chick growth(Hedd et al. 2006; Hipfner and Galbraith 2013). Nonetheless, A study on nestlings showed they can cope with food shortages by using morphological allocation such as prioritizing skeletal growth over mass reserve and through adrenocortical suppression (Sears and Hatch 2008). While we mostly understand the foraging habits of chick rearing auklets, they forage different items for themselves than for their chicks (Davoren and Burger 1999). Generally, rhinoceros auklets do indeed show high behavioural plasticity in foraging habits, within and between seasons (Davoren 2000). The variable reproductive success of auklets is most likely due to changes in the biotic and abiotic environment, with bill load prey composition showing high variability between years (Davoren 2000; Cunningham et al. 2018).

Middleton Island, Alaska (59.42° N, 146.32° W) is an 8 km long and 1.6 km wide island situated in the Gulf of Alaska (Crowley et al. 1997). This biological research station has been monitoring the rhinoceros auklet population since 1977 (Hatch 1984). Collection of food samples has been the main monitoring aspect of the population since 1993 (see Figure 1).

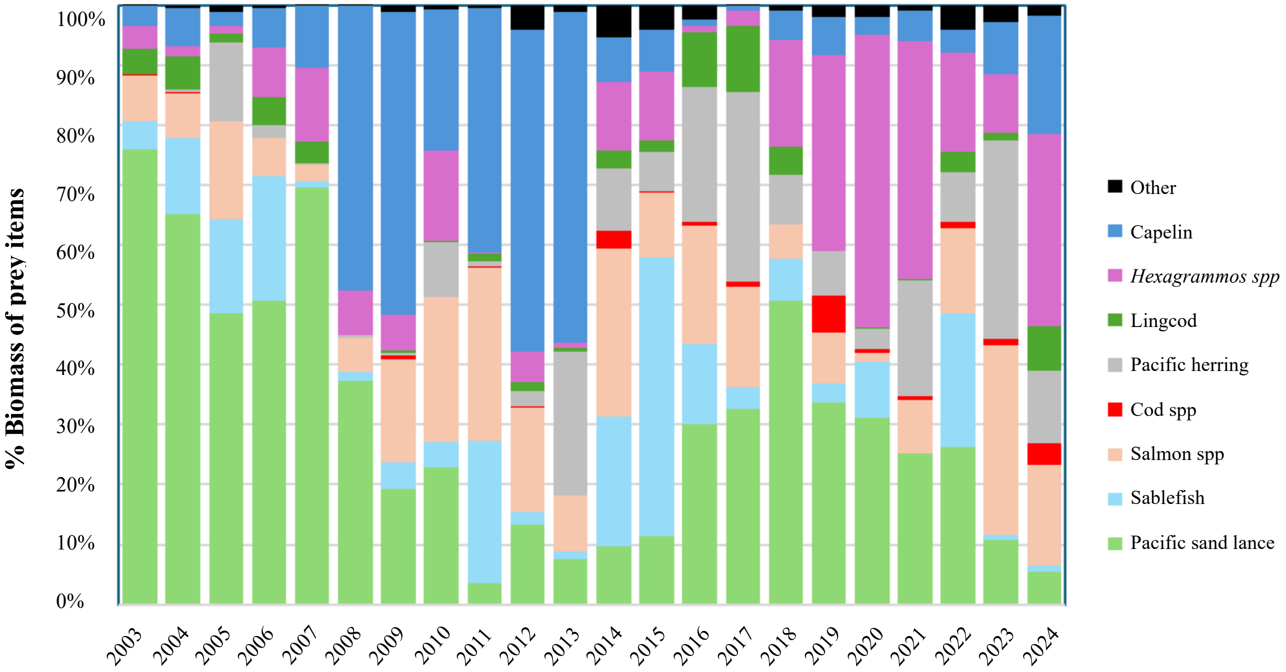

Figure 1. Proportion of total biomass of prey observed in auklets diets through the years, modified from Solmon et al. 2025 (unpublished).

However, since 2017 and up until 2024, 188 artificial nest boxes have been buried and installed in two of the subcolonies on Middleton Island. The artificial burrows consist of two parts: an L-shaped wooden box made with ½-inch-thick plywood treated with wood preservative and a corrugated plastic tubing as an entrance tunnel. The top of the box is equipped with an access lid to the nesting chamber and the floor is made of wire mesh. Nest boxes are buried about 15 cm underground, partially filled with soil, and then marked with a uniquely numbered stake. Combined with the RFID (Radio Frequency Identification) automatic resighting system being set up since 2022 (Marcouiller et al. 2024), we have been able to slowly implement individual based monitoring. Personality is a new avenue being explored in this study system which has so far mostly been focused on diet samples.

NOTE ON CHAPTER 1

This chapter corresponds to a manuscript I plan on submitting to the journal of *Animal Behaviour* as first author. The data in this chapter was collected by me and interns of the Institute for Seabird Research and Conservation on Middleton Island (Alaska). This study was conceptualized by me with the supervision of Dr. Kyle Elliott (McGill University) and the help of Dr. Shannon Whelan (Institute for Seabird Research and Conservation). This manuscript was written and revised in with these three authors.

CHAPTER 1. Unfaithful but still successful: Low mate and site fidelity in shy rhinoceros auklets does not affect reproductive success

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Abstract

In animals with biparental care, animal personality can impact an individual's reproductive success through both individual or partner traits. Bolder individuals (more willing to take risks) tend to reproduce more successfully, and the higher reproductive success may lead to higher mate and site fidelity. To test this idea, we studied personality, reproduction and mate choice in a burrow-nesting seabird, the rhinoceros auklet (*Cerorhinca monocerata*) in two years. To obtain personality scores we ran a Principal Components Analysis (PCA) behavioural for two behavioural assays: a novel object video test and a human intrusion hand test. Auklet personality scores were repeatable within individuals and across years, but there was no assortative mating with personality or association with reproductive success. However, shyer individuals were more likely to switch sites and mates. We conclude that shy individuals may be less inclined to engage in intraspecific competition for mates and territories, opting instead to invest in forming a new match, but with minimal impact on overall fitness.

Keywords: seabird, personality, boldness, mate choice, reproduction, site fidelity, divorce, nest box, auk

Introduction

It is now well established that personality—defined as consistent, repeatable differences in behavior among individuals—exists in non-human animals (Gosling and John 1999; Locurto 2006; Griffin et al. 2015; Roche et al. 2016; Réale et al. 2007). One of the most extensively studied aspects of personality is the shyness-boldness continuum (Sloan Wilson et al. 1994; Sih et al. 2004). Boldness refers to an individual's propensity to take risks (Stamps 2007; White et al. 2013). This trait is particularly significant because it intersects with key questions about life history trade-offs (Wolf et al. 2007; Bell et al. 2009). Specifically, shyer individuals may tend to prioritize future fitness by avoiding risky but potentially rewarding activities, whereas bolder individuals, often with lower expectations of future survival or reproduction, may be more likely to pursue high-risk, high-reward strategies (Wolf et al. 2007).

Personality may impact fitness through reproductive success, as bolder individuals in many taxa reproduce more successfully, but at higher mortality costs (Smith and Blumstein 2008). However, there are other taxa where the reverse is true; young bolder bighorn sheep (*Ovis canadensis*) rams had high survival but low reproductive success early in life. However, bolder rams had higher reproductive success later in life (Réale et al. 2009). We must therefore consider factors such as age, sex and the natural history of each species when considering fitness consequences of personality. The effects of personality on fitness likely depend on environment, such as prey availability and foraging conditions (Clermont et al. 2023).

While personality may impact reproduction directly it may also affect reproduction indirectly through mate choice (Chira 2014). Individuals will sometimes select a mate based on their own and/or their conspecifics' personality (Schuett et al. 2010). For example, animals may choose to mate with a similar personality individual (i.e. assortative mating) (González-Medina et al. 2020).

Choosing a mate with the right personality isn't just a choice of which traits to pass off to the offspring, but also a matter of compatibility. Black-legged kittiwakes (*Rissa* t*ridactyla*) with similar boldness levels, for example, were more likely to successfully breed and to stay together (McCully et al. 2023). Personality compatibility may be advantageous in socially monogamous species which exercise bi-parental care through pair coordination (Burtka and Grindstaff 20 15; Spoon et al. 2006). Yet, assortative mating may not be the only viable pairing strategy: disassortative mating has also been observed in various species (Both et al. 2005; Martin-Wintle et al. 2017). Selecting for a mate with a different personality may be helpful in mitigating challenges related to contrasting environmental conditions between breeding seasons (Dingemanse et al. 2004). The fitness advantages of having a mate with a specific personality may only be beneficial for certain species, or rather for certain contexts.

Mate selection via personality may be particularly relevant in long-lived species with mate retention that are sexually monomorphic, where mate choice may be less based on morphology. For example, black-legged kittiwakes have assortative mating with a positive effect of boldness on reproductive success (Collins et al. 2019). However, bold black-browed albatross tend to forage closer to the colony and shallower, but this may not always be advantageous as shyer females had higher reproductive success in low quality years (Patrick and Weimerskirch 2014). Finally, personality may also affect fitness in long-lived animals with biparental care, such as seabirds, through fidelity. While divorce is widespread, the individual drivers of it aren't fully understood, but seem to depend on an individual's sex, size and age (Wheelwright and Teplitsky 2017; Pelletier and Guillemette 2022). Individual and pair personality may be an important component (Sun et al. 2022).

Here we explore the link between boldness (measured with a novel object test), reproduction and mate choice in the rhinoceros auklet (*Cerorhinca monocerata*). Auklets exhibit highly variable interindividual nest attendance patterns and incubation rates (Blight et al. 2010), showing individual differences in strategies during breeding. Coordination may have a role to play in mate choice as rhinoceros auklets have been shown to synchronize their foraging activities during pre-laying (Kubo et al. 2018). We hypothesized that (H1) auklets perform assortative mating as it leads to better coordination which affects their reproductive success. We predicted that personality scores of mates will be correlated and pairs with similar personality scores will have higher reproductive success. Alternatively, auklets may perform disassortative mating (H2) and pairs with different personality scores could have higher reproductive success. As shy and bold individuals will employ different foraging strategies, a pair with higher differences may be able to mitigate contrasting environmental conditions better when provisioning for a chick. In the eventuality of no trends in mate choice (H3), we predicted that bolder individuals will have higher reproductive success. Finally, we also hypothesized that (H4) boldness affects fidelity in the rhinoceros auklet, predicting that bolder individuals will be more likely to stay at a site or with their previous mate.

Methods

Study system

We studied the reproductive success and personality of a burrow-nesting auk, the rhinoceros auklet (*Cerorhinca monocerata*), breeding in artificial nest boxes on Middleton Island, Alaska (59.42° N, 146.32° W) during the 2023 and 2024 breeding seasons Breeding pairs of rhinoceros auklets lay one egg usually in late April to early May (Hatch 1984). They have highly variable interindividual nest attendance patterns and incubation rates, but incubation lasts ~45 days with individuals taking 1 to 4 day shifts (Blight et al. 2010; Wilson and Manuwal 1986). When the chick is a few days old, parents stop attending during the day and deliver food at night. A total of 120 boxes were buried in a section of a rhinoceros auklet colony between 2017 and 2018. Boxes are installed in early April, right before the auklets' egg laying phase. The boxes consist of two parts: a ½ inch-thick plywood nest chamber and a corrugated plastic tube which serves as an entrance tunnel. The bottom part of the box is made of metal mesh wire, with a thick layer of soil covering it. Boxes are buried about 6 inches underground, with uniquely numbered stakes identifying them. All boxes installed pre-2024 are L-shaped, with an access hatch allowing for easy access to the nest chamber. Nest boxes are ideal as they provide for easy access to the birds without compromising the burrow's structural integrity, as well as providing uniformization of the environment in behavioural studies.

Figure 2. A rhinoceros auklet nest box unburied. (1) is the entrance tube and the opening through which the first behaviour test was conducted (see Behavioural assay section). (2) is the access hatch, through which the hand test is conducted. (3) is the location of the nest chamber.

Data collection

Productivity monitoring

Productivity monitoring has been conducted on the Middleton Island auklet colony since 2003. Since 2018, nest boxes have been monitored as well. The reproductive success data for this study was collected in the context of this long-term monitoring. A first check to identify the contents of boxes was first conducted 16 May 2023 and 25 May 2024. Boxes that were active were then examined every 5 days. Each check consisted of plugging the entrance of the box to make sure the adult did not escape, and then noting the contents of the box (presence of a bird, presence or absence of an egg (warm, cold, broken), presence of a chick). When an egg is first found we floated it to estimate laying date (Liebezeit et al. 2007). The egg is carefully retrieved from the nest chamber and submerged in water. If the egg is sinking, we measured the angle at which it rests at the bottom of the container. If the egg was floating, we measured the height at which it floats above the water line. We used the floatation technique and formula from Sun et al. (2020). For a sinking egg, we used the following equation:

$$\textit{Lay date} = \textit{Date measured} - (0.002 * \textit{floating angle}^2 + 0.078 * \textit{floating angle} + 1.16)$$

For a floating egg, we used the following equation:

$$\textit{Lay date} = \textit{Date measured} - (2.014 * \textit{floating height} + 20.027)$$

Once a hatched chick was found, the regular checks stopped. Chick weight (g) and wing chord (mm) was measured at 5 and 20 days. We collected the following reproductive success measures: fledge success (1 = for a burrow whose chick fledged, 0 = for a burrow that did not fledge a chick, including eggs that did not hatch), daily chick weight gain, daily chick wing growth and laying date. Our study only included nest boxes in which an auklet laid an egg.

Behavioural assays

We performed behaviour tests on a total of 18 burrows that had an incubated egg (n = 35 birds, as one nest abandoned before we were able to test for the mate) in 2023. We exclusively assessed incubating birds as only birds which have an egg spend the day in the colony (in other words, nest boxes were only regularly occupied by incubating adults). We performed tests on 31 burrows in 2024 (n = 61 birds). We reassessed n = 23 (12 boxes) of the 2024 sample birds to test for interannual repeatability. We aimed to perform the tests 3 times per breeding season per bird to test for repeatability of the behaviours, with around 5 days in between tests. We captured individuals only after the first test, to band and identify them. Since some birds abandoned the nest and there was often one parent incubating much more than the other, we actually tested birds an average of 2.189 times per year, and 2.811 times in total (for both 2023 and 2024). Two behavioural assays were performed, one after the other. All behavioural assays were performed between mid to late incubation.

Endoscope novel object test

We measured boldness with two tests. The first personality assessment was a novel object test where we entered an endoscope camera from the main entrance. A coloured ping pong ball attached to the end of the camera served as the novel object. The bird’s reaction to this test may be similar to how an individual would behave to a predator, an unrecognized conspecific, or another foreign threat entering the burrow entrance. Once the object was in front of the bird, we recorded the individual’s reaction to the novel object for 2 min. Videos were later analysed according to an ethogram (Table 2).

After this test was conducted, we waited 10 minutes, which was always enough time for the bird to start incubating the egg again. We then performed the second test.

Hand test

This test occurred between the endoscope test and right before the capture of the individual. We opened the access hatch to the nest box and placed a hand in front of the bird. This might be similar to how an individual would react to a threat that breaks through the burrow surface, or if poor weather exposes the nest chamber. We then waited 10 seconds and recorded the behaviours in Table 2.

Table 2: Ethogram depicting the behavioural states associated with the endoscope novel object test and the hand test. The position of the bird relative to the bird are divided into three behavioural state events (on the egg, next to the egg, and off the egg). The time allotments for each behaviour were recorded. The number of bites to the novel object are behavioural point events. For the hand test, each test yielded one of three mutually exclusive state events (staying on the egg, moving away from the object, and running away towards the exit). Each bite and peck to the novel object was recorded as a point event.

Behavioural State	Test	Type of Event	Description
On egg	Endoscope	State Event	Bird stays on the egg, incubating
Next to egg	Endoscope	State Event	Bird moves next to egg, not incubating
Off egg	Endoscope	State Event	Bird runs away from the egg, towards entrance
Bite	Endoscope	Point Event	Biting at novel object
Bite (B)	Hand test	Point event	A prolonged bite, holding on to the hand
Peck (P)	Hand test	Point Event	Pecking quickly and softly at the hand
Move (M)	Hand test	State Event	Moving, but not running, away from the hand
Stay (S)	Hand test	State Event	Staying on the egg
Run (R)	Hand test	State Event	Running away from the hand towards exit

Once the test was performed, we retrieved the bird from the nest and placed it in a handling bag to reduce stress. We then wrote down the band number or banded the bird if necessary. Birds were also PIT (Passive Integrated Transponder) tagged as part of a long-term RFID resighting project.

PIT tagging does not impact their reproductive success (Marcouillier et al. 2024). Since rhinoceros auklets are sexually monomorphic, we also took a brachial vein blood sample to DNA sex them (Addison et al. 2008). Average handling time was 5 min and never exceeded 10 min. To minimize disruption, we placed a piece of black Tesa tape (tesa tape inc. 5825 Carnegie Boulevard, Charlotte, North Carolina 28209) on the first mate we handled, to easily be able to identify the mates for subsequent behaviour tests without having to pull the bird out. The purpose of performing both methods was to compare it to the endoscope technique. The hand test method is convenient as behaviours can be recorded whenever an individual must be handled, therefore not adding any extra disturbance.

Genetic testing

Blood samples were preserved on DBS (Dry Blood Spot) absorbent filter paper. Following Griffiths et al.'s method, we determined the sexes of the sample birds by DNA extraction of the blood samples and PCR (Polymerase Chain Reaction) amplification. We used the P2F (5'-TCTGCATCGCTAAATCCTT) and P8R (5'- CTCCCAAGGATGAGRAAYTG) primers.

Statistical analyses

All statistical analyses and plots were performed in RStudio 2024.4.2.764 (Posit Team 2024) using R version 4.3.2 (2023-10-31). Linear mixed effect models (LMMs) were fitted using the lme4 package (Bates et al. 2015). Bayesian mixed models were calculated using the MCMCglmm (Markov Chain Monte Carlo generalized linear mixed model) package (Hadfield 2010). Graphics and figures were plotted using the ggplot2 (Wickham 2016).

Personality scores

We ran a Principal Component Analysis (PCA) on centred-scaled behavioural states and point events of both behavioural assays. For the video test, we extracted the values for the time allocated on the egg, next to the egg and off the egg (all mutually exclusive). For the hand test, we used a degree of movement, with staying on the egg being a 0, moving away being a 1 and running being a 2. We also inputted the total number of bites and pecks during both tests. We decided to use PC1 and PC2 for the rest of the analyses as it explained 58% of the total variance, as two measures of boldness.

Repeatability analysis

To determine whether the behavioural states could be classified as a measure of personality, we assessed the repeatability of the first two components of our Principal Component Analysis (PC1 and PC2). To do so, we implemented the approach proposed by Araya-Ajoy et al. (2015). We fitted linear mixed-effects models (LMM) to partition variance components across and within years. We used general bird ID, Band, and the combination of bird and year, Band_year, as two random effects with year as a fixed effect to control for the potential average difference in the behaviour between years. PC1 and PC2 were our response variables. The model formula was specified as:

$$PC_i = \alpha + \beta \times Year + u_{Band} + u_{Band\_Year} + \epsilon$$

where α is the population intercept, β is the effect of Year on PC_i ($i = 1$ or 2), u_{Band} *and* u_{Band_Year} are random effects, and ϵ is the residual error.

Normality of the residuals was tested for each of our mixed models using the Shapiro-Wilk test and by visualizing them using Q-Q plots.

Long-term repeatability (R_{lt}) was calculated as:

$$R_{lt} = \frac{\sigma^2_{Band}}{\sigma^2_{Band} + \sigma^2_{Band\_year} + \sigma^2_{Residual}}$$

and short-term repeatability (R_{st}) was calculated as:

$$R_{st} = \frac{\sigma^2_{Band} + \sigma^2_{Band\_year}}{\sigma^2_{Band} + \sigma^2_{Band\_year} + \sigma^2_{Residual}}$$

Where σ^2_{Band} is the variance component attributed to differences between individuals, $\sigma^2_{Band\_year}$ is the variance component associated with individual-by-year interactions and $\sigma^2_{Residual}$ is the residual variance

Since PC1 showed high variance and was repeatable both inter- and intra-annually with no effect of year (year had an effect on PC2, and had a long term repeatability bellow the 0.3 threshold, see Results section), we used it as a measure of boldness for our following analyses. We considered individuals with a low PC1 score bold, and inversely an individual with a high PC1 score as shy.

Sex and assortative mating analysis

We obtained the sexes of 74 individuals, 37 males and 37 females. To assess whether there were sex differences in boldness, we performed a Welch Two-Sample t-test, comparing PC1 scores between males and females.

We tested for the presence of assortative mating based on boldness by using a Bayesian bivariate mixed model, with each mate's PC1 score as fixed effects, as described in Class et al. (2017). We used nestbox per year ID as well as pair ID as random effects. This way, we assessed the covariance in boldness between mates at three levels:

- Between pairs through years (random effect is pair ID)
- Between pairs within years (random effect is nest box per year ID)
- Residual within pairs.

We specified inverse-Wishart priors for variance parameters, with V set to the identity matrix (I_2) and degrees of belief (ν) matching the order of the matrices (2). Priors were divided by the number of random effects, 3, to account for scaling. To assess robustness, we tested alternative ν values (0.1, 1, and 3), which did not impact posterior distributions. Both traits were modeled to assume a Gaussian distribution. We ran 130,000 iterations with a 30,000 burn-in and a thinning interval of 100.

We calculated the correlation estimates from the (co)variance matrices of the bivariate model following similar methods as Clermont et al. (2019). Correlation coefficients were extracted using the formula:

$$r_{X,\,Y} = \frac{C_{X,\,Y}}{\sqrt{(V_X \times V_Y)}}$$

where $C_{X,\,Y}$ is the covariance between the two traits, and V_X and V_Y are their respective variances.

Personality and reproductive success

To test for the effects of personality on reproductive success, we first extracted four PC1 metrics: (1) the absolute PC1 difference between mates, (2) the PC1 score of the boldest mate, (3) the PC1 score of the shyest mate, and (4) the average PC1 score for each nest box. We then tested the effect of each of these metrics on different reproductive success measures: (1) fledging success, (2) hatching success, (3) daily wing growth (mm), (4) daily weight gain (g), and (5) laying date. For models with binary values (fledging and hatching success), we fitted generalized linear models (GLMs) with a binomial error distribution and logit link function. The following formula was used:

$$\mathit{logit}\ (\pi) = \alpha + \beta \times \mathit{PC1\ metric}$$

where π is the probability of hatching or fledging, α is the intercept, and β is the effect of the PC1 metric. For models with continuous values (daily wing growth and daily weight gain, lay date), we fitted linear mixed models (LMMs) with year as a random effect. The following formula was used:

$$\mathit{success\ measure} = \alpha + \beta \times \mathit{PC1\ metric} + u_{year} + \epsilon$$

where success measure represents either daily wing growth, daily weight gain or julian laying date, α is the intercept, β is the effect of the PC1 metric, u_{year} is the random effect of the study year, and ϵ is the residual error. For our LMMs, normality of the residuals was tested for each of our models using the Shapiro-Wilk test and by visualizing them using Q-Q plots. For our GLMs, we assessed model fit with diagnostic residual plots.

Personality and fidelity

To investigate the relationship between pair and individual personality on fidelity, we used general linear models (GLMs) with binomial error distribution. We ran four models, testing for the effect of pair fidelity (whether the pair had bred together in the past or was confirmed to be new) and site fidelity (whether the bird had bred at that specific nest site before) on pair differences in PC1 scores and individual PC1 scores.

2023 vs 2024 productivity

To compare the reproductive success of rhinoceros auklets nesting in nest boxes between 2023 and 2024, we extracted three productivity metrics: (i) the percentage of eggs laid out of all 121 boxes, (ii) the percentage of eggs laid which successfully hatched (hatch success), and (iii) percentage of nest boxes which laid an egg that successfully fledged a chick (fledge success).

Results

Principal Component Analysis (PCA) of behavioural states

We ran a total of 208 single behavioural assays on 74 unique individuals over two years. Over 57% of the variance was explained by the first two principal components (see Table 3), and so we dropped all subsequent principal components, and used PC1 and PC2 as measures of personality. The Principal Component Analysis (PCA) of the behavioural states yielded six total components. The loadings for the first two principal components for each variable are represented in Table 4.

Table 3. Summary of the Principal Component Analysis (PCA) results showing standard deviation, and proportion of variance.

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**
Standard deviation	1.50	1.09	1.00	0.95	0.80	0.0085
Proportion of variance	0.35	0.20	0.17	0.15	0.11	0.00

Table 4. Loadings for PC1 and PC2 of each behaviour, here staying on the egg, being next to the egg and completely being off the egg (from the video test), and degree of movement, biting and pecking during the hand test. Negative values PC1 values represent behaviours we interpret as bold (staying on the egg, pecking at the novel object) and positive PC1 values represent shy or antagonistic behaviours towards the novel object (running away, staying off the egg or biting).

	PC1	**PC2**
On Egg	-0.63	-0.16
Next to Egg	0.45	0.65
Off Egg	0.39	-0.62
Movement	0.42	-0.29
Bites	0.25	-0.063
Pecks	-0.052	0.28

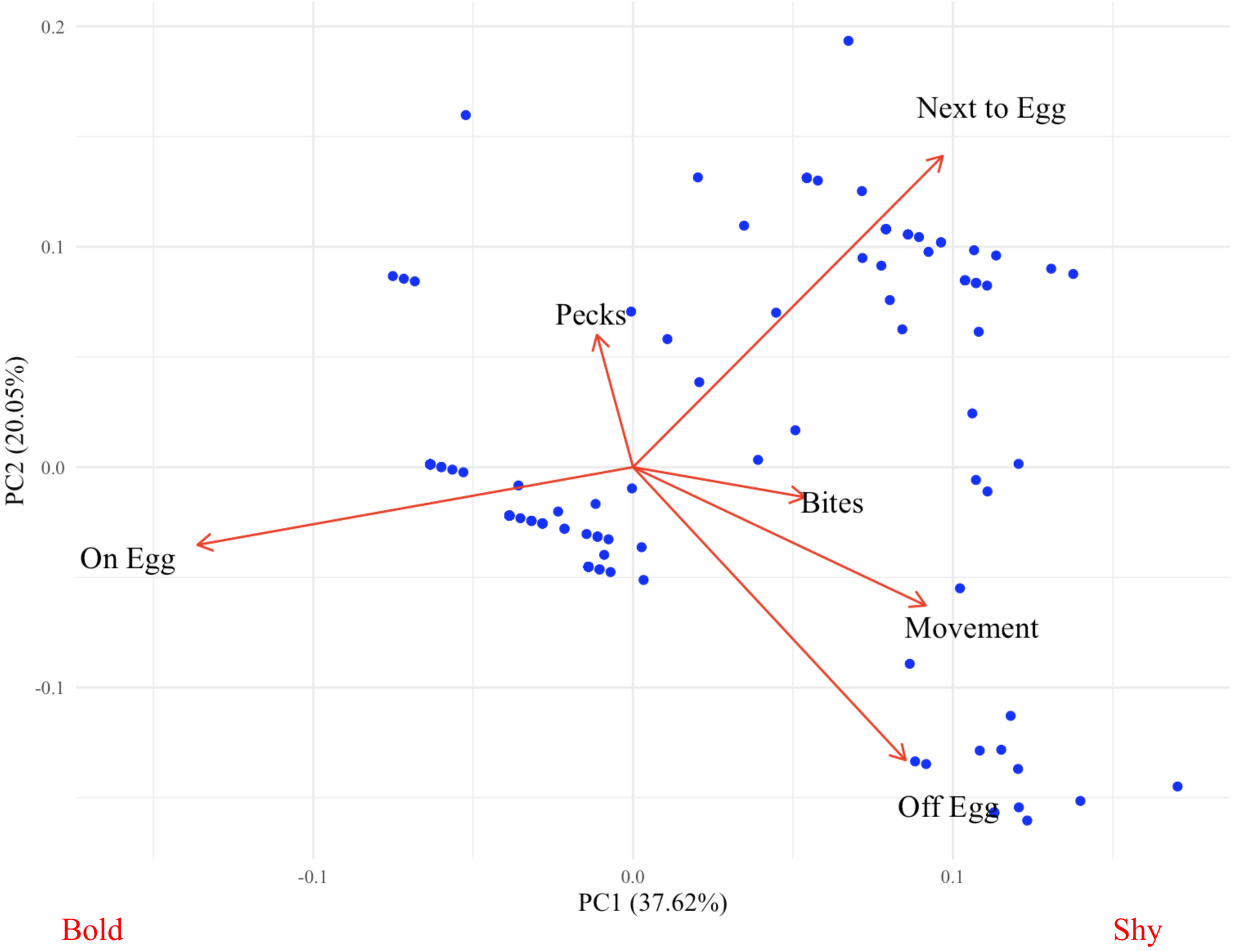

Figure 3. Principal Component Analysis (PCA) of behavioural states from the behavioural assays performed on rhinoceros auklets. Each point represents one test on one bird. The arrows and their associated labels represent the loadings for the behavioural states during both the endoscope test and the hand test (e.g., Bites, Pecks, Movement, etc.). The PC1 component seems to represent the bold-shy continuum of individuals, with lower values representing bolder individuals and higher values representing shy individuals. Higher PC1 scores represent risk-averse individuals. PC2 does not seem to represent a quantifiable trait of animal personality. The main driver of the difference in traits seems to be whether the bird stayed on the egg or not, meaning a risky situation did not affect their commitment to the egg, which we here interpret as boldness.

Repeatability analysis

We estimated the repeatability of PC1 and PC2 using linear mixed models, accounting for both long-term (between-individual) and short-term (within-year) variation.

PC1 had high repeatability (>0.3) within years and across years (Table 4), indicating that a substantial proportion of variation in PC1 is explained by consistent individual differences. On the other hand, PC2's among-individual variance was lower, with the variance attributable to individual differences across years being negligible. As a result, we could only calculate long term repeatability for PC2, keeping in mind the lack of variance at the Band_year level suggests that individual differences do not vary meaningfully across years. PC2 had low long term repeatability (<0.3).

The fixed effect of year (2023 or 2024) on PC1 was not significant ($\beta = -0.069$, $p = 0.47$), indicating that PC1 scores did not systematically differ between years. However, for PC2, we found a significant effect of year ($\beta = -0.197$, $p = 0.013$) suggesting that PC2 scores differed between years. For these reasons, we decided to exclude PC2 from further analysis, and focus on PC1 scores instead.

Table 5. Variance components and repeatability estimates for PC1 and PC2 within and across years in rhinoceros auklets.

Trait	Among-individual variance	Year-specific individual variance	Residual variance	Long-term repeatability	Short-term repeatability
PC1	1.39	0.02	0.75	0.65	0.65
PC2	0.32	0	0.86	0.28	NA

Personality analyses

There was no significant difference in PC1 scores between males and females ($t_{204} = 1.11$, p = 0.27; Females = 0.12+/- -0.17; Males = -0.11+/- 0.64). There was also no covariance nor correlation, in pair boldness scores, within and across years, as seen in Table 6. Since all 95% CRI values include zero, we conclude these results suggest there is no boldness based assortative mating between pairs

Table 6. Covariance and correlation levels between pairs of auklets through years, within years as well as at the residual within pair level. All values are reported with their associated 95% CRI between brackets.

Level	Covariance	Correlation
Between-pairs through years	0.12 [-0.51; 0.80]	0.13 [-0.56; 0.59]
Between pairs within years	0.029 [-0.48; 0.53]	0.039 [-0.51; 0.67]
Residual within pairs	0.060 [-0.51; 0.52]	0.081 [-0.55; 0.63]

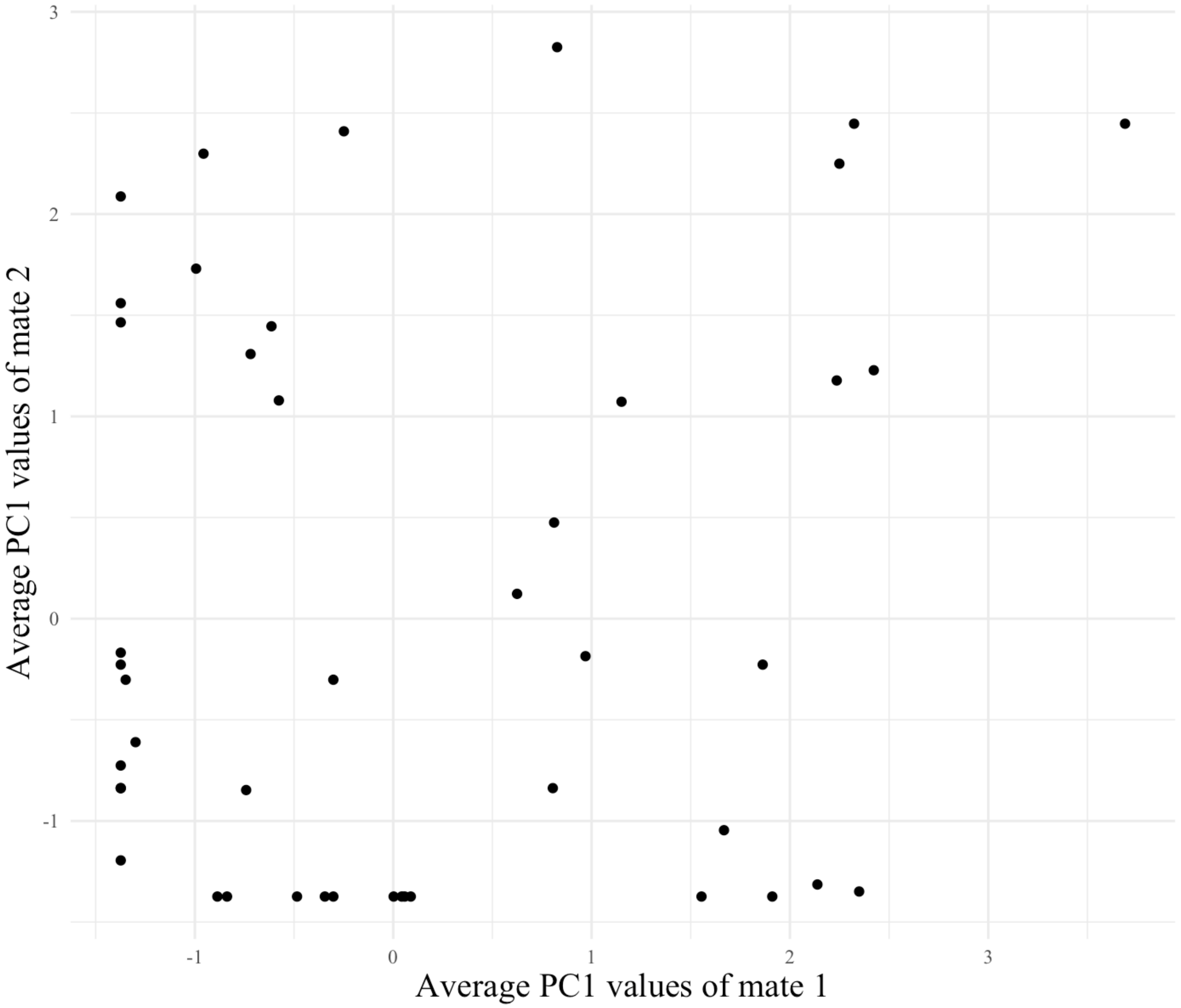

Figure 4. Scatterplot depicting average PC1 values of mate 2 in function of the average PC1 values of mate 1. While there is a slight positive slope (r = 0.14), the relationship is not significant (p = 0.84). There seems to be no trend in mate choice according to boldness, whether it be assortative mating (similar PC1 values) or disassortative mating (opposite PC1 values).

The 20 linear mixed effect models (LMMs) and general linear models (GLMs) we ran on our n = 45 breeding pairs did not reveal any evidence for the effect of PC1 scores (boldness) on reproductive success. The four personality metrics we extracted did not have any statistically significant effect on any of the reproductive success measures. We summarize the model outputs into the table below.

Table 7. Effects of personality metrics (difference in pair PC1 scores, PC1 of the boldest mate, PC1 of the shyest mate, and average PC1 scores of a pair) on reproductive success measures (hatching and fledging success, daily wing growth and daily weight gain of the chicks and laying date). General linear models (GLMs) were used for binary outcomes (hatch and fledge success) while linear mixed effect models were used for the continuous outcomes.

Reproductive success measure	**Personality metric**	**Estimate**	**Standard Error (SE)**	**t-value**	**p-value**
Fledge Success	Pair PC1 difference	0.069	0.29	0.24	0.81
Fledge Success	PC1 of boldest mate	0.14	0.29	0.50	0.62
Fledge Success	PC1 of shyest mate	0.16	0.24	0.64	0.52
Fledge Success	Average pair PC1	0.19	0.30	0.64	0.52
Hatch Success	Pair PC1 difference	0.00089	0.29	0.0030	0.99
Hatch Success	PC1 of boldest mate	0.085	0.29	0.30	0.77
Hatch Success	PC1 of shyest mate	0.064	0.24	0.26	0.80
Hatch Success	Average pair PC1	0.092	0.30	0.31	0.76
Daily Wing Growth	Pair PC1 difference	-0.21	0.11	-1.86	0.08
Daily Wing Growth	PC1 of boldest mate	0.12	0.12	1.04	0.31

Daily Wing Growth	PC1 of shyest mate	-0.068	0.11	-0.64	0.53
Daily Wing Growth	Average pair PC1	0.023	0.13	0.18	0.86
Daily Weight Gain	Pair PC1 difference	0.015	0.35	0.04	0.97
Daily Weight Gain	PC1 of boldest mate	-0.016	0.34	-0.05	0.96
Daily Weight Gain	PC1 of shyest mate	-0.0013	0.31	-0.0040	0.99
Daily Weight Gain	Average pair PC1	-0.010	0.37	-0.03	0.98
Lay Date	Pair PC1 difference	1.42	0.80	1.77	0.09
Lay Date	PC1 of boldest mate	0.31	0.83	0.37	0.72
Lay Date	PC1 of shyest mate	1.33	0.70	1.90	0.07
Lay Date	Average pair PC1	1.12	0.86	1.30	0.20

Birds in new pairs had significantly higher PC1 scores (Estimate = 0.75, SE = 0.26, $p < 0.01$). Birds that had changed nest sites between breeding seasons also had higher PC1 scores (Estimate = 0.34, SE = 0.36, $p = 0.35$). Thus, shyer birds tend to find themselves in new pairs and new nest sites each breeding season. Pair status and new site status did not, however, have any significant effect on difference in mate PC1 scores ($p = 0.15$, $p = 0.35$; Table 6).

Table 8. Summary of general linear models (GLMs) examining the relationship between site and mate fidelity and boldness (PC1).

Model	**Predictor**	**Estimate**	**Standard Error**	**t-value**	**p-value**
Difference in mate PC1s ~ Pair status	New Pair (Y)	0.67	0.46	1.47	0.15
PC1 ~ Pair status	New Pair (Y)	0.75	0.26	2.84	**0.005 ****
Difference in mate PC1s ~ New site status	New Box (Y)	0.34	0.36	0.94	0.35
PC1~ Pair New site status	New Box (Y)	0.66	0.24	2.74	**0.006 ****

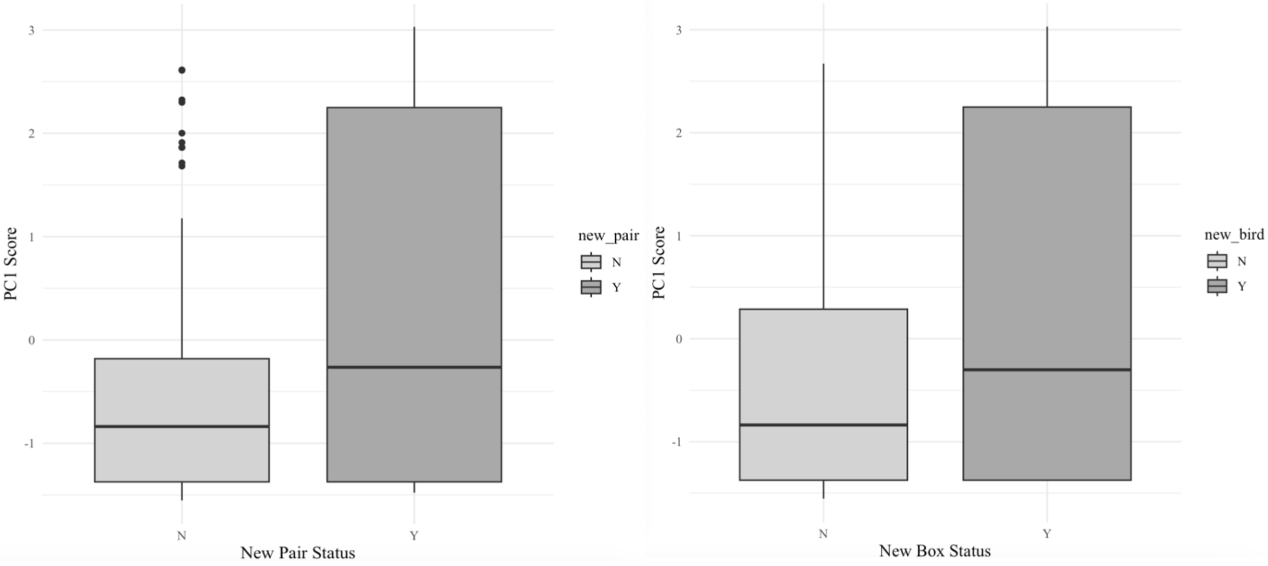

Figure 5. Boxplots depicting the significant effects of pair status (new (Y) and old (N)) and nest box status (new (Y) and old (N)) on personality scores PC1. For birds in a new box (n = 18), the median PC1 score was of -0.84 (IQR = 1.19, min = -1.13, max = 2.61). For birds in an old box (n = 28), the median PC1 score was of -0.30 (IQR = 3.62, min = -1.37, max = 3.03). For birds in an old pair (n = 15), the median PC1 score was of -0.84 (IQR = 1.19, min = -1.55, max = 2.61). For new birds in a new pair (n = 11), the median PC1 score was of -0.27 (IQR = 3.62, min = -1.48, max = 3.03). Both boxplots represent a statistically significant ($p < 0.01$) difference in PC1 scores between birds in new pairs and new boxes, suggesting shyer birds are associated with lower site and mate fidelity.

2023 vs 2024 productivity

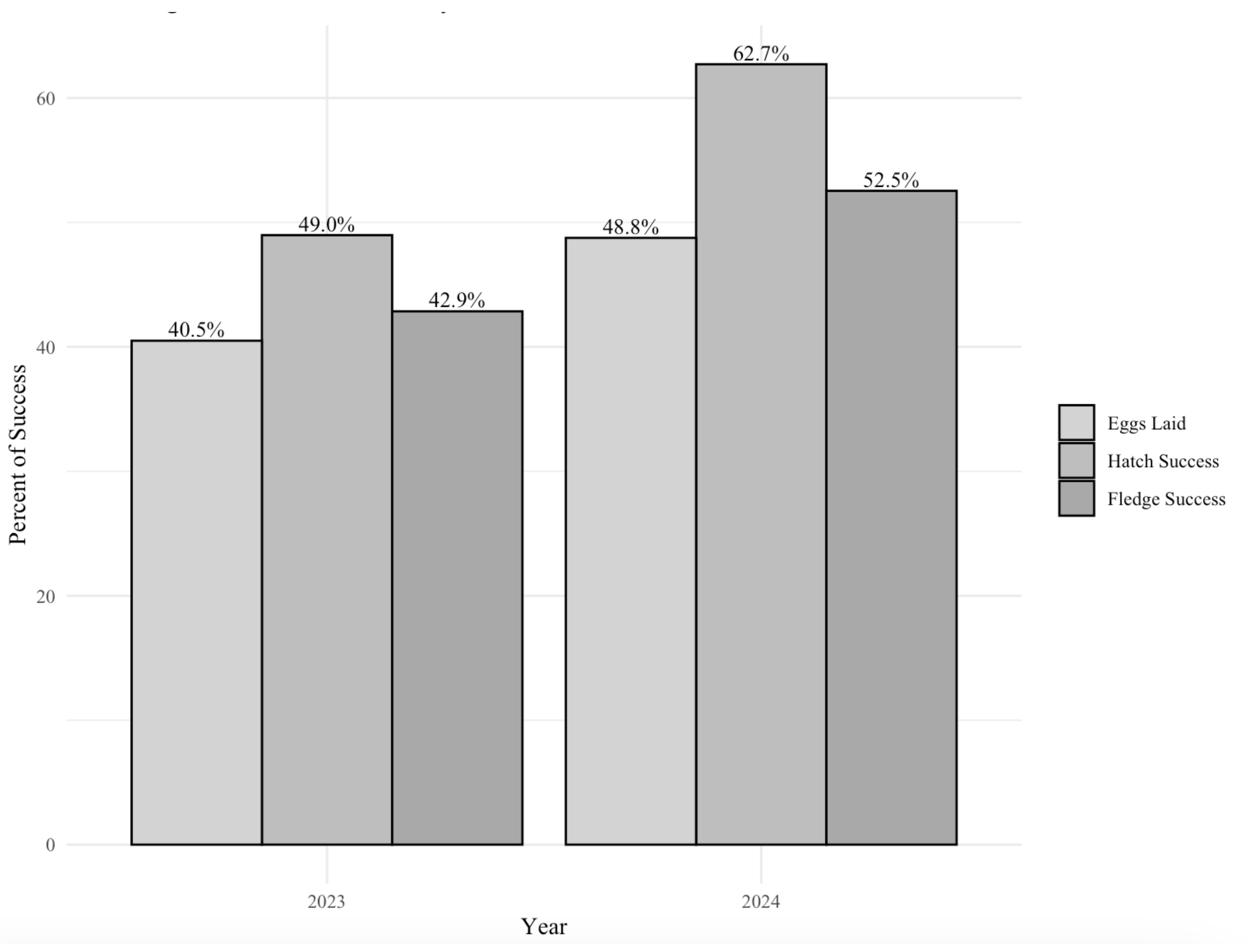

Figure 6. Bar plot comparing three productivity metrics of the rhinoceros auklet nest box colony (total n = 121 nests). Out of the nest boxes that laid an egg (n = 49 in 2023 and n = 59 in 2024), 49% successfully hatched an egg in 2023 compared to the higher 62.7% of 2024. 42.9% of nests which had a breeding attempt successfully fledged a chick in 2023, while 52.5% fledged a chick in 2024.

Discussion

We assessed the personality of rhinoceros auklets nesting on Middleton Island in 2023 and 2024 and explored the link between boldness, reproduction, mate choice and fidelity. Understanding how personality is related to these life history traits may help elucidate how individual auklets navigate fitness trade-offs. Auklet personality scores were repeatable within individuals and across years. There was no assortative mating with boldness or association with reproductive success. However, shyer individuals were more likely to switch sites and mates.

Personality in the rhinoceros auklet

Boldness was repeatable in the rhinoceros auklet within individuals and across two years. We interpreted the first component of our PCA (PC1) as the bold-shy continuum (2). Lower values, such as staying on the egg and pecking at the novel object, represented bold behaviours. Deciding to stay on the egg despite an intruder entering the burrow (here the novel object) represents a risky behaviour, as is pecking curiously at the novel object. In contrast, higher PC1 values reflected shy behaviours, such as running, and represented more risk-averse personalities. While pecking falls under bold behaviours and biting under shy behaviours, the biggest indicator of boldness seems to be whether the individual stayed on the egg or not. Biting was closely associated with running away, thus associated with neophobic behaviours.

Our auklet population had a range of boldness scores, demonstrating that rather than being a binary trait, this personality measure is continuous (Réale et al. 2007). If we consider a negative PC1 score as portraying generally bold individuals, we had 26 bold individuals and 48 shy individuals. Auks tend to be sensitive to human disturbance and so it makes sense that more individuals are shy within the population (Rodway et al. 1996; Gjerdrum et al. 2003; Sydeman et al. 2017; Smith et al. 2024). However, the ratio of shy to bold may also be colony specific. A study on wandering albatross (*Diomedea exulans*) found that denser colonies had a higher proportion of shyer individuals than less-dense colonies (Patrick et al. 2013). The subcolony where we studied auklets is one of the densest and biggest on the island. It may be that smaller subcolonies contain overall bolder individuals. A smaller colony may be more prone to predation by gulls, which are the main predator to auklets on Middleton Island (Brunton 1999). This ecological context may select for bolder individuals that will stay on the egg. As part of another project, we installed camera traps which revealed that all foreign intrusions to the burrow were due to conspecifics, and not predators (E. Miranda, pers. obs.). Being shy may then be advantageous, by avoiding aggressive actions that could damage the egg.

Boldness, mate choice and reproductive success

Male and female auklets had similar PC1 scores. There was no assortative nor disassortative mating based on boldness; some birds mated with highly similar individuals and some with extremely dissimilar individuals (Figure 3). Difference between personality scores within a pair did not affect reproductive success. We therefore failed to reject our null hypotheses associated with H1 (auklets perform assortative mating) and H2 (auklets perform disassortative mating);

rather, auklets do not seem to select their mate according to boldness. Pair boldness and individual boldness also had no effect on reproductive success (H3).

Interestingly, shyer birds did not abandon more, even after human handling. While this may seem counterintuitive, since shyer birds ran away when encountering a risk, shyer individuals appear as committed to their eggs and chicks as bolder individuals. Our results do not follow the trend of many studies that link boldness to higher reproductive success (Stamps 2007; Smith and Blumstein 2008; Collins et al. 2019), with bolder individuals trading off higher reproductive success for lower individual fitness and survival. There is evidence in the literature of shyness positively affecting reproductive success in seabirds depending on the quality of the year (Patrick and Weimerskirch 2014). Few studies, however, report no effect at all, perhaps due to the file drawer effect where negative results are less likely to be presented (Lortie et al. 2007; Garamszegi et al. 2012). In short, for rhinoceros auklets, boldness is repeatable and constant but does not directly affect reproductive success.

Mate and site fidelity

Boldness influenced mate and site fidelity (H4). Birds in new pairs and birds that switched nest sites between breeding seasons were shyer than established pairs (Figure 4). The difference in pair personality was not affected by the age of the pair, and so seems to be truly an attribute of the “individual”. Our results are interesting because other studies have reported high site fidelity in the rhinoceros auklet (Kubo et al. 2018). Moreover, auks usually have high mate retention (Moody et al. 2005; Gousy-Leblanc et al. 2023). For our auklet colony, 11/26 (42%) birds in 2023 found themselves in a new pair in 2024. While some of these birds may be widows instead of divorcees, adult puffin survival rates are usually high (Ashcroft 1979), meaning it would be extremely unlikely that 42% of birds would have been widowed after one year. While we acknowledge that some of these repairings may be due to to mortality in the pair, we assume that some may also be due to divorce. For the sake of semantics, we will call instances of a bird finding itself in a new pair a "repairing" instead of a divorce. Still, divorce rates in other auks are low (common murres *Uria aalge* = 9% per year, Atlantic puffins *Fratercula arctica* = 8% per year; Ashcroft 1979; Moody et al. 2005; Jeschke et al. 2007). Another burrowing auk, the crested auklet (*Aethia cristatella*), had similar rates of recoupling, at 31% (Fraser et al. 2004). Still, these rates, combined with a 39% nest site switching rate, seem abnormally high. The high rate of remating in 2024 may have been caused by the lower reproductive success rates in 2023 (see Figure 5). One of the drivers of divorce in seabirds is a failed breeding success in the previous year, providing a possible explanation as to why we observed high rates of remating in 2024 (Catry et al. 1997; Wheelwright and Teplitsky 2017; Mercier et al. 2021; Wagner et al. 2022; Gousy-Leblanc et al. 2023).

Regardless of whether the repairing rate was higher in 2023-24, birds that had recoupled and moved boxes tended to be shyer. Predation at our study site is not a big risk for reproduction. However, intraspecific competition and kleptoparasitism by gulls may be drivers for site switching (Coulson 2002). Shyer birds may be less willing to partake in intraspecific competition for mates and sites, choosing to invest in a new match instead. Both strategies show the life-history trade-offs of boldness: staying in the same box and fighting for your nest site and mate or switching and taking the gamble of being successful in the following year. The current versus future reproduction dilemma is apparent here, although we did not see an effect of recoupling on reproductive success in 2024. Unlike what we've observed, seabird pairs that have been together for a long time tend to do better (Wagner et al. 2022; Bebbington and Groothuis 2023; Gousy-Leblanc et al. 2023). Perhaps the potential negative effects of remating would be apparent in a poor-quality year (2024 was a good year). A study on northern gannets (*Sula bassana*), for example, showed that after a bad year, individuals that recoupled were successful if the following year had good foraging conditions (Pelletier and Guillemette 2022).

Our results underline the importance not to conflate neophobia with shyness. Shy individuals will often engage in exploratory behaviours to avoid risky situations (for example, competition), such as foraging further, exploring new patches, and here, changing sites and mates (Patrick and Weimerskirch 2014). The adverse responses to the novel object tests did not extend to new mates and sites for our auklets.

Implications

The emergence of studies in animal personality paints a strong case for its importance, through its environmental, ecological and behavioural implications (Wolf and Weissing 2012). This holds especially in seabirds which often serve as indicators of ecosystem health (Piatt et al. 2007; Le Bohec et al. 2013). Notably, environmental degradation may favour shyer birds through time (Jeffries et al. 2021). The implications of a potential loss of personality diversity in seabirds are still unclear, particularly since the scope of species studied and of questions asked has been limited thus far. Burrowing auks are extremely compelling because of how sensitive they are, both to variations in their environment and to investigator disturbance. The decade starting in 2014 was the warmest on record in the Gulf of Alaska with mass starvation for many auks (Renner et al. 2024), and worsening oceanic conditions may favour shyer birds that are more likely to forage further and explore more (Jeffries et al. 2021). We can imagine this trend holding true for our auklet population as well: as the environment degrades, mate and site switching may become more common, favouring shyer birds. Habitat degradation does decrease intraspecific functional diversity in populations, and it seems that this effect could extend to personality as well (Cianciaruso et al. 2009; Albert et al. 2012; Morelli 2018). A loss in personality diversity is alarming since it may lead to cryptic function loss, whereby certain functions associated with a species may be lost (McConkey and O'Farrill 2015). Understanding which strategies shy and bold auklets prefer not only sheds light onto how individuals may face poor-quality years, but also the trends a population may follow as environmental conditions worsen.

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GENERAL DISCUSSION

This thesis examined the links between boldness, reproductive success, fidelity and mate choice in the rhinoceros auklet. Here we discuss our findings as well as limitations in methodology and theory. Finally, we consider the potentials of expanding the use of rhinoceros auklets for ecosystem monitoring on Middleton Island.

Chapter Summary and Highlights

In the data chapter we performed behavioural assays on rhinoceros auklets (*Cerrorhinca monocertata*) nesting on Middleton Island (Alaska). It was initially unclear whether the tests would be successful, as there is little to no published literature on performing personality tests on burrowing animals, and none on seabirds. It seemed that approaching a threat from the access hatch of the nest box vs. the entrance presented very different threats to the animal. I decided to perform two tests, one where the novel object would be presented from the natural entrance of the burrow (simulating a conspecific or a predator entering the burrow), and one when we retrieved the bird through the access hatch (measuring the reaction to a human). Both tests ended up yielding similar results as seen in the PCA Analysis (Figure 2), with birds running away at the novel object also moving away from my hand. That and the high inter-year repeatability of personality are probably some of the most interesting and meaningful results of the study. No auk species, to my knowledge has been assessed for personality. The reliability of the test results was therefore both unexpected and noteworthy.

I found no assortative mating or effect of personality on reproductive success. However, birds that had switched mates and nest sites in previous years were significantly shyer than faithful birds. Another interesting finding was how high the recoupling rates were. Although we cannot state assuredly that divorce occurred (both mates need to be found at the colony), it seems that auklets were experiencing higher than normal rates (42% per year compared to 8% per year in Atlantic puffins *Fratercula arctica*; Ashcroft 1979). Recoupling in seabirds is a strategy often employed after poor quality years (Mercier et al. 2021; Gousy-Leblanc et al. 2023), and we can therefore postulate that the trends of shyer birds being favoured as climate change progresses as theorized by Jeffries et al. (2021) could occur for the rhinoceros auklet as well. Nonetheless, there was no effect of either strategy on reproductive success, thus it becomes difficult to envision how this trait would be favoured over time. I must note though that 2024 seemed to be a good productivity year for not only the auklets, but also all bird species on Middleton Island, with record-breaking early laying dates for all species (E. Miranda, pers. obs.). It may well be that we observed little effects on fitness due to the good quality and abundance of prey that year.

An exciting finding not reported directly in the data chapter, is the discovery of two homosexual pairs. Since rhinoceros auklets are monomorphic (Gaston and Dechesne 1996), I performed blood card genetic testing in the fall. I originally wanted to assess whether there were sex-differences in boldness levels but instead found two male-male pairings. Homosexuality has been recorded in over 130 bird species (Bagemihl 1999). While most of these recorded behaviours tend to be coupled with heterosexual pairings, some seabird species, mostly gulls and albatross, have shown socially monogamous long-term pairings (Conover 1984), The Laysan albatross (*Phoebastria immutabilis*) even reaches up to 30% of homosexual pairings in some colonies (Zuk and Bailey 2008). It's important to note that most of these homosexual pairings recorded in seabirds seem to be of a female-female nature (Conover 1984; Mills 1991; Zuk and Bailey 2008). An exception is penguins, with various cases of male homosexual behaviours being recorded (Davis et al. 1998; Pincemy et al. 2010; Russell et al. 2012). Under monogamous bird species, long-term homosexual pairings are almost always female-female (MacFarlane et al. 2010), making this finding surprising. Male homosexual behaviour is usually associated with polygynous species, with homosexual behaviours in socially monogamous species with high levels of male parental care being rare (MacFarlane et al. 2010). Still, the fact that two pairs of rhinoceros auklets were incubating an egg, (and for one of the pairs, successfully raised a chick) is fascinating. One of the male-male pairs was separated in the following year, with the male being with a female this time. Our automated antenna RFID (Radio-Frequency Idenfitication) system, however, showed that the old male mate was visiting the burrow each night in 2024, perhaps caring for the egg and the chick as well. If the female was present in past years, it would explain how these two male birds were able to have access to a fertilized egg. Perhaps this finding underlines the importance in investigating the hidden life of the rhinoceros auklet further, as pairing may not be as simple as male-female, as we often assume for auk species.

Limitations

As mentioned before, assessing the personality of a burrowing seabird was challenging as literature on the appropriate methodology was limited. Rhinoceros auklets are also an extremely sensitive species, and the right balance between being able to test for repeatability through recurring tests and minimizing disturbance was difficult to achieve. Individuals also had extremely variable incubation shift differences and patterns, with some pairs even leaving the egg unattended for days. Egg neglect was higher than the literature suggested, with chicks being successfully raised for nests that partook in it.

Perhaps the main limitation had little to do with the study species itself but rather the method of the novel object test, which we used to assess boldness in the rhinoceros auklet. I acknowledge that the study followed a quite vague definition of boldness, which seems to be a recurring problem throughout animal personality literature. According to Réale et al., the novel object test is used to assess an animal within the exploration/avoidance continuum (Réale et al. 2007). However, most seabird studies use this test to measure boldness (Patrick and Weimerskirch 2014; Morandini and Ferrer 2019; Harris et al. 2019; Collins et al. 2019 amongst many). Boldness is the most measured trait (Conrad et al. 2011), perhaps due to a positive feedback loop of animal studies mentioning it much more frequently than other traits. There seems to be a lack of consensus, however, on how exactly to measure it and what it means (Greggor et al. 2015): Réale et al. defines boldness as the response an individual may have to a risky situation but non novel situations. Paradoxically, other literature includes novel situations as a part of measuring boldness (Toms et al. 2010). In general, boldness is measured in a variety of different ways, with novel environment and novel object tests being the most popular (Carter et al. 2012).

Therefore, if we strictly follow the presumption that neophobic assays should be testing for the cognitive response to novel stimuli, then our study has not assessed boldness in the rhinoceros auklet. Yet, the birds we deemed shy (which we would deem as less exploratory if we considered for the novel object test measure that instead) were not neophobic towards new mates or new sites, quite the opposite. Perhaps the answer lies wherein a test can measure for multiple traits (Réale et al. 2007), and a novel object test could test for both exploration/avoidance and boldness. A study on domestic rabbits tried to determine which tests best assessed exploration, boldness and anxiety concluded that the novel object test represented both boldness and exploration factors (Andersson et al. 2014). Finally, the nature of repeating tests with novel objects seems contradictory. While repeating tests is necessary to be able to assure the behaviours we're measuring are in fact personality, it did cross my mind that the object may not be as "new" to a bird after its first encounter with it. Repeated novel object tests on rainbow trout (*Onchorhyncus mykiss*) showed that individuals changed their reaction depending on whether they had good or bad outcomes to the test, with shy individuals with good outcomes becoming bolder and vice versa (Frost et al. 2006). Finally, it may also be worthwhile to question where the hand test fits into a novel object test: while I considered it almost analogous to the ball entering the burrow, a hand which later picks up a bird is not the same as a true novel object being presented. While this is a limitation in the conceptualization of the study, individuals responded similarly to the two tests. Such questions were a big limitation in designing my study and interpreting the behaviours that the rhinoceros auklets did in response to the test. Overall, I believe to improve upon this study I would've needed: i) clearer guidelines and consensus in the literature on what is boldness and how to measure it and ii) a better understanding of the auklet's nighttime habits.

Future Endeavours

Fortunately, better understanding the rhinoceros auklet's natural history may be possible thanks to the automated monitoring system which I helped set up in 2023 (Marcouillier et al. 2024). RFID (Radio-Frequency Identification) PIT (Passive Integrated Transponder) tagging is a cheap and simple relatively new technology which uniquely identifies individuals (Gibbons and Andrews 2004). PIT tags are passive electronic microchips which are activated when a reader comes close them (Zydlewski et al. 2006). PIT tags are an ideal technology because they are easy to apply, very small (for most seabirds they represent less than 1% of their body mass), and permanent. They do not need an external power source, and unless they migrate or get rejected from the animal's body, they stay inside the individual for the remainder of its lifetime.

By placing antennas at the entrance of the burrows of tagged individuals, we have been able to monitor their movements, including at night. We found that neither implanted nor leg band PIT tags increased nest abandonment or affected reproductive success of the auklets (see Figure 6), demonstrating this tagging method to be safe for these birds, despite them previously reacting poorly to biologging tags even bellow 3% body mass (Sun et al. 2020; Marcouiller et al. 2024). For now, it has been difficult to interpret the data to extrapolate accurate switchover and incubation bouts. In 2023 and 2024, I set up infrared cameras to cross-validate the RFID data. Future work could interpret rhinoceros auklet nest attendance data through this low disturbance method. Moreover, I believe this data could be interesting to further explore questions related to animal personality.

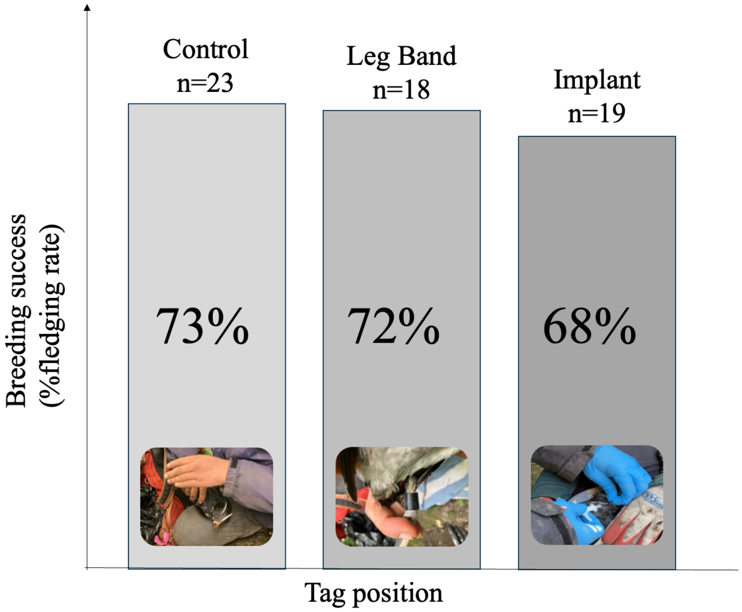

Figure 7. Figure modified from Marcouiller et al. 2024. Fledging rates (from nest boxes with an egg that hatched) from control birds (handled but not tagged), leg banded birds (3D printed nylon bands with a PIT tag attached to it) and implanted birds (subcutaneous neck injected PIT tag). There was no significant tag effect measured on breeding success.

Personality and nest attendance have been linked to reproductive success in many bird species (Schuett et al. 2011; Fox and Millam 2014; Le Bot et al. 2014). In some bird species, pairs with similar personalities coordinate incubation better which leads to higher reproductive success (Spoon et al. 2006). A few studies have even used PIT tagging to study nest attendance behaviours in seabirds (Zangmeister et al. 2009; Taylor et al. 2012; Tyson et al. 2017). The rhinoceros auklet has highly variable interindividual nest attendance patterns and incubation rates (Blight et al. 2010). Pairs of rhinoceros auklet synchronize their foraging activities during pre-laying (Kubo et al. 2018). Knowing this, I would like to understand if pair and individual personality affects incubation patterns, as well as whether shy individuals are more prone to egg neglect compared to bold individuals.

The individual personalities of auklets, such as boldness, exploration, and aggression, could offer a valuable tool for monitoring populations in the context of conservation. Behaviour is often a more immediate and sensitive indicator of environmental stressors than traditional measures like reproductive success or population size, which may only reflect changes after significant declines (Scott and Sloman 2004; Sih et al. 2011; Tuomainen and Candolin 2011). For example, shifts in individual behaviour, such as altered foraging patterns (Dunphy et al. 2020) or increased aggression in response to disturbance (Grace and Anderson 2014), could serve as early warning signals of deteriorating habitat conditions or emerging threats like climate change, predation, or human interference. Monitoring these behavioural traits across a population could help detect subtle changes in the health or stability of a colony long before noticeable effects on reproduction or overall numbers occur. This approach could enhance the ability to proactively address conservation concerns, providing a timelier response to emerging environmental pressures that might otherwise go unnoticed until it is too late.

THESIS CONCLUSIONS

Seabird personality affects multiple aspects of their life history, from mate choice to foraging habits (Harris 2019; Patrick and Weimerskirch 2015; Collins et al. 2019). A common finding within this taxon is that shyer individuals tend to be more exploratory and flexible in behaviours such as foraging habits, while bold individuals will prioritize routine-like behaviours (Traisnel and Pichegru 2017; Patrick and Weimerskitch 2015; Patrick and Weimerskirch 2014; Gillies et al. 2023; Krüger et al. 2019). This phenomenon has raised concerns on whether degrading environmental conditions will decrease personality diversity in seabirds in favour for shyer individuals (Traisnel and Pichegru 2017**;** Jeffries et al. 2020). Most studies, however, have been performed on gulls and albatross, and have yet to inspect other groups of seabirds. Moreover, they have almost exclusively focused on foraging habits. We therefore explored the impact of boldness on reproduction and mate choice in the rhinoceros auklet (*Cerrorhinca monocertata*). As a burrowing auk, this type of seabird has yet to be assessed for personality. We successfully obtained boldness scores through a Principal Component Analysis (PCA) of two behavioural assays. Boldness was indeed present in the auklets and repeatable between and through years. Personality had no effect on reproductive success, but that bolder birds were more likely to be faithful to both sites and mates, than bolder birds. This study therefore reiterates the idea of bolder seabirds being more repeatable and stable in their life history choices. Future research should focus on exploiting the RFID (Radio-Frequency Identification) study system set up for rhinoceros auklets on Middleton Island (Alaska) to assess whether personality is tied to nest attendance patterns, egg neglect and incubation bouts in this species.

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