SEABIRD PERSONALITY AND INDIVIDUAL BEHAVIOURAL CONSISTENCY IN THE CANADIAN NORTH ATLANTIC

By

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Preface

This thesis was written using a grouped manuscript style following the guidelines outlined by the University of Manitoba Faculty of Graduate Studies. I confirm that the research described in this thesis was conducted in adherence with guidelines of the Canadian Council of Animal Care (Protocol numbers: F16-017, F20-017). I, Matthew John Legard, declare that this thesis contains my original research for which I performed the majority of the work. The roles and contribution of all authors are described below for each chapter.

Chapter 1: A non-invasive method during routine handling indicates docility in a wild, crevice-nesting seabird.

Matthew Legard: Conceptualization, Data collection, Formal analysis, Investigation, Methodology, Writing - original draft.
Gail Davoren: Funding acquisition, Resources, Supervision, Writing - review & editing.

Chapter 2: Individual consistency in foraging behaviour is influenced by prey availability in a breeding seabird.

Matthew Legard: Conceptualization, Data collection, Formal analysis, Investigation, Methodology, Writing - original draft.
Lauren Lescure: Data collection, Writing - review & editing.
Gail Davoren: Funding acquisition, Resources, Supervision, Writing - review & editing.

Chapter 3: The behaviour of individual razorbills (*Alca torda*) during the non-breeding season is consistent but not related to personality.

Matthew Legard: Conceptualization, Data collection, Formal analysis, Investigation, Methodology, Writing - original draft.
Mark Dodds; Antony Diamond; David Fifield; Heather Major: Writing - review & editing.
Robert Ronconi: Funding acquisition, Writing - review & editing.
Gail Davoren: Funding acquisition, Resources, Supervision, Writing - review & editing.

Chapter 4: Diversity in non-breeding distribution differs across seabird species in the northwest Atlantic.

Matthew Legard: Conceptualization, Data collection, Formal analysis, Investigation, Methodology, Writing - original draft.
Mark Baran; Mark Dodds; David Fifield; Grant Gilchrist; Jean-François Rail; Ulrike Kubetzki; Allison Patterson; Robert Ronconi; Gregory Robertson; Data collection, Writing - review & editing.
Kyle Elliot; William Montevecchi; Stefan Garthe; Heather Major; Antony Diamond: Data collection, Funding acquisition, Writing - review & editing.
Gail Davoren: Funding acquisition, Resources, Supervision, Writing - review & editing.

Thesis Abstract

Animal personality (i.e., consistent individual behaviour over time/across contexts) is made up of distinct trait continuums (e.g., docile-aggressive; docility) that can play an important role in shaping the behavioural responses of animals, and therefore, can influence fitness. Understanding personality in animal populations can be a useful tool to aid conservation decisions. To date, limited research on personality has been carried out in seabirds, especially species from the family Alcidae. This family, which includes the razorbill (*Alca torda*), is characterised by a stout body which facilitates diving but results in high energetic costs of flight.

In comparison to personality, individual consistency in seabird behaviour (e.g., migratory route) is well studied, but studies rarely compare across species. If individuals within a population behave consistently (e.g., migratory site fidelity), but differences are present among individuals (i.e., behavioural diversity), this variation may expose components of populations to varying threats (e.g., offshore wind development). Therefore, understanding this behavioural variation across and within species will aid in the protection of populations with lower diversity, which are more likely to experience population declines.

The aims of this thesis were to:

1. Determine the best method for quantifying the docile-aggressive trait in razorbills (**Ch.1**).
2. Investigate relationships between docility and razorbill behaviour during the breeding (**Ch.2**) and non-breeding (**Ch.3**) periods.
4. Explore behavioural diversity in migratory routes of seabird species that breed in Atlantic Canada (**Ch.4**).

In Chapter 1, I found that different behavioural tests had varying suitability for identifying docility in razorbills. Of the tests, standardized observer ratings were the best test for quantifying docility in razorbills and potentially other hard to observe species. In Chapter 2, I found that razorbills exhibit consistent behaviour during the breeding period, but this consistency is context dependent (i.e., varying prey availability periods) and not related to docility. Additionally, I found no relationship between fledging success and docility. In Chapter 3, I found individual consistency in razorbill non-breeding behaviours but no relationships between any observed non-breeding behaviours and docility. Finally, in Chapter 4, I found varying levels of behavioural diversity both within and across seabird families (Alcidae, Laridae and Sulidae).

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I would like to acknowledge the stewards of the land that I called home for 3 years in Winnipeg. The University of Manitoba campuses are located on the original lands of the Anishinaabeg, Cree, Oji-Cree, Dakota and Dene peoples and on the homeland of the Metis Nation. Newfoundland, where the research was conducted, is the unceded ancestral homelands of the Beothuk. I respect the treaties that were made on these lands and acknowledge the harms of the past as we attempt to move forward in partnership with Indigenous communities.

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General Introduction

Animal personality is defined as consistent between-individual differences that are stable across contexts and persist through time (Stamps & Groothuis, 2010; Wolf & Weissing, 2012). These differences are common (Wolf et al., 2007), present between individuals of the same size, sex and age (Bell, 2007; Muller and Muller, 2015) and have been found in numerous animal groups throughout the animal kingdom (Sih et al., 2004; Wolf and Weissing, 2012). These animal groups include birds, mammals, fish, reptiles, amphibians, arthropods, insects, cephalopods and molluscs (Bell et al., 2009). This discovery of widespread animal personality is a result of a significant increase in targeted research in the last few decades (Grace and Anderson, 2014). The five commonly studied personality traits are activity, sociability, boldness, exploration and aggressiveness (Kaiser and Muller, 2021; Merrick and Koprowski, 2017; Réale et al., 2007), and these traits lie along continuums such as shy-bold or docile-aggressive. Personality traits also form behavioural syndromes of correlated traits, for example, boldness, aggression and exploration are commonly related (Bell, 2007; Réale et al., 2009).

There are two main methods of assessing personality in animals: behavioural coding and observer ratings (Carter et al., 2013). Behavioural coding involves observing the frequency, duration or latency of discrete, well-defined behaviours and subsequently has limited human bias (Kaiser and Müller, 2021; Petelle & Blumstein, 2014). Alternately, observer ratings involve using standardised scales to assess a suite of behaviours and are therefore more subjective but less time consuming (Kaiser and Müller, 2021; Ebenau et al., 2020). Relationships commonly seen between the two methods (Gosling, 2008; Koski, 2011) indicate that simultaneous application can be beneficial (Carter et al., 2013). Observer ratings are more common in studies of captive animals because their reliability increases with observer experience of the study animals (e.g., Powell & Svoke, 2008; Torgerson-White, 2014). Non-captive animal personality assessment by observer ratings has now begun (e.g., Arden et al., 2023; Baker et al., 2016) and there is evidence that observers with no prior experience can provide reliable ratings of personality traits in wild animals (Petelle & Blumstein, 2014).

There is growing evidence that personality is a key driver of population dynamics, as individuals with varying personalities respond differently to changing environmental conditions, thereby influencing their fitness (Dall et al., 2004; Mathot et al, 2012; Smith and Blumstien, 2008). Indeed, personality traits appear to be heritable (Carter et al., 2013) and, thus, represent important diversity for evolutionary change (Kaiser and Müller, 2021). For example, personality is often related to resource acquisition, anti-predator behaviour and reproductive success (Menzies et al., 2013; Wolf and Weissing, 2012). Additionally, personality traits may lead to sub-optimal behaviour in certain situations (Sih et al., 2004). For example, bold individuals may have a competitive advantage over shy conspecifics but may also have a higher risk of predation due to lower risk aversion (Wolf and Weissing, 2012). Personality, however, may also cause individuals to only use a part of the species' total niche, which may benefit populations by reducing intraspecific competition through resource partitioning (Ceia and Ramos, 2015).

Personality in Seabirds

As with other taxonomic groups, personality has been identified in seabirds, primarily as the shy-bold continuum (e.g., Collins et al., 2019; Harris et al., 2020; Kruger et al., 2019; Patrick et al., 2017; Traisnel and Pichegru, 2018). Personality traits in seabirds have been related to foraging during the breeding period, migration during the non-breeding period and reproductive rates/fitness. In relation to foraging, bolder individuals have generally been classed as specialists and shyer individuals as generalists (Harris et al., 2020; Jeffries et al., 2021; Krüger et al., 2019; Pereira et al., 2024). In addition, exploitation of food patches is usually associated with the shy end of the boldness continuum (Jeffries et al., 2021; Patrick et al., 2017). In comparison, bold individuals usually take more risks (Carter et al., 2013). For example, these individuals may forage in areas with greater densities of competitors (Patrick & Weimerskirch, 2017). Unlike relationships during the breeding season (e.g., foraging behaviour), there has been limited investigation into relationships between personality and non-breeding behaviour in seabirds (e.g., migration). One study, however, has showed that bolder Cory's shearwaters (*Calonectris borealis*) migrate away from the breeding colony, while shyer birds remain year-round residents around the colony (Gatt et al. 2021).

Despite the relationships between behaviour and personality in seabirds, few studies have investigated the fitness effects of these relationships (Patrick and Weimerskirch, 2014), and across those that have there are mixed results. For example, boldness-related differences in reproductive success have been observed in some species (Collins et al., 2019; Harris et al., 2020; Patrick and Weimerskirch, 2014) but not in others (Krüger et al., 2019; Patrick et al., 2017; van de Walle et al., 2024). This lack of a relationship has even remained the case when prey is available in varying quantities across years (Krüger et al., 2019) as different traits may be suited to different environmental conditions (Jeffries et al., 2021; Traisnel and Pichegru, 2018).

Individual Consistency & Among Individual Variation in Seabirds

Individual consistency across a wide range of behaviours throughout the annual cycle (e.g., foraging, migration) is also common in seabirds (Biagiotti Barchiesi et al., 2023; Ceia and Ramos, 2015; Phillips et al., 2017). Examples related to foraging include consistency in diet and movement patterns (e.g., Patrick et al., 2013; Patrick and Weimerskirch 2014; Woo et al., 2008), and individual consistency (i.e., site fidelity) has also been found in non-breeding movement and distribution patterns (e.g., Fifield et al., 2014; Franklin et al., 2022; Guilford et al., 2011). These and other examples of consistent between-individual differences may be related to personality due to their high repeatability over time. Consistency in individual behaviour has likely evolved due to the relationships between consistency and efficiency (Rebstock et al., 2022). For example, individual strategies, that are learned and remembered over the lifetime of an individual (i.e., memory; Dall et al., 2005), may increase foraging efficiency and reduce energy expenditure (Phillips et al., 2017), with subsequent benefits to fitness.

Due to individual consistency, most of the behavioural variation within animal populations is often explained by differences among individuals rather than within individuals (Araújo et al., 2011; Bolnick et al., 2011; Dall et al., 2012). Therefore, populations with greater amounts of between-individual variation have greater behavioural diversity. Importantly, species and populations with lower behavioural diversity are more vulnerable to environmental change (Wolf and Weissing, 2012) and subsequently are experiencing population declines (Clavel et al., 2011). This vulnerability may be increased when individuals within such populations are highly consistent leading to potentially sub-optimal behaviour under changing environmental conditions. In contrast, high behavioural diversity may allow a larger number of ecological niches to be exploited (Ceia and Ramos, 2015) and may mitigate the effects of increased environmental variability or a local disaster (e.g., oil spill). Identifying species and populations with lower behavioural diversity will be valuable for seabird conservation as marine environments become more variable due to climate change (Weber et al., 2021) and experience increasing numbers of threats (e.g., rapid offshore wind development; Williams et al., 2024).

Study Species and Location

Several seabird species that breed in the Canadian North Atlantic will be studied during this research. Seabirds are ideal model species for studies of personality as behavioural studies can be carried out on land at their breeding colony and distribution and foraging behaviour can be tracked at sea. Additionally, seabirds are long-lived, allowing fitness consequences of personality to be assessed (Patrick et al., 2017). Furthermore, seabirds tend to have high nest site fidelity which facilitates study of individuals across multiple years. Razorbills (*Alca torda*) will be the primary study species (Chapters 1-4), a member of the family Alcidae which is characterized by a stout body and high body mass to wing ratio which results in a high energetic cost of flight relative to other species (Elliott et al., 2013). Razorbills breed at colonies across the North Atlantic, nesting in crevices among boulders. They are central place foragers during breeding, capturing small forage fish such as capelin (*Mallotus villosus*) to provide for a single chick each year (Lavers et al., 2020). Razorbill chicks fledge after ~21 days following a 35-day incubation period. They weigh 25% of adult body mass and are cared for by the male at sea until adult mass is achieved and flight feathers have developed (Lavers et al., 2020). Razorbills do not breed until they reach three to six years of age and can live for up to 40 years. They spend the non-breeding period at sea, during which they complete flight and contour feather moult. Different feathers moult at different times of the year and they are flightless whilst replacing primary and secondary wing feathers (Dunn et al., 2020).

The razorbills studied here breed on James Island, on the northeast coast of Newfoundland (Figure I). This island is <1 km across, with a grassy interior and a coastal area made up of rocks and boulders with roughly 3000 breeding pairs of razorbills (Environment and Climate Change Canada unpublished data). Other seabird species investigated in this study (Chapter 4) include American herring gull (*Larus smithsonianus*), Atlantic puffin (*Fratercula arctica*), glaucous gull (*Larus hyperboreus*), northern gannet (*Morus bassanus*) and thick-billed murre (*Uria lomvia*). The study populations of these species are found breeding at different colonies across the Canadian North Atlantic: Bonaventure Island, Coats Island, Funk Island, Gull Island, James Island and Machias Seal Island (Figure I).

Capelin is the main forage fish in the Northwest Atlantic (Carscadden and Vilhjálmsson, 2002) and it dominates the coastal Newfoundland marine ecosystem when it migrates inshore to spawn in the summer (Davoren, 2024). This forage fish species plays a key role transferring energy to higher trophic levels (Buren et al., 2019) and is relied on by numerous species including seabirds such as the razorbill whose chick-rearing period coincides with capelin spawning (Gulka et al., 2017; Lescure et al., 2023). During the early 1990s, the capelin population crashed and has not recovered (Buren et al., 2019). Additionally, the timing of arrival inshore to spawn has recently become highly variable (Davoren, 2024). This has likely been caused by changes in seasonal sea ice dynamics and zooplankton community abundance and composition (Buren et al., 2014).

The objectives of this thesis were to:

1. Determine the best method for quantifying the docile-aggressive trait in razorbills (**Ch.1**).
2. Investigate relationships between docility and razorbill behaviour during the breeding (**Ch.2**) and non-breeding (**Ch.3**) periods.
4. Explore behavioural diversity in migratory routes of seabird species that breed in Atlantic Canada (**Ch.4**).

Significance

Quantifying personality in species is important because these individual level differences in behaviour are a key source of biodiversity within populations and, therefore, affect their stability, persistence and resilience (Wolf and Weissing, 2012). Understanding personality in seabirds and other marine taxa is important due to the increasing pressures facing the marine environment. For example, overfishing is a significant threat, with forage fish now making up a third of global catch (Pikitch et al., 2012). Additionally, another major threat is climate change with sea surface temperatures predicted to rise 1.4°C by 2070 (Han et al., 2019). This is especially the case in the study area as the Northwest Atlantic is experiencing increased rates of warming compared to other Atlantic regions (Pershing et al., 2015). Understanding how razorbill populations and personality types within them respond to this greater environmental variability is vital. For example, more variable prey availability may favour generalists over specialists within the population that are less reliant on a particular prey species or location. Therefore, studying personality traits in animals can aid in the development of management strategies that protect larger contingents of populations (MacKinlay & Shaw, 2023). Indeed, there are a growing number of personality studies that inform conservation (e.g., Arden et al., 2023; Collins et al., 2022).

Furthermore, identifying species and populations that have low levels of behavioural diversity will allow them to be prioritised for conservation measures, as they are more likely to experience declines due to environmental change and threats (Clavel et al., 2011).

References

Araújo, M. S., Bolnick, D. I., & Layman, C. A. (2011). The ecological causes of individual specialisation. *Ecol. Lett.*, 14(9), 948–958. https://doi.org/10.1111/j.1461-0248.2011.01662.x

Arden, R., Abdellaoui, A., Li, Q., Zheng, Y., Wang, D., & Su, Y. (2023). Majestic tigers: personality structure in the great Amur cat. *R. Soc. Open Sci.*, 10(4), 1–11. https://doi.org/10.1098/rsos.220957

Baker, L., Lawrence, M. S., Toews, M., Kuling, S., & Fraser, D. (2016). Personality differences in a translocated population of endangered kangaroo rats (*Dipodomys stephensi*) and implications for conservation success. *Behaviour*, 153(13–14), 1795–1816. https://doi.org/10.1163/1568539X-00003380

Bell, A. M. (2007). Animal personalities. *Nature*, 447, 539–540. https://doi.org/10.1038/44759a

Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: a meta-analysis. *Anim. Behav.*, 77(4), 771–783. https://doi.org/10.1016/j.anbehav.2008.12.022

Biagiotti Barchiesi, C.M., Biondi, L. M., & García, G. O. (2023). A systematic review of trends in research on seabird behavioral flexibility. *Mar. Ornithol.*, 51, 293–300. http://doi.org/10.5038/2074-1235.51.2.1546

Bolnick, D. I., Amarasekare, P., Araújo, M., Bürger, R., Levine, J. M., Novak, M., Rudolf, V. HW., Schreiber, S. J., Urban, M. C., & Vasseur, D. (2011). Why intraspecific trait variation matters in community ecology. *Trends Ecol. Evol.*, 26(4), 183–192. http://doi.org/10.1016/j.tree.2011.01.009

Buren, A. D, Koen-Alonso, M., Pepin, P., Mowbray, F., Nakashima, B., Stenson, G., Ollerhead, N. & Montevecchi, W. A. (2014). Bottom-up regulation of capelin, a keystone forage species. *PLoS ONE*. 9(2), 1–11. https://doi:10.1371/journal.pone.0087589.

Buren, A. D., Murphy, H. M., Adamack, A. T., Davoren, G. K., Koen-Alonso, M., Montevecchi, W. A., Mowbray, F. K., Pepin, P., Regular, P. M., … Robert, D. (2019). The collapse and continued low productivity of a keystone forage fish species. *Mar. Ecol. Prog. Ser.* 616, 155–170. https://doi:10.3354/meps12924.

Carscadden, J. E., & Vilhjálmsson, H. (2002). Capelin - What are they good for? *ICES J. Mar. Sci.*, 59(5), 863–869. https://doi.org/10.1006/jmsc.2002.1283

Carter, A. J., Feeney, W. E., Marshall, H. H., Cowlishaw, G., & Heinsohn, R. (2013). Animal personality: what are behavioural ecologists measuring? *Biol. Rev.*, 88(2), 465–475. http://hdl.handle.net/10871/19094

Ceia, F. R., & Ramos, J. A. (2015). Individual specialization in the foraging and feeding strategies of seabirds: a review. *Mar. Biol.*, 162(10), 1923–1938. https://doi.org/10.1007/s00227-015-2735-4

Clavel, J., Julliard, R., & Devictor, V. (2011). Worldwide decline of specialist species: toward a global functional homogenization? *Front. Ecol. Environ.*, 9(4), 222–228. https://doi.org/10.1890/080216

Collins, S. M., Hatch, S. A., Elliott, K. H., & Jacobs, S. R. (2019). Boldness, mate choice and reproductive success in *Rissa tridactyla*. *Anim. Behav.*, 154, 67–74. https://doi.org/10.1016/j.anbehav.2019.06.007

Collins, S. M., Hendrix, J. G., Webber, Q. M. R., Boyle, S. P., Kingdon, K. A., Blackmore, R. J., d'Entremont, K. J. N., Hogg, J., Ibáñez, J. P., Kennah, J. L., Lamarre, J., Mejías, M., Newediuk, L., Richards, C., Schwedak, K., Wijekulathilake, C., & Turner, J. W. (2022). Bibliometric investigation of the integration of animal personality in conservation contexts. *Conserv. Biol.*, 1–13. https://doi.org/10.1111/cobi.14021

Dall, S. R. X., Houston, A. I., & McNamara, J. M. (2004). The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecol. Lett.*, 7(8), 734–739. https://doi.org/10.1111/j.1461-0248.2004.00618.x

Dall, S. R. X., Bell, A. M., Bolnick, D. I., & Ratnieks, F. L. W. (2012). An evolutionary ecology of individual differences. *Ecol. Lett.*, 15(10), 1189–1198. https://doi.org/10.1111/j.1461-0248.2012.01846.x

Dall, S. R. X., Giraldeau, L. A., Olsson, O., McNamara, J. M., & Stephens, D. W. (2005). Information and its use by animals in evolutionary ecology. *Trends Ecol. Evol.*, 20(4), 187–193. https://doi.org/10.1016/j.tree.2005.01.010

Davoren, G. K. (2024). Variable forage fish biomass and phenology influence marine predator diet, foraging behavior, and species interactions in coastal Newfoundland, Canada. *ICES J. Mar. Sci.*, 1–14. https://doi.org/10.1093/icesjms/fsae021

Dunn, R. E., Wanless, S., Daunt, F., Harris, M. P., & Green, J. A. (2020). A year in the life of a North Atlantic seabird: behavioural and energetic adjustments during the annual cycle. *Sci. Rep.*, 10(1), 1–11. https://doi.org/10.1038/s41598-020-62842-x

Ebenau, A., von Borell, C., Penke, L., Ostner, J., & Schulke, O. (2020). Supplemental material for integrative personality assessment in wild Assamese macaques (*Macaca assamensis*). *J. Comp. Psychol.*, 134(1), 27–41. https://doi.org/10.1037/com0000190.supp

Elliott, K. H., Ricklefs, R. E., Gaston, A. J., Hatch, S. A., Speakman, J. R., & Davoren, G. K. (2013). High flight costs, but low dive costs, in auks support the biomechanical hypothesis for flightlessness in penguins. *PNAS*, 110(23), 9380–9384. https://doi.org/10.1073/pnas.1304838110

Fifield, D. A., Montevecchi, W. A., Garthe, S., Robertson, G. J., Kubetzki, U., & Rail, JF. (2014). Migratory tactics and wintering areas of northern gannets (*Morus bassanus*) breeding in North America. *Ornithol. Monogr*. 79, 1–63. https://doi:10.1642/aoum.79-1.

Franklin, K. A., Norris, K., Gill, J. A., Ratcliffe, N., Bonnet-Lebrun, A.-S., Butler, S. J., Cole, N. C., Jones, C. G., Lisovski, S., Ruhomaun, K., Tatayah, V., & Nicoll, M. A. C. (2022). Individual consistency in migration strategies of a tropical seabird, the Round Island petrel. *Mov. Ecol.*, 10, 1–14. https://doi.org/10.1186/s40462-022-00311-y

Gatt, M. C., Granadeiro, J. P., & Catry, P. (2021). Migrants and residents of a long-lived seabird differ in their behavioural response to a stressor. *J. Avian Biol.*, 52(2), 1–8. https://doi.org/10.1111/jav.02589

Gosling, S. D. (2008). Personality in non-human Animals. *Soc. Pers. Psychol. Compass*, 2(2), 985–1001. https://doi.org/10.1111/j.1751-9004.2008.00087.x

Grace, J, & Anderson, D. (2014). Personality correlates with contextual plasticity in a free-living, long-lived seabird. *Behaviour*. 151(9), 1281–1311. https://doi:10.1163/1568539X-00003185.

Guilford, T., Freeman, R., Boyle, D., Dean, B., Kirk, H., Phillips, R., & Perrins, C. (2011). A dispersive migration in the Atlantic Puffin and its implications for migratory navigation. *PLoS ONE*, 6(7), 1–8. https://doi.org/10.1371/journal.pone.0021336

Gulka, J., Carvalho, P. C., Jenkins, E., Johnson, K., Maynard, L., & Davoren, G. K. (2017). Dietary niche shifts of multiple marine predators under varying prey availability on the northeast Newfoundland coast. Front. Mar. Sci., 4, 1–11. https://doi.org/10.3389/fmars.2017.00324

Han, G., Ma, Z., Long, Z., Perrie, W., & Chassé, J. (2019). Climate change on Newfoundland and Labrador shelves: results from a regional downscaled ocean and sea-ice model under an A1B forcing scenario 2011–2069. Atmos. - Ocean. 57(1), 3–17. https://doi:10.1080/07055900.2017.1417110.

Harris, S. M., Descamps, S., Sneddon, L. U., Bertrand, P., Chastel, O., & Patrick, S. C. (2020). Personality predicts foraging site fidelity and trip repeatability in a marine predator. *J. Anim. Ecol.*, 89(1), 68–79. https://doi.org/10.1111/1365-2656.13106

Jeffries, P. M., Patrick, S. C., & Potts, J. R. (2021). Be different to be better: the effect of personality on optimal foraging with incomplete knowledge. *Theor. Ecol.*, 1–13. https://doi.org/10.1007/s12080-021-00517-7

Kaiser, M. I., & Müller, C. (2021). What is an animal personality? *Biol. Philos.*, 36(1), 1–25. https://doi.org/10.1007/s10539-020-09776-w

Koski, S. E. (2011). How to measure animal personality and why does it matter? Integrating the psychological and biological approaches to animal personality. In Inoue-Murayama M, Kawamura S, & A. Weiss (Eds.), From Genes to Animal Behaviour (pp. 115–136). Springer. https://doi.org/10.1007/978-4-431-53892-9_5

Krüger, L., Pereira, J. M., Paiva, V. H., & Ramos, J. A. (2019). Personality influences foraging of a seabird under contrasting environmental conditions. *JEMBE*, 516, 123–131. https://doi.org/10.1016/j.jembe.2019.04.003

Lavers, J., Hipfner, M., & Chapdelaine, G. (2020). Razorbill (*Alca torda*). In Billerman SM (Ed.), Birds of the World (1.0). Cornell Lab of Ornithology.

Lescure, L., Gulka, J., & Davoren, G. (2023). Increased foraging effort and reduced chick condition of razorbills under lower prey biomass in coastal Newfoundland, Canada. *Mar. Ecol. Prog. Ser.*, 709, 109–123. https://doi.org/10.3354/meps14286

MacKinlay, R. D., & Shaw, R. C. (2023). A systematic review of animal personality in conservation science. *Conserv. Biol.*, 37(1), 1–16. https://doi.org/10.1111/cobi.13935

Mathot, K. J., Wright, J., Kempenaers, B., & Dingemanse, N. J. (2012). Adaptive strategies for managing uncertainty may explain personality-related differences in behavioural plasticity. *Oikos*, 121(7), 1009–1020. https://doi.org/10.1111/j.1600-0706.2012.20339.x

Menzies, A. K., Timonin, M. E., McGuire, L. P., & Willis, C. K. R. (2013). Personality variation in little brown bats. *PLoS One*, 8(11). https://doi.org/10.1371/journal.pone.0080230

Merrick, M. J., & Koprowski, J. L. (2017). Should we consider individual behavior differences in applied wildlife conservation studies? *Biol. Conserv.*, 209, 34–44. https://doi.org/10.1016/j.biocon.2017.01.021

Müller, T., & Müller, C. (2015). Behavioural phenotypes over the lifetime of a holometabolous insect. *Front. Zool.*, 12(1). https://doi.org/10.1186/1742-9994-12-S1-S8

Patrick, S. C., Charmantier, A., & Weimerskirch, H. (2013). Differences in boldness are repeatable and heritable in a long-lived marine predator. *Ecol. Evol.*, 3(13), 4291–4299. https://doi.org/10.1002/ece3.748

Patrick, S. C., & Weimerskirch, H. (2014). Personality, foraging and fitness consequences in a long lived seabird. *PLoS ONE*, 9(2), 1–11. https://doi.org/10.1371/journal.pone.0087269

Patrick, S. C., & Weimerskirch, H. (2017). Reproductive success is driven by local site fidelity despite stronger specialisation by individuals for large-scale habitat preference. *J. Anim. Ecol.*, 86(3), 674–682. https://doi.org/10.1111/1365-2656.12636

Patrick, S. C., Pinaud, D., & Weimerskirch, H. (2017). Boldness predicts an individual's position along an exploration–exploitation foraging trade-off. *J. Anim. Ecol.*, 86(5), 1257–1268. https://doi.org/10.1111/1365-2656.12724

Pereira, J. M., Ramos, J. A., Ceia, F. R., Krüger, L., Marques, A. M., & Paiva, V. H. (2024). Boldness predicts foraging behaviour, habitat use and chick growth in a central place marine predator. *Oecologia*. https://doi.org/10.1007/s00442-024-05557-4

Pershing, A. J., Alexander, M. A., Hernandez, C. M., Kerr, L. A., Bris, A. L., Mills, K. E., Nye, J. A., Record, N. R., Scannell, H. A., Scott, J. D., Sherwood, G. D., & Thomas, A. C. (2015). Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. *Sci.*, 350(6262), 809–812. https://doi.org/10.1126/science.aac9819

Petelle, M. B., & Blumstein, D. T. (2014). A critical evaluation of subjective ratings: unacquainted observers can reliably assess certain personality traits. *Curr. Zool.*, 60(2), 162–169. https://academic.oup.com/cz/article/60/2/162/1804160

Phillips, R. A., Lewis, S., González-Solís, J., & Daunt, F. (2017). Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds. *Mar. Ecol. Prog. Ser.*, 578, 117–150. https://doi.org/10.3354/meps12217

Pikitch, E., Boersma, P., Boyd, I., Conover, D., Cury, P., Essington, T., Heppel, S., Houde, E., Mangel, M., Pauly, D., Plaganyi, E., Sainsbury, K., Steneck, R., & Santora, C. (2012). Little fish big impact: managing a crucial link in ocean food webs. www.lenfestocean.org.

Powell, D. M., & Svoke, J. T. (2008). Novel environmental enrichment may provide a tool for rapid assessment of animal personality: a case study with giant pandas (*Ailuropoda melanoleuca*). *J. Appl. Anim. Welf. Sci.*, 11(4), 301–318. https://doi.org/10.1080/10888700802329673

Réale, D., Martin, J., Coltman, D. W., Poissant, J., & Festa-Bianchet, M. (2009). Male personality, life-history strategies and reproductive success in a promiscuous mammal. *J. Evol. Biol.*, 22(8), 1599–1607. https://doi.org/10.1111/j.1420-9101.2009.01781.x

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biol. Rev.*, 82(2), 291–318. https://doi.org/10.1111/j.1469-185X.2007.00010.x

Rebstock, G. A., Abrahms, B., & Boersma, P. D. (2022). Site fidelity increases reproductive success by increasing foraging efficiency in a marine predator. *Behav. Ecol.*, 33(4), 868–875. https://doi.org/10.1093/beheco/arac052

Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.*, 19(7), 372–378. https://doi.org/10.1016/j.tree.2004.04.009

Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: a meta-analysis. *Behav. Ecol.*, 19(2), 448–455. https://doi.org/10.1093/beheco/arm144

Stamps, J., & Groothuis, T. G. G. (2010). The development of animal personality: relevance, concepts and perspectives. *Biol. Rev.*, 85(2), 301–325. https://doi.org/10.1111/j.1469-185X.2009.00103.x

Torgerson-White, L. L. (2014). Rating methodology, personality axes, and behavioural plasticity: a case study in African lions. *Anim. Behav. Cogn.*, 1(3), 230–248. https://doi.org/10.12966/abc.08.02.2014

Traisnel, G., & Pichegru, L. (2018). Does it always pay to defend one’s nest? A case study in African penguin. *J. Ethol.*, 124(1), 74–83. https://doi.org/10.1111/eth.12704 van de Walle, J., Sun, R., Fay, R., Patrick, S. C., Barbraud, C., Delord, K., Weimerkirch, H., & Jenouvrier, S. (2024). The impact of boldness on demographic rates and life-history outcomes in the wandering albatross. *J. Anim. Ecol.*, 93, 676–690. https://doi.org/10.1111/1365-2656.14077

Weber, S. B., Richardson, A. J., Brown, J., Bolton, M., Clark, B. L., Godley, B. J., Leat, E., Oppel, S., Shearer, L., Soetaert, K. E. R., Weber, N., & Broderick, A. C. (2021). Direct evidence of a prey depletion "halo" surrounding a pelagic predator colony. *PNAS*, 118(28), 1–8. https://doi.org/10.1073/pnas.2101325118/-/DCSupplemental

Williams, K. A., Gulka, J., Cook, A. S. C. P., Diehl, R. H., Farnsworth, A., Goyert, H., Hein, C., Loring, P., Mizrahi, D., Petersen, I. K., Peterson, T., Press, K. M. C., & Stenhouse, I. J. (2024). A framework for studying the effects of offshore wind energy development on birds and bats in the Eastern United States. *Front. Mar. Sci.*, 11, 1–18. https://doi.org/10.3389/fmars.2024.1274052

Wolf, M., Van Doorn, G. S., Leimar, O., & Weissing, F. J. (2007). Life-history trade-offs favour the evolution of animal personalities. *Nature*, 447, 581–584. https://doi.org/10.1038/nature05835

Wolf, M., & Weissing, F. J. (2012). Animal personalities: Consequences for ecology and evolution. *Trends Ecol. Evol.*, 27(8), 452–461. https://doi.org/10.1016/j.tree.2012.05.001

Woo, K. J., Elliott, K. H., Davidson, M., Gaston, A. J., & Davoren, G. K. (2008). Individual specialization in diet by a generalist marine predator reflects specialization in foraging behaviour. *J. Anim. Ecol.*, 77(6), 1082–1091. https://doi.org/10.1111/j.1365-2656.2008.01429.x

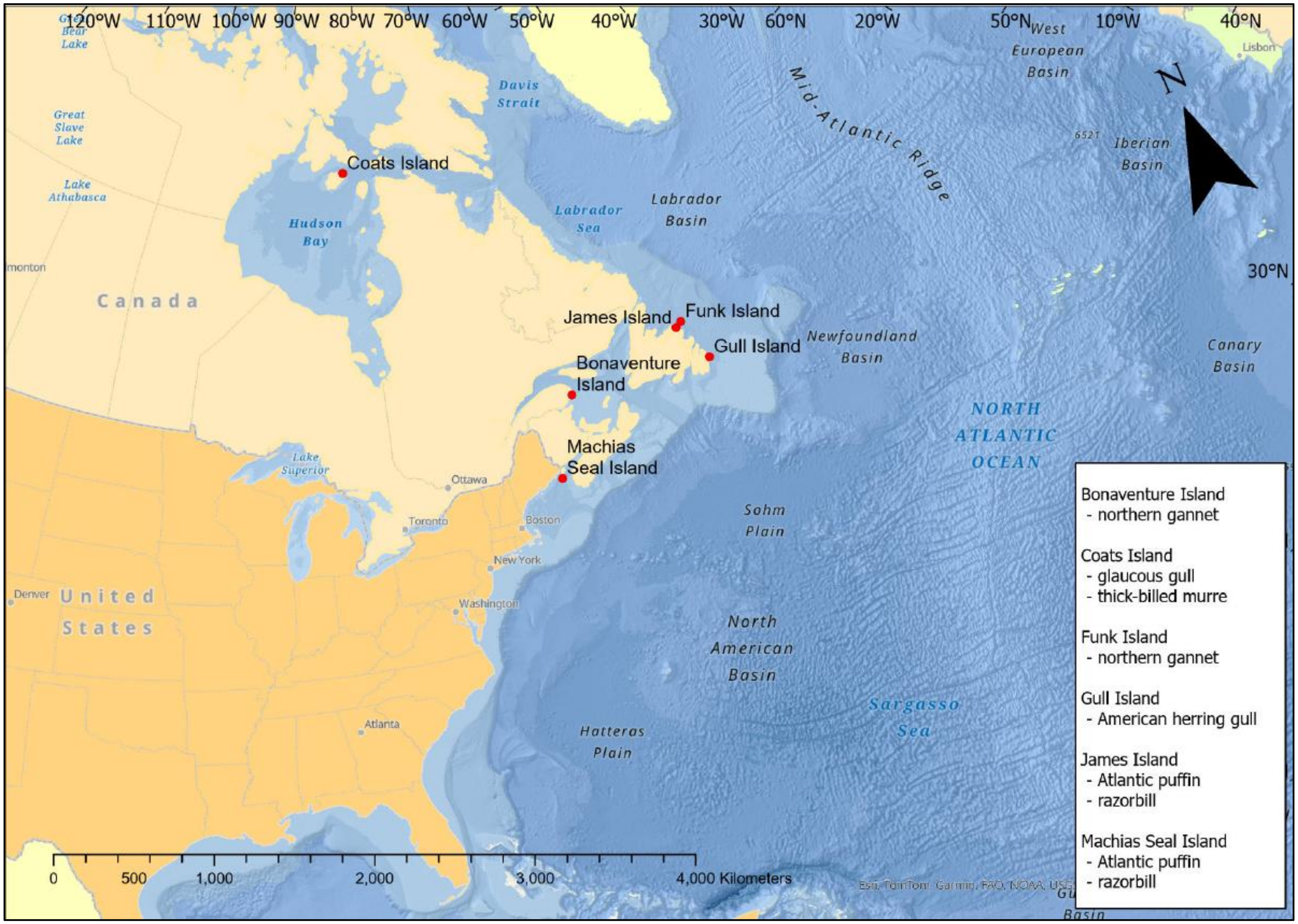

Figure I. The location of the seabird breeding colonies where data were collected for this study, with the species present at each island shown.

Chapter 1: A non-invasive method during routine handling indicates docility in a wild, crevice-nesting seabird.

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Abstract

Personality traits have been identified in many animals but species that are hard to observe in the wild present unique challenges. We aimed to determine an appropriate method for identifying docility in a crevice-nesting seabird (razorbill, *Alca torda*) by conducting three tests associated with this trait. Two tests used quantitative behavioural coding (crevice extraction, restraint), while the other used qualitative observer ratings (routine handling). Chick-rearing razorbills (n = 44) in Newfoundland, Canada were tested across two years (2021, 2022), with 16 tested in both years. Observer ratings during routine handling had the highest repeatability (*R* = 0.527, 95% CI: 0.007 - 0.831), compared to quantified scores during extraction (*R* = 0.157, 95% CI: 0 - 0.399) and restraint (*R* = 0.041, 95% CI: 0 - 0.294) tests. Overall, findings suggest that observer ratings may be a good method to quantify personality traits in species that are hard to observe in the wild.

Introduction

Animal personality is defined as consistent between-individual differences that are stable across contexts and persist through time (Stamps & Groothuis, 2010; Wolf & Weissing, 2012). These differences are present among individuals of the same size, sex, and age (Bell, 2007; Müller & Müller, 2015) and have been found in numerous animal groups throughout the animal kingdom (Sih et al., 2004; Wolf et al., 2007; Wolf & Weissing, 2012). The five commonly studied personality traits are activity, sociability, boldness, exploration, and aggressiveness (Réale et al., 2007; Sih et al., 2004). These traits are continuums with a range of potential expressed behaviours such as shy to bold or docile to aggressive. As studying personality traits in animals can aid in the development of management strategies that protect larger contingents of populations (MacKinlay & Shaw, 2023), there are a growing number of personality studies that inform conservation (e.g., Arden et al., 2023; Collins et al., 2022).

There are two main methods of assessing personality traits in animals: behavioural coding and observer ratings (Carter et al., 2013; Gosling, 2001). Behavioural coding involves observing and quantifying the frequency and duration of discrete, well-defined behaviours (Kaiser & Müller, 2021) and, thus, is an objective method with limited human bias (Petelle & Blumstein, 2014). Alternatively, observer ratings involve using standardised scales to assess a suite of behaviours (Kaiser & Müller, 2021) and, thus, are more subjective but less time consuming to administer (Ebenau et al., 2020). Observer ratings are common in captive studies because the reliability of ratings increases with experience with the study animals (e.g., Powell & Svoke, 2008; Torgerson-White, 2014). The use of observer ratings on non-captive animals, however, has begun (e.g., Arden et al., 2023; Baker et al., 2016) and there is evidence that standardised ratings by observers with no prior experience with the study individuals can also be an effective way of measuring a personality trait in wild animals (Petelle & Blumstein, 2014). To account for the advantages and disadvantages of both methods, simultaneous use is recommended (Highfill et al., 2010) and scores from the two methods are often correlated when measuring the same personality trait (e.g., Gosling, 2008; Koski, 2011). Although studies using both methods are growing in frequency (Carter et al., 2013), they are still rare (e.g., Baker et al., 2016).

As with other taxonomic groups, personality traits have been investigated and identified in seabirds. Boldness, the most studied trait across all taxa (Kaiser & Müller, 2021), has been the only trait to receive significant attention; however, and only a small proportion of seabird species have been studied (Table 1). In seabirds, responses to novel items (e.g., avoidance, attack) by parental birds at nest sites during incubation or chick-rearing are typically used as an appropriate test of boldness (e.g., Collins et al., 2019; Harris et al., 2020), although assessment of responses to human approach of nest sites has also been used (e.g., Traisnel & Pichegru, 2018, 2019a, 2019b). For some species, however, these methods are not feasible. Indeed, many seabirds breed in dense colonies which promotes work at night to minimize disturbance, leading to issues illuminating and observing responses of focal individuals to a stimulus (e.g., novel object, human approach). These issues are amplified for species that nest in crevices or burrows, resulting in few studies on personality traits in these species (e.g., Gatt et al., 2021) and emphasizing a need for alternative approaches to study personality traits. In the adults and young of other taxa, the docile-aggressive continuum (hereafter referred to as docility) has been assessed through responses to capture and handling (e.g., Petelle et al., 2013; Poissant et al., 2013; Réale et al., 2000; Trnka et al., 2018), suggesting that this approach may be appropriate to test for personality traits in these harder to study species.

As there is substantial evidence that personality is commonplace throughout the animal kingdom (Sih et al., 2004), our objective was to determine an appropriate method for quantifying a personality trait in species that are hard to observe naturally in the wild (e.g., burrow/crevice nesting, nocturnal or semi-fossorial species). Specifically, we measured the behavioural responses of chick-rearing razorbills (*Alca torda*), a seabird of the family Alcidae, during three tests in a similar behavioural context (nest extraction, restraint, routine handling). Razorbills are an ideal model species for this study because they nest in crevices, where direct observations are not possible, and they nest at high densities (Lavers et al., 2020), making research at night preferable to minimise colony-level disturbance. Additionally, razorbills have high nest site fidelity (Lavers et al., 2020), facilitating personality studies on the same individuals across years. As all three tests assess responses to capture and handling, the behaviours measured likely relate to the docility personality trait (Bonnot et al., 2018; Poissant et al., 2013). A combination of behavioural coding and observer ratings was used to examine the effectiveness of each method at measuring personality in the wild for this species. If all tests are effective at quantifying consistent behavioural differences among individuals, we predict that individual responses will be highly repeatable across years. If a test is not appropriate, however, we predict that responses will not be repeatable. As this is the first study to investigate individual behavioural differences in a seabird species from the family Alcidae and to explore methods for quantifying a personality trait in a wild crevice-nesting seabird, this study will inform methods of future personality studies on this and other similarly hard to observe species.

Methods

Study Species and Study Site

Similar to other seabirds, razorbills are long-lived (~40 years), sexually monomorphic and have delayed sexual maturity (3 - 6 years; Lavers et al., 2020). Razorbills lay a single egg each year that both parents incubate for ~35 days and chicks fledge after a short rearing period (16 - 21 days) at 30% of adult body mass (~700 g; Lavers et al., 2020). We studied razorbills breeding on James Island on the northeast coast of Newfoundland, Canada. This island is < 1 km across, with a grassy interior and a coastal area made up of rocks and boulders. Razorbills nest along the coastal area in rock crevices that are only large enough for the adult pair and offspring, a behaviour common across their North Atlantic range (Lavers et al., 2020). A total of ~2,700 breeding pairs of razorbills nest on the island in high densities (0.69 ± 0.17 nests per m^2; Environment and Climate Change Canada unpublished data), along with multiple other seabird species.

Personality Testing

Chick-rearing razorbills captured in previous years (2017, 2019-2020) for tracking studies were targeted for personality testing because rock crevices were individually marked to facilitate recapture across years. Although we targeted previously captured birds, recapture rates were lower than expected and, thus, many (40%) had not been previously captured. Of the birds previously captured, most had only been captured once for bird-borne tag deployment. As razorbills are sexually monomorphic, blood was sampled during routine handling (see below) for genetic sex determination (see methods in: Gulka & Davoren, 2019; Lescure et al., 2023). Age of focal birds could not be determined, however, because razorbills do not possess age-related characteristics (e.g., varying plumage colour). To minimise the probability of nest abandonment, all tests were carried out on chick-rearing razorbills (8 July – 4 August 2021, 11 July – 4 August 2022) at night (0100 - 0400 hours, Newfoundland Daylight Time, NDT) under the illumination of red headlamps as the birds appeared to respond less to red relative to white light. To ensure that repeatability of responses could be determined if present, the tests were repeated using the same procedures on recaptured individuals across two years (Menzies et al., 2013; Petelle & Blumstein, 2014; Sánchez-Tójar et al., 2022). As behavioural responses can change with the competence and technique of the handler, we ensured all three handlers during this study had equivalent levels of animal handling experience. As behavioural responses can also change throughout the breeding season in seabirds (e.g., boldness; Collins et al, 2019), the chick body mass of the tested parental bird was measured during testing, and the development stage of each chick was characterised as early (50 - 100 g), mid (100 - 150 g) and late (> 151 g). Finally, because all observations were carried out on focal individuals in the field, it was not possible to record data using a blind design.

For the first test, we quantitatively measured the response of each parent (i.e., behavioural coding) to capture at the nest and removal from the rock crevice (methods adapted from Gatt et al., 2021). When possible, birds were extracted from the nest by holding the bird from behind, allowing control of the wings to prevent harm. The researcher extracting the bird quantified four metrics during extraction, including the presence/absence and frequency of struggling, resisting, biting and vocalising (Table 2). Specifically, each of the four metrics were scored as absent (0) or present (1), and the biting and struggling metrics were also given a score of 2 if continuous. These values were summed across all four metrics to determine an overall test score on a scale of 0-6 (Table 2). The same researcher carried out all nest extractions throughout the study. As crevice complexity might influence the difficulty of extraction and, thus, a bird's response to extraction, each crevice was qualitatively assessed based on four criteria to derive a crevice complexity index. The four criteria included crevice height and depth (low, 1; medium; 2, high, 3), the number of possible exits, and the area within the crevice (small, 1; large, 2). The value from each criterion was summed to determine the complexity index for each crevice. These values were all collected by the same two individuals in the first year and values were considered consistent across both years due to high nest site fidelity in razorbills.

For the second test, we measured an individual's response to routine handling using observer ratings. Routine handling occurred immediately after nest extraction and involved the following conducted in the same order: banding with a standard metal band, attachment/removal of tracking devices (i.e., geolocators, time-depth recorders) on plastic leg bands, blood/feather sampling, and body measurements (i.e., mass, wing chord, tarsus). For full details on this process, see Runnells et al. (2024). During handling, observers were instructed not to discuss the bird's behaviour and once the bird was released, each observer stated their rating simultaneously to ensure independent assessments. Ratings were on a scale of 1 to 5 and were based on qualitative assessments of the combined presence and frequency of a suite of observable behaviours (Table 2). Extreme values (1 and 5) indicate that all behavioural responses were considered low, or high, respectively. Intermediate values (2/3/4) indicate each observer's judgment after consideration of responses to all five behavioural questions.

For the observer ratings, we attempted to minimise the disadvantages associated with this method in a number of ways. First, novice observers (Observer 1, Observer 2) were always accompanied by an experienced observer (MJL). The same two observers (MJL, Observer 1) conducted ratings in 2021 and 2022, and a third observer was added in 2022 (Observer 2). Second, prior to conducting observer ratings in the field, all observers underwent training, which involved practicing rating using bird handling videos to gain familiarity with assessing behaviour and the rating questionnaire. Third, during initial instruction and throughout testing, it was emphasised that all observers were to remain consistent with their own ratings to minimise the influence of other observers. Fourth, observers were not provided with the previous scores for an individual bird. The numbers of birds tested each year (30 birds/year) plus the one-year duration between tests also made it unlikely that observers remembered previous scores for each individual. Finally, all ratings were noted immediately following handling to prevent memory recall bias/error.

For the third test, we quantitatively measured each individual's response to restraint (i.e. behavioural coding) by placing the adult bird in a cotton cloth bag that was tied to ensure a snug fit to the body. The bag with the bird was then placed in a small plastic box for 5 min (methods adapted from Elliott et al., 2014). During this period, we quantified the amount of struggling and heavy breathing as: motionless, no heavy breathing (1), one-two struggles, no heavy breathing (2), one-two struggles, heavy breathing (3), and three or more struggles, heavy breathing (4). As birds were in a bag, it was not possible to accurately measure breath frequency and, thus, we coded the behaviour as presence or absence of heavy breathing. Struggles were defined as movements that lasted > 2 s. If the bird reached the maximum score before the end of the test, the test was terminated to eliminate unnecessary handling time. As the bag used might influence an individual's response to restraint, the bag used for each test was recorded (three bags were used). The same researcher carried out all observations of the restraint test throughout the study.

Data Analysis

All data processing and statistical analysis were carried out in R version 4.3.0 (R Core Team, 2023). For observer ratings, the agreement (or similarity) in ratings among researchers is one of the main methodological concerns (Kaiser & Müller, 2021; Petelle & Blumstein, 2014). Although it is not necessary for the rating values to be the same across observers, high agreement in ratings between observers is necessary for observer ratings to be a robust measure of personality.

Therefore, we assessed the agreement of observer ratings between each pair of experienced and novice observers in each year using Kendall's coefficient of concordance (Kendall's W) in the *irr* package (Gamer et al., 2019). Kendall's W is a non-parametric rank correlation metric that assesses agreement among the ratings of two or more observers (Legendre, 2005), where values range between 0 (no agreement) and 1 (complete agreement), with > 0.6 typically considered high agreement (Gearhart et al., 2013). Due to high agreement between observers (see below), averaged observer ratings for each bird within each year were used in analyses. Averaged observer ratings were considered to be a continuous variable as values were no longer integers.

Within each year, pairwise correlations between scores/ratings of the three tests were assessed during exploratory analysis using Spearman's Rank Correlation tests to investigate whether the behavioural responses to each test may represent the same personality trait (i.e., docility) or a behavioural syndrome (i.e., correlated traits such as aggression and boldness; Bell, 2007). We also used a mixed Principal Component Analysis (PCA) using the *FAMD* function in the *FactoMineR* package (Le et al., 2008) on our restraint and extraction scores (ordinal data, integers) and averaged observer ratings (continuous non-integers) to reduce all test scores/ratings within each year into a single continuous variable (PC1), as is typical in studies with multiple tests or multiple observed behaviours within tests (e.g., Baker et al., 2016; Martinig et al., 2022). PC1 is hereafter referred to as the 'response index'.

To determine whether an individual's behaviour during each test was repeatable, we calculated adjusted repeatability (*R*). Adjusted repeatability is a population level measure that determines how much of the variation in the dataset is due to within-individual variation (Bell et al., 2009) by dividing the variance among individuals by the sum of the variance among individuals and the residual within-individual variance (Biro & Stamps, 2015). To calculate adjusted repeatability, we carried out generalized linear mixed models (GLMM) on observer ratings and the response index (Gaussian data) and cumulative link mixed models (CLMM) on extraction and restraint scores (ordinal data). The *rpt* (*rptR* package; Stoffel et al., 2017) and *clmm* (*ordinal* package; Christensen, 2023) functions were used to carry out GLMMs and CLMMs, respectively. Adjusted repeatability is calculated directly by the *rpt* function along with associated 95% confidence intervals (parametric bootstrapping, n=1000) and a *p* value (Stoffel et al., 2017). Alternatively, adjusted repeatability was calculated manually from the CLMM output and confidence intervals (95%) were generated using the *r.con* function in the *psych* package (Revelle, 2024). All personality-tested individuals, including those that were tested only once, were included in the analysis to increase precision of the among-individual variation (Nakagawa & Schielzeth, 2010). The fixed factors included in all repeatability analyses were chick development stage, year, and sex of the tested parent, along with one additional fixed factor for each response variable, which was crevice complexity for the extraction score model, bag ID for the restraint score model and observer pair ID for the observer rating model. Although age could not be added as a factor, we tried to control for age in the experimental design by only testing mature adults that were currently rearing chicks. Model assumptions were verified when appropriate by plotting residuals against fitted values and against each predictor in the model (Zuur & Ieno, 2016).

Ethical note

This research was conducted in accordance with the Canadian Council for Animal Care (Protocol F20-017/1/2) and under Canadian Master Banding Permit (10873). All efforts were taken to reduce animal use, minimise the handling time for each individual, and limit disturbance to the wider seabird colony. Additionally, the individuals used were part of a long-term study where several overlapping scientific objectives were met.

Results

In total, personality tests were conducted on 44 unique individuals in two breeding seasons (2021, 2022), with 30 assessments in each year. We tested 30 individuals in 2021, with the goal of testing as many of these individuals again during 2022 to facilitate repeatability analyses across years. However, it was only possible to recapture 16 of the original 30 from 2021. Therefore, 14 more individuals were added to maintain a sample size of 30 individuals per year for measures of between-individual variation. Observer ratings were conducted during all 60 assessments, while 59 and 58 restraint and extraction scores were conducted, respectively. Conducting all three tests took on average 17 mins 52 s (± 3 mins 56 s) per bird.

There was high agreement (Kendall's W = 0.70 – 0.83) in observer ratings between experienced/novice observer pairs in both 2021 and 2022 (Figure 1), with complete agreement between observers for 38% of the birds tested, and similar levels of complete agreement across all 5 rating levels (11 - 34%). Additionally, high agreement remained consistent throughout each study year, as indicated by limited differences during initial and late testing (Figure 1). Overall, these highly consistent rating values across observers suggest that observer ratings are a robust metric to assess individual differences.

During exploratory analysis, we investigated whether the behavioural responses to each test may represent the same personality trait (i.e., docility) or a behavioural syndrome. We found that pairwise correlations during 2021 of personality test scores/ratings were positive and significant between observer ratings and restraint scores (Figure 2C) and extraction scores (Figure 2E), but not between extraction and restraint scores (Figure 2A). During 2022, scores/ratings were not significantly correlated (Figure 2B, 2D, 2F). During 2021, the response index (PC1) explained 23% of the variation in the dataset and was highly correlated with the three original test scores/ratings (extraction scores = 0.720, observer ratings = 0.780, restraint scores = 0.780). By contrast, the response index (PC1) in 2022 explained 21% of the variation in the dataset and had weaker correlations with the three original test scores/ratings (extraction scores = 0.630, observer ratings = 0.630, restraint scores = 0.580).

The GLMMs and CLMMs revealed that the fixed effects did not have a significant effect on the test scores, ratings or response index (Table 3). Adjusted repeatability varied among test scores/ratings and the response index (Figure 3). Repeatability of the observer ratings over the two-year period was significant and high (R = 0.527, 95% CI: 0.007-0.831, p = 0.011), as indicated by a greater number of individuals with consistent differences (i.e. parallel lines in Figure 3C). Repeatability of the response index was also high and significant (R = 0.519, 95% CI: 0.025-0.769, p = 0.019). By contrast, adjusted repeatability was lower for restraint scores (R = 0.041, 95% CI: 0-0.294) and extraction scores (R = 0.157, 95% CI: 0-0.399), which was also indicated by fewer individuals with consistent differences between individuals (Figure 3A, 3B). Model validation indicated no concerns.

Discussion

Our findings show that after controlling for fixed effects (e.g., chick development stage, year, and sex), consistent individual differences in behaviours associated with a personality trait (docility) are present in razorbills, adding to the growing evidence that personality traits are common throughout the animal kingdom (Sih et al., 2004; Wolf et al., 2007; Wolf & Weissing, 2012). The differences in repeatability among our three tests, however, suggest that not all tests were appropriate (e.g., not compatible with the study species, not effectively standardised) for quantifying a personality trait in razorbills. Observer ratings were highly consistent between observers and produced more repeatable results than the other two tests. These findings suggest that standardised, independent observer ratings during routine handling is an appropriate method to assess personality for this species, and possibly other hard to observe species. Although the repeatability of the response index (PC1) was also high, it may not be an appropriate metric of personality as it incorporates test scores with limited to no repeatability. Indeed, even though combining multiple tests can be an informative method of personality trait assessment, especially when incorporating both consistency across time and across contexts (Sih et al., 2012; Wolf et al., 2007), all tests must be repeatable and assess the same trait for this to be effective.

Presence of Personality

Key requirements for the identification of a personality trait were met in our study. First, we found observable differences in behaviour among individuals, and second, these differences were consistent over time (i.e., highly repeatable). Indeed, repeatability values from our observer ratings (R = 0.527, 95% CI: 0.007 - 0.831) were greater than the average animal repeatability reported in the literature (R = 0.37; Bell et al., 2009) and comparable with those found in other seabird studies that investigated personality (e.g., boldness: 0.37 - 0.68; Collins et al., 2019; Harris et al., 2020; Patrick et al., 2013, 2017). It is also notable that our high repeatability was found with a one-year duration between tests because repeatability has been reported to decrease with greater duration between tests (e.g., great tits, *Parus major*; Dingemanse et al., 2002), due to greater opportunity for developmental change (Bell et al., 2009). Although our study did not assess behaviour across contexts, this requirement may not be achievable in all studies, due to practical constraints (e.g., time, equipment, species ecology), as was likely the case in many previous seabird personality studies (Table 1). In these cases, consistency across time may be sufficient to confirm the presence of a personality trait (Kaiser & Müller, 2021). Overall, our findings support numerous studies that have confirmed avian personality (Bell et al., 2009) in both field and captive settings (Pogány et al., 2018) across all five main personality traits (van Oers & Naguib, 2013). Additionally, our findings support more recent studies confirming the presence of personality traits in seabirds (Table 1) as well as the prevalence of individual behavioural consistency in this taxonomic group (Ceia & Ramos, 2015).

It is important to consider which personality traits our observer ratings are measuring. In other taxa (e.g., mammals), an individual's response to capture and handling has been used to measure docility (docile – aggressive continuum; Petelle et al., 2013; Poissant et al., 2013), with higher frequencies of struggling-type behaviours associated with lower docility (Réale et al., 2000). Similar to our study, other studies using capture and handling methods to assess personality traits have also frequently used the relative judgement of experienced animal handlers to score docility (i.e., observer ratings; Bonnot et al., 2018; Martin & Réale, 2008; Petelle et al., 2013). Docility has been shown to form a behavioural syndrome with boldness (Bell, 2007; Réale et al., 2009) and docility and boldness are also related to an animal's stress response (Bonnot et al., 2018; Carere et al., 2010; Ellis et al., 2006). Therefore, the repeatable behavioural differences in razorbills in this study are likely strongly related to docility whilst also being potentially influenced by the boldness of an individual. Overall, our study suggests that personality is present in razorbills, as the repeatable behaviours observed can be linked to personality traits.

Personality Assessment Methods

The low repeatability of behavioural responses to the extraction and restraint tests and the lack of correlations between test scores during one year (2022) may be due to factors limiting our ability to standardise the administration of these tests. Indeed, standardised assessment is vital (Martinig et al., 2022; Sánchez-Tójar et al., 2022) and assessing personality can be complicated by factors during testing that are difficult to control (Burns, 2008). Repeatability estimates can be influenced by interactions between individuals and their environment (e.g., food availability, temperature; Martin & Réale, 2008; Nussey et al., 2007), with even small environmental changes having the potential to influence behavioural expression (Niemelä et al., 2019). In our study, each nest crevice presented its own unique extraction scenario due to varying crevice complexity and the initial orientation of the bird, which likely combined to influence the extraction score. Indeed, Gatt et al. (2021) standardised their personality tests during nest extraction of another burrow-nesting species (Cory's shearwater, *Calonectris borealis*) by only removing birds facing the burrow entrance, which was the primary orientation encountered. Although many razorbills were encountered oriented away from the crevice entrance and were extracted from behind, others were oriented differently which precluded standardising extraction orientation. For the restraint test, it was difficult to standardise how snug the cloth bag was during testing regardless of whether the same bag was used. If these confounding factors could be addressed consistently across all study individuals (e.g., bags designed for the study species with a quick secure closure mechanism), then restraint and extraction tests may be more appropriate personality tests in this and other burrow/crevice-nesting species.

In contrast to the extraction and restraint scores, observer ratings were highly repeatable in razorbills, likely because we addressed the main limitations of this method. Specifically, all observers were trained prior to personality testing and then produced independent ratings of individual birds using a standardised process focusing on simple, observable behaviours. Training addressed the concern that observers may interpret behaviours differently (Uher & Visalberghi, 2016), with the high agreement in ratings between observers suggesting this was not an issue. Despite our observers having limited experience with the study species/individuals and two of the three having no prior experience conducting observer ratings, the high agreement between observers supports the application of observer ratings to wild animals (Petelle & Blumstein, 2014). Although, observer ratings can be biased if sex and age are known (Uher & Visalberghi, 2016), these biases were eliminated because our study species (razorbill) is sexually monomorphic and does not possess age-related characteristics (e.g., varying plumage colour). When sex and age are known, it will be important to account for these biases in the study design and statistical analyses. With these factors considered, observer ratings appeared to be an appropriate and effective method of personality assessment for this species and a method of high potential for other hard to observe species. One caveat, however, is that observer ratings are likely most accurate for individuals at the extreme ends of the personality trait continuum being assessed (Torgerson-White, 2014), although this was not the case in our study.

Conclusion

In conclusion, there is support for personality being present in razorbills when considering the responses to capture and handling are likely linked to docility, as observed in other taxa (Petelle et al., 2013; Poissant et al., 2013). Although our methods differ from those used in other seabird personality studies, which impacts our ability to directly compare repeatability values with these studies (Sánchez-Tójar et al., 2022), observation limitations with our crevice-nesting study species required us to identify a different appropriate method. Overall, standardised, independent observer ratings were found to be the best of the three tests for quantifying repeatable behavioural responses in this crevice-nesting seabird, highlighting the potential value of observer ratings when studying personality in other cryptic wild animals. Indeed, if researchers are handling wild animals for other scientific objectives, observer ratings may provide a low-cost, time-efficient method to test for personality (Ebenau et al., 2020) with highly repeatable results after carefully addressing and controlling for the potential pitfalls of this method. Furthermore, stress on study animals can be minimized as ratings do not require separate tests and can be carried out in conjunction with routine handling (e.g., banding, body measurements), which also may facilitate larger sample sizes. Our results also highlight the benefit of an initial multi-test approach to assessing personality traits in animals, allowing the determination of an appropriate test. As personality traits can both directly and indirectly influence fitness, due to their correlation with movement and foraging decisions (Collins et al., 2019; Santicchia et al., 2018; Smith & Blumstein, 2008), identifying personality and between-individual differences within a species is vital to understand species-specific tolerances to increasing anthropogenic threats

(Krüger et al., 2019). Therefore, routinely using observer ratings as an effective personality assessment method in wild animals may contribute towards the conservation of many species.

References

Arden, R., Abdellaoui, A., Li, Q., Zheng, Y., Wang, D., & Su, Y. (2023). Majestic tigers: personality structure in the great Amur cat. R. Soc. Open Sci., 10(4), 1–11. https://doi.org/10.1098/rsos.220957

Baker, L., Lawrence, M. S., Toews, M., Kuling, S., & Fraser, D. (2016). Personality differences in a translocated population of endangered kangaroo rats (*Dipodomys stephensi*) and implications for conservation success. *Behaviour*, 153(13–14), 1795–1816. https://doi.org/10.1163/1568539X-00003380

Bell, A. M. (2007). Animal personalities. *Nature*, 447, 539–540. https://doi.org/10.1038/44759a

Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: a meta-analysis. *Anim. Behav.*, 77(4), 771–783. https://doi.org/10.1016/j.anbehav.2008.12.022

Biro, P. A., & Stamps, J. A. (2015). Using repeatability to study physiological and behavioural traits: Ignore time-related change at your peril. *Anim. Behav.*, 105, 223–230. https://doi.org/10.1016/j.anbehav.2015.04.008

Bonnot, N. C., Bergvall, U. A., Jarnemo, A., & Kjellander, P. (2018). Who's afraid of the big bad wolf? Variation in the stress response among personalities and populations in a large wild herbivore. *Oecologia*, 188(1), 85–95. https://doi.org/10.1007/s00442-018-4174-7

Burns, J. G. (2008). The validity of three tests of temperament in guppies (*Poecilia reticulata*). *J. Comp. Psychol.*, 122(4), 344–356. https://doi.org/10.1037/0735-7036.122.4.344

Carere, C., Caramaschi, D., & Fawcett, T. W. (2010). Covariation between personalities and individual differences in coping with stress: converging evidence and hypotheses. *Curr. Zool.*, 56(6), 728–740. https://doi.org/10.1093/czoolo/56.6.723

Carter, A. J., Feeney, W. E., Marshall, H. H., Cowlishaw, G., & Heinsohn, R. (2013). Animal personality: what are behavioural ecologists measuring? *Biol. Rev.*, 88(2), 465–475. http://hdl.handle.net/10871/19094

Ceia, F. R., & Ramos, J. A. (2015). Individual specialization in the foraging and feeding strategies of seabirds: a review. *Mar. Biol.*, 162(10), 1923–1938. https://doi.org/10.1007/s00227-015-2735-4

Christensen, R. H. B. (2023). Ordinal regression models for ordinal data (R package version 2023.12-4).

Collins, S. M., Hatch, S. A., Elliott, K. H., & Jacobs, S. R. (2019). Boldness, mate choice and reproductive success in *Rissa tridactyla*. *Anim. Behav.*, 154, 67–74. https://doi.org/10.1016/j.anbehav.2019.06.007

Collins, S. M., Hendrix, J. G., Webber, Q. M. R., Boyle, S. P., Kingdon, K. A., Blackmore, R. J., d'Entremont, K. J. N., Hogg, J., Ibáñez, J. P., Kennah, J. L., Lamarre, J., Mejías, M., Newediuk, L., Richards, C., Schwedak, K., Wijekulathilake, C., & Turner, J. W. (2022). Bibliometric investigation of the integration of animal personality in conservation contexts. *Conserv. Biol.*, 1–13. https://doi.org/10.1111/cobi.14021

Dingemanse, N. J., Both, C., Drent, P. J., Van Oers, K., & Van Noordwijk, A. J. (2002). Repeatability and heritability of exploratory behaviour in great tits from the wild. *Anim. Behav.*, 64(6), 929–938. https://doi.org/10.1006/anbe.2002.2006

Ebenau, A., von Borell, C., Penke, L., Ostner, J., & Schulke, O. (2020). Supplemental material for integrative personality assessment in wild Assamese macaques (*Macaca assamensis*). *J. Comp. Psychol.*, 134(1), 27–41. https://doi.org/10.1037/com0000190.supp

Elliott, K. H., O'Reilly, K. M., Hatch, S. A., Gaston, A. J., Hare, J. F., & Anderson, W. G. (2014). The prudent parent meets old age: a high stress response in very old seabirds supports the terminal restraint hypothesis. *Horm. Behav.*, 66(5), 828–837. https://doi.org/10.1016/j.yhbeh.2014.11.001

Ellis, B. J., Jackson, J. J., & Boyce, W. T. (2006). The stress response systems: universality and adaptive individual differences. *Dev. Rev.*, 26(2), 175–212. https://doi.org/10.1016/j.dr.2006.02.004

Gamer, M., Lemon, J., & Fellows, I. (2019). irr: various coefficients of interrater reliability and agreement (R package version 0.84.1)

Gatt, M. C., Granadeiro, J. P., & Catry, P. (2021). Migrants and residents of a long-lived seabird differ in their behavioural response to a stressor. *J. Avian Biol.*, 52(2), 1–8. https://doi.org/10.1111/jav.02589

Gearhart, A., Booth, D. T., Sedivec, K., & Schauer, C. (2013). Use of Kendall's coefficient of concordance to assess agreement among observers of very high resolution imagery. *Geocarto Int.*, 28(6), 517–526. https://doi.org/10.1080/10106049.2012.725775

Gosling, S. D. (2001). From mice to men what can we learn about personality from animal research. *Psychol. Bull.*, 127, 45–86. https://doi.org/10.1037/0033-2909.127.1.45

Gosling, S. D. (2008). Personality in non-human Animals. *Soc. Pers. Psychol. Compass*, 2(2), 985–1001. https://doi.org/10.1111/j.1751-9004.2008.00087.x

Grace, J.K. & Anderson, D.J. (2014). Personality correlates with contextual plasticity in a free-living, long-lived seabird. *Behaviour*, 151, 1281-1311. https://doi.org/10.1163/1568539X-00003185.

Gulka, J., & Davoren, G. K. (2019). High individual flexibility in the foraging behaviour of a marine predator, the common murre. *Mar. Biol.*, 166(83), 1–16. https://doi.org/10.1007/s00227-019-3530-4

Harris, S. M., Descamps, S., Sneddon, L. U., Bertrand, P., Chastel, O., & Patrick, S. C. (2020). Personality predicts foraging site fidelity and trip repeatability in a marine predator. *J. Anim. Ecol.*, 89(1), 68–79. https://doi.org/10.1111/1365-2656.13106

Highfill, L., Hanbury, D., Kristiansen, R., Kuczaj, S., & Watson, S. (2010). Rating vs. coding in animal personality research. *Zoo Biol.*, 29(4), 509–516. https://doi.org/10.1002/zoo.20279

Kaiser, M. I., & Müller, C. (2021). What is an animal personality? *Biol. Philos.*, 36(1), 1–25. https://doi.org/10.1007/s10539-020-09776-w

Koski, S. E. (2011). How to measure animal personality and why does it matter? Integrating the psychological and biological approaches to animal personality. In Inoue-Murayama M, Kawamura S, & A. Weiss (Eds.), From Genes to Animal Behaviour (pp. 115–136). Springer. https://doi.org/10.1007/978-4-431-53892-9_5

Krüger, L., Pereira, J. M., Paiva, V. H., & Ramos, J. A. (2019). Personality influences foraging of a seabird under contrasting environmental conditions. *JEMBE*, 516, 123–131. https://doi.org/10.1016/j.jembe.2019.04.003

Lavers, J., Hipfner, M., & Chapdelaine, G. (2020). Razorbill (*Alca torda*). In Billerman SM (Ed.), Birds of the World (1.0). Cornell Lab of Ornithology.

Le, S., Josse, J., & Husson, F. (2008). FactoMineR: an R package for multivariate analysis. *J. Stat. Softw.*, 25(1), 1–18. https://doi.org/10.18637/jss.v025.i01

Legendre, P. (2005). Species associations: the Kendall coefficient of concordance revisited. *JABES*, 10(2), 226–245. https://doi.org/10.1198/108571105X46642

Lescure, L., Gulka, J., & Davoren, G. (2023). Increased foraging effort and reduced chick condition of razorbills under lower prey biomass in coastal Newfoundland, Canada. *Mar. Ecol. Prog. Ser.*, 709, 109–123. https://doi.org/10.3354/meps14286

MacKinlay, R. D., & Shaw, R. C. (2023). A systematic review of animal personality in conservation science. *Conserv. Biol.*, 37(1), 1–16. https://doi.org/10.1111/cobi.13935

Martin, J. G. A., & Réale, D. (2008). Temperament, risk assessment and habituation to novelty in eastern chipmunks, *Tamias striatus*. *Anim. Behav.*, 75(1), 309–318. https://doi.org/10.1016/j.anbehav.2007.05.026

Martinig, A. R., Karst, H. J., Siracusa, E. R., Studd, E. K., McAdam, A. G., Dantzer, B., Delaney, D. M., Lane, J. E., Pokharel, P., & Boutin, S. (2022). Animal personality: a comparison of standardized assays and focal observations in North American red squirrels. *Anim. Behav.*, 190, 221–232. https://doi.org/10.1016/j.anbehav.2022.05.012

Menzies, A. K., Timonin, M. E., McGuire, L. P., & Willis, C. K. R. (2013). Personality variation in little brown bats. *PLoS One*, 8(11). https://doi.org/10.1371/journal.pone.0080230

Morandini, V. & Ferrer, M. (2019). Nutritional condition determines behavioural response of nestling Black-browed albatrosses to a shy-bold continuum test. *Ethol. Ecol. Evol.* 31, 266-276. https://doi.org/10.1080/03949370.2019.1592229.

Müller, T., & Müller, C. (2015). Behavioural phenotypes over the lifetime of a holometabolous insect. *Front. Zool.*, 12(1). https://doi.org/10.1186/1742-9994-12-S1-S8

Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: A practical guide for biologists. *Biol. Rev.*, 85(4), 935–956. https://doi.org/10.1111/j.1469-185X.2010.00141.x

Niemelä, P. T., Niehoff, P. P., Gasparini, C., Dingemanse, N. J., & Tuni, C. (2019). Crickets become behaviourally more stable when raised under higher temperatures. *Behav. Ecol. Sociobiol.*, 73(6), 1–12. https://doi.org/10.1007/s00265-019-2689-5

Nussey, D. H., Wilson, A. J., & Brommer, J. E. (2007). The evolutionary ecology of individual phenotypic plasticity in wild populations. *J. Evol. Biol.*, 20(3), 831–844. https://doi.org/10.1111/j.1420-9101.2007.01300.x

Patrick, S.C. & Weimerskirch, H. (2014). Personality, foraging and fitness consequences in a long lived seabird. *PLoS One,* 9. https://doi.org/10.1371/journal.pone.0087269.

Patrick, S. C., Charmantier, A., & Weimerskirch, H. (2013). Differences in boldness are repeatable and heritable in a long-lived marine predator. *Ecol. Evol.*, 3(13), 4291–4299. https://doi.org/10.1002/ece3.748

Patrick, S. C., Pinaud, D., & Weimerskirch, H. (2017). Boldness predicts an individual's position along an exploration–exploitation foraging trade-off. *J. Anim. Ecol.*, 86(5), 1257–1268. https://doi.org/10.1111/1365-2656.12724

Petelle, M. B., & Blumstein, D. T. (2014). A critical evaluation of subjective ratings: unacquainted observers can reliably assess certain personality traits. *Curr. Zool.*, 60(2), 162–169. https://academic.oup.com/cz/article/60/2/162/1804160

Petelle, M. B., McCoy, D. E., Alejandro, V., Martin, J. G. A., & Blumstein, D. T. (2013). Development of boldness and docility in yellow-bellied marmots. *Anim. Behav.*, 86(6), 1147–1154. https://doi.org/10.1016/j.anbehav.2013.09.016

Pogány, Á., Vincze, E., Szurovecz, Z., Kosztolányi, A., Barta, Z., Székely, T., & Riebel, K. (2018). Personality assortative female mating preferences in a songbird. *Behaviour*, 155(6), 481–503. https://doi.org/10.1163/1568539X-00003500

Poissant, J., Réale, D., Martin, J. G. A., Festa-Bianchet, M., & Coltman, D. W. (2013). A quantitative trait locus analysis of personality in wild bighorn sheep. *Ecol. Evol.*, 3(3), 474–481. https://doi.org/10.1002/ece3.468

Powell, D. M., & Svoke, J. T. (2008). Novel environmental enrichment may provide a tool for rapid assessment of animal personality: a case study with giant pandas (*Ailuropoda melanoleuca*). *J. Appl. Anim. Welf. Sci.*, 11(4), 301–318. https://doi.org/10.1080/10888700802329673

R Core Team. (2023). R: a language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/

Réale, D., Gallant, B. Y., Leblanc, M., & Festa-Bianchet, M. (2000). Consistency of temperament in bighorn ewes and correlates with behaviour and life history. *Anim. Behav.*, 60(5), 589–597. https://doi.org/10.1006/anbe.2000.1530

Réale, D., Martin, J., Coltman, D. W., Poissant, J., & Festa-Bianchet, M. (2009). Male personality, life-history strategies and reproductive success in a promiscuous mammal. *J. Evol. Biol.*, 22(8), 1599–1607. https://doi.org/10.1111/j.1420-9101.2009.01781.x

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biol. Rev.*, 82(2), 291–318. https://doi.org/10.1111/j.1469-185X.2007.00010.x

Revelle, W. (2024). psych: Procedures for Psychological, Psychometric and Personality Research (R package version 2.4.6).

Runnells, E., Montevecchi, W., & Davoren, G. (2024). Spatiotemporal and isotopic niche overlap among Atlantic puffins, razorbills, and common murres during the non-breeding season in the Northwest Atlantic. *Mar. Ecol. Prog. Ser.*, 739, 241–256. https://doi.org/10.3354/meps14614

Sánchez-Tójar, A., Moiron, M., & Niemelä, P. T. (2022). Terminology use in animal personality research: a self-report questionnaire and a systematic review. *Proc. R. Soc. B.*, 289, 1–9. https://doi.org/10.1098/rspb.2021.2259

Santicchia, F., Gagnaison, C., Bisi, F., Martinoli, A., Matthysen, E., Bertolino, S., & Wauters, L. A. (2018). Habitat-dependent effects of personality on survival and reproduction in red squirrels. *Behav. Ecol. Sociobiol.*, 72(8), 1–13. https://doi.org/10.1007/s00265-018-2546-y

Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.*, 19(7), 372–378. https://doi.org/10.1016/j.tree.2004.04.009

Sih, A., Cote, J., Evans, M., Fogarty, S., & Pruitt, J. (2012). Ecological implications of behavioural syndromes. *Ecol. Lett.*, 15(3), 278–289. https://doi.org/10.1111/j.1461-0248.2011.01731.x

Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: a meta-analysis. *Behav. Ecol.*, 19(2), 448–455. https://doi.org/10.1093/beheco/arm144

Stamps, J., & Groothuis, T. G. G. (2010). The development of animal personality: relevance, concepts and perspectives. *Biol. Rev.*, 85(2), 301–325. https://doi.org/10.1111/j.1469-185X.2009.00103.x

Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2017). rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods Ecol. Evol.*, 8(11), 1639–1644. https://doi.org/10.1111/2041-210X.12797

Torgerson-White, L. L. (2014). Rating methodology, personality axes, and behavioural plasticity: a case study in African lions. *Anim. Behav. Cogn.*, 1(3), 230–248. https://doi.org/10.12966/abc.08.02.2014

Traisnel, G., & Pichegru, L. (2018). Does it always pay to defend one's nest? A case study in African penguin. *J. Ethol.*, 124(1), 74–83. https://doi.org/10.1111/eth.12704

Traisnel, G., & Pichegru, L. (2019a). Boldness at the nest predicts foraging and diving behaviour of female but not male African penguins. *Anim. Behav.*, 150, 113–125. https://doi.org/10.1016/j.anbehav.2019.02.003

Traisnel, G., & Pichegru, L. (2019b). Success comes with consistency in hard times: foraging repeatability relates to sex and breeding output in African penguins. *Mar. Ecol. Prog. Ser.*, 608, 279–289. https://doi.org/10.3354/meps12827

Trnka, A., Samaš, P., & Grim, T. (2018). Consistent individual and sex-specific differences in behaviour of common cuckoo chicks: is there a potential impact on host-parasite coevolutionary dynamics? *Behaviour*, 155, 1051–1072. https://doi.org/10.2307/26640531

Uher, J., & Visalberghi, E. (2016). Observations versus assessments of personality: a five-method multi-species study reveals numerous biases in ratings and methodological limitations of standardised assessments. *J. Res. Pers.*, 61, 61–79. https://doi.org/10.1016/j.jrp.2016.02.003

van Oers, K., & Naguib, M. (2013). Avian Personality. In C. Carere & D. Maestripieri (Eds.), Animal Personalities: Behaviour, Physiology and Evolution (pp. 66–95). University of Chicago Press. http://ebookcentral.proquest.com/lib/umanitoba/detail.action?docID=1110069.

Wolf, M., Van Doorn, G. S., Leimar, O., & Weissing, F. J. (2007). Life-history trade-offs favour the evolution of animal personalities. *Nature*, 447, 581–584. https://doi.org/10.1038/nature05835

Wolf, M., & Weissing, F. J. (2012). Animal personalities: Consequences for ecology and evolution. *Trends Ecol. Evol.*, 27(8), 452–461. https://doi.org/10.1016/j.tree.2012.05.001

Zuur, A. F., & Ieno, E. N. (2016). A protocol for conducting and presenting results of regression-type analyses. *Methods Ecol. Evol.*, 7(6), 636–645. https://doi.org/10.1111/2041-210X.12577

Table 1. Behavioural assessments that have been conducted on breeding seabirds, indicating the study species, assessment type and target personality trait, if applicable.

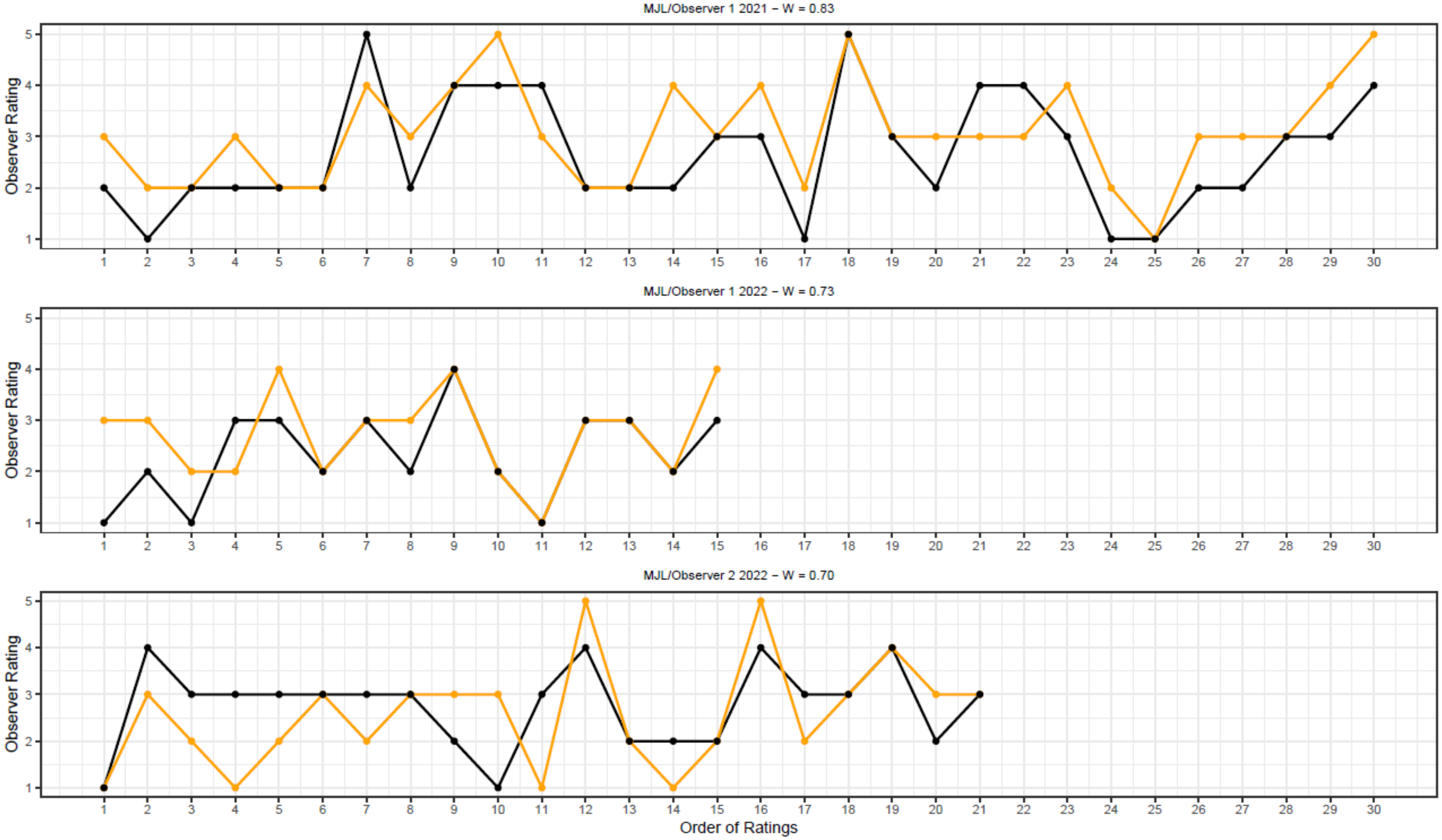
Species	Trait	Test	Reference
African penguin (*Spheniscus demersus*)	boldness	human approach	Traisnel and Pichegru, 2018
	boldness	human approach	Traisnel and Pichegru, 2019a
	boldness	human approach	Traisnel and Pichegru, 2019b
black-browed albatross (*Thalassarche melanophris*)	boldness	novel item	Patrick and Weimerskirch, 2014
	boldness	novel item	Morandini and Ferrer, 2019
black-legged kittiwake (*Rissa tridactyla*)		restraint test	Elliot et al., 2014
	boldness	novel item	Collins et al., 2019
	boldness	novel item	Harris et al., 2020
Cory's shearwater *(Calonectris borealis*)	boldness	novel item	Kruger et al., 2019
	exploration	novel environment	Gatt et al., 2021
	boldness	nest extraction	
Nazca booby (*Sula granti*)	aggression	human approach	Grace and Anderson, 2014
	boldness	novel item	
	sociality	sociality test	
thick-billed murre (*Uria lomvia*)		restraint test	Elliot et al., 2014
wandering albatross (*Diomedea exulans*)	boldness	human approach	Patrick et al., 2013
	boldness	human approach	Patrick et al., 2014

Table 2. Behaviours considered during crevice extraction and observer ratings that contributed to the corresponding personality score/rating. For the extraction test, responses were scored as: no (0), yes (1) and yes - continuous (2). These were then summed to give a value from 0-6. For observer ratings, a value between 1 and 5 was subjectively rated by considering all five behaviours simultaneously.

Behaviour	Response		
Extraction Test			
Did the bird struggle in the initial three seconds once captured?	no	yes	
Did the bird resist extraction from the nest by continuing to struggle?	no	yes	continuous
Did the bird bite, or attempt to bite, at any point during extraction from the nest?	no	yes	continuous
Did the bird vocalise at any point during extraction from the nest?	no	yes	
Observer Ratings			
Did the bird bite the handler?	no		yes
If so, how many times?	once	a few	many
Did the bird try to escape being handled?	no		yes
If so, how many times?	once	a few	many
Did the bird vocalise during handling?	no		yes
If so, how many times?	once	a few	many
How difficult was it to take measurements (e.g., weights and lengths) from the bird?	low	moderate	hard
How difficult was it to take samples (e.g., blood and feathers) from the bird?	low	moderate	hard

Table 3. Statistical test results for the fixed effects included in each adjusted repeatability model for each of the four response variables: extraction score, restraint score (CLMM models: df, χ^2 and *p*), observer rating and response index (GLMM models: df, F and *p*). ‘Additional’ refers to the other fixed effect added to the model for each response variable: crevice complexity (extraction score), bag ID (restraint score), and observer pair ID (observer rating).

	Extraction			Restraint			Observer			Response index		
Effect	df	χ^2	*p*	df	χ^2	*p*	df	F	*p*	df	F	*p*
Sex	2.0	0.827	0.661	2.0	1.344	0.511	41.1	0.448	0.642	41.1	0.302	0.741
Year	1.0	0.003	0.956	1.0	2.090	0.148	26.9	0.269	0.608	25.7	0.000	0.983
Chick stage	3.0	5.735	0.125	3.0	2.751	0.432	43.9	0.995	0.404	48.0	0.930	0.434
Additional	1.0	0.127	0.721	3.0	1.649	0.648	38.6	0.688	0.565			


MJL/Observer 1 2021 – W = 0.83

MJL/Observer 1 2022 – W = 0.73

MJL/Observer 2 2022 – W = 0.70

Figure 1. Observer ratings for each razorbill given by each observer (black (MJL)/orange (Observer 1/Observer 2)) from the three observer pairs across the two years (2021 and 2022). Note the x axis is ordered chronologically, where the first bird tested by both observers in each year is ‘1’. Kendall’s W values for each observer pair are also shown.

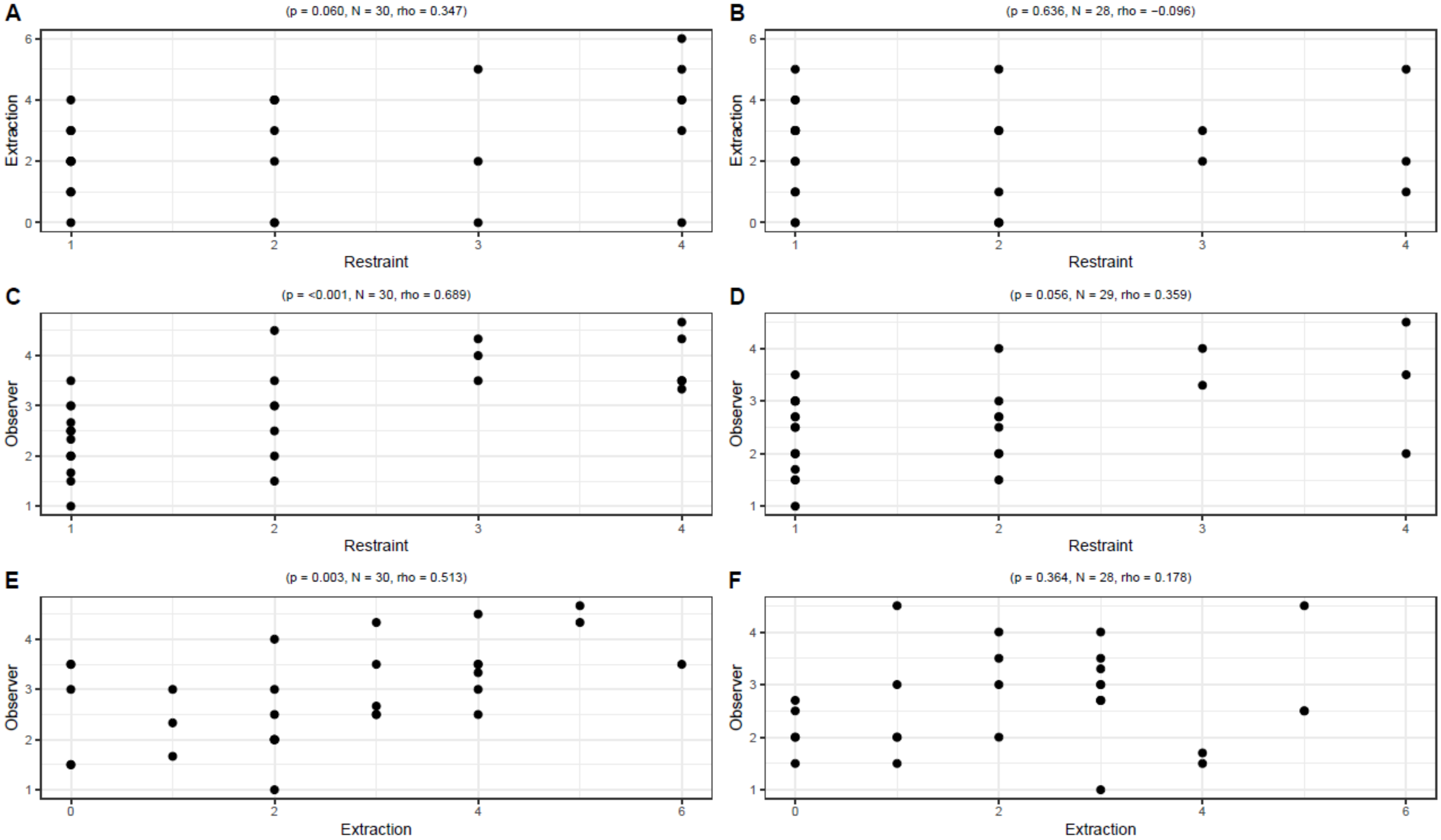


Figure 2. Correlations between the extraction and restraint test scores in 2021/2022 (**A**, **B**), the restraint test scores and observer ratings in 2021/2022 (**C**, **D**) and the observer ratings and extraction test scores in 2021/2022 (**E**, **F**). The Spearman's rho and p-values are indicated for each pairwise correlation.

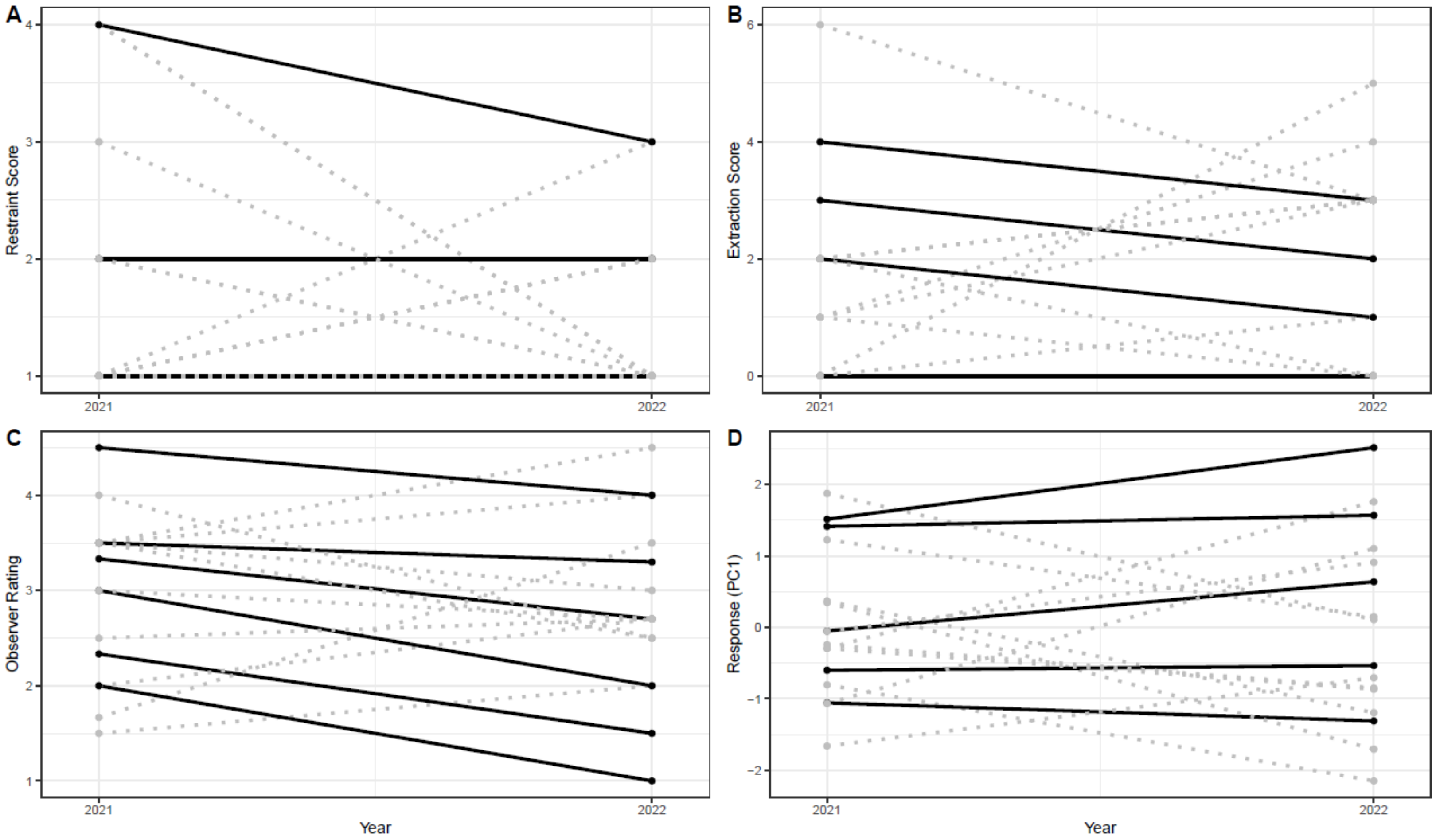


Figure 3. Test scores/ratings and the response index in 2021 and 2022 for each bird tested in both years (n=16 for observer ratings and response index, n=15 for extraction and restraint tests), with each line representing a different individual. **A**, **B**, **C** and **D** show restraint, extraction, observer, and response index scores/ratings, respectively. In each plot, some individuals are highlighted (black line) to visualise the greater number of consistent differences between individuals in observer ratings and the response index relative to other test scores.

Link between Chapters 1 & 2

In Chapter 1, I conducted three different behavioural tests to determine the best method for quantifying personality in razorbills, a crevice nesting seabird species of the family Alcidae. Of these tests, standardized observer ratings were the best individual test for quantifying the aggressive-docile trait in this seabird species, and potentially other species that are hard to observe naturally (e.g., nocturnal). In Chapter 2, I aimed to use these measures of personality (observer ratings) to place individual razorbills on the aggressive-docile continuum, and then relate their docility to behaviour during the breeding season (e.g., foraging distance and location) and fledging success.

Chapter 2: Individual consistency in foraging behaviour is influenced by prey availability in a breeding seabird.

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Abstract

Individual behavioural consistency has been identified throughout the animal kingdom and is commonly observed in foraging behaviour. Foraging consistency has been linked to several extrinsic (e.g., prey availability) and intrinsic factors (e.g., age, sex), including animal personality, and can influence fitness. We investigated consistency in the foraging behaviour of a pursuit-diving seabird (razorbill, *Alca torda*) under varying prey availability (2019-2020, 2023), and whether foraging behaviour (2023) or fledging success (2020-2023) are related to animal personality. During 2019-2023, we measured repeatability (R) of foraging trip characteristics (i.e., number of dives, foraging effort index) and average dive depth per foraging trip of chick-rearing razorbills (bird-borne tracking devices; 2019-2020, 2023), along with personality (docile-aggressive; observer ratings; 2021-2023), fledging success (nest monitoring; 2020-2023) and prey availability (forage fish biomass; 2019-2023) in coastal Newfoundland, Canada. Individual consistency in razorbills varied with prey availability. Razorbill foraging locations were only spatially consistent under high prey availability, while dive depth (R = 0.12 - 0.74) and foraging trip characteristics were not repeatable (R = 0.00 - 0.25) regardless of prey context. Personality was not related to foraging behaviour metrics in one year (2023) or fledging success across years, despite annually varying prey availability. Overall, these results highlight the importance of accounting for varying prey availability when investigating consistency in foraging behaviour, and that individuals with differing personality may have similar reproductive success across varying prey conditions.

Introduction

Most of the behavioural variation within an animal population is often explained by differences among individuals rather than within individuals (Araújo et al., 2011; Bolnick et al., 2011; Dall et al., 2012). Variation among individuals may be linked to factors such as age, sex and physiology (Araújo et al., 2011), but this variation can remain once these factors have been accounted for (Bolnick et al., 2003). The remaining variation may be related to personality, which is common across the animal kingdom (Sih et al., 2004; Wolf et al., 2007; Wolf & Weissing, 2012). Animal personalities are expressed as consistent differences between individuals that persist through time and are constant across contexts (Stamps & Groothuis, 2010). The five frequently studied personality traits are boldness, sociability, activity, aggressiveness, and exploration (Réale et al., 2007). These traits are continuums with a wide range of expressed behaviours (e.g., docile – aggressive, shy – bold) and form behavioural syndromes of correlated traits (e.g., boldness and aggression, Réale et al., 2009). Behavioural syndromes allow researchers to indirectly investigate how behaviour (e.g., foraging) is related to one trait (e.g., boldness) by investigating a correlated trait (e.g., aggression, Patrick et al., 2017).

In seabirds, there is increasing evidence that individual consistency is common (Biagiotti Barchiesi et al., 2023) and can persist over long periods (Patrick & Weimerskirch, 2014; Ramírez et al., 2016). For example, seabirds commonly show consistency in foraging location (e.g., Harris et al., 2020a; Patrick & Weimerskirch, 2014; Wakefield et al., 2015), dive behaviour (Woo et al., 2008) and diet (e.g., Ceia & Ramos, 2015; Connan et al., 2017; Zango et al., 2019). In some studies, foraging behaviour differences among breeding seabirds have been related to boldness, a personality trait, with shyer individuals typically being classified as generalists and bolder individuals as specialists (Harris et al., 2020a; Jeffries et al., 2021; Krüger et al., 2019; Pereira et al., 2024). Along with being more generalist, shyer seabirds may exploit food patches for longer than bolder individuals (Jeffries et al., 2021; Patrick et al., 2017) and take fewer risks than bolder individuals (Carter et al., 2013), such as foraging under lower competitor densities (i.e., further from the breeding colony; Harris et al., 2020a; Kruger et al., 2019; Patrick & Weimerskirch, 2017).

Personality-related differences may influence fitness, due to impacts on resource acquisition (Menzies et al., 2013; Pereira et al., 2024). While some seabird studies have not found an effect of personality on fitness (Krüger et al., 2019; Van de Walle et al., 2024), others found a positive relationship between boldness and reproductive output (Collins et al., 2019; Pereira et al., 2024). Bolder, more aggressive individuals may benefit from a specialist strategy and have increased fitness under good foraging conditions (i.e., high prey availability), due to the positive relationships between specialisation, foraging efficiency and reproductive success (Rebstock et al., 2022; Van Den Bosch et al., 2019). In comparison, shyer, more docile individuals may benefit from the greater flexibility of a generalist strategy under poor foraging conditions (Jeffries et al., 2021; Krüger et al., 2019). Additionally, bolder animals are predicted to invest more in their present breeding attempt due to their higher risk prone tendencies (Dammhahn & Almeling, 2012), while shyer individuals may take less risks and be more willing to abandon a breeding attempt when conditions change (Cole & Quinn, 2014).

During breeding in coastal Newfoundland, seabirds rely on capelin (*Mallotus villosus*), a key forage fish in the Northwest Atlantic (Carscadden & Vilhjálmsson, 2002), as prey (Gulka et al., 2019; Jenkins & Davoren, 2021; Lescure et al., 2023). The razorbill (*Alca torda*), a member of the family Alcidae (hereafter 'alcid'), has been shown to alter their foraging behaviour and diet under varying capelin biomass among years (Davoren, 2024; Gulka et al., 2019; Lescure et al., 2023). Razorbills raise one chick per year over a short period (16-21 days) to fledge at 30% of adult body mass (Lavers et al., 2020) and the energetically demanding chick-rearing period typically coincides with the inshore arrival of spawning capelin (Carscadden et al., 2002; Davoren, 2024). The Newfoundland capelin population crashed in the early 1990s, however, and has not recovered (Buren et al., 2019), which has been associated with highly variable capelin biomass both within and among years (Davoren, 2024; Davoren et al., 2025). As personality was recently described in razorbills (aggressive-docile continuum, hereafter 'docility'; Legard and Davoren, 2025; Chapter 1), razorbills in this system are a good model species to investigate the relationships between personality and individual consistency under dynamic prey conditions. Indeed, relationships between individual consistency in foraging behaviour, fledging success, personality and prey availability have not been studied in alcids.

The first objective of this study was to investigate the consistency in foraging behaviour (i.e., foraging location, foraging effort, number of dives, dive depth) of chick-rearing razorbills under varying prey contexts (high/low availability), both within years (before/after capelin spawning) and among years. The second objective was to investigate whether foraging behaviour was related to animal personality and whether consistency in foraging location was related to animal personality on a subset of data (2023). We also examined whether fledging success was related to animal personality. To achieve these objectives, we combined foraging behaviour of chick-rearing razorbills (bird-borne tracking devices; 2019-2020, 2023) with personality assessments (observer ratings; 2021-2023), fledging success (nest monitoring; 2020-2023) and prey biomass estimates (spawning capelin surveys; 2019-2023) on the northeast coast of Newfoundland, Canada. We hypothesized that razorbills exhibit consistent individual behaviour (i.e. high repeatability) and that the level of spatial consistency will be related to docility. Due to the positive correlations between boldness and aggression (Sih et al., 2004), we predicted that aggressive individuals will be more consistent in their foraging locations and make shorter trips (i.e., distance and duration) compared to docile individuals. We also predicted that in years of lower capelin biomass, docile individuals will have higher fledging success as they exhibit more generalist behaviour than aggressive individuals and, therefore, are more able to exploit different types of prey.

Methods

We investigated foraging behaviour and fledging success of razorbills rearing chicks on James Island, a small rocky island roughly 1 km across on the northeast coast of Newfoundland, Canada (Figure 1). Approximately 2750 pairs of razorbills breed on this island between May and August (Environment and Climate Change Canada unpublished data), along with several other seabird species.

Prey Availability

A fine-scale (~15 km) hydroacoustic survey (Figure 1) was conducted approximately weekly over a cluster of annually persistent capelin spawning sites to quantify capelin biomass from mid-July to mid-August in each study year. See Davoren et al. (2025) for a full description of the survey methods. In brief, capelin biomass (gm^{-2}) was quantified for each 100 m during each survey using a surface-towed echosounding system (70 kHz transducer), which were then averaged to determine the mean capelin biomass per survey. The survey with the peak biomass for each year was identified, allowing inter-annual comparisons of capelin biomass in the study area. These surveys have been conducted annually since 2009 (Davoren, 2024; Davoren et al., 2025), allowing each study year to be compared to the long-term average (mean ± SD, 0.14 ± 0.06 gm^{-2}). Each year was classified as high (> 0.20 gm^{-2}), average (0.09 - 0.19 gm^{-2}) or low (< 0.09 gm^{-2}) for capelin biomass. Equipment difficulties during 2021 resulted in a lack of capelin biomass estimates and, thus, peak capelin biomass was imputed using a Principal Components Analysis (PCA) incorporating many annual capelin metrics (e.g., biomass, length, mass, date of first spawning) in JMP 16 Pro (Page et al., 2018). Additionally, each year was also split into two capelin availability periods: before (lower availability) and after (higher availability) the first day of spawning. This was achieved by regularly monitoring known capelin spawning sites (intertidal: 2 d; subtidal: 3-6 d) for the presence of fertilised capelin eggs adhered to the substrate, following Crook et al. (2017).

Foraging Behaviour

Tracking devices were deployed on chick rearing razorbills during July and August in 2019, 2020 and 2023 (Table 1). Like other alcid species, razorbills lack sexual dimorphism, outward age-related characteristics, and have limited physiological differences between mature individuals (Lavers et al., 2020) and, thus, age and sex were initially unknown for all tagged birds. Across these years, only three razorbills were tagged in more than one year and, thus, most tagged individuals differed across years and capelin availability periods within years. GPS tags were deployed during all three years, while additional time-depth recorder (TDR) tags were deployed in 2020 and tags deployed in 2023 were combination GPS-TDR tags (Table 1). Chick-rearing birds were captured at the nest during the night (0100 - 0400 hours, Newfoundland Daylight Time, NDT) to minimise colony disturbance and the risk of nest abandonment. GPS and GPS-TDR tags were attached to the scapula feathers using TESA® tape and cable ties, while TDR tags deployed in 2020 were attached to plastic leg bands with cable ties. All tag and attachment materials had a combined weight of < 20 g, and when considering potential tag effects (Vandenabeele et al., 2012), this is less than 3% of the body mass of adult razorbills captured at James Island (701 ± 52 g). GPS tags recorded a location (latitude and longitude) every 10 min and TDR tags recorded pressure and temperature every 5/6 s (2023/2020) when wet. While Catlog GPS tags had to be retrieved for data download during 2019 and 2020, data were remotely downloaded to a base station (AstraEa 2.4GHz 18dBi microstrip antenna) in 2023, which was set up within 75 m of nest sites with tagged birds. For full details on 2019/2020 deployments see Lescure et al. (2023).

Foraging trips were defined as the bird having travelled > 250 m from the nest site for longer than 10 min. The 250 m buffer was chosen because alcids, such as razorbills, are known to land on the water close to the colony after returning from and before leaving on foraging trips (Burger, 1997). Additionally, trips without at least one foraging dive (see definition below) were removed as they were unlikely to be trips for foraging (Linnebjerg et al., 2013). For each foraging trip, the following characteristics were calculated using the *tripSplit* and *tripSummary* functions in the R package *track2KBA* (Beal et al., 2021): total duration (h), maximum distance from the nest (km), and total distance travelled (km). A PCA was carried out (*FactoMineR* package; Le et al., 2008) to reduce these three highly correlated ($r^2 = 0.821 - 0.978$, p values: < 0.001) foraging trip characteristics across all years into a single variable (PC1). PC1 is hereafter referred to as 'foraging effort' because flight costs are high for alcids (Elliott et al., 2013) and, therefore, trips of greater duration and distance likely have higher energetic cost. Dive characteristics (i.e., dive depth, duration) were also quantified from TDRs in 2020 and 2023 using the R package *diveMove* (Luque, 2007). Foraging dives were defined as dives > 1.5 m and > 5 s (Lescure et al., 2023). For each foraging trip, the average dive depth, along with the number of dives were quantified for analyses. Average dive duration per trip was not included in analyses because dive depth and dive duration were highly correlated (2020, N = 13175, $r^2 = 0.795$, $p = < 0.001$; 2023, N = 5477, $r^2 = 0.824$, $p = < 0.001$).

Personality

All razorbills that were captured between 2021 and 2023 (for tag deployment/retrieval), including many birds previously tagged in 2019 and 2020, underwent personality assessment, following Legard and Davoren (2025; Chapter 1). In brief, observer ratings of docility were completed by two or three observers, whereby each observer independently rated each bird based on the presence/absence of a range of observable behaviours (i.e., biting, vocalising, struggling, resisting) during routine handling (i.e., tag deployment, morphometric measurements, feather sampling). In 2023, most tagged individuals (18 out of 20 birds) were assessed twice (at tag deployment and retrieval). Although not all tagged birds were assessed for personality twice, observer ratings were consistent across observers and repeatable across personality assessments for individuals that were assessed more than once (Legard and Davoren, 2025; Chapter 1). Ratings for each individual were averaged across observers after each personality assessment, then averaged across assessments in the same year, if applicable, and finally across assessments in different years, to generate a single docility score for each individual.

Fledging Success

To quantify fledging success, nests with personality assessed birds were checked at night (0100 – 0400 hours, Newfoundland Daylight Time, NDT) every 2-5 days during 2020-2022, when three to four 5-10 day trips were made to the colony and every 2 days during 2023 when researchers remained on the colony throughout late incubation and chick-rearing (~6 weeks). Birds were personality assessed for other research projects (Legard and Davoren, 2025; Chapter 1), resulting in 18, 38, 43 and 61 nests being monitored during the four respective years (2020-2023), with some of the same nests monitored across years. During a nest check, we recorded whether the nest had an egg, a chick or was empty. If a chick was present, the stage of feather development was recorded (early: downy feathers; middle: flight feather eruption; late: downy feathers lost) and chicks were opportunistically weighed when time permitted using a Pesola scale (300 g). These nest monitoring data were integrated with the published range of the chick-rearing period (16-21 days), daily average weight gain of chicks (10 g/d) and average fledging weight (210-215 g; Lavers et al., 2020) to estimate whether empty nests indicated successful or unsuccessful fledging. An empty nest was considered 'successful' if it met all the following criteria at the last sighting: the chick was in a later feather development stage, the chick was above the published minimum chick-rearing duration (16+ days since estimated or observed hatch), and the chick was above published average fledge weight (>190 g). If a nest only met 1-2 of these criteria, it was considered 'probably successful'. An empty nest was considered 'unsuccessful' if it met one or more of the following criteria: the chick was not observed in a later feather development stage, chick-rearing duration was shorter than the published minimum, the chick did not reach the published average fledge weight, or the chick was found dead in nest. Nests were classified as ‘unknown’ when there was insufficient information to make a classification (e.g., if the nest was only monitored during early chick rearing and not revisited). This resulted in four categories describing the probability of fledging success for each personality-assessed nest: successful (2), probably successful (1), not successful (0) and unknown. Nests with an unknown status were omitted from analyses.

Statistical Analysis

All data processing and statistical analyses were carried out in R version 4.3.0 (R Core Team, 2023). As intra- and inter-annual variation in capelin biomass influences razorbill foraging behaviour and location (Lescure et al., 2023) and individuals were not tracked across prey contexts (i.e. prey availability periods within years, varying capelin biomass across years), we could not distinguish if high among-individual variation resulted from differences across tagged individuals or from individuals shifting their foraging behaviour across contexts. Therefore, consistency of razorbill foraging behaviour (i.e., repeatability) was examined separately for each prey availability period within each year.

To assess the relationships between personality and behaviour, a subset of tagged and personality-assessed birds (n=20) during 2023 were used. During 2023, emphasis was placed on obtaining multiple trips per individual through longer term tag deployments as higher repeated measures within individuals is more beneficial when investigating individual consistency than a greater number of tagged individuals (Wolak et al., 2012). Due to this emphasis, 2023 was the only year with a sufficient sample size of personality-assessed individuals tracked on multiple foraging trips. During analyses, model assumptions were confirmed in all cases following protocols outlined in Zuur & Ieno (2016).

Spatial consistency in foraging locations was quantified as Earth Mover's Distance (EMD) values using the *emd* function in the R package *move* (Kranstauber et al., 2021). EMD values are calculated by comparing the proximity between two different spatial distributions (Franklin et al., 2022; Kranstauber et al., 2021) and provide a value of dissimilarity (in km), unlike spatial overlap indices which provide the same value for proximity and dissimilarity when two distributions do not overlap (Kranstauber et al., 2017). Greater variation between two distributions results in higher EMD values (Franklin et al., 2022). An EMD value was calculated for each possible foraging track combination within and between individuals within each capelin availability period in each year. Geographical coordinates were used as the input and the Haversine function was applied to account for distributions that stretch over large distances to address the spherical surface of the Earth (Franklin et al., 2022; Kranstauber et al., 2017). Generalised linear models (GLM) were then used to compare EMD values (response variables) between individuals versus within individuals in each capelin availability period in each year to determine if individuals were spatially consistent (i.e., significantly lower within- versus between-individual EMD values). All EMD values were continuous and normally distributed except for the period after capelin spawning in 2019 and 2023, which were right-skewed and, thus, models were run with the Gaussian and Gamma error families, respectively.

To determine whether more docile versus more aggressive birds varied in their spatial consistency, a generalized linear mixed model (GLMM) was run on the subset of personality-assessed birds from 2023. Within-individual EMD values (Gaussian distribution) were used as the response variable, with docility score (continuous) as a fixed effect and individual as a random factor.

To quantify consistency of foraging trip and dive characteristics, adjusted repeatability was calculated using GLMMs for foraging effort (i.e., PC1), the number of dives per trip and average dive depth per trip (response variables) within each capelin availability period in each year using the *rpt* function in the *rptR* package (Stoffel et al., 2017). Repeatability (*R*) values vary from 0-1, with 0 indicating low and 1 indicating high repeatability (i.e. high consistency). Repeatability is calculated by dividing the variance among individuals by the sum of the variance among individuals and the residual within-individual variance (Bell et al., 2009). All tagged individuals, including those that were tracked for one foraging trip, were included in the analysis to increase the precision of the calculated between-individual variation (Nakagawa & Schielzeth, 2010). Adjusted repeatability allows fixed factors to be accounted for in the analysis (Biro & Stamps, 2015). The fixed factors included in all analyses were day of the year (ordinal date) and time of day (day/overnight), as some trips occurred only during daylight ('day'), while others started during daylight but continued through the night and ended the following morning ('overnight'). Sex was also included in 2019 and 2020 models but was not available for 2023 and, thus, was not included in the models for this year. Personality (docility score: continuous) was also added as a fixed factor for 2023 analyses to determine the relationships between personality and foraging behaviour. Analyses were completed with a Gaussian distribution for foraging effort and average dive depth per trip, while a Poisson distribution was used for the number of dives per trip (count data). Parametric bootstrapping (n=1000) was used in all models to quantify 95% confidence intervals.

To determine whether personality influenced fledging success in each year, we ran cumulative link models (CLMs, *ordinal* package; Christensen, 2023) for each year separately with fledge success as the response variable (ordinal) and docility score (continuous) as the fixed factor. This allowed us to determine whether personality influenced fledge success within each year and results were qualitatively compared across years of varying capelin biomass. A cumulative link mixed model (CLMM) with all years combined, an interaction between year and personality and individual as a random factor was not possible because not all nests had a known outcome in each year, resulting in an unbalanced design.

Ethical Note

This research was conducted under a Canadian Master Banding Permit (No. 10873) and in accordance with the Canadian Council for Animal Care (Protocols F16-017, F20-017). All efforts were made to limit animal use, reduce the handling times, and prevent disturbance to the seabird colony. Additionally, the individuals used were part of a long-term study where multiple overlapping scientific objectives were achieved from research activities. The authors declare no conflict of interest.

Results

Each tag was deployed for 1-11 days across the three years, resulting in 261 foraging trips across all tagged individuals: 72 trips in 2019, 37 trips in 2020 and 152 trips in 2023 (Table 1). During 2020 and 2023, 13175 and 5477 foraging dives were recorded, respectively. The foraging effort variable (PC1) explained 92% of the variation in the foraging trip characteristics and was highly positively correlated with the three original foraging trip characteristics (total trip duration =

0.923, maximum trip distance = 0.974, total trip distance = 0.982). There were a range of docility scores across all tagged birds, tagged birds in 2023 and nests with a known fledge success (Figure S1). The date of first spawning and peak capelin biomass varied across years. During 2019, spawning started on July 22 and peak biomass was 0.098 gm^{-2} ('average biomass'), while in 2020 spawning started on July 29 and peak biomass was 0.005 gm^{-2} ('low biomass'). During 2021 spawning started on July 17 and peak biomass was estimated to be 0.121 gm^{-2} ('average biomass'), while during 2022 and 2023 spawning started on July 11 and 12, respectively, and peak biomass was 0.228 gm^{-2} and 0.215 gm^{-2} ('high biomass'), respectively. During 2023, early spawning resulted in birds being tagged only after capelin began spawning.

Consistency, Repeatability and Personality

When examining spatial consistency within capelin availability periods during each year, within-individual EMD values were significantly lower than between-individual values after capelin began spawning during 2019, along with a similar tendency during 2023 (Figure 2A, Table 2), suggesting that razorbills were more spatially consistent in their foraging trips once spawning capelin arrived inshore (Figure 3). By contrast, within- and between-individual EMD values did not differ before spawning in 2019 or during either capelin availability period in 2020 (Figure 2A, Table 2), illustrating much lower spatial consistency (Figure 3). Finally, there was no relationship between docility and within-individual EMD values within one prey availability period (i.e., after capelin spawning during 2023; t = -0.992, $p = 0.335$; Figure 2B).

Foraging effort was not repeatable within capelin availability periods in any year (Table 3). While sex did not influence foraging effort, overnight trips had significantly higher effort than day trips in all capelin availability periods except before capelin spawned in 2019 (Table 3). Additionally, foraging effort increased throughout the period after capelin began spawning in 2023 (Table 3). The number of dives per foraging trip was not repeatable within capelin availability periods in any year, whereas overnight trips had significantly higher numbers of dives than day trips in 2020 and 2023 (Table 3). Finally, average dive depth per trip had high but not significant repeatability in both capelin availability periods during 2020 and comparatively lower and still not significant repeatability in 2023 (Table 3).

During 2023, repeatability of foraging effort, number of dives per trip and dive depth remained low when personality was considered, and personality did not significantly influence any of these characteristics (Table 3). Foraging effort was significantly influenced by date, increasing with the days after capelin spawning, and by time of day, being higher in overnight relative to day trips (Table 3, Figure 4). Additionally, there were more dives during overnight relative to day trips (Table 3, Figure 4).

Fledging Success

Personality did not influence fledging success in any year (2020: z = 0.121, *p* = 0.904; 2021: z = -1.270, *p* = 0.204; 2022: z = 1.947, *p* = 0.052; 2023: z = 0.766, *p* = 0.443, Figure 5), but there was a trend towards higher success in more docile individuals in 2022.

Discussion

Our results show that chick-rearing razorbills can be consistent in their foraging behaviour in different prey availability periods (i.e., before or after spawning spawning) within years. The degree of consistency, however, varied across these periods, which partially aligned with our prediction. Indeed, spatial consistency in foraging locations was only observed after capelin began spawning in the study area in years where capelin biomass was near or above the long-term average (2019, 2023). By contrast, foraging effort and number of dives per trip were not repeatable within any prey context and were more influenced by time of day and date of the trip during chick rearing. Contrary to our prediction, personality within the 2023 subset did not relate to spatial consistency, nor were any foraging metrics influenced by personality. Overall, these results partially align with studies showing consistency in seabird behaviour (Biagiotti Barchiesi et al., 2023) but contrast with those showing that seabird foraging behaviour metrics are related to personality (e.g., Harris et al., 2020a; Krüger et al., 2019; Pereira et al., 2024). Finally, also opposing our prediction, limited differences in fledge success along the docile-aggressive continuum suggest that all trait types may have similar degrees of success under varying prey conditions.

Individual consistency

Razorbill spatial consistency was dependent on the prey context, with the highest levels of consistency in foraging location when capelin was spawning nearby the colony and likely in sufficient abundance to become the dominant prey type (2019 and 2023; Davoren, 2024). This spatial consistency is not surprising given the spawning behaviour of capelin in the study area (Davoren et al., 2006). Although the capelin population collapsed in the 1990s, capelin becomes locally abundant at inshore spawning sites (Davoren et al., 2025), which are known to be spatially persistent across years (Davoren, 2013) if key environmental features (i.e., suitable sediment grain size, temperature) are annually consistent (Crook et al., 2017; Penton & Davoren, 2012). Indeed, capelin is briefly (2-3 weeks) highly abundant relative to the other prey species (e.g., sand lance) at these spawning sites in coastal areas (Davoren et al., 2025), which results in large multi-species predator aggregations that include breeding and non-breeding seabirds plus large predatory fish (i.e., Atlantic cod, *Gadus morhua*) and humpback whales (*Megaptera novaeangliae*, Davoren, 2013). In support, spatial consistency was low in 2020 when capelin biomass was the lowest on record in the last decade and capelin did not spawn at these annually persistent spawning sites (Davoren, 2024).

Although the repeatability of average razorbill dive depth was not significant and varied across years and capelin availability periods within years (Table 3), high repeatability values were found (*R* > 0.6 in 2020), suggesting a level of individual consistency. Indeed, there was high and significant repeatability of dive depth of individual dives across all prey contexts and years (Figure S2, Table S1). Therefore, a lower number of repeated measures per individual by using average dive depth per trip may have impacted our ability to estimate repeatability (Wolak et al., 2012). Consistent differences in dive depth among individual may be explained by the positive relationship between specialisation and foraging efficiency (Rebstock et al., 2022). For example, learning and remembering individual for catching prey over the lifetime of an individual (i.e., memory; Dall et al., 2005), may potentially increase foraging efficiency and reduce energy expenditure (Phillips et al., 2017). Indeed, long-term individual prey capture techniques have previously been observed in other marine predators (common minke whale, *Balaenoptera acutorostrata*, Hoelzel et al., 1989; bottlenose dolphins, *Tursiops* spp., Sargeant et al., 2005). Furthermore, consistency in individual dive depths has been observed in seabirds (Phillips et al., 2017), along with another alcid species (thick-billed murre, *Uria lomvia*, Woo et al., 2008), and the latter study speculated that variation was caused by individual differences.

Personality

In comparison to other seabird studies (e.g., Harris et al., 2020a; Krüger et al., 2019), we did not find relationships between foraging behaviour and personality in the one year this was investigated (2023). Our ability to detect an influence of personality on razorbill foraging behaviour, however, may have been impacted by limitations with our study design. A higher number of repeat tracks and tracking individuals across contexts might have provided a greater opportunity to observe differences among individuals related to personality. For example, we were unable to determine if individuals maintained different foraging behaviour across prey contexts (i.e., across years and across pre- and post-spawning periods within years), which would be likely if influenced by personality.

The influence of date on razorbill foraging behaviour may have reduced our ability to detect varying foraging behaviour with personality. More docile birds were tracked close to the spawning initiation date, while more aggressive birds were tracked later in this capelin availability period (Figure 4). As inshore capelin biomass and predictably located spawning aggregations both decrease with days from the date of first spawning (Davoren et al., 2025), both of these prey changes could have reduced our ability to detect varying foraging behaviour with personality. In support, date had a significant negative effect on foraging effort in 2023 after capelin began spawning, which has been found in other seabird studies on the northeast Newfoundland coast (common murre, *Uria aalge*, Gulka et al., 2019; razorbills, Lescure et al., 2023).

The high influence of time of day on razorbill foraging behaviour may have further reduced our ability to detect varying foraging behaviour with personality. Individuals along the docile-aggressive continuum conducted similar proportions of day and overnight trips, which differed significantly in all foraging trip characteristics (Figure S3). Overnight trips had more dives and were longer in both total duration and total distance, which resulted in greater foraging effort (Figure S3). Bimodal foraging trip duration (short and long trips) has been observed previously in razorbills (Benvenuti et al., 2001) and several other alcid species (Evans et al., 2013; Fayet et al., 2021; Symons & Diamond, 2022; Welcker et al., 2009). The increased effort of longer trips may be offset by reaching more profitable prey aggregations farther from the colony (Welcker et al., 2009), or an increase in foraging efficiency. For example, dives in overnight (long) trips were typically clustered before sunset and at sunrise in this study. Dives in the evening may allow feeding for self-maintenance, providing time to fully digest food and secrete waste, thereby reducing flight costs back to the colony (Gabrielsen, 1996). By contrast, dives when light levels become sufficient for visual foraging during the morning (i.e., greater than 90% of dives were during twilight or daylight) may be an efficient time for catching prey for chick-provisioning. Indeed, both capelin and sand lance undergo regular diel movement patterns (Davoren et al., 2006; Morrison & Davoren, 2024), with capelin spending the night at the surface but move into deeper water during the day (Davoren et al., 2006), while sand lance burrow in the sediment during the night but exit during dawn when they are most vulnerable to capture (Morrison & Davoren, 2024). Dawn and dusk may therefore provide an opportunity to efficiently catch both species either at the surface or as they transition between habitats.

Similar to some other studies (e.g., Harris et al., 2020a), sex did not influence any of our observed foraging behaviours. Relationships between foraging behaviour, personality and sex, however, have been observed in other seabird species. For example, in African penguins (*Spheniscus* *demersus*), bolder females are more flexible in their foraging behaviour (i.e., more sinuous tracks) than bolder males (Traisnel and Pichegru, 2019a; 2019b). Similarly, in wandering albatross (*Diomedea exulans*), bolder females prioritised travel during foraging (i.e., explorative), while shyer females prioritised searching (i.e., exploitation), but there was no difference along the shy-bold continuum in males (Patrick et al., 2017; Gillies et al., 2023). In wandering albatross, however, this sex-related difference may be explained by higher wing loading (mass per unit wing area) in males compared to females (Shaffer et al., 2001), that may influence flight decisions in males and reduce the observable effect of personality (Gillies et al., 2023).

Fledging success

In this study, there is little evidence for an effect of personality on fledging success over the four years (2020-2023) despite annual variation in capelin availability. This aligns with the results from other studies on seabirds that have not always found a link between personality and reproductive success (e.g., Krüger et al., 2019). We found that more docile individuals had a trend towards higher fledging success in one of the four years, which contradicts previous studies that have found the opposite relationship, with higher success in bolder, more aggressive individuals (Collins et al., 2019; Harris et al., 2020b). These studies that linked boldness to reproductive success are, however, relatively short in duration (1-2 years) compared to the lifespan of the study species (> 10 years), while in longer studies, such as ours (4 years), and Van de Walle et al. (2024; 12 years), there are weaker or no associations between personality and reproductive success. Our findings may support the concept that for the observed behavioural variation to persist across animal populations, a mechanism (e.g., fluctuating selection) must exist to maintain it (Gosling, 2001). Therefore, longer studies are potentially more likely to show variations in the relationship between personality and fitness. Indeed, consistent behaviour resulting from personality may lead to trade-offs as a rewarding behaviour in one context may be costly in another (Sih et al., 2004), and these trade-offs may play a key role in maintaining behavioural variation (Stamps, 2007; Wolf et al., 2007). In seabirds, bolder individuals (i.e., specialists) may be vulnerable under poorer environmental conditions that favour shyer individuals (i.e., generalists; Jeffries et al., 2021). For example, chick growth of bold parents was observed to be slower in low prey years compared to shy parents in African penguins (*Spheniscus demersus*; Traisnel & Pichegru, 2018). This was not observed in our study, however, as there was no difference in fledging success and success did not vary with personality in the year with the lowest capelin biomass on record (Davoren, 2024), but the sample size for this year is the lowest in our study. In summary, fluctuating selection based on yearly inter-annual variations in environmental pressures may maintain the behavioural variation seen in seabirds (Dingemanse et al., 2004; Patrick & Weimerskirch, 2014), and longer studies may be required to understand variation in relationship between personality and fitness (e.g., Van de Walle et al., 2024).

When interpreting our findings on razorbill fledging success, other important points should be considered. For example, the docility of only one parent was known, but relationships between the personality composition of a breeding pair and reproductive behaviour have been shown (McCully et al., 2022). Therefore, the lack of a significant effect of personality on fledging success in this study could be explained by the male and female having differing personalities, with the costs of one trait type potentially being buffered by the benefits of the opposite trait in the partner. Additionally, the age of individuals in this study was unknown, but reproductive success is known to change with age in a long-lived species as foraging efficiency has been shown to increase with experience (Votier et al., 2017). Finally, we only measured fledging success, or the success of nests that produced a chick. Although we did not find an immediate relationship between fledging success and personality, there could be impacts on offspring quality or recruitment, as well as hatching success or the probability of breeding (e.g., Van de Walle et al., 2024), all of which could influence lifetime reproductive success. As long-lived species tend to follow a conservative life history strategy, favouring survival over reproductive output in any given year (Gaillard et al., 1998), breeding may be discontinued at any stage under extreme prey scarcity if continued breeding may impact future reproductive potential (Hamel et al., 2018). Abandoning breeding attempts may be more likely in shyer individuals as these individuals are more risk averse (Carter et al., 2013; Cole & Quinn, 2014). Conversely, bolder individuals that invest heavily in the current breeding attempt (Dammhahn & Almeling, 2012) may skip the next breeding season to recover, as seen in wandering albatross (*Diomedea exulans*, Van de Walle et al., 2024). Therefore, when considering the long-term relationships between personality and fitness, it is important to monitor both whether individuals attempted to breed, as well as the success of the breeding attempt from the start of incubation.

Conclusion

In conclusion, chick-rearing razorbills exhibit behavioural consistency, but this consistency is influenced by the availability of spawning capelin, the main forage fish prey species in the area, with little to no influence of personality (i.e., docility) or sex. Studying individual foraging consistency is important because it may result in individuals using only a small portion of the population-level foraging niche (Bolnick et al., 2003), which can result in individuals segregating horizontally in space (Barger et al., 2016; Wakefield et al., 2015), vertically in depth (Shoji et al.,

2015) or in diet (Linnebjerg et al., 2013; Phillips et al., 2017), thereby leading to reduced intraspecific competition. Individual consistency may also be a key mechanism for increasing foraging efficiency in razorbills during the energetically demanding chick-rearing period, especially as consistency has been observed to increase foraging efficiency in other seabirds (Rebstock et al., 2022; Van Den Bosch et al., 2019). With increasing changes in marine ecosystems that result in multiple simultaneous threats (Dias et al., 2019), it is becoming critical to understand a species' ability to behaviourally respond to these changes (Audet & Lefebvre, 2017). Studying personality traits can help to understand constraints to these responses and, thus, develop strategies to protect larger proportions of populations (MacKinlay & Shaw, 2023). For example, seabird populations have been predicted to become less diverse with a greater proportion of shyer individuals as they likely have higher success in more variable and poorer conditions (Jeffries et al., 2021). This study, however, suggests that both docile and aggressive birds may have similar fledging success. Our findings also indicate that prey abundance and behaviour should be considered when investigating seabird behavioural consistency (Harris et al., 2020a), because these metrics change the foraging context for seabirds and, thus, may influence whether individual consistency is detected.

References

Araújo, M. S., Bolnick, D. I., & Layman, C. A. (2011). The ecological causes of individual specialisation. *Ecol. Lett.*, 14(9), 948–958. https://doi.org/10.1111/j.1461-0248.2011.01662.x

Audet, J. N., & Lefebvre, L. (2017). What's flexible in behavioral flexibility? *Behav. Ecol.*, 28(4), 943–947. https://doi.org/10.1093/beheco/arx007

Barger, C. P., Young, R. C., Will, A., Ito, M., & Kitaysky, A. S. (2016). Resource Partitioning between sympatric seabird species increases during chick-rearing. *Ecosphere*, 7(9), 1–15. https://doi.org/10.1002/ecs2.1447

Beal, M., Oppel, S., Handley, J., Pearmain, E. J., Morera-Pujol, V., Carneiro, A. P. B., Davies, T. E., Phillips, R. A., Taylor, P. R., Miller, M. G. R., Franco, A. M. A., Catry, I., Patrício, A. R., Regalla, A., Staniland, I., Boyd, C., Catry, P., & Dias, M. P. (2021). track2KBA: an R package for identifying important sites for biodiversity from tracking data. *Methods Ecol. Evol.*, 12(12), 2372–2378. https://doi.org/10.1111/2041-210X.13713

Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: a meta-analysis. *Anim. Behav.*, 77(4), 771–783. https://doi.org/10.1016/j.anbehav.2008.12.022

Benvenuti, S., Dall'Antonia, L., & Lyngs, P. (2001). Foraging behaviour and time allocation of chick-rearing razorbills *Alca torda* at Græsholmen, central Baltic Sea. *Ibis*, 143(4), 402–412. https://doi.org/10.1111/j.1474-919x.2001.tb04941.x

Biagiotti Barchiesi, M., Biondi, L. M., & García, G. O. (2023). A systematic review of trends in research on seabird behavioral flexibility. *Mar. Ornithol.*, 51, 293–300. http://doi.org/10.5038/2074-1235.51.2.1546

Biro, P. A., & Stamps, J. A. (2015). Using repeatability to study physiological and behavioural traits: Ignore time-related change at your peril. *Anim. Behav.*, 105, 223–230. https://doi.org/10.1016/j.anbehav.2015.04.008

Bolnick, D. I., Amarasekare, P., Araújo, M., Bürger, R., Levine, J. M., Novak, M., Rudolf, V. HW., Schreiber, S. J., Urban, M. C., & Vasseur, D. (2011). Why intraspecific trait variation matters in community ecology. *Trends Ecol. Evol.*, 26(4), 183–192.

Bolnick, D. I., Svanbäck, J., Fordyce, L., Yang, J., Davis, D., & Darrin, C. (2003). The ecology of individuals: incidence and implications of individual specialization. *Am. Nat.*, 161(1), 1–30.

Buren, A. D., Murphy, H. M., Adamack, A. T., Davoren, G. K., Koen-Alonso, M., Montevecchi, W. A., Mowbray, F. K., Pepin, P., Regular, P. M., Robert, D., Rose, G. A., Stenson, G. B., & Varkey, D. (2019). The collapse and continued low productivity of a keystone forage fish species. *Mar. Ecol. Prog. Ser.*, 616, 155–170. https://doi.org/10.3354/meps12924

Burger, A. E. (1997). Arrival and departure behavior of common murres at colonies: evidence for an information halo? *Waterbirds*, 20(1), 55–65. https://doi.org/10.2307/1521764

Carscadden, J. E., Frank, K. T., & Leggett, W. C. (2002). Ecosystem changes and the effects on capelin (*Mallotus villosus*), a major forage species. *Can. J. Fish. Aquat. Sci.*, 58, 73–85. https://doi.org/10.1139/cjfas-58-1-73

Carscadden, J. E., & Vilhjálmsson, H. (2002). Capelin - What are they good for? *ICES J. Mar. Sci.*, 59(5), 863–869. https://doi.org/10.1006/jmsc.2002.1283

Carter, A. J., Feeney, W. E., Marshall, H. H., Cowlishaw, G., & Heinsohn, R. (2013). Animal personality: what are behavioural ecologists measuring? *Biol. Rev.*, 88(2), 465–475. http:// 10.1111/brv.12007

Ceia, F. R., & Ramos, J. A. (2015). Individual specialization in the foraging and feeding strategies of seabirds: a review. *Mar. Biol.*, 162(10), 1923–1938. https://doi.org/10.1007/s00227-015-2735-4

Christensen, R. H. B. (2023). Ordinal regression models for ordinal data (R package version 2023.12-4).

Cole, E. F., & Quinn, J. L. (2014). Shy birds play it safe: personality in captivity predicts risk responsiveness during reproduction in the wild. *Biol. Lett.*, 10(5), 1–4. https://doi.org/10.1098/rsbl.2014.0178

Collins, S. M., Hatch, S. A., Elliott, K. H., & Jacobs, S. R. (2019). Boldness, mate choice and reproductive success in *Rissa tridactyla*. *Anim. Behav.*, 154, 67–74. https://doi.org/10.1016/j.anbehav.2019.06.007

Connan, M., Bonnevie, B. T., Hagen, C., van der Lingen, C. D., & McQuaid, C. (2017). Diet specialization in a colonial seabird studied using three complementary dietary techniques: effects of intrinsic and extrinsic factors. *Mar. Biol.*, 164(8), 1–20. https://doi.org/10.1007/s00227-017-3201-2

Crook, K. A., Maxner, E., & Davoren, G. K. (2017). Temperature-based spawning habitat selection by Capelin (*Mallotus villosus*) in Newfoundland. *ICES J. Mar. Sci.*, 74(6), 1622–1629. https://doi.org/10.1093/icesjms/fsx023

Dall, S. R. X., Bell, A. M., Bolnick, D. I., & Ratnieks, F. L. W. (2012). An evolutionary ecology of individual differences. *Ecol. Lett.*, 15(10), 1189–1198. https://doi.org/10.1111/j.1461-0248.2012.01846.x

Dall, S. R. X., Giraldeau, L. A., Olsson, O., McNamara, J. M., & Stephens, D. W. (2005). Information and its use by animals in evolutionary ecology. *Trends Ecol. Evol.*, 20(4), 187–193. https://doi.org/10.1016/j.tree.2005.01.010

Dammhahn, M., & Almeling, L. (2012). Is risk taking during foraging a personality trait? A field test for cross-context consistency in boldness. *Anim. Behav.*, 84(5), 1131–1139. https://doi.org/10.1016/j.anbehav.2012.08.014

Davoren, G. K. (2013). Distribution of marine predator hotspots explained by persistent areas of prey. *Mar. Biol.*, 160(12), 3043–3058. https://doi.org/10.1007/s00227-013-2294-5

Davoren, G. K. (2024). Variable forage fish biomass and phenology influence marine predator diet, foraging behavior, and species interactions in coastal Newfoundland, Canada. *ICES J. Mar. Sci.*, 1–14. https://doi.org/10.1093/icesjms/fsae021

Davoren, G. K., Anderson, J. T., & Montevecchi, W. A. (2006). Shoal behaviour and maturity relations of spawning capelin (*Mallotus villosus*) off Newfoundland: demersal spawning and diel vertical movement patterns. *Can. J. Fish. Aquat. Sci.*, 63(2), 268–284. https://doi.org/10.1139/f05-204

Davoren, G. K., Maynard, L. D., Johnson, K. F., Carvalho, P. C., Gulka, J., Jenkins, E., Lescure, L. M., Runnells, E., & Tripp, A. (2025). Aggregative responses of marine predators to a pulsed resource. *J. Anim. Ecol.*, 1–16. https://doi.org/10.1111/1365-2656.14214

Dias, M. P., Martin, R., Pearmain, E. J., Burfield, I. J., Small, C., Phillips, R. A. 4, Yates, O., Lascelles, B., Borboroglu, P. G., & Croxall, J. P. (2019). Threats to seabirds: a global assessment. *Biol. Conserv.*, 237, 525–537. https://10.1016/j.biocon.2019.06.033

Dingemanse, N. J., Both, C., Drent, P. J., & Tinbergen, J. M. (2004). Fitness consequences of avian personalities in a fluctuating environment. *Proc. R. Soc. B.*, 271, 847–852. https://doi.org/10.1098/rspb.2004.2680

Elliott, K. H., Ricklefs, R. E., Gaston, A. J., Hatch, S. A., Speakman, J. R., & Davoren, G. K. (2013). High flight costs, but low dive costs, in auks support the biomechanical hypothesis for flightlessness in penguins. *PNAS*, 110(23), 9380–9384. https://doi.org/10.1073/pnas.1304838110

Evans, T. J., Kadin, M., Olsson, O., & Åkesson, S. (2013). Foraging behaviour of common murres in the Baltic Sea, recorded by simultaneous attachment of GPS and time-depth recorder devices. *Mar. Ecol. Prog. Ser.*, 475, 277–289. https://doi.org/10.3354/meps10125

Fayet, A. L., Clucas, G. V., Anker-Nilssen, T., Syposz, M., & Hansen, E. S. (2021). Local prey shortages drive foraging costs and breeding success in a declining seabird, the Atlantic puffin. *J. Anim. Ecol.*, 90(5), 1152–1164. https://doi.org/10.1111/1365-2656.13442

Franklin, K. A., Norris, K., Gill, J. A., Ratcliffe, N., Bonnet-Lebrun, A.-S., Butler, S. J., Cole, N. C., Jones, C. G., Lisovski, S., Ruhomaun, K., Tatayah, V., & Nicoll, M. A. C. (2022). Individual consistency in migration strategies of a tropical seabird, the Round Island petrel. *Mov. Ecol.*, 10, 1–14. https://doi.org/10.1186/s40462-022-00311-y

Gabrielsen, G. W. (1996). Energy expenditure of breeding common murres. In W. A. Montevecchi (Ed.), Studies of High Latitude Seabirds, 4. Trophic Relationships and Energetics of Endotherms in Cold Ocean Systems.

Gaillard, J.-M., Festa-Bianchest, M., & Yoccoz, N. G. (1998). Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends Ecol. Evol.*, 13(2), 58–63. https://doi.org/10.1016/S0169-5347(97)01237-8

Gillies, N., Weimerskirch, H., Thorley, J., Clay, T. A., Martín López, L. M., Joo, R., Basille, M., & Patrick, S. C. (2023). Boldness predicts plasticity in flight responses to winds. *J. Anim. Ecol.*, 92(9), 1730–1742. https://doi.org/10.1111/1365-2656.13968

Gosling, S. D. (2001). From mice to men what can we learn about personality from animal research. *Psychol. Bull.*, 127, 45–86.

Gulka, J., Ronconi, R. A., & Davoren, G. K. (2019). Spatial segregation contrasting dietary overlap: niche partitioning of two sympatric alcids during shifting resource availability. *Mar. Biol.*, 166(9). https://doi.org/10.1007/s00227-019-3553-x

Hamel, S., Gaillard, J. M., & Yoccoz, N. G. (2018). Introduction to individual heterogeneity – the causes and consequences of a fundamental biological process. *Oikos*, 127(5), 643–647. https://doi.org/10.1111/oik.05222

Harris, S. M., Descamps, S., Sneddon, L. U., Bertrand, P., Chastel, O., & Patrick, S. C. (2020a). Personality predicts foraging site fidelity and trip repeatability in a marine predator. *J. Anim. Ecol.*, 89(1), 68–79. https://doi.org/10.1111/1365-2656.13106

Harris, S. M., Descamps, S., Sneddon, L. U., Cairo, M., Bertrand, P., & Patrick, S. C. (2020b). Personality-specific carry-over effects on breeding. *Proc. R. Soc. B.*, 287, 1–9. https://doi.org/10.1098/rspb.2020.2381

Hoelzel, A. R., Dorsey, E. M., & Stern, S. J. (1989). The foraging specializations of individual minke whales. Anim. Behav., 38, 786–794. https://doi/10.1016/S0003-3472(89)80111-3

Jeffries, P. M., Patrick, S. C., & Potts, J. R. (2021). Be different to be better: the effect of personality on optimal foraging with incomplete knowledge. *Theor. Ecol.*, 1–13. https://doi.org/10.1007/s12080-021-00517-7

Jenkins, E. J., & Davoren, G. K. (2021). Seabird species- and assemblage-level isotopic niche shifts associated with changing prey availability during breeding in coastal Newfoundland. *Ibis*, 163(1), 183–196. https://doi.org/10.1111/ibi.12873

Kranstauber, B., Smolla, M., & Safi, K. (2017). Similarity in spatial utilization distributions measured by the earth mover's distance. *Methods Ecol. Evol.*, 8(2), 155–160. https://doi.org/10.1111/2041-210X.12649

Kranstauber, B., Smolla, M., & Scharf, A. (2021). move: visualising and analysing animal track data (R package version 4.1.6)

Krüger, L., Pereira, J. M., Paiva, V. H., & Ramos, J. A. (2019). Personality influences foraging of a seabird under contrasting environmental conditions. *JEMBE*, 516, 123–131. https://doi.org/10.1016/j.jembe.2019.04.003

Lavers, J., Hipfner, M., & Chapdelaine, G. (2020). Razorbill (*Alca torda*). In Billerman SM (Ed.), Birds of the world (1.0). Cornell Lab of Ornithology.

Le, S., Josse, J., & Husson, F. (2008). FactoMineR: an R package for multivariate analysis. *J. Stat. Softw.*, 25(1), 1–18.

Legard, M. J., & Davoren, G. K. (2025). A non-invasive method during routine handling indicates docility in a wild, crevice-nesting seabird. *Behaviour*, 1–22. https://doi.org/10.1163/1568539X-bja10298

Lescure, L., Gulka, J., & Davoren, G. (2023). Increased foraging effort and reduced chick condition of razorbills under lower prey biomass in coastal Newfoundland, Canada. *Mar. Ecol. Prog. Ser.*, 709, 109–123. https://doi.org/10.3354/meps14286

Linnebjerg, J. F., Fort, J., Guilford, T., Reuleaux, A., Mosbech, A., & Frederiksen, M. (2013). Sympatric breeding auks shift between dietary and spatial resource partitioning across the annual cycle. *PLoS One*, 8(8), 1–10. https://doi.org/10.1371/journal.pone.0072987

Luque, S. P. (2007). Diving behaviour analysis in R. *R News*, 7(3), 8–14.

MacKinlay, R. D., & Shaw, R. C. (2023). A systematic review of animal personality in conservation science. *Conserv. Biol.*, 37(1), 1–16. https://doi.org/10.1111/cobi.13935

McCully, F. R., Weimerskirch, H., Cornell, S. J., Hatchwell, B. J., Cairo, M., & Patrick, S. C. (2022). Partner intrinsic characteristics influence foraging trip duration, but not coordination of care in wandering albatrosses *Diomedea exulans*. *Ecol. Evol.*, 12, 1–13. https://doi.org/10.1002/ece3.9621

Menzies, A. K., Timonin, M. E., McGuire, L. P., & Willis, C. K. R. (2013). Personality variation in little brown bats. *PLoS One*, 8(11). https://doi.org/10.1371/journal.pone.0080230

Morrison, S. M., & Davoren, G. K. (2024). Habitat characteristics and diel patterns of sand lance (*Ammodytes* spp.) in coastal Newfoundland. *Environ. Biol. Fish.*, 107(4), 443–457. https://doi.org/10.1007/s10641-024-01540-3

Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: A practical guide for biologists. *Biol. Rev.*, 85(4), 935–956. https://doi.org/10.1111/j.1469-185X.2010.00141.x

Page, M., Gotwalt, C. & Wilson, A.G. (2018). Automated data imputation: extending low rank matrix imputation techniques for statistical prediction modeling. http://www.lib.ncsu.edu/resolver/1840.20/35520

Patrick, S. C., Pinaud, D., & Weimerskirch, H. (2017). Boldness predicts an individual's position along an exploration–exploitation foraging trade-off. *J. Anim. Ecol.*, 86(5), 1257–1268. https://doi.org/10.1111/1365-2656.12724

Patrick, S. C., & Weimerskirch, H. (2014). Personality, foraging and fitness consequences in a long lived seabird. *PLoS One*, 9(2), 1–11. https://doi.org/10.1371/journal.pone.0087269

Patrick, S. C., & Weimerskirch, H. (2017). Reproductive success is driven by local site fidelity despite stronger specialisation by individuals for large-scale habitat preference. *J. Anim. Ecol.*, 86(3), 674–682. https://doi.org/10.1111/1365-2656.12636

Penton, P. M., & Davoren, G. K. (2012). Physical characteristics of persistent deep-water spawning sites of capelin: importance for delimiting critical marine habitats. *Mar. Biol. Res.*, 8(8), 778–783. https://doi.org/10.1080/17451000.2012.678858

Pereira, J. M., Ramos, J. A., Ceia, F. R., Krüger, L., Marques, A. M., & Paiva, V. H. (2024). Boldness predicts foraging behaviour, habitat use and chick growth in a central place marine predator. *Oecologia*. https://doi.org/10.1007/s00442-024-05557-4

Phillips, R. A., Lewis, S., González-Solís, J., & Daunt, F. (2017). Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds. *Mar. Ecol. Prog. Ser.*, 578, 117–150. https://doi.org/10.3354/meps12217

R Core Team. (2023). R: a language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/

Ramírez, I., Paiva, V. H., Fagundes, I., Menezes, D., Silva, I., Ceia, F. R., Phillips, R. A., Ramos, J. A., & Garthe, S. (2016). Conservation implications of consistent foraging and trophic ecology in a rare petrel species. *Anim. Conserv.*, 19(2), 139–152. https://doi.org/10.1111/acv.12227

Réale, D., Martin, J., Coltman, D. W., Poissant, J., & Festa-Bianchet, M. (2009). Male personality, life-history strategies and reproductive success in a promiscuous mammal. *J. Evol. Biol.*, 22(8), 1599–1607. https://doi.org/10.1111/j.1420-9101.2009.01781.x

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biol. Rev.*, 82(2), 291–318. https://doi.org/10.1111/j.1469-185X.2007.00010.x

Rebstock, G. A., Abrahms, B., & Boersma, P. D. (2022). Site fidelity increases reproductive success by increasing foraging efficiency in a marine predator. *Behav. Ecol.*, 33(4), 868–875. https://doi.org/10.1093/beheco/arac052

Sargeant, B. L., Mann, J., Berggren, P., & Krützen, M. (2005). Specialization and development of beach hunting, a rare foraging behavior, by wild bottlenose dolphins (*Tursiops* sp.). *Can. J. Zool.*, 83(11), 1400–1410. https://doi.org/10.1139/z05-136

Shaffer, S. A., Weimerskirch, H., & Costa, D. P. (2001). Functional significance of sexual dimorphism in wandering albatrosses, *Diomedea exulans*. *Funct. Ecol.*, 15(2), 203–210. https://doi.org/10.1046/j.1365-2435.2001.00514.x

Shoji, A., Elliott, K., Fayet, A., Boyle, D., Perrins, C., & Guilford, T. (2015). Foraging behaviour of sympatric razorbills and puffins. *Mar. Ecol. Prog. Ser.*, 520, 257–267. https://doi.org/10.2307/24895065

Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.*, 19(7), 372–378. https://doi.org/10.1016/j.tree.2004.04.009

Stamps, J. A. (2007). Growth-mortality tradeoffs and “personality traits” in animals. *Ecol. Lett.*, 10(5), 355–363. https://doi.org/10.1111/j.1461-0248.2007.01034.x

Stamps, J., & Groothuis, T. G. G. (2010). The development of animal personality: relevance, concepts and perspectives. *Biol. Rev.*, 85(2), 301–325. https://doi.org/10.1111/j.1469-185X.2009.00103.x

Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2017). rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods Ecol. Evol.*, 8(11), 1639–1644. https://doi.org/10.1111/2041-210X.12797

Symons, S. C., & Diamond, A. W. (2022). Resource partitioning in Atlantic puffins and razorbills facing declining food: an analysis of feeding areas and dive behaviour in relation to diet. *Mar. Ecol. Prog. Ser.*, 699, 153–165. https://doi.org/10.3354/meps14172

Traisnel, G., & Pichegru, L. (2018). Does it always pay to defend one’s nest? A case study in African penguin. *J. Ethol.*, 124(1), 74–83. https://doi.org/10.1111/eth.12704

Traisnel, G., & Pichegru, L. (2019a). Boldness at the nest predicts foraging and diving behaviour of female but not male African penguins. *Anim. Behav.*, 150, 113–125. https://doi.org/10.1016/j.anbehav.2019.02.003

Traisnel, G., & Pichegru, L. (2019b). Success comes with consistency in hard times: foraging repeatability relates to sex and breeding output in African penguins. *Mar. Ecol. Prog. Ser.*, 608, 279–289. https://doi.org/10.3354/meps12827

Van Den Bosch, M., Baert, J. M., Müller, W., Lens, L., & Stienen, E. W. M. (2019). Specialization reduces foraging effort and improves breeding performance in a generalist bird. *Behav. Ecol.*, 30(3), 792–800. https://doi.org/10.1093/beheco/arz016

Van de Walle, J., Sun, R., Fay, R., Patrick, S. C., Barbraud, C., Delord, K., Weimerkirch, H., & Jenouvrier, S. (2024). The impact of boldness on demographic rates and life-history outcomes in the wandering albatross. *J. Anim. Ecol.* https://doi.org/10.1111/1365-2656.14077

Vandenabeele, S. P., Shepard, E. L., Grogan, A., & Wilson, R. P. (2012). When three per cent may not be three per cent; device-equipped seabirds experience variable flight constraints. *Mar. Biol.*, 159(1), 1–14. https://doi.org/10.1007/s00227-011-1784-6

Votier, S. C., Fayet, A. L., Bearhop, S., Bodey, T. W., Clark, B. L., Grecian, J., Guilford, T., Hamer, K. C., Jeglinski, J. W. E., Morgan, G., Wakefield, E., & Patrick, S. C. (2017). Effects of age and reproductive status on individual foraging site fidelity in a long-lived marine predator. *Proc. R. Soc. B.*, 284, 1–7. https://doi.org/10.1098/rspb.2017.1068

Wakefield, E. D., Cleasby, I. R., Bearhop, S., Bodey, T. W., Davies, R. D., Miller, P. I., Newton, J., Votier, S. C., & Hamer, K. C. (2015). Long-term individual foraging site fidelity - why some gannets don't change their spots. *Ecology*, 96(11), 3058–3074. https://doi.org/10.1890/14-1300.1

Welcker, J., Harding, A. M. A., Karnovsky, N. J., Steen, H., Strøm, H., & Gabrielsen, G. W. (2009). Flexibility in the bimodal foraging strategy of a high Arctic alcid, the little auk *Alle alle*. *J. Avian Biol.*, 40(4), 388–399. https://doi.org/10.1111/j.1600-048X.2008.04620.x

Wolak, M. E., Fairbairn, D. J., & Paulsen, Y. R. (2012). Guidelines for estimating repeatability. *Methods Ecol. Evol.*, 3(1), 129–137. https://doi.org/10.1111/j.2041-210X.2011.00125.x

Wolf, M., Van Doorn, G. S., Leimar, O., & Weissing, F. J. (2007). Life-history trade-offs favour the evolution of animal personalities. *Nature*, 447, 581–584. https://doi.org/10.1038/nature05835

Wolf, M., & Weissing, F. J. (2012). Animal personalities: Consequences for ecology and evolution. *Trends Ecol. Evol.*, 27(8), 452–461. https://doi.org/10.1016/j.tree.2012.05.001

Woo, K. J., Elliott, K. H., Davidson, M., Gaston, A. J., & Davoren, G. K. (2008). Individual specialization in diet by a generalist marine predator reflects specialization in foraging behaviour. *J. Anim. Ecol.*, 77(6), 1082–1091. https://doi.org/10.1111/j.1365-2656.2008.01429.x

Zango, L., Reyes-González, J. M., Militão, T., Zajková, Z., Álvarez-Alonso, E., Ramos, R., & González-Solís, J. (2019). Year-round individual specialization in the feeding ecology of a long-lived seabird. *Sci. Rep.*, 9, 1–12. https://doi.org/10.1038/s41598-019-48214-0

Zuur, A. F., & Ieno, E. N. (2016). A protocol for conducting and presenting results of regression-type analyses. *Methods Ecol. Evol.*, 7(6), 636–645. https://doi.org/10.1111/2041-210X.12577

Table 1. Summary of tags deployed on chick rearing razorbills from James Island, Newfoundland, during 2019, 2020 and 2023 both before and after capelin spawning in July and August.

	2019		2020		2023
	Before	After	Before	After	Before
Individuals tracked	4	14	12	8	20
Total trips	19	53	19	18	152
Trips per individual	2 - 4	1 - 11	1 - 3	1 - 6	3 - 18
Tags deployed/data retrieved	10/4	20/14	19/12	17/8	20/20
Tracking days per individual	2-4	1-11	1-3	1-6	2-11
Range of deployment dates	17 – 23 Jul	26 Jul – 9 Aug	13 – 21 Jul	27 Jul – 15 Aug	17 Jul – 1 Aug
Tag model	Catlog Gen 2		Catlog Gen 2 + Lotek LAT 1800		Ecotone URIA-300
Tag weight (g)	13		13 + 6 (TDR)		15

Table 2. Results of generalised linear models (GLMs) examining the spatial consistency of chick-rearing razorbill foraging trips by comparing between- and within-individual Earth Mover's Distance (EMD values) in each capelin availability period (before/after spawning) during 2019, 2020, and 2023. Periods with significantly lower EMD values within-individuals compared to between-individuals (i.e. spatially consistent) are highlighted in bold.

Year	Period	Estimate ± SE	t value	*p* value
2019	Intercept	18.322 ± 1.904	9.624	<0.001
	Before	4.824 ± 4.257	1.133	0.263
	Intercept	0.149 ± 0.003	56.766	<0.001
	After	**0.066 ± 0.012**	**5.305**	**<0.001**
2020	Intercept	39.080 ± 1.618	24.16	<0.001
	Before	2.126 ± 6.437	0.33	0.742
	Intercept	58.516 ± 3.230	18.005	<0.001
	After	-11.547 ± 8.719	-1.324	0.187
2023	Intercept	0.130 ± 0.001	109.750	<0.001
	After	0.009 ± 0.005	1.809	0.071

Table 3. Repeatability values (*R*) for each razorbill foraging trip and dive characteristic in each capelin availability period (before/after spawning) in each year. Bootstrapped 95% confidence intervals and *p* values are shown along with t, df and *p* values for each fixed effect. Significant *R* values and fixed effects are shown in bold.

			Adjusted Repeatability			Fixed Factors															
						Sex				Time of day				Date				Personality			
Year	Trip	Period	*R*	95% CI	*p*	Est ± SE	t	df	*p*	Est ± SE	t	df	*p*	Est ± SE	t	df	*p*	Est ± SE	t	df	*p*
2019	'Effort'	Before	0.000	0.000 - 0.964	0.500	-1.933 ± 5.103	-0.379	5.0	0.720	9.694 ± 4.319	2.244	5.0	0.075	-3.422 ± 2.554	-1.340	4.8	0.240				
		After	0.043	0.000 - 0.368	1.000	3.115 ± 1.458	2.136	7.3	0.069	**5.521 ± 1.285**	**4.298**	**4.8**	**<0.001**	1.041 ± 1.527	0.682	1.5	0.506				
2020	'Effort'	Before	0.252	0.000 - 0.858	0.403	-9.843 ± 1.062	-0.093	1.2	0.928	**4.097 ± 9.086**	**4.509**	**1.4**	**<0.001**	-4.911 ± 2.875	-1.708	8.6	0.124				
		After	0.008	0.000 - 0.740	0.500	-1.729 ± 1.229	-1.407	4.8	0.221	**4.649 ± 1.145**	**4.059**	**1.3**	**0.002**	-1.332 ± 9.027	-1.469	4.7	0.206				
	No. of dives	Before	0.000	0.000 - 0.914	1.000	2.810 ± 1.399	0.201	1.4	0.844	**3.006 ± 1.269**	**2.368**	**1.4**	**0.033**	3.364 ± 3.558	0.095	1.4	0.926				
		After	0.000	0.000 - 0.598	1.000	-1.396 ± 1.396	-1.000	3.4	0.383	**4.010 ± 1.136**	**3.531**	**9.0**	**0.006**	-2.971 ± 1.033	-0.288	3.4	0.791				
	Dive depth	Before	0.743	0.000 - 0.969	0.074	-2.395 ± 3.488	-0.694	1.0	0.503	3.010 ± 2.189	1.375	8.5	0.205	-1.585 ± 9.454	-0.168	1.4	0.869				
		After	0.623	0.198 - 0.925	0.352	4.614 ± 2.770	0.167	3.2	0.877	**3.599 ± 1.295**	**2.779**	**7.5**	**0.026**	1.076 ± 2.010	0.054	3.9	0.960				
2023	'Effort'	After	0.025	0.000 - 0.142	0.474					**1.135 ± 6.139**	**18.485**	**1.4**	**<0.001**	**4.119 ± 7.222**	**5.703**	**1.8**	**<0.001**	2.845 ± 5.648	0.050	1.9	0.960
	No. of dives	After	0.051	0.000 - 0.145	0.102					**4.076 ± 6.383**	**6.386**	**1.5**	**<0.001**	1.482 ± 8.320	1.782	2.0	0.090	6.432 ± 6.535	0.098	1.7	0.923
	Dive depth	After	0.124	0.000 - 0.315	0.157					8.950 ± 9.697	0.923	1.4	0.358	1.510 ± 1.448	1.043	2.5	0.307	2.136 ± 1.167	1.830	1.6	0.086

Table S1. Repeatability values (*R*) for razorbill individual dive depths in 2020 (before/after capelin spawning), and in 2023. Bootstrapped 95% confidence intervals and *p* values are also shown. Significant *R* values are shown in bold.

	Year	Group	*R*	95% CI	*p*
Dive depth	2020	**Before**	**0.307**	**0.103 - 0.468**	**<0.001**
		After	**0.598**	**0.198 - 0.793**	**<0.001**
	2023	**After**	**0.136**	**0.064 - 0.216**	**<0.001**

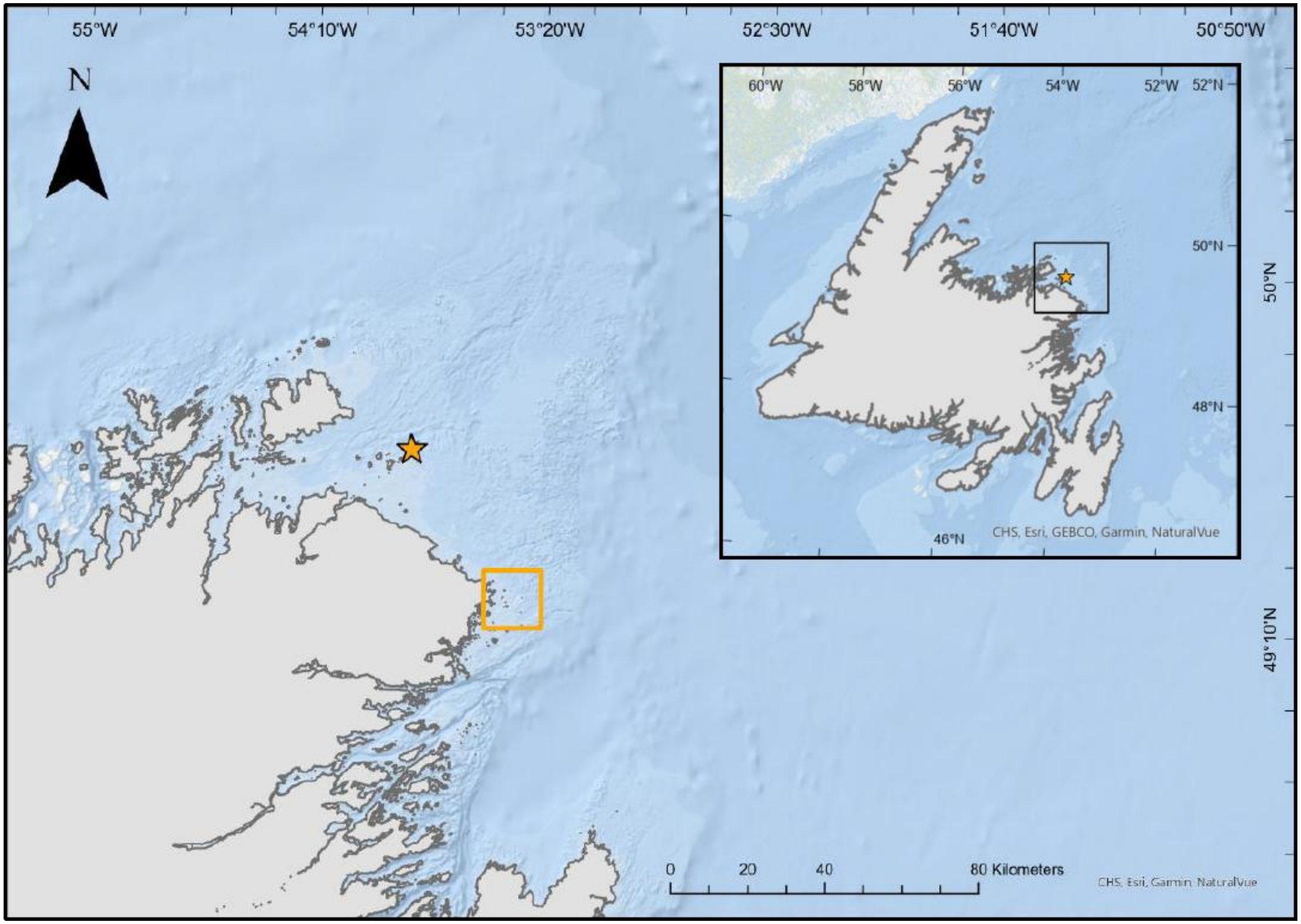

Figure 1. The location of the study breeding colony, James Island (orange star), part of the Wadham Islands archipelago, on the northeast coast of Newfoundland, Canada. The map also shows the location of the hydroacoustic survey area (orange box) to measure capelin biomass (see Davoren et al. 2025 for details).

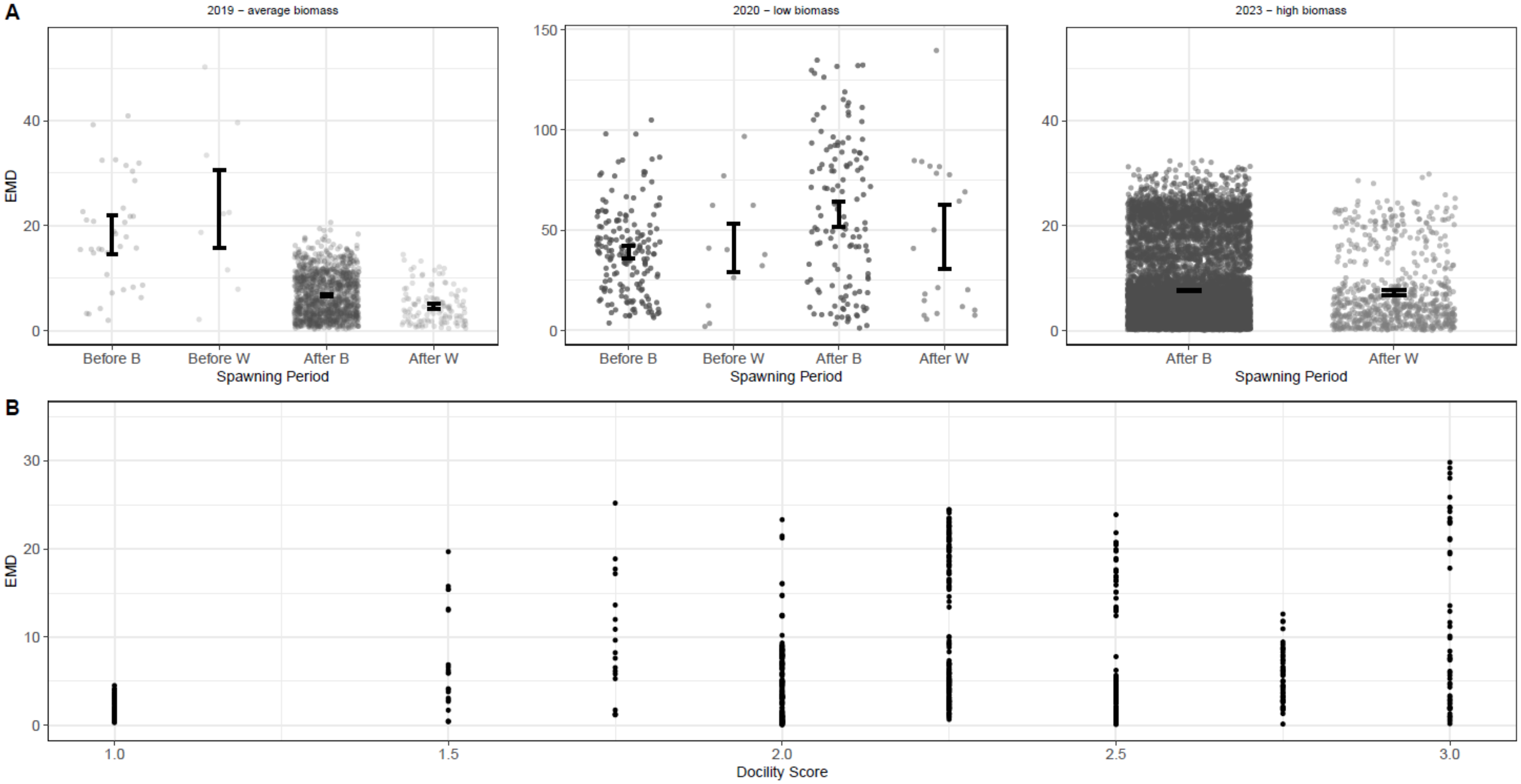

Figure 2. Earth mover's distance (EMD) values for between (B) and within-individual (W) differences in foraging track locations of chick-rearing razorbills on the northeast Newfoundland coast during each capelin availability period (before/after spawning) in each year (**A**). Note the difference in y-axis scale in 2020, illustrating varying spatial consistency across years. Also note that during 2023, birds were tagged only after capelin spawning began. Predicted EMD values from a generalised linear model (GLM) are shown as error bars with 95% confidence intervals. Within individual earth mover's distance (EMD) values along the docile-aggressive continuum within 2023 (**B**).

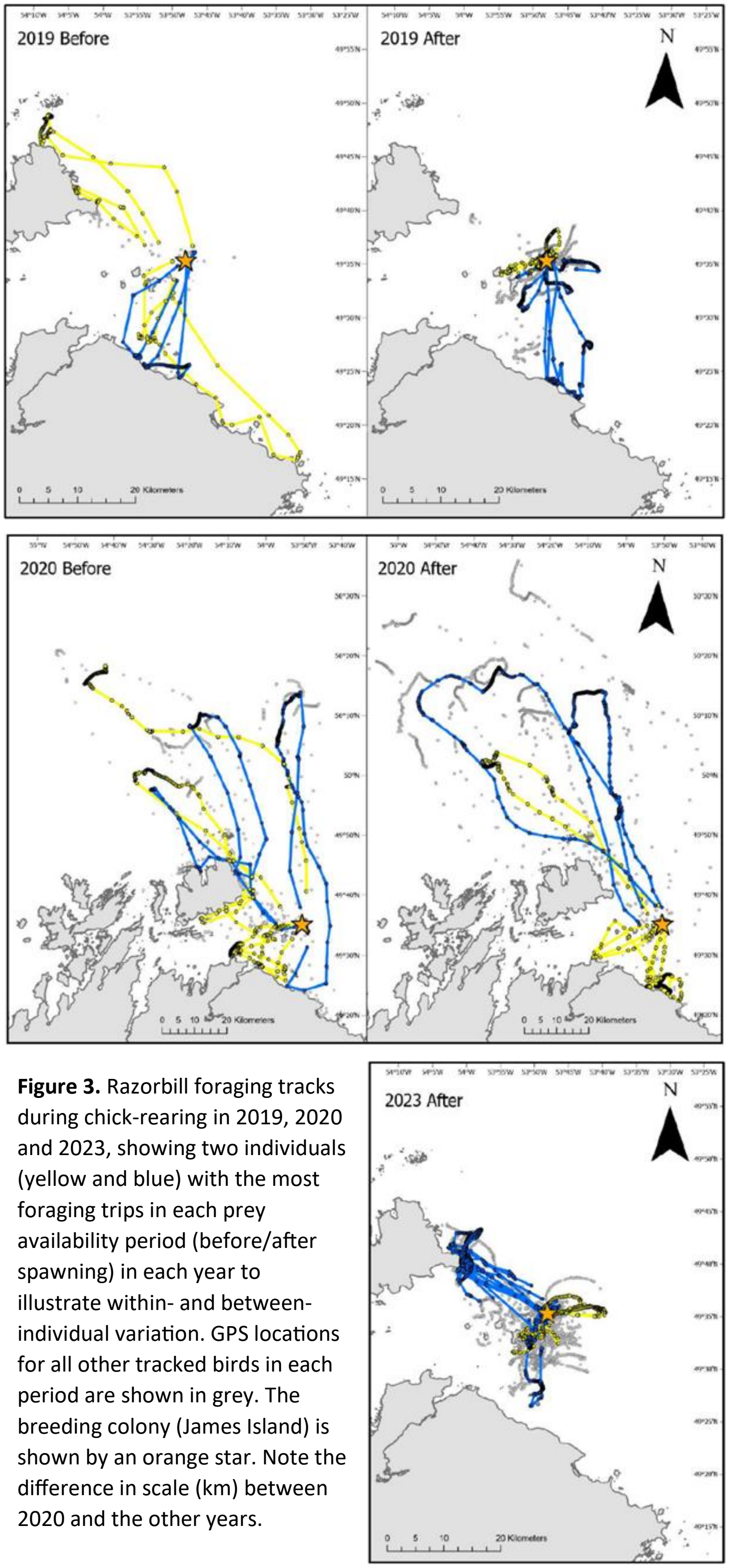

Figure 3. Razorbill foraging tracks during chick-rearing in 2019, 2020 and 2023, showing two individuals (yellow and blue) with the most foraging trips in each prey availability period (before/after spawning) in each year to illustrate within- and between-individual variation. GPS locations for all other tracked birds in each period are shown in grey. The breeding colony (James Island) is shown by an orange star. Note the difference in scale (km) between 2020 and the other years.

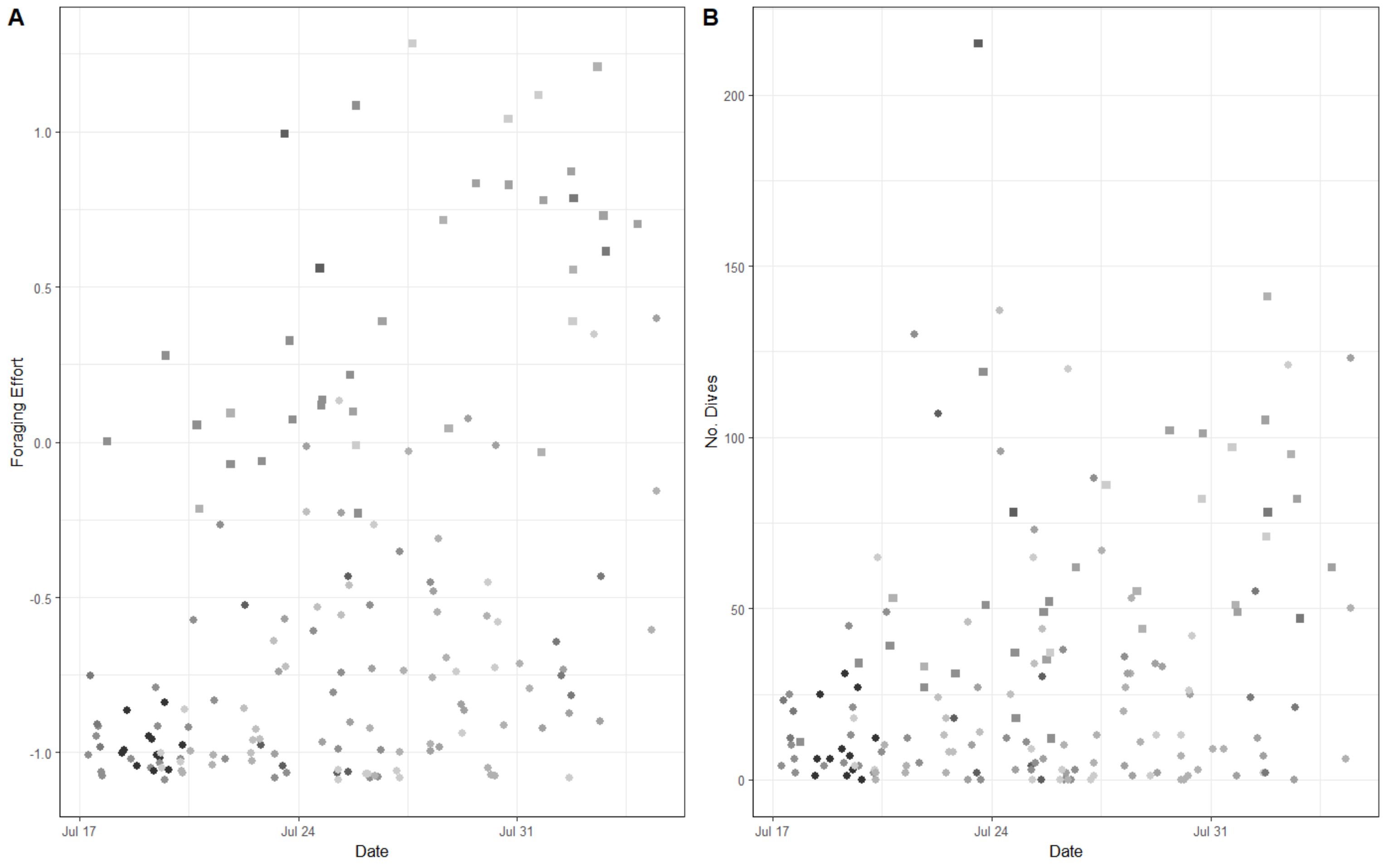

Figure 4. Foraging effort (**A**) and number of dives (**B**) per trip throughout 2023 with the time of day of the trip shown by squares (overnight) and circles (day). Points are shaded along the docile-aggressive continuum, with darker and lighter shading showing individual birds at the docile and aggressive ends of the continuum, respectively.

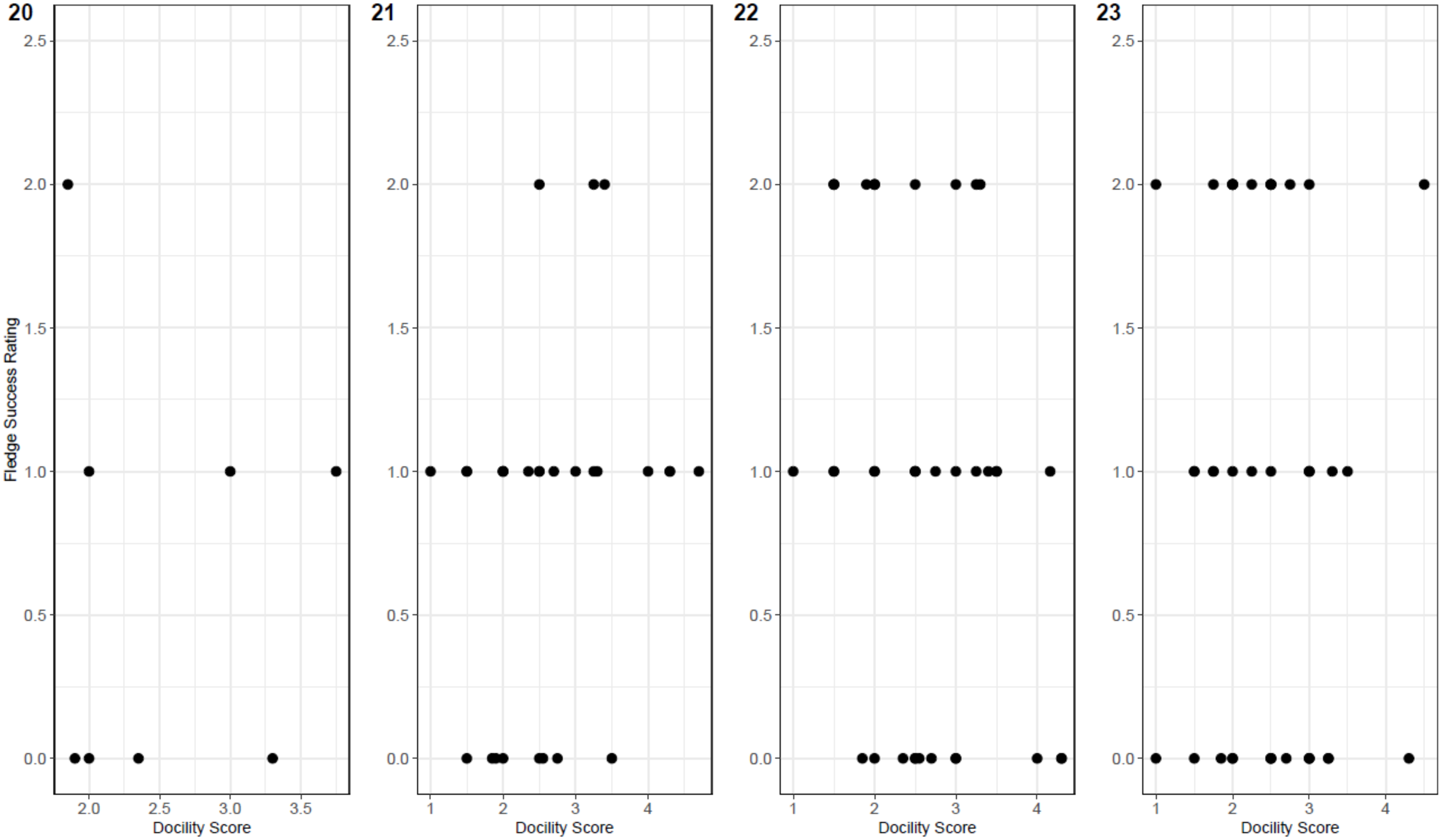

Figure 5. Razorbill fledge success (successful = 2, probably successful = 1, unsuccessful = 0) along the docile-aggressive continuum in 2020 (n=8), 2021 (n=28), 2022 (n=38) and 2023 (n=42).

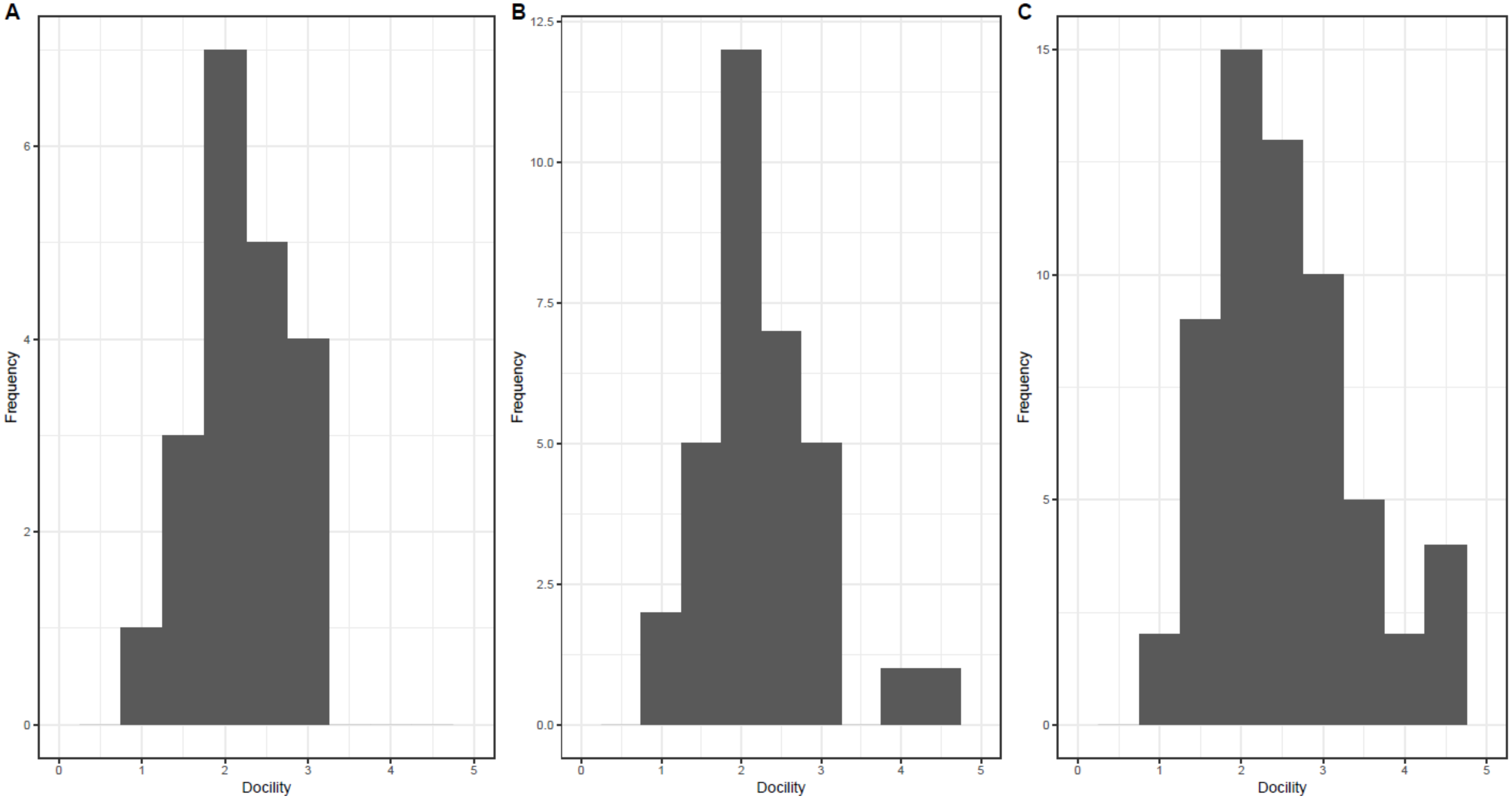

Figure S1. Distribution of docility scores within: (**A**) GPS (global positioning system) tagged razorbills in 2023, (**B**) GPS tagged razorbills across all years (2019-2020, 2023) and (**C**) razorbills with known fledge success in at least one year (2020-2023).

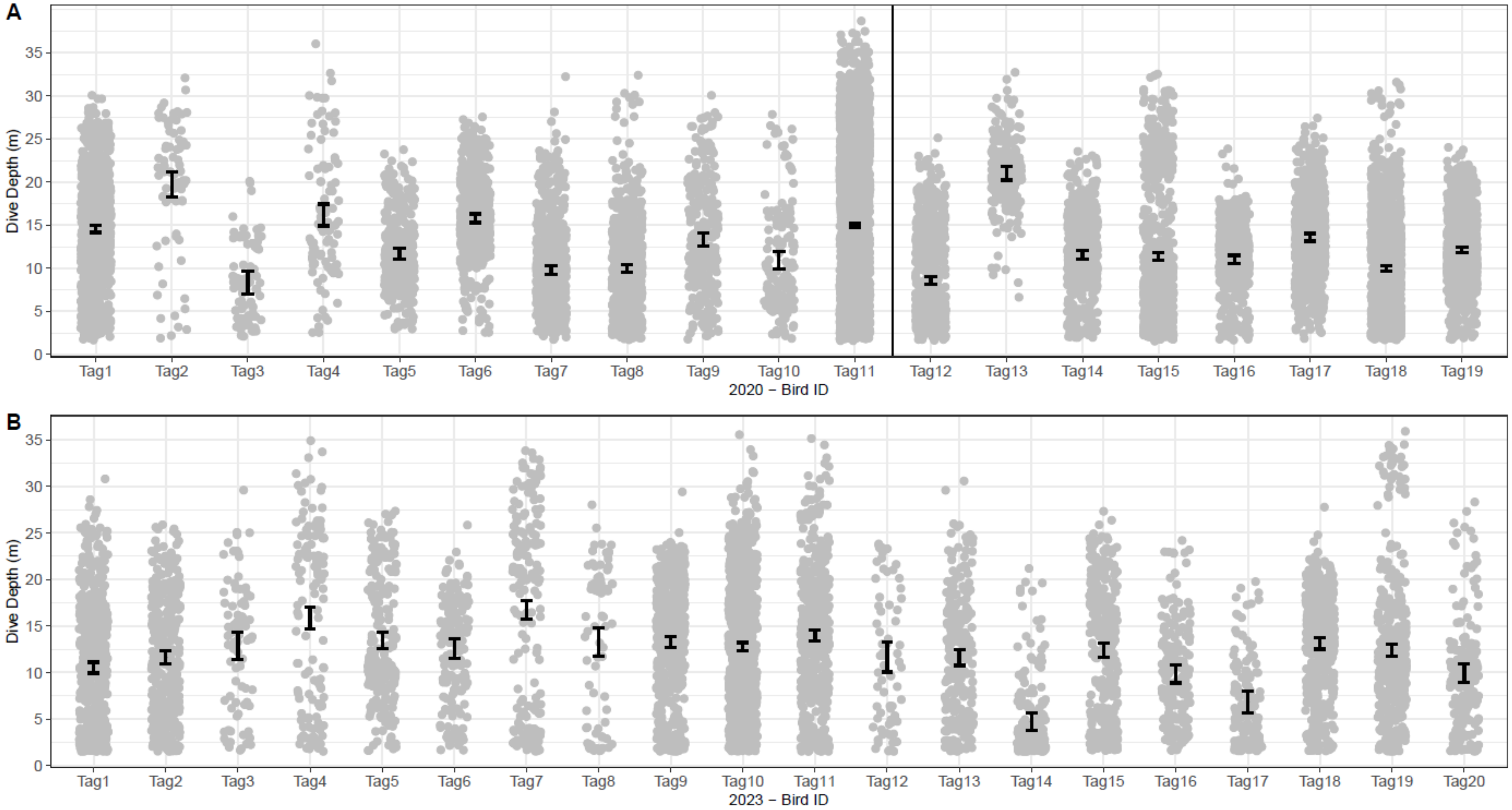

Figure S2. The dive depths of each tagged razorbill collected with time-depth recorders (TDRs) in 2020 (**A**) and 2023 (**B**). The vertical line in A divides the birds into those tagged before capelin spawned in 2020 (left) and those that were tagged after capelin spawned (right). Predicted depth values for each individual from a generalised linear model (GLM) are shown as error bars with 95% confidence intervals.

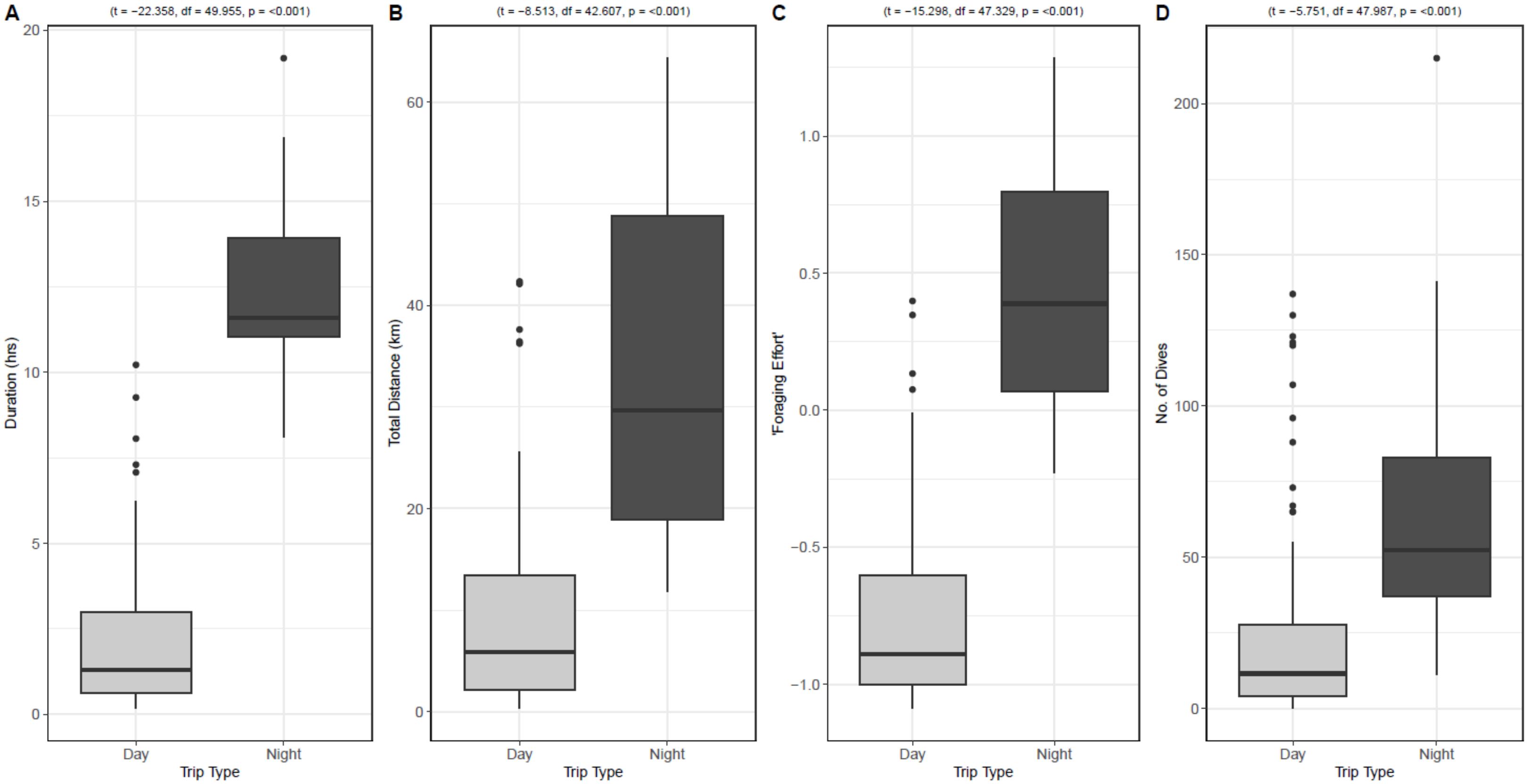

Figure S3. Razorbill foraging trip duration (**A**), total distance (**B**), ‘foraging effort’ (**C**), and number of dives (**D**) for day and overnight (night) trips in 2023. Statistical results (t, df and *p*) from t-tests comparing the trip types are shown above.

Link between Chapters 2 & 3

In Chapter 2, I found no relationships between personality (aggressive-docile continuum, using observer ratings developed in Chapter 1) and razorbill behaviour (e.g., foraging distance, location) or fledging success during the breeding season. Instead, razorbill behaviour was dependent on the prey context (i.e., high or low capelin availability). For example, razorbills were spatially consistent in their foraging locations when capelin was present in the study area to spawn and the dominant prey type (i.e., years where peak capelin biomass was at least equal to the decadal average). In Chapter 3, I aimed to relate the aggressive-docile continuum (observer ratings) to razorbill behaviour during the non-breeding season (e.g., migratory location, foraging dive depth), an understudied period of the annual cycle of seabirds.

Chapter 3: The behaviour of individual razorbills (*Alca torda*) during the non-breeding season is consistent but not related to personality.

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Abstract

Within-individual consistency and between-individual variation in migratory (e.g., timing and location) and foraging (e.g., dive depth or trophic level) behaviour have been observed in many species, including seabirds. Migratory differences among individuals within species have been linked to factors, such as age, sex and animal personality, and may have fitness consequences. Therefore, we aimed to investigate individual consistency in migratory behaviour (i.e. location, distance), foraging dive depth and dietary metrics for razorbills (*Alca torda*) during non-breeding seasons across years and whether these behaviours were related to personality. Between 2017-2023, we deployed light-level geolocator (GLS) and combination geolocator time-depth recorder (GLS/TDR) tags on personality-tested razorbills (docile-aggressive continuum) during chick-rearing in coastal Newfoundland, Canada and collected feathers (head, belly, secondary) to quantify stable isotope ratios of nitrogen ($\delta^{15}N$) as a proxy of trophic level. Razorbills displayed higher between-individual relative to within-individual variation (i.e., high repeatability, R) in their overwintering locations, the distances travelled north ($R = 0.592$) and south ($R = 0.564$) from the colony, average daily dive depth ($R = 0.108$), and $\delta^{15}N$ values ($R = 0.128$). These behaviours, however, were not related to personality. Overall, the small but consistent differences in migratory location and foraging behaviour suggest that environmental conditions causing negative fitness consequences may be experienced by certain subsets of the population, thereby minimizing the impacts of localized threats at the population-level. Although relationships between personality and behaviour were not observed, we suggest future studies investigate personality to understand the between-individual variation shown in a growing number of studies.

Introduction

Migration, or seasonal movements between breeding and non-breeding areas (Newton, 2008), likely evolves in animals in response to resource availability, which varies over temporal and spatial scales (McNamara & Dall, 2010). Indeed, migration is likely to evolve if reproduction is more successful in one location, but winter survival is higher at a different location (Lack, 1954; Stearns, 1992). Within species, site fidelity of individuals to non-breeding locations is common across animal taxa (mammals: Bradshaw et al., 2004; reptiles: Broderick et al., 2007; birds: Phillips et al., 2005) and may evolve to increase familiarity with the resources available in the local environment (McNamara & Dall, 2010; Newton, 2008).

Animal non-breeding periods are comparatively less well studied than breeding periods (Bell et al., 2009), and this is especially the case in seabirds (Dunn et al., 2019). In seabirds, the non-breeding season is typically a period of migration with many species travelling large distances from the breeding grounds to reach non-breeding areas (Nelson, 2002). Although seabird species may vary in their migratory distance (Fort et al., 2013), they often follow consistent routes, possibly reflecting environmental processes that concentrate prey (e.g., oceanic upwellings; Fort et al., 2012). Studying seabird migration is challenging due to the large distances involved (e.g., across oceanic basins; Webster & Marra, 2005) but technological advancements, such as the reduction in size of tracking devices, have reduced the reliance on visual observations of identification bands (Franklin et al., 2022a), thereby facilitating the study of migratory patterns without the biases associated with coastal resights (Fort et al., 2012).

There is increasing evidence that many seabird species exhibit consistent individual differences in migratory behaviour (e.g., location, timing; Biagiotti Barchiesi et al., 2023; Ceia & Ramos, 2015; Franklin et al., 2022b; Phillips et al., 2017). These individual differences in behaviour can be related to factors such as sex, age or physiology (Araújo et al., 2011). Indeed, differences in migratory distance or location within a species, known as 'differential migration', are known to result from different age groups or sexes segregating in time or space, possibly to reduce competition or facilitate earlier arrival to the breeding colony (Cristol et al., 1999). Individual differences, however, persist within sexes and age classes (Bolnick et al., 2003; Carneiro et al., 2017) and may be linked to animal personality (Wolf & Weissing, 2012). Animal personality is defined as consistent variation among individuals that persists both temporally and across contexts (Stamps & Groothuis, 2010). Five main personality traits are regularly studied (Réale et al., 2007), each with a wide range of potential behaviours that vary along continuums (e.g., docile – aggressive, shy – bold). Individual traits can correlate with others to form behavioural syndromes (e.g., boldness and aggression, Réale et al., 2009) and have been linked to exploratory and foraging behaviour (Wolf & Weissing, 2012). In general, bolder individuals typically take more risks (Montiglio et al., 2018) and are more repeatable in their behaviour (i.e., specialists) compared to shyer individuals (i.e., generalists; Gibelli & Dubois, 2017). Therefore, personality can both influence and place limitations on individual behaviours (Dall et al., 2004; Mathot et al., 2012), such as migration (Gatt et al., 2021).

Consistent individual differences in seabird behaviour during breeding (e.g., foraging distance and location) have been related to personality (Harris et al., 2020; Krüger et al., 2019; Pereira et al., 2024). Indeed, shyer individuals have been shown to forage further from the breeding colony, potentially in a less competitive environment (Harris et al., 2020; Kruger et al., 2019; Patrick & Weimerskirch, 2017). Few studies, however, have linked personality and non-breeding behaviours, including migration distance and location. This may stem from few studies intentionally collecting repeat migration tracks, resulting in low sample sizes (Franklin et al., 2022a; McFarlane Tranquilla et al., 2014). As personality influences seabird movement in the breeding season (e.g., Harris et al., 2020), it is also a possible driver of migration differences within species due to the relationships between traits such as boldness and exploration (Merrick & Koprowski, 2017). Indeed, Gatt et al. (2021) found that bolder Cory's shearwater (*Calonectris borealis*) were migrants compared to shyer birds which were year-round residents near the breeding colony. Although personality was not investigated in the other seabird studies that showed high within-individual consistency, consistent differences in migratory behaviour across individuals (e.g., Anderson et al., 2020) suggest underlying personality differences may be responsible.

In addition to migratory consistency in seabirds, individual consistency has also been observed in behaviours related to foraging such as dive depth, prey type or trophic level (Phillips et al., 2017). Like animal tracking, there have also been advancements in techniques available to study consistency in metrics related to diet (e.g., stable isotope analysis; Kernaléguen et al., 2015). In marine systems, stable isotope ratios in consumer tissues reflect those in their prey with some modification (Phillips et al., 2009) and stable isotope analysis (SIA) is now increasingly used to investigate consistency in trophic level or foraging habitat (Carneiro et al., 2017). In particular, nitrogen stable isotope ratios are related to differences in trophic level, with higher nitrogen stable isotope ratios ($\delta^{15}N$) indicating feeding at a higher trophic level (Bearhop et al., 2000). As different tissues integrate stable isotope ratios from diet over varying timescales (Bearhop et al., 2002), each tissue type reflects diet from a different period of the annual cycle. For example, feathers reflect diet when the feather is grown as keratin is inert once synthesised (Ceia & Ramos, 2015). Therefore, the similarity in stable isotope ratios from the same tissue type that are formed during different periods (e.g., feathers) can be used as a proxy of individual dietary consistency (Wakefield et al., 2015). It is important to note, however, that because stable isotope ratios vary spatially and temporally (Moreno et al., 2016), these baseline shifts must be accounted for (Araújo et al., 2011).

Razorbills (*Alca torda*) are a member of the Family Alcidae (hereafter 'alcids') and are found across the North Atlantic (Lavers et al., 2020). Alcids are characterized by a stout body and high body mass to wing ratio which facilitates wing-propelled pursuit diving but results in a high energetic cost of flight relative to other bird species (Elliott et al., 2013). Like other alcids, razorbills are long-lived (up to 40 yr), take several years to reach sexual maturity (4-5 yr), have limited physiological differences among mature individuals and lack outward age- or sex-related characteristics (Lavers et al., 2020). Both sexes share parental care during chick rearing but once chicks fledge at ~30% of adult body mass, the male cares for the single chick at sea for 1-2 months (Gaston & Jones, 1998). Razorbills spend the non-breeding period (September to April) at sea, during which they moult (Lavers et al., 2020). Different feather types moult at different times of the year (flight feathers: autumn; contour feathers: autumn/winter/spring; Glew et al., 2019; Lavers et al., 2020), and they are flightless whilst replacing primary and secondary flight feathers (Dunn et al., 2020). Consistent individual differences in migration were reported in three closely related alcid species: Atlantic puffin (*Fratercula arctica*; Guilford et al., 2011), common murre

(*Uria aalge*) and thick-billed murre (*Uria lomvia*; McFarlane Tranquilla et al., 2014). Personality was also recently identified in razorbills (aggressive-docile continuum, hereafter 'docility'; Legard and Davoren, 2025; Chapter 1), therefore, razorbills may be a good model species to investigate links between personality and migratory behaviour.

The first objective of this study was to investigate individual behavioural consistency in razorbills during the non-breeding season. The second objective was to determine whether behaviours (i.e., migration location and distance, foraging dive depth, trophic level) are influenced by personality. To do this, assessments of personality (observer ratings; 2021-2023) along the docile-aggressive continuum were performed on chick-rearing razorbills on the northeast coast of Newfoundland, Canada, and non-breeding migration and dive depth (bird-borne devices; 2017-2018, 2019-2024) were combined with stable isotope ratios of nitrogen from three different feather types (2017, 2019-2024) representing different parts of the non-breeding season. We hypothesized that razorbills exhibit consistent individual behaviour, and that this behaviour is related to docility. We predicted that razorbills would have higher between-individual relative to within-individual variation (i.e., high repeatability) for all observed behaviours. Due to correlations among aggression, boldness and exploration (Sih et al., 2004), we predicted that aggressive individuals will migrate greater distances from the breeding colony and be more consistent in use of non-breeding locations than docile individuals. Additionally, due to the possible competitive advantage of bolder individuals, we predicted aggressive individuals would forage at a higher trophic level. This study is the first to investigate the relationships between individual consistency in behaviour during the non-breeding season combined with personality in a species from the family Alcidae and among the first in seabirds in general.

Methods

We captured chick-rearing razorbills for tag deployment/retrieval during July-August 2017, 2019-2024 on James Island on the northeast coast of Newfoundland, Canada (Figure 1), home to ~2,750 breeding pairs (Environment and Climate Change Canada unpublished data). Between 2021 and 2023, all razorbills captured for tag deployment/retrieval, including birds tagged in previous years (2017, 2019, 2020), underwent personality assessments, following Legard and Davoren (2025; Chapter 1). In brief, observer ratings were conducted to assess personality along the docile-aggressive continuum by two or three observers, with each observer independently rating each bird on a scale from 1 to 5 during routine handling (e.g., tag deployment, feather sampling; see below) across a range of observable behaviours (e.g., biting, vocalising). Ratings were averaged across observers, and then across years, to create one docility-aggressive score for each individual. Ratings were consistent across years in individuals that were assessed in more than one year (Legard and Davoren, 2025; Chapter 1).

Data and Sample Collection

Archival, light-weight Global Location Sensor (GLS) tags, GLS-Time-Depth Recorder (TDR) tags or TDR tags were deployed on chick-rearing razorbills during 2017 and between 2019-2022 (Table 1). Four different tag types were used: Biotrack MK3006 (GLS), Migrate Technology Intigeo C330 (GLS), Lotek Lat1800 (TDR) and Lotek Lat2800 (GLS-TDR, see details in Table 1). All tag types were attached to a plastic band and deployed on the left tarsus of the bird. The tag and plastic band had a combined weight of 4.0 – 7.0 g, which is less than 1% of the body mass of adult razorbills captured at James Island (701 ± 52 g), when considering potential tag effects (Vandenabeele et al., 2012). Tags were retrieved during subsequent breeding seasons (2018, 2020-2024; retrieval rate = 51%, Table 1, Table 2). Tag deployments and retrievals took place at night (01:00 - 04:00) to minimise colony disturbance and nest abandonment.

All tags had immersion (wet/dry) and temperature sensors, while TDR tags also had pressure sensors (depth) and GLS also had light sensors. The four tag types recorded data at different intervals. Migrate Technology GLS tags (C330) recorded light (continuous scale, full daylight curve) every 5 min, a wet/dry value every 30 s (proportion of wet to dry recorded every 10 min), and temperature when the tag was wet continuously for 20 min (minimum, maximum and mean temperature recorded for every 8 h). GLS Biotrack tags (MK3006) recorded light (binary, yes/no light) every 10 min, a wet/dry value every 3 s (proportion of wet to dry recorded every 10 min), and temperature when the tag was wet continuously for 20 min, 40 min, and 4 h. Lotek TDR (Lat1800) tags recorded pressure, immersion and temperature every 6 s (5 retrieved tags) or 10 s (2 retrieved tags), while Lotek GLS-TDR tags (Lat2800) recorded all parameters every 10 s (light: continuous scale, full daylight curve). Due to varying recordings intervals and memory, battery life varied among tag types, but all recorded at least one full non-breeding period.

Three feather types were collected from each razorbill (head, belly, secondaries) upon tag deployment and retrieval (Table 2). Three to five head and belly feathers were plucked by hand and the tip (~ 2 cm^2) of the first secondary feather was collected for stable isotope analysis (SIA).

Data and Sample Processing

Daily location estimates

To calibrate the GLS tags, we followed Runnells et al. (2024). In brief, a small number (n=10) of previously deployed C330 tags were attached to plastic common murre decoys and placed in the ocean close to James Island for 3-7 d. Solar angles were calculated using the GeoLight package (Lisovski & Hahn, 2013), generating values ranging from -2.98° to -5.63° (-4.54° ± 0.82°).

The departure/arrival dates from/to the colony for each tagged bird were estimated and used to subset the raw light data to the non-breeding period. For GLS (Migrate Technology) and GLS-TDR (Lotek) tags, the arrival date was defined as the first day with lower light levels (i.e., below a set threshold) during daylight hours, indicating that the bird was in the shaded rock crevice (i.e., had begun nesting). The departure date was similarly defined as the last day in the autumn with lower light levels during the day. This was not possible for GLS (Biotrack) tags as light data were collected in a binary fashion (yes/no light). Therefore, immersion data were used to estimate arrival/departure dates for these tags, where the first and last days where the tag was continuously dry for 6 hours was used to indicate presence on the breeding colony.

Geolocator data processing followed frequently used methods (e.g., Runnells et al., 2024). Twilights (sunrise and sunset) were determined from raw light data using the *preprocesslight* function from the package *TWGeos* (Lisovski et al., 2016). An additional preliminary step was required prior to this for GLS-TDR (Lotek) tags as these tags did not automatically adjust for time drift throughout the deployment period (see Supplementary Materials). Different light thresholds were required for each tag type as they measured light on different scales (see Supplementary

Material). Processed twilight data were then used to estimate movement tracks using the R package *probGLS* (Merkel, 2021) that produces two location estimates per day, one for each twilight event (sunrise and sunset; see details in Merkel et al., 2016). In brief, this process involved generating 2000 possible locations for each twilight event based on the timing of the estimated twilights, the potential uncertainty around these times and a random solar angle from the input range (-3° to -6°). Each of these 2000 locations was then weighted based on sea surface temperature (SST) and sea ice cover, along with razorbill flight speeds. Specifically, location estimates were constrained by satellite-derived SST and ice cover data (downloaded from the National Oceanic and Atmospheric Administration; NOAA). Locations with an SST > 2°C from the tag-recorded temperature or with 100% ice cover were considered unreasonable. This difference of 2°C for SST was selected following preliminary exploration of movement tracks, where a difference of 3°C produced tracks with unreasonable distances between consecutive twilight events (>1500 km). Flight speeds of razorbills were estimated following (Buckingham et al., 2022), which was informed by flight speeds of several bird species (Pennycuick, 1987) and further constrained by a study on razorbills (Thaxter et al., 2010). The algorithm then used a biased random walk with forward particle sampling to randomly select one location for each twilight event based on assigned weights, repeating the process from one twilight event to the next and generating one movement track for the tag deployment. This step was repeated to get 100 movement tracks for each tag deployment and the geographic median track was output as the final movement track. For full details on preliminary steps leading up to the use of *probGLS*, and the required input parameters, see Supplementary Material (Table S1).

Dive behaviour

Foraging dive characteristics (i.e., dive depth, duration) were quantified from TDRs using the R package *diveMove* (Luque, 2007). Foraging dives were defined as dives >1.5 m (Lescure et al., 2023). Because of the large number of dives recorded per tag (69337 ± 16673), dives were subsampled for each individual by constraining to only include the non-breeding period (October 1 to March 31) and then calculating the mean daily dive depth during this this period. This resulted in ~180 data points per individual. Dive duration was not included in analyses because dive duration and depth were highly correlated (N = 1594733, r2 = 0.660, p = < 0.001).

Feather stable isotope analysis

Feathers were washed twice in 0.25 M Sodium Hydroxide (NaOH) solution to remove dirt (Bearhop et al., 2002), rinsed in deionized water twice and then dried. All samples were then shipped to the Chemical Tracers Lab (University of Windsor, ONT, Canada) where stable isotope ratios of nitrogen ($\delta^{15}N$) were quantified using an Elemental Analyzer – Isotope Ratio Mass Spectrometer (Thermo Delta V). For full details on this process, see Carvalho et al. (2022) and Runnells et al. (2024). The nitrogen stable isotope ratios of feathers are reported in standard δ notation (units: parts per mil, ‰) relative to ratios of the universal standard (atmospheric N_2; Bond & Jones 2009). Instrument accuracy, based on certified values of USGS 40 (n = 60) analysed throughout runs, showed a difference from the certified value of 0.08‰ for $\delta^{15}N$. Precision was determined as ≤0.48‰ for $\delta^{15}N$ using the standard deviation of repeat analyses of 4 standards: USGS 40, NIST1577c, tilapia muscle and urea (all n = 60).

Data Analysis

All data processing and statistical analysis were carried out in R version 4.3.0 (R Core Team, 2023). During analyses, model assumptions were confirmed in all cases following protocols outlined in Zuur & Ieno (2016).

Non-breeding spatial consistency within and among individuals was quantified as Earth Mover's Distance (EMD) values using the *emd* function in the R package *move* (Kranstauber et al., 2021). This metric provides a dissimilarity value of the average distance between two spatial distributions (km) even when they do not overlap (Franklin et al., 2022b; Kranstauber et al., 2017). EMD values are continuous, where two identical distributions have a value of zero and values increase as the difference between distributions increases (Franklin et al., 2022b). The Haversine function was applied to account for distributions that stretch over large distances (spherical surface of the Earth) and geographical coordinates were used as the input (Franklin et al., 2022b; Kranstauber et al., 2017). EMD values were calculated for all possible between-individual and within-individual migration track combinations, based on one daily location estimate (morning twilight). To compare the level of within-individual consistency to between-individual differences of all tagged birds, individuals with movement tracks but had not been personality tested were also included (n=4).

The maximum dispersal distance from the colony for each individual's track was quantified as the distance between the breeding colony and the maximum north and south latitudes (± 200 km due to known GLS error, Merkel et al., 2016). Distance was calculated based on latitude as this was the main direction travelled by razorbills during non-breeding, with minimal movement east into the Atlantic Ocean and west due to land (Runnells et al., 2024).

To quantify consistency in space use, we compared the within- versus between-individual EMD values (response variable) using a general linear model (GLM). If within individual EMD values were significantly lower than between individuals, this indicated greater spatial similarity within individuals than among individuals (i.e. higher individual consistency). As the EMD values were non-negative, continuous and normally distributed, a gaussian error family and identity link was used. To compare within- and between-individual differences, the predict function was used to generate a predicted value and 95% confidence intervals for each from the output of the GLM. An additional generalised linear mixed model (GLMM) was also used to determine the influence of personality (i.e., docility score) and sex on within-individual EMD values, a proxy of spatial consistency. Individual was included as a random factor and the model was run with a gaussian distribution and identity as the link function.

To quantify the consistency of non-spatial behavioural metrics and assess the influence of personality on behaviour, adjusted repeatability was calculated using GLMMs. The maximum distance travelled north and south, average daily dive depth and $\delta^{15}N$ values were the response variables. These GLMMs were completed using the *rpt* function in the *rptR* package (Stoffel et al., 2017). Repeatability (*R*) is calculated by dividing the variance among individuals by the sum of the variance among individuals and the residual within-individual variance (Bell et al., 2009), where *R* varies between 0 (low) and 1 (high). Adjusted repeatability allows fixed factors to be included in the analysis (Biro & Stamps, 2015) and is, therefore, recommended as it is important that biologically relevant factors that explain between individual differences are incorporated

(Carneiro et al., 2017). The fixed factors included in analyses of distances travelled north/south and $\delta^{15}N$ were personality (i.e., docility score), sex and year (defined as distinct non-breeding periods) and were personality (i.e., docility score), sex and month for average dive depth. Month was included in this analysis as data exploration showed variable average dive depth across months during the non-breeding period (Figure S1). Additionally, feather type was included as a fixed factor for the repeatability analysis of $\delta^{15}N$ values, as data exploration also showed variation in $\delta^{15}N$ among feather types (Figure S2). All analyses were completed with a Gaussian distribution and parametric bootstrapping (n=1000) was used in all models to quantify 95% confidence intervals.

Ethical Note

This research was conducted under a Canadian Master Banding Permit (10873) and in agreement with the Canadian Council for Animal Care (Protocols F16-017, F20-017). All attempts were made to minimise animal use, limit the handling duration for each individual (15 min 8 sec ± 4 min 35 sec), and avoid disturbance to the seabird colony. Additionally, the individuals used were part of a long-term study population where multiple converging scientific objectives were achieved from all research (e.g., Runnells et al., 2024).

Results

GLS tagged razorbills from James Island (Table 1) spent the non-breeding period on the east coasts of Canada and the USA and particularly spent time in the Labrador Sea, Gulf of St Lawrence and the Gulf of Maine (Figure 1). During the non-breeding period, TDR tagged razorbills (Table 1) had an average dive depth of 14.6 ± 9.3 m.

When examining spatial consistency across non-breeding periods, within-individual EMD values (324 ± 134 km) were significantly lower than between-individual values (408 ± 202 km; df = 990, t = -3.695, *p* = <0.001; Figure 2, Figure 3), showing that razorbills consistently used similar areas across consecutive non-breeding periods. Within-individual EMD values, a proxy of spatial consistency, however, did not vary with personality along the docile-aggressive continuum (df = 8.7, F = 0.552, *p* = 0.477) or between sexes (df = 10.7, F = 0.489, *p* = 0.626). Additionally, there was no relationship between individual consistency and the number of years between two tracked migrations (the number of years between two tracks from the same individual was up to 5 years; N = 19, r^2 = 0.368, *p* = 0.121).

Razorbills were significantly repeatable in the maximum distance they travelled north (970 ± 582 km) and south (1187 ± 299 km) from the breeding colony (Table 3). While there was no effect of year on the distance travelled north or south, and sex on the distance travelled south, there was a significant effect of sex on the distance travelled north, with females (1186 ± 482 km) travelling farther north than males (597 ± 381 km; Table 3, Figure S3). Personality did not influence either the distance travelled north or south (Table 3).

There was also low but significant repeatability in daily average dive depths (12.2 ± 7.6, min = 1.8 max = 39.1 m) of razorbills (Figure 4, Table 3). Personality and sex did not influence daily average dive depth (Table 3). Daily average dive depth was significantly affected by month throughout the non-breeding season (Table 3), with shallower dives in midwinter (11.0 ± 7.0 m; November, December, January) compared to the months following and prior to the breeding season (13.9 ± 7.1 m; October, February, March; Figure S1).

Similar to dive depth, $\delta^{15}N$ values from feather samples had low but significant repeatability across all birds (Figure 5). While there was no effect of personality or sex on $\delta^{15}N$ values, values varied significantly across feather types (Table 3), with significantly lower $\delta^{15}N$ values in head feathers compared to belly and secondary feathers (Figure S2).

Discussion

In line with our prediction, our results show that individual razorbills are consistent in their behaviour during the non-breeding season. Consistency within individuals is shown by the spatial consistency of overwintering locations and the repeatability in average daily dive depth, $\delta^{15}N$ values and the distances travelled north and south from the breeding colony. Overall, these results align with studies showing consistency in seabird behaviour (Biagiotti Barchiesi et al., 2023; Ceia & Ramos, 2015; Phillips et al., 2017) and relate closely to a study showing razorbills can be consistent in their behaviour during the breeding season (Legard et al. in press; Chapter 2). In contrast to our prediction, however, we did not find relationships between any non-breeding behaviours and docility. These results contrast with the one study showing relationships between personality and seabird migratory behaviour during the non-breeding season in Cory's shearwater (Gatt et al., 2021).

Personality

Although personality in seabirds has been linked with reproductive success, foraging behaviour and distribution (Collins et al., 2019; Gatt et al., 2021; Harris et al., 2020; Krüger et al., 2019; Patrick & Weimerskirch, 2014), we found no relationship between docility and any of the observed non-breeding behaviours in this study. Indeed, the only behaviour that was influenced by an intrinsic factor (i.e., sex) was the distance travelled north, while there was no influence of sex or docility for all other behaviours investigated. This suggests that the small but consistent differences in migratory location and foraging behaviour (e.g., dive depth and trophic level) in razorbills are related to other unmeasured factors (e.g., age, physiology). Indeed, foraging behaviour and efficiency may vary among age classes within species (Phillips et al., 2017) and physiological differences may impact foraging technique or ability (Bolnick et al., 2003). It is also possible that personality influenced behaviours not investigated here (e.g., migratory timing, frequency of breeding attempts). Interestingly, relationships were also not found between personality and foraging behaviours during the breeding season in razorbills, with a greater effect of local forage fish prey availability than any other factor (Legard et al. in press; Chapter 2).

Individual Consistency

Razorbills displayed high levels of spatial consistency in their overwintering migrations and high repeatability in the distance travelled north and south from the breeding colony. These findings match numerous studies that have found high levels of site fidelity in migratory location in seabirds (e.g., Delord et al., 2019; Grist et al., 2014; Ramírez et al., 2016). Seabird site fidelity likely results from knowledge gained prior to maturity (Guilford et al., 2011; Péron & Grémillet, 2013). For instance, individuals may learn predictable prey locations, with oceanographic features (e.g., ocean fronts, shelf and ice edges, coastal upwellings) and seasonal temperature and salinity gradients resulting in predictable prey on multiple temporal and spatial scales (Phillips et al., 2017; Wakefield et al., 2009). In support, it is common to find greater consistency in species that are found in areas with higher resource predictability (Phillips et al., 2005). Abundant prey are known to occur at locations razorbills consistently returned to during non-breeding. For example, high prey densities can be found in the Labrador Sea during the autumn (Figure 1: A; Davoren et al., 2002). Additionally, sand lance (*Ammodytes* spp.), a highly profitable prey type for seabirds, are found in the Gulf of Maine during the winter (Figure 1: B; Staudinger et al., 2020), where they are also known to be major dietary component for razorbills, common murre and Atlantic puffins during the summer (Scopel et al., 2019). Individual consistency might be higher in alcids relative to other seabirds as they are flightless during flight feather moult (Lavers et al., 2020), therefore, constraining movement within specific profitable moulting areas (Frederiksen et al., 2012). In support, the consistent use of non-breeding locations has been reported for other alcid species (e.g., common and thick-billed murre; McFarlane Tranquilla et al., 2014). Although individuals may be less consistent if individuals are tracked over longer periods due to changing prey availability over time (Berthold et al., 2004; Carneiro et al., 2017), individual consistency of razorbills were similarly high across two or three tracked migrations and when tracked migrations were not across consecutive non-breeding periods (e.g., up to five years apart). As this study used GLS tags that have relatively high spatial inaccuracy (± 150 km Halpin et al., 2021; Lisovski et al., 2020); compared to other tag types (e.g., global positioning system tags; GPS), the level of spatial consistency may be underestimated (Franklin et al., 2022a). For example, a bird overwintering in the same location in two successive years may be estimated to be up to 300 km apart in any direction due to the error associated with GLS location estimates, while this error would be significantly lower for GPS tags (< 50 m).

Along with the high repeatability in distances travelled north and south, females travelled further north than males. Northward travel occurred immediately following the breeding season and, thus, may be related to males being unable to travel large distances while they care for their flightless chick (Gaston & Jones, 1998). By contrast, most females moved north into the Labrador Sea, a known profitable prey area (Davoren et al., 2002), possibly to replenish energy expended during the breeding period. This resulted in temporary differential migration, but there was no spatial segregation between the sexes following this period. Sexual segregation during migration, including in monomorphic species (e.g., sooty shearwater; *Puffinus griseus*; Hedd et al., 2014), is widespread in seabirds and occurs over a wide range of spatial and temporal scales (Catry et al., 2005). Differential migration can result from the availability of multiple profitable wintering areas or divergent mobility constraints, as was likely the case for male razorbills in this study. This differential migration may have the added benefit of reducing intra-specific competition through niche partitioning of the sexes (Miller et al., 2018; Oppel et al., 2015; Phillips et al., 2004), benefiting chick growth and survival rates in razorbills.

Razorbills also exhibited low but significant repeatability in both average daily dive depth (R = 0.108) and trophic level ($\delta^{15}N$; R = 0.128). These results are suggestive of consistent differences among individuals in diet and foraging behaviour (i.e., individual specialisation), which have been observed in 80% of tested seabird species, across many taxa including alcids (Ceia & Ramos, 2015). Indeed, many studies using stomach content and stable isotope analyses have shown consistent individual differences in habitat use, prey type, or trophic level (Phillips et al., 2017). Specialisation is predicted to provide a selective advantage due to increased foraging efficiency from higher proficiency at locating and handling certain prey types (Phillips et al., 2017; Rebstock et al., 2022; Van Den Bosch et al., 2019; Weimerskirch, 2007). Although the location of foraging dives was not known and bathymetry may constrain dive depth in shallower areas, consistent dive depth may also represent habitat-related foraging preferences.

There were temporal factors that influenced within-individual differences in dive depth (i.e., month; Figure S1) and trophic level (i.e., feather type; Figure S2) throughout the non-breeding period. Importantly, the significant repeatability in these response variables shows that individual differences remained consistent throughout the non-breeding period despite this variation, which we accounted for by incorporating temporal fixed factors when calculating adjusted repeatability. Within-individual variation is expected, as individual foraging consistency can vary over time (e.g., across years; Ceia et al., 2014; within years; Harris et al., 2013) and some specialisations are relatively short lived (Wakefield et al., 2015). Additionally, repeatability of foraging behaviour likely declines over longer timescales due to changes in prey availability (Woo et al., 2008). The reduction in average daily dive depth during the winter months (Figure S1) may be explained by lower light levels in the winter resulting in lower light penetration into the water column. Similarly, changes in $\delta^{15}N$ values may be explained as stable isotope ratios change spatially due to a variety of factors (depth, nutrient source, primary productivity; Moreno et al., 2016). Given the large distances travelled by razorbills, spatial and temporal baseline shifts can confound direct comparisons of the trophic level of tissues grown in different regions at different times if not corrected (Araújo et al., 2011; Moreno et al., 2016).

Conclusion

Overall, razorbills exhibit both spatial and foraging behavioural consistency during the non-breeding season. Understanding this between-individual variation is important as some subsets of populations may be more vulnerable to environmental change than others (Dingemanse & Wolf, 2013). As razorbills occupy different non-breeding locations with potentially varying environmental characteristics, negative effects on survival or reproductive success in the following breeding season may occur only in part of a population (Baak et al., 2021; Jeffries et al., 2021; Wolf & Weissing, 2012). Alternatively, within-species spatial segregation, along with differences in diet and foraging behaviour, may reduce intraspecific competition and result in higher reproductive success for the entire population (Barger et al., 2016; de Grissac et al., 2016; Linnebjerg et al., 2013; Phillips et al., 2017; Shoji et al., 2015; Wakefield et al., 2015). This segregation may also increase the resilience of a species to anthropogenic risks by limiting the impact of a localised threat (Clavel et al., 2011). For example, specific localised threats to razorbills include the regulated harvest of murres in coastal Newfoundland (Newfoundland turr hunt; Montevecchi et al., 2007), during which razorbills can be misidentified as murres (Lavers et al., 2009), and the vulnerability to oil spills in the Gulf of Maine due to the high density of oil related shipping in the area. Overall, understanding population and individual level differences can be beneficial for conservation (Baak et al., 2021), such as informing the locations of marine protected areas (Davies et al., 2021; Hanson et al., 2020; Hindell et al., 2020) that can contribute to the persistence of species (Beal et al., 2023). Finally, although relationships between personality and behaviour were not observed in this study, investigating personality traits alongside individual consistency can be another tool to help design conservation strategies that protect larger proportions of populations (MacKinlay & Shaw, 2023).

References

Anderson, C. M., Gilchrist, H. G., Ronconi, R. A., Shlepr, K. R., Clark, D. E., Fifield, D. A., Robertson, G. J., & Mallory, M. L. (2020). Both short and long-distance migrants use energy-minimizing migration strategies in North American herring gulls. *Mov. Ecol.*, 8(1). https://doi.org/10.1186/s40462-020-00207-9

Araújo, M. S., Bolnick, D. I., & Layman, C. A. (2011). The ecological causes of individual specialisation. *Ecol. Lett.*, 14(9), 948–958. https://doi.org/10.1111/j.1461-0248.2011.01662.x

Baak, J. E., Patterson, A., Grant Gilchrist, H., & Elliott, K. H. (2021). First evidence of diverging migration and overwintering strategies in glaucous gulls (*Larus hyperboreus*) from the Canadian Arctic. *Anim. Migr.*, 8(1), 98–109. https://doi.org/10.1515/ami-2020-0107

Barger, C. P., Young, R. C., Will, A., Ito, M., & Kitaysky, A. S. (2016). Resource Partitioning between sympatric seabird species increases during chick-rearing. *Ecosphere*, 7(9), 1–15. https://doi.org/10.1002/ecs2.1447

Beal, M., Catry, P., Phillips, R. A., Oppel, S., Arnould, J. P. Y., Bogdanova, M. I., Bolton, M., Carneiro, A. P. B., Clatterbuck, C., Conners, M., Daunt, F., Delord, K., Elliott, K., Fromant, A., Granadeiro, J. P., Green, J. A., Halsey, L., Hamer, K. C., Ito, M., … Dias, M. P. (2023). Quantifying annual spatial consistency in chick-rearing seabirds to inform important site identification. *Biol. Conserv.*, 281, 1–14. https://doi.org/10.1016/j.biocon.2023.109994

Bearhop, S., Teece, M. A., Waldron, S., & Furness, R. W. (2000). Influence of lipid and uric Acid on δ^{13}C and δ^{15}N values of avian blood: implications for trophic studies. *Auk*, 117(2), 504–507. https://doi.org/10.2307/4089734

Bearhop, S., Waldron, S., Votier, S. C., & Furness, R. W. (2002). Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. *Physiol. Biochem. Zool.*, 75(5), 451–458. https://doi.org/10.1086/342800

Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: a meta-analysis. *Anim. Behav.*, 77(4), 771–783. https://doi.org/10.1016/j.anbehav.2008.12.022

Berthold, P., Kaatz, M., & Querner, U. (2004). Long-term satellite tracking of white stork (*Ciconia ciconia*) migration: constancy versus variability. *J. Ornithol.*, 145(4), 356–359. https://doi.org/10.1007/s10336-004-0049-2

Biro, P. A., & Stamps, J. A. (2015). Using repeatability to study physiological and behavioural traits: Ignore time-related change at your peril. *Anim. Behav.*, 105, 223–230. https://doi.org/10.1016/j.anbehav.2015.04.008

Bolnick, D. I., Svanbäck, J., Fordyce, L., Yang, J., Davis, D., & Darrin, C. (2003). The ecology of individuals: incidence and implications of individual specialization. *Am. Nat.*, 161(1), 1–30. https://doi.org/10.1086/343878

Bradshaw, C. J. A., Hindell, M. A., Sumner, M. D., & Michael, K. J. (2004). Loyalty pays: potential life history consequences of fidelity to marine foraging regions by southern elephant seals. *Anim. Behav.*, 68(6), 1349–1360. https://doi.org/10.1016/j.anbehav.2003.12.013

Broderick, A. C., Coyne, M. S., Fuller, W. J., Glen, F., & Godley, B. J. (2007). Fidelity and over-wintering of sea turtles. *Proc. R. Soc. B.*, 274(1617), 1533–1539. https://doi.org/10.1098/rspb.2007.0211

Buckingham, L., Bogdanova, M., Green, J., Dunn, R., Wanless, S., Bennett, S., Bevan, R., Call, A., Canham, M., Corse, C., Harris, M., Heward, C., Jardine, D., Lennon, J., Parnaby, D., Redfern, C., Scott, L., Swann, R., Ward, R., … Daunt, F. (2022). Interspecific variation in non-breeding aggregation: a multi-colony tracking study of two sympatric seabirds. *Mar. Ecol. Prog. Ser.*, 684, 181–197. https://doi.org/10.3354/meps13960

Biagiotti Barchiesi, M., Biondi, L. M., & García, G. O. (2023). A systematic review of trends in research on seabird behavioral flexibility. *Mar. Ornithol.*, 51, 293–300. http://doi.org/10.5038/2074-1235.51.2.1546

Carneiro, A. P. B., Bonnet-Lebrun, A. S., Manica, A., Staniland, I. J., & Phillips, R. A. (2017). Methods for detecting and quantifying individual specialisation in movement and foraging strategies of marine predators. *Mar. Ecol. Prog. Ser.*, 578, 151–166. https://doi.org/10.3354/meps12215

Carvalho, P. C., Ronconi, R. A., Bugoni, L., & Davoren, G. K. (2022). Moult chronology and strategies of sympatric Great (*Ardenna gravis*) and Sooty (*A. grisea*) Shearwaters based on stable isotope analysis. *Ibis*, 164(4), 998–1012. https://doi.org/10.1111/ibi.13060

Catry, P., Phillips, R. A., & Croxall, J. P. (2005). Sexual segregation in birds: patterns, processes and implications for conservation. In K. E. Ruckstuhl & P. Neuhaus (Eds.), Sexual Segregation in Vertebrates: Ecology of the Two Sexes (pp. 351–387). Cambridge University Press.

Ceia, F. R., Paiva, V. H., Garthe, S., Marques, J. C., & Ramos, J. A. (2014). Can variations in the spatial distribution at sea and isotopic niche width be associated with consistency in the isotopic niche of a pelagic seabird species? *Mar. Biol.*, 161(8), 1861–1872. https://doi.org/10.1007/s00227-014-2468-9

Ceia, F. R., & Ramos, J. A. (2015). Individual specialization in the foraging and feeding strategies of seabirds: a review. *Mar. Biol.*, 162(10), 1923–1938. https://doi.org/10.1007/s00227-015-2735-4

Clavel, J., Julliard, R., & Devictor, V. (2011). Worldwide decline of specialist species: toward a global functional homogenization? *Front. Ecol. Environ.*, 9(4), 222–228. https://doi.org/10.1890/080216

Collins, S. M., Hatch, S. A., Elliott, K. H., & Jacobs, S. R. (2019). Boldness, mate choice and reproductive success in *Rissa tridactyla*. *Anim. Behav.*, 154, 67–74. https://doi.org/10.1016/j.anbehav.2019.06.007

Cristol, D. A., Baker, M. B., & Carbone, C. (1999). Latitudinal segregation by age and sex class. In V. J. Nolan, E. D. Ketterson, & C. F. Thompson (Eds.), Current Ornithology (Vol. 15, pp. 33–88). Plenum Press.

Dall, S. R. X., Houston, A. I., & McNamara, J. M. (2004). The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecol. Lett.*, 7(8), 734–739. https://doi.org/10.1111/j.1461-0248.2004.00618.x

Davies, T. E., Carneiro, A. P. B., Tarzia, M., Wakefield, E., Hennicke, J. C., Frederiksen, M., Hansen, E. S., Campos, B., Hazin, C., Lascelles, B., Anker-Nilssen, T., Arnardóttir, H., Barrett, R. T., Biscoito, M., Bollache, L., Boulinier, T., Catry, P., Ceia, F. R., Chastel, O., … Dias, M. P. (2021). Multispecies tracking reveals a major seabird hotspot in the North Atlantic. *Conserv. Lett.*, 14(5), 1–14. https://doi.org/10.1111/conl.12824

Davoren, G. K., Montevecchi, W. A., & Anderson, J. T. (2002). Scale-dependent associations of predators and prey: constraints imposed by flightlessness of common murres. *Mar. Ecol. Prog. Ser.*, 245, 259–272. https://doi.org/10.3354/meps245259

de Grissac, S., Börger, L., Guitteaud, A., & Weimerskirch, H. (2016). Contrasting movement strategies among juvenile albatrosses and petrels. *Sci. Rep.*, 6, 1–12. https://doi.org/10.1038/srep26103

Delord, K., Barbraud, C., Pinaud, D., Ruault, S., Patrick, S. C., & Weimerskirch, H. (2019). Individual consistency in the non-breeding behaviour of a long-distance migrant seabird, the grey petrel *Procellaria cinerea*. *Mar. Ornithol.*, 47, 93–103. http://doi.org/10.5038/2074-1235.47.1.1298

Dingemanse, N. J., & Wolf, M. (2013). Between-individual differences in behavioural plasticity within populations: causes and consequences. *Anim. Behav.*, 85(5), 1031–1039. https://doi.org/10.1016/j.anbehav.2012.12.032

Dunn, R. E., Wanless, S., Daunt, F., Harris, M. P., & Green, J. A. (2020). A year in the life of a North Atlantic seabird: behavioural and energetic adjustments during the annual cycle. *Sci. Rep.*, 10(1), 1–11. https://doi.org/10.1038/s41598-020-62842-x

Dunn, R. E., Wanless, S., Green, J. A., Harris, M. P., & Daunt, F. (2019). Effects of body size, sex, parental care and moult strategies on auk diving behaviour outside the breeding season. *J. Avian Biol.*, 50(7), 1–14. https://doi.org/10.1111/jav.02012

Elliott, K. H., Ricklefs, R. E., Gaston, A. J., Hatch, S. A., Speakman, J. R., & Davoren, G. K. (2013). High flight costs, but low dive costs, in auks support the biomechanical hypothesis for flightlessness in penguins. *PNAS*, 110(23), 9380–9384. https://doi.org/10.1073/pnas.1304838110

Fort, J., Pettex, E., Tremblay, Y., Lorentsen, S.-H., Garthe, S., Votier, S., Pons, J. B., Siorat, F., Furness, R. W., Grecian, J., Bearhop, S., Montevecchi, W. A., & Grémillet, D. (2012). Meta-population evidence of oriented chain migration in northern gannets (*Morus bassanus*). *Front. Ecol. Environ.*, 10(5), 237–242. https://doi.org/10.1890/l

Fort, J., Steen, H., Strøm, H., Tremblay, Y., Grønningsæter, E., Pettex, E., Porter, W. P., & Grémillet, D. (2013). Energetic consequences of contrasting winter migratory strategies in a sympatric Arctic seabird duet. *J. Avian Biol.*, 44(3), 255–262. https://doi.org/10.1111/j.1600-048X.2012.00128.x

Franklin, K. A., Norris, K., Gill, J. A., Ratcliffe, N., Bonnet-Lebrun, A.-S., Butler, S. J., Cole, N. C., Jones, C. G., Lisovski, S., Ruhomaun, K., Tatayah, V., & Nicoll, M. A. C. (2022a). Individual consistency in migration strategies of a tropical seabird, the Round Island petrel. *Mov. Ecol.*, 10, 1–14. https://doi.org/10.1186/s40462-022-00311-y

Franklin, K. A., Nicoll, M. A. C., Butler, S. J., Norris, K., Ratcliffe, N., Nakagawa, S., & Gill, J. A. (2022b). Individual repeatability of avian migration phenology: a systematic review and meta-analysis. *J. Anim. Ecol.*, 1–15. https://doi.org/10.1111/1365-2656.13697

Frederiksen, M., Moe, B., Daunt, F., Phillips, R. A., Barrett, R. T., Bogdanova, M. I., Boulinier, T., Chardine, J. W., Chastel, O., Chivers, L. S., Christensen-Dalsgaard, S., Clément-Chastel, C., Colhoun, K., Freeman, R., Gaston, A. J., González-Solís, J., Goutte, A., Grémillet, D., Guilford, T., … Anker-Nilssen, T. (2012). Multicolony tracking reveals the winter distribution of a pelagic seabird on an ocean basin scale. *Diversity Distrib.*, 18(6), 530–542. https://doi.org/10.1111/j.1472-4642.2011.00864.x

Gaston, A. J., & Jones, I. L. (1998). The auks: Alcidae. Oxford University Press.

Gatt, M. C., Granadeiro, J. P., & Catry, P. (2021). Migrants and residents of a long-lived seabird differ in their behavioural response to a stressor. *J. Avian Biol.*, 52(2), 1–8. https://doi.org/10.1111/jav.02589

Gibelli, J., & Dubois, F. (2017). Does personality affect the ability of individuals to track and respond to changing conditions? *Behav. Ecol.*, 28(1), 101–107. https://doi.org/10.1093/BEHECO/ARW137

Glew, K. S. J., Wanless, S., Harris, M. P., Daunt, F., Erikstad, K. E., Strøm, H., Speakman, J. R., Kürten, B., & Trueman, C. N. (2019). Sympatric Atlantic puffins and razorbills show contrasting responses to adverse marine conditions during winter foraging within the North Sea. *Mov. Ecol.*, 7(1), 1–14. https://doi.org/10.1186/s40462-019-0174-4

Grist, H., Daunt, F., Wanless, S., Nelson, E. J., Harris, M. P., Newell, M., Burthe, S., & Reid, J. M. (2014). Site fidelity and individual variation in winter location in partially migratory European shags. *PLoS ONE*, 9(6), 1–14. https://doi.org/10.1371/journal.pone.0098562

Guilford, T., Freeman, R., Boyle, D., Dean, B., Kirk, H., Phillips, R., & Perrins, C. (2011). A dispersive migration in the atlantic Puffin and its implications for migratory navigation. *PLoS ONE*, 6(7), 1–8. https://doi.org/10.1371/journal.pone.0021336

Halpin, L. R., Ross, J. D., Ramos, R., Mott, R., Carlile, N., Golding, N., Reyes-González, J. M., Militão, T., De Felipe, F., Zajková, Z., Cruz-Flores, M., Saldanha, S., Morera-Pujol, V., Navarro-Herrero, L., Zango, L., González-Solís, J., & Clarke, R. H. (2021). Double-tagging scores of seabirds reveals that light-level geolocator accuracy is limited by species idiosyncrasies and equatorial solar profiles. *Methods Ecol. Evol.*, 21(11), 2243–2255. https://doi/10.1111/2041-210X.13698

Hanson, J. O., Rhodes, J. R., Butchart, S. H. M., Buchanan, G. M., Rondinini, C., Ficetola, G. F., & Fuller, R. A. (2020). Global conservation of species' niches. *Nature*, 580(7802), 232–234. https://doi.org/10.1038/s41586-020-2138-7

Harris, S. M., Descamps, S., Sneddon, L. U., Bertrand, P., Chastel, O., & Patrick, S. C. (2020). Personality predicts foraging site fidelity and trip repeatability in a marine predator. *J. Anim. Ecol.*, 89(1), 68–79. https://doi.org/10.1111/1365-2656.13106

Harris, S., Raya Rey, A., Phillips, R. A., & Quintana, F. (2013). Sexual segregation in timing of foraging by imperial shags (*Phalacrocorax atriceps*): is it always ladies first? *Mar. Biol.*, 160(5), 1249–1258. https://doi.org/10.1007/s00227-013-2177-9

Hedd, A., Montevecchi, W. A., Phillips, R. A., & Fifield, D. A. (2014). Seasonal sexual segregation by monomorphic sooty shearwaters *Puffinus griseus* reflects different reproductive roles during the pre-laying period. *PLoS ONE*, 9(1), 1–11. https://doi.org/10.1371/journal.pone.0085572

Hindell, M. A., Reisinger, R. R., Ropert-Coudert, Y., Hückstädt, L. A., Trathan, P. N., Bornemann, H., Charrassin, J. B., Chown, S. L., Costa, D. P., Danis, B., Lea, M. A., Thompson, D., Torres, L. G., Van de Putte, A. P., Alderman, R., Andrews-Goff, V., Arthur, B., Ballard, G., Bengtson, J., … Raymond, B. (2020). Tracking of marine predators to protect Southern Ocean ecosystems. *Nature*, 580(7801), 87–92. https://doi.org/10.1038/s41586-020-2126-y

Jeffries, P. M., Patrick, S. C., & Potts, J. R. (2021). Be different to be better: the effect of personality on optimal foraging with incomplete knowledge. *Theor. Ecol.*, 1–13. https://doi.org/10.1007/s12080-021-00517-7

Kernaléguen, L., Cherel, Y., Knox, T. C., Baylis, A. M. M., & Arnould, J. P. Y. (2015). Sexual niche segregation and gender-specific individual specialisation in a highly dimorphic marine mammal. *PLoS ONE*, 10(8), 1–15. https://doi.org/10.1371/journal.pone.0133018

Kranstauber, B., Smolla, M., & Safi, K. (2017). Similarity in spatial utilization distributions measured by the earth mover’s distance. *Methods Ecol. Evol.*, 8(2), 155–160. https://doi.org/10.1111/2041-210X.12649

Kranstauber, B., Smolla, M., & Scharf, A. (2021). move: visualising and analysing animal track data (R package version 4.1.6.).

Krüger, L., Pereira, J. M., Paiva, V. H., & Ramos, J. A. (2019). Personality influences foraging of a seabird under contrasting environmental conditions. *JEMBE*, 516, 123–131. https://doi.org/10.1016/j.jembe.2019.04.003

Lack, D. (1954). The natural regulation of animal numbers. Clarendon Press.

Lavers, J. L., Hipfner, M., & Chapdelaine, G. (2020). Razorbill (*Alca torda*). In Billerman SM (Ed.), Birds of the World (1.0). Cornell Lab of Ornithology.

Lavers, J. L., Jones, I. L., Robertson, G. J., & Diamond, A. W. (2009). Contrasting population trends at two razorbill colonies in Atlantic Canada: additive effects of fox predation and hunting mortality? *Avian Conserv. Ecol.*, 4(2), 1–17. https://doi.org/10.5751/ACE-00322-040203

Legard, M. J., & Davoren, G. K. (2025). A non-invasive method during routine handling indicates docility in a wild, crevice-nesting seabird. *Behaviour*, 1–22. https://doi.org/10.1163/1568539X-bja10298

Lescure, L., Gulka, J., & Davoren, G. (2023). Increased foraging effort and reduced chick condition of razorbills under lower prey biomass in coastal Newfoundland, Canada. *Mar. Ecol. Prog. Ser.*, 709, 109–123. https://doi.org/10.3354/meps14286

Linnebjerg, J. F., Fort, J., Guilford, T., Reuleaux, A., Mosbech, A., & Frederiksen, M. (2013). Sympatric breeding auks shift between dietary and spatial resource partitioning across the annual cycle. *PLoS ONE*, 8(8), 1–10. https://doi.org/10.1371/journal.pone.0072987

Lisovski, S., Bauer, S., Briedis, M., Davidson, S. C., Dhanjal-Adams, K. L., Hallworth, M. T., Karagicheva, J., Meier, C. M., Merkel, B., Ouwehand, J., Pedersen, L., Rakhimberdiev, E., Roberto-Charron, A., Seavy, N. E., Sumner, M. D., Taylor, C. M., Wotherspoon, S. J., & Bridge, E. S. (2020). Light-level geolocator analyses: a user's guide. *J. Anim. Ecol.*, 89(1), 221–236. https://doi.org/10.1111/1365-2656.13036

Lisovski, S., & Hahn, S. (2013). GeoLight - processing and analysing light-based geolocation in R. *Methods Ecol. Evol.*, 3, 1055–1059. https://doi.org/10.1111/j.2041-210X.2012.00248.x

Lisovski, S., Wotherspoon, S., & Sumner, M. (2016). TWGeos: basic data processing for light-level geolocation archival tags (R package version 0.1.2.).

Luque, S. P. (2007). Diving behaviour analysis in R. *R News*, 7(3), 8–14.

MacKinlay, R. D., & Shaw, R. C. (2023). A systematic review of animal personality in conservation science. *Conserv. Biol.*, 37(1), 1–16. https://doi.org/10.1111/cobi.13935

Mathot, K. J., Wright, J., Kempenaers, B., & Dingemanse, N. J. (2012). Adaptive strategies for managing uncertainty may explain personality-related differences in behavioural plasticity. *Oikos*, 121(7), 1009–1020. https://doi.org/10.1111/j.1600-0706.2012.20339.x

McFarlane Tranquilla, L. A., Montevecchi, W. A., Fifield, D. A., Hedd, A., Gaston, A. J., Robertson, G. J., & Phillips, R. A. (2014). Individual winter movement strategies in two species of murre (*Uria* spp.) in the Northwest Atlantic. *PLoS ONE*, 9(4), 1–13. https://doi.org/10.1371/journal.pone.0090583

McNamara, J. M., & Dall, S. R. X. (2010). Information is a fitness enhancing resource. *Oikos*, 119(2), 231–236. https://doi.org/10.1111/j.1600-0706.2009.17509.x

Merkel, B. (2021). probGLS: probabilistic algorithm for geolocation data (R package version 0.9.5).

Merkel, B., Phillips, R. A., Descamps, S., Yoccoz, N. G., Moe, B., & Strøm, H. (2016). A probabilistic algorithm to process geolocation data. *Mov. Ecol.*, 4(1). https://doi.org/10.1186/s40462-016-0091-8

Merrick, M. J., & Koprowski, J. L. (2017). Should we consider individual behavior differences in applied wildlife conservation studies? *Biol. Conserv.*, 209, 34–44. https://doi.org/10.1016/j.biocon.2017.01.021

Miller, M. G. R., Silva, F. R. O., Machovsky-Capuska, G. E., & Congdon, B. C. (2018). Sexual segregation in tropical seabirds: drivers of sex-specific foraging in the brown booby *Sula leucogaster*. *J. Ornithol.*, 159(2), 425–437. https://doi.org/10.1007/s10336-017-1512-1

Montevecchi, W. A., Chaffey, H., & Burke, C. M. (2007). Hunting for security: changes in the exploitation of marine birds in Newfoundland and Labrador. In C. C. Parrish, N. J. Turner, & S. M. Solberg (Eds.), Resetting the Kitchen Table (pp. 99–116). Nova Science Publishers.

Montiglio, P.-O., Dammhahn, M., Dubuc Messier, G., & Réale, D. (2018). The pace-of-life syndrome revisited: the role of ecological conditions and natural history on the slow-fast continuum. *Behav. Ecol. Sociobiol.*, 72(7), 1–9. https://doi.org/10.1007/s00265-018-2526-2

Moreno, R., Stowasser, G., Mcgill, R. A. R., Bearhop, S., & Phillips, R. A. (2016). Assessing the structure and temporal dynamics of seabird communities: the challenge of capturing marine ecosystem complexity. *J. Anim. Ecol.*, 85(1), 199–212. https://doi.org/10.1111/1365-2656.12434

Nelson, J. B. (2002). The Atlantic Gannet (2nd ed.). Fennix Books.

Newton, I. (2008). The Migration Ecology of Birds. Academic Press.

Oppel, S., Beard, A., Fox, D., Mackley, E., Leat, E., Henry, L., Clingham, E., Fowler, N., Sim, J., Sommerfeld, J., Weber, N., Weber, S., & Bolton, M. (2015). Foraging distribution of a tropical seabird supports Ashmole’s hypothesis of population regulation. *Behav. Ecol. Sociobiol.*, 69(6), 915–926. https://doi.org/10.1007/s00265-015-1903-3

Patrick, S. C., & Weimerskirch, H. (2014). Personality, foraging and fitness consequences in a long lived seabird. *PLoS ONE*, 9(2), 1–11. https://doi.org/10.1371/journal.pone.0087269

Patrick, S. C., & Weimerskirch, H. (2017). Reproductive success is driven by local site fidelity despite stronger specialisation by individuals for large-scale habitat preference. *J. Anim. Ecol.*, 86(3), 674–682. https://doi.org/10.1111/1365-2656.12636

Pennycuick, C. J. (1987). Flight of Auks (Alcidae) and other northern seabirds compared with southern procellariiformes: ornithodolite observations. *JEB*, 128, 335–347. https://doi.org/10.1242/jeb.128.1.335

Pereira, J. M., Ramos, J. A., Ceia, F. R., Krüger, L., Marques, A. M., & Paiva, V. H. (2024). Boldness predicts foraging behaviour, habitat use and chick growth in a central place marine predator. *Oecologia*. https://doi.org/10.1007/s00442-024-05557-4

Péron, C., & Grémillet, D. (2013). Tracking through life stages: adult, immature and juvenile autumn migration in a long-lived seabird. *PLoS ONE*, 8(8), 1–14. https://doi.org/10.1371/journal.pone.0072713

Phillips, R. A., Bearhop, S., McGill, R. A. R., & Dawson, D. A. (2009). Stable isotopes reveal individual variation in migration strategies and habitat preferences in a suite of seabirds during the nonbreeding period. *Oecologia*, 160(4), 795–806. https://doi.org/10.1007/s00442-009-1342-9

Phillips, R. A., Lewis, S., González-Solís, J., & Daunt, F. (2017). Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds. *Mar. Ecol. Prog. Ser.*, 578, 117–150. https://doi.org/10.3354/meps12217

Phillips, R. A., Silk, J. R. D., Croxall, J. P., Afanasyev, V., & Bennett, V. J. (2005). Summer distribution and migration of nonbreeding albatrosses: individual consistencies and implications for conservation. *Ecology*, 86(9), 2386–2396.

Phillips, R. A., Silk, J. R. D., Phalan, B., Catry, P., & Croxall, J. P. (2004). Seasonal sexual segregation in two *Thalassarche* albatross species: competitive exclusion, reproductive role specializaion or foraging niche divergence? *Proc. R. Soc. B.*, 271(1545), 1283–1291. https://doi.org/10.1098/rspb.2004.2718

R Core Team. (2023). R: a language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/

Ramírez, I., Paiva, V. H., Fagundes, I., Menezes, D., Silva, I., Ceia, F. R., Phillips, R. A., Ramos, J. A., & Garthe, S. (2016). Conservation implications of consistent foraging and trophic ecology in a rare petrel species. *Anim. Conserv.*, 19(2), 139–152. https://doi.org/10.1111/acv.12227

Réale, D., Martin, J., Coltman, D. W., Poissant, J., & Festa-Bianchet, M. (2009). Male personality, life-history strategies and reproductive success in a promiscuous mammal. *J. Evol. Biol.*, 22(8), 1599–1607. https://doi.org/10.1111/j.1420-9101.2009.01781.x

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biol. Rev.*, 82(2), 291–318. https://doi.org/10.1111/j.1469-185X.2007.00010.x

Rebstock, G. A., Abrahms, B., & Boersma, P. D. (2022). Site fidelity increases reproductive success by increasing foraging efficiency in a marine predator. *Behav. Ecol.*, 33(4), 868–875. https://doi.org/10.1093/beheco/arac052

Runnells, E., Montevecchi, W., & Davoren, G. (2024). Spatiotemporal and isotopic niche overlap among Atlantic puffins, razorbills, and common murres during the non-breeding season in the Northwest Atlantic. *Mar. Ecol. Prog. Ser.*, 739, 241–256. https://doi.org/10.3354/meps14614

Scopel, L., Diamond, A., Kress, S., & Shannon, P. (2019). Varied breeding responses of seabirds to a regime shift in prey base in the Gulf of Maine. *Mar. Ecol. Prog. Ser.*, 626, 177–196. https://doi.org/10.3354/meps13048

Shoji, A., Elliott, K., Fayet, A., Boyle, D., Perrins, C., & Guilford, T. (2015). Foraging behaviour of sympatric razorbills and puffins. *Mar. Ecol. Prog. Ser.*, 520, 257–267. https://doi.org/10.2307/24895065

Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.*, 19(7), 372–378. https://doi.org/10.1016/j.tree.2004.04.009

Stamps, J., & Groothuis, T. G. G. (2010). The development of animal personality: relevance, concepts and perspectives. *Biol. Rev.*, 85(2), 301–325. https://doi.org/10.1111/j.1469-185X.2009.00103.x

Staudinger, M. D., Goyert, H., Suca, J. J., Coleman, K., Welch, L., Llopiz, J. K., Wiley, D., Altman, I., Applegate, A., Auster, P., Baumann, H., Beaty, J., Boelke, D., Kaufman, L., Loring, P., Moxley, J., Paton, S., Powers, K., Richardson, D., … Steinmetz, H. (2020). The role of sand lances (*Ammodytes* sp.) in the Northwest Atlantic Ecosystem: A synthesis of current knowledge with implications for conservation and management. *Fish Fish.*, 21(3), 522–556. https://doi.org/10.1111/faf.12445

Stearns, S. (1992). The evolution of life histories. Oxford University Press.

Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2017). rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods Ecol. Evol.*, 8(11), 1639–1644. https://doi.org/10.1111/2041-210X.12797

Thaxter, C. B., Wanless, S., Daunt, F., Harris, M. P., Benvenuti, S., Watanuki, Y., Grémillet, D., & Hamer, K. C. (2010). Influence of wing loading on the trade-off between pursuit-diving and flight in common guillemots and razorbills. *JEB*, 213(7), 1018–1025. https://doi.org/10.1242/jeb.037390

Van Den Bosch, M., Baert, J. M., Müller, W., Lens, L., & Stienen, E. W. M. (2019). Specialization reduces foraging effort and improves breeding performance in a generalist bird. *Behav. Ecol.*, 30(3), 792–800. https://doi.org/10.1093/beheco/arz016

Vandenabeele, S. P., Shepard, E. L., Grogan, A., & Wilson, R. P. (2012). When three per cent may not be three per cent; device-equipped seabirds experience variable flight constraints. *Mar. Biol.*, 159(1), 1–14. https://doi.org/10.1007/s00227-011-1784-6

Wakefield, E. D., Cleasby, I. R., Bearhop, S., Bodey, T. W., Davies, R. D., Miller, P. I., Newton, J., Votier, S. C., & Hamer, K. C. (2015). Long-term individual foraging site fidelity - why some gannets don't change their spots. *Ecology*, 96(11), 3058–3074.

Wakefield, E. D., Phillips, R. A., & Matthiopoulos, J. (2009). Quantifying habitat use and preferences of pelagic seabirds using individual movement data: a review. *Mar. Ecol. Prog. Ser.*, 391, 165–182. https://doi.org/10.3354/meps08203

Webster, M. S., & Marra, P. P. (2005). The importance of understanding migratory connectivity and seasonal interactions. In R. Greenberg & P. P. Marra (Eds.), Birds of Two Worlds: The Ecology and Evolution of Migration (pp. 199–209). John Hopkins University Press.

Weimerskirch, H. (2007). Are seabirds foraging for unpredictable resources? *Deep-Sea Res. II: Top. Stud. Oceanogr.*, 54(3–4), 211–223. https://doi.org/10.1016/j.dsr2.2006.11.013

Wolf, M., & Weissing, F. J. (2012). Animal personalities: Consequences for ecology and evolution. *Trends Ecol. Evol.*, 27(8), 452–461. https://doi.org/10.1016/j.tree.2012.05.001

Woo, K. J., Elliott, K. H., Davidson, M., Gaston, A. J., & Davoren, G. K. (2008). Individual specialization in diet by a generalist marine predator reflects specialization in foraging behaviour. *J. Anim. Ecol.*, 77(6), 1082–1091. https://doi.org/10.1111/j.1365-2656.2008.01429.x

Zuur, A. F., & Ieno, E. N. (2016). A protocol for conducting and presenting results of regression-type analyses. *Methods Ecol. Evol.*, 7(6), 636–645. https://doi.org/10.1111/2041-210X.12577

Table 1. Summary of bird borne tags deployed on chick rearing razorbills from James Island, Newfoundland (2017 and 2019-2022).

	Tag Type			
	Biotrack MK3006	Migrate Technology Ltd C330	Lotek Lat1800	Lotek Lat2800
Years deployed	2017	2019-2022	2019	2021-2022
No. tags deployed	12	45	21	30
No. tags retrieved (%)	4 (33%)	28 (62%)	7 (33%)	16 (53%)
Tag weight (g)	4.00 ± 0.20	4.48 ± 0.19	6.00 ± 0.20	6.51 ± 0.20

Table 2. Summary of sample sizes, with the number of individuals with multiple years of data for each data type.

	Number of individuals with data from:				
	1 year	2 years	3 years	4 years	5 years
Non-breeding migration (GLS)	16	10	4	/	/
Diet (feather SIA)	/	17	11	2	3
Foraging behaviour (TDR)	16	5	/	/	/

Table 3. Repeatability (*R*) values for distance travelled north and south, average dive depth and δ^{15}N in razorbills. The 95% confidence intervals for repeatability are presented and t, df and *p* values for each fixed effect are reported. Significant *R* values and fixed effects are shown in bold.

				Fixed Factors											
	Adjusted Repeatability			Personality			Sex			Year/Month			Feather		
	R	95% CI	*p*	F	df	*p*	F	df	*p*	F	df	*p*	F	df	*p*
Distance north	**0.592**	**0.154 - 0.837**	**0.020**	0.269	19.3	0.610	**6.055**	**17.6**	**0.010**	2.461	20.8	0.132			
Distance south	**0.595**	**0.151 - 0.830**	**0.011**	0.223	18.5	0.881	0.160	16.7	0.853	3.691	20.1	0.069			
Dive depth	**0.108**	**0.005 - 0.181**	**<0.001**	0.149	15.2	0.705	1.947	15.2	0.179	**18.552**	**4254.8**	**<0.001**			
δ^{15}N	**0.128**	**0.024 - 0.245**	**0.002**	0.894	28.9	0.352	0.006	29.5	0.995	**4.789**	**256.6**	**0.030**	**44.973**	**232.2**	**<0.001**

Table S1. Table showing all the input parameters for *probGLS* (https://rdrr.io/github/benjamin-merkel/probGLS/) used in this study, and a description of the methodology and/or options for the input. Variations between the three tag types used (C330, MK3006 and Lat2800) are also shown. More details available in supplementary text for some elements (*).

Input parameter:	Input (C330 & MK3006 / Lat2800)	Input description by tag type:	
		C330 & MK3006	Lat2800
trn *	light data	Twilights processed in *TWGeos* from raw light data.	Twilights processed in *TWGeos* from raw light data subset to lowest light value in each 5 min period. Following manual time drift adjustment.
sensor *	SST data	Raw SST data.	SST estimation from raw temperature data using R code from *seabiRds* package (Patterson, 2023). Average calculated for 8-hour periods.
act	immersion data	Raw immersion data.	Proportion of wet to dry generated for 5 min periods (value out of 30) from raw immersion data.
tagging.date	tag specific	Date of tag deployment.	
retrieval.date	tag specific	Date of tag retrieval.	
loess.quartile	NULL	If not 'NULL' then the *GeoLight loessFilter* function is used before running iterations.	
tagging.location	-53.78, 49.58	Longitude and latitude of tag deployment (decimal degrees).	
particle.number	2000	Number of possible locations generated for each twilight event.	
iteration.number	100	Number of tracks generated to calculate the geographic median track from.	
sunrise.sd	2.49, 0.94, 0	Twilight error structure for open habitat species such as seabirds: shape/scale/delay values defining uncertainty for each twilight event, following a log normal distribution.	
sunset.sd			
range.solar *	-6, -3	Solar angle range deemed appropriate for deployment on this species in this location following calculation of solar angles in *GeoLight* from a calibration period.	
boundary.box	-85, -1, 25, 70	The area within which the movement track occurs, locations are not produced outside of this box. Decimal degree coordinates.	
speed.dry *	16, 0.2, 17	Three values, expected, associated standard deviation and maximum speeds in m/s^{-1} for when the tag is wet (on water) or dry (flying).	
speed.wet *	1, 1.3, 5		
sst.sd *	calculated per individual / 0.2	A value for the standard deviation around the tag measured SST. Typically found in tag manual (e.g., Lotek Lat2800 tags ± 0.2°C)	
max.sst.diff *	2	The range around the tag recorded SST that the algorithm can place a location based on the supplementary satellite recorded SST data.	
east.west.comp	F	If 'T' then apply Biotrack east west movement compensation applied.	
landmask	T	If 'T' then no locations possible on land.	
ice.conc.cutoff	1	The percentage of sea ice cover a bird is assumed not to be associated with (1=100%).	
tol	0.08	Used to define equinox periods by setting the tolerance on the sine of the solar declination. When the solar declination is close to zero (at the equinoxes) latitude estimates are less accurate. Where the sine of the solar declination is less than set 'tol', the latitude estimates are returned as NA.	
distance.method	'ellipsoid'	How distances between locations are calculated, 'spherical' or 'ellipsoid'.	
wetdry.resolution	30 / 10	Frequency of wet/dry recordings by the tag in seconds.	
NOAA.OI.location	-	Computer location of required environmental data.	

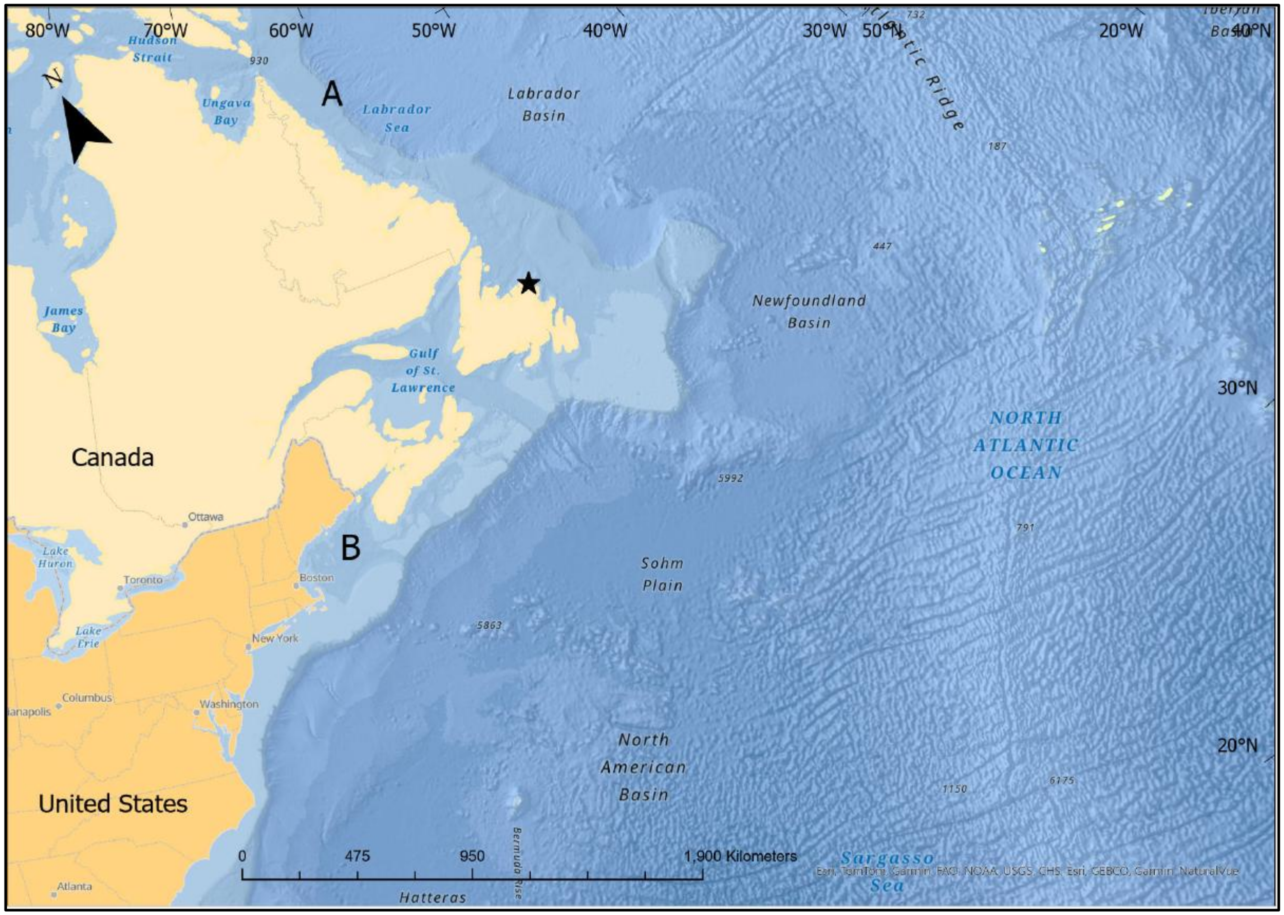

Figure 1. The location of the study breeding colony, James Island (black star), on the northeast coast of Newfoundland, Canada. The Labrador Sea (**A**) and Gulf of Maine (**B**) are indicated.

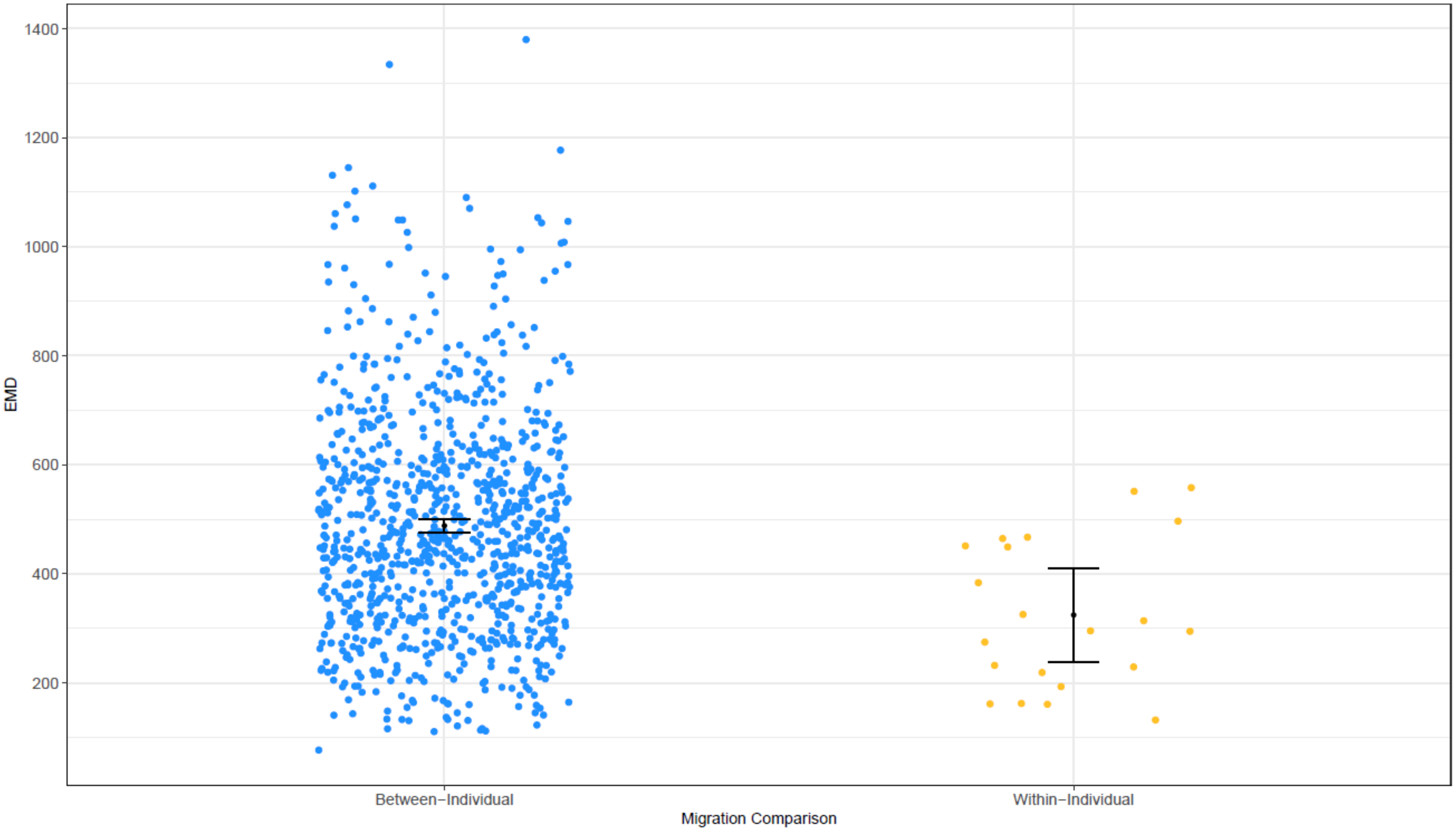

Figure 2. Earth mover's distance (EMD) values for between and within-individual differences in migratory track locations of non-breeding razorbills in the northwest Atlantic. Predicted EMD values from a generalised linear model (GLM) are shown as error bars with 95% confidence intervals.

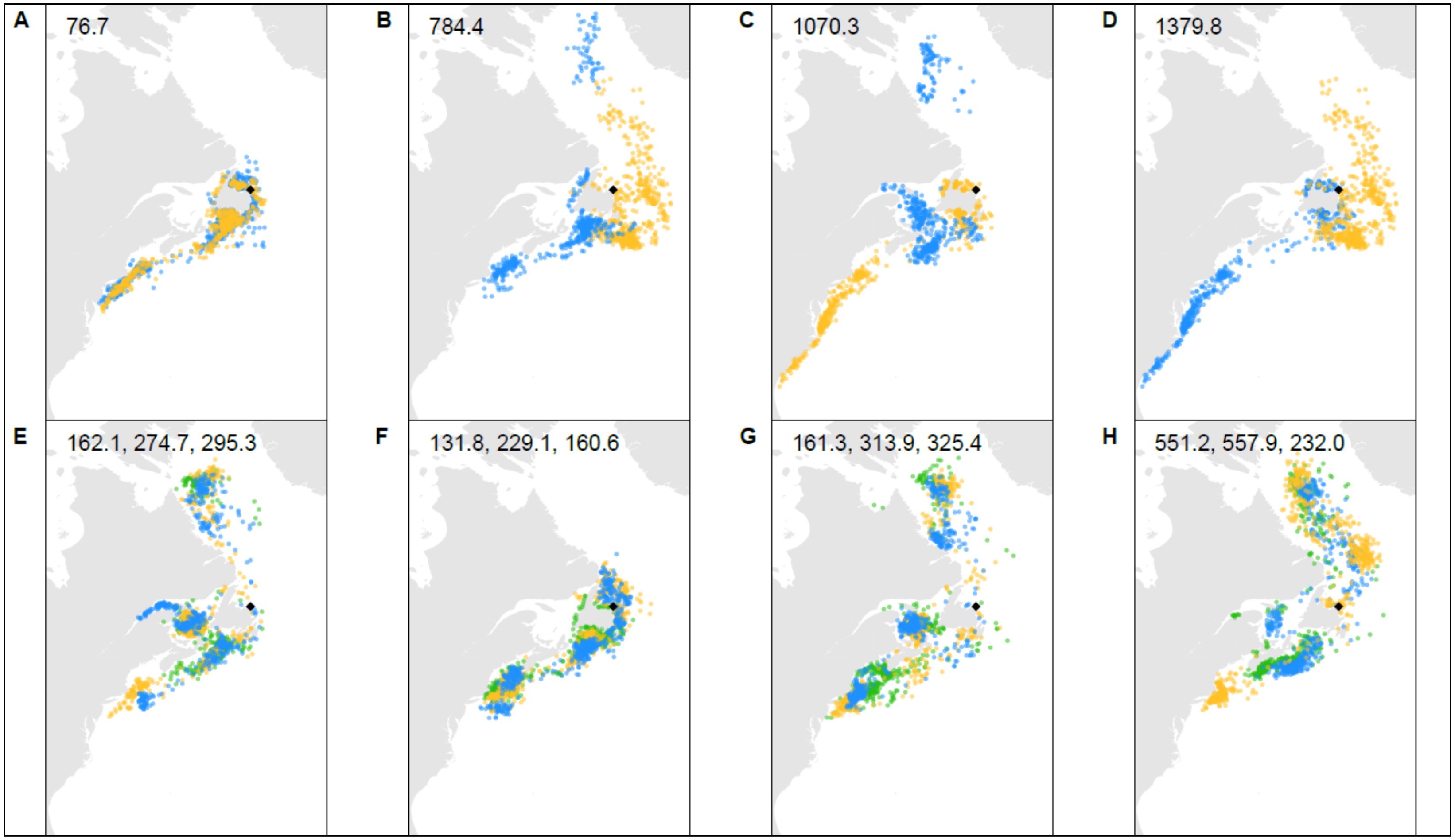

Figure 3. Razorbill migratory tracks during non-breeding. Examples of between-individual differences (**A**, **B**, **C**, **D**) with each bird shown in a different colour (blue and orange). Examples of within-individual differences (**E**, **F**, **G**, **H**) with each year shown in a different colour (blue, orange and green). EMD values (km) are indicated for each comparison or set of comparisons.

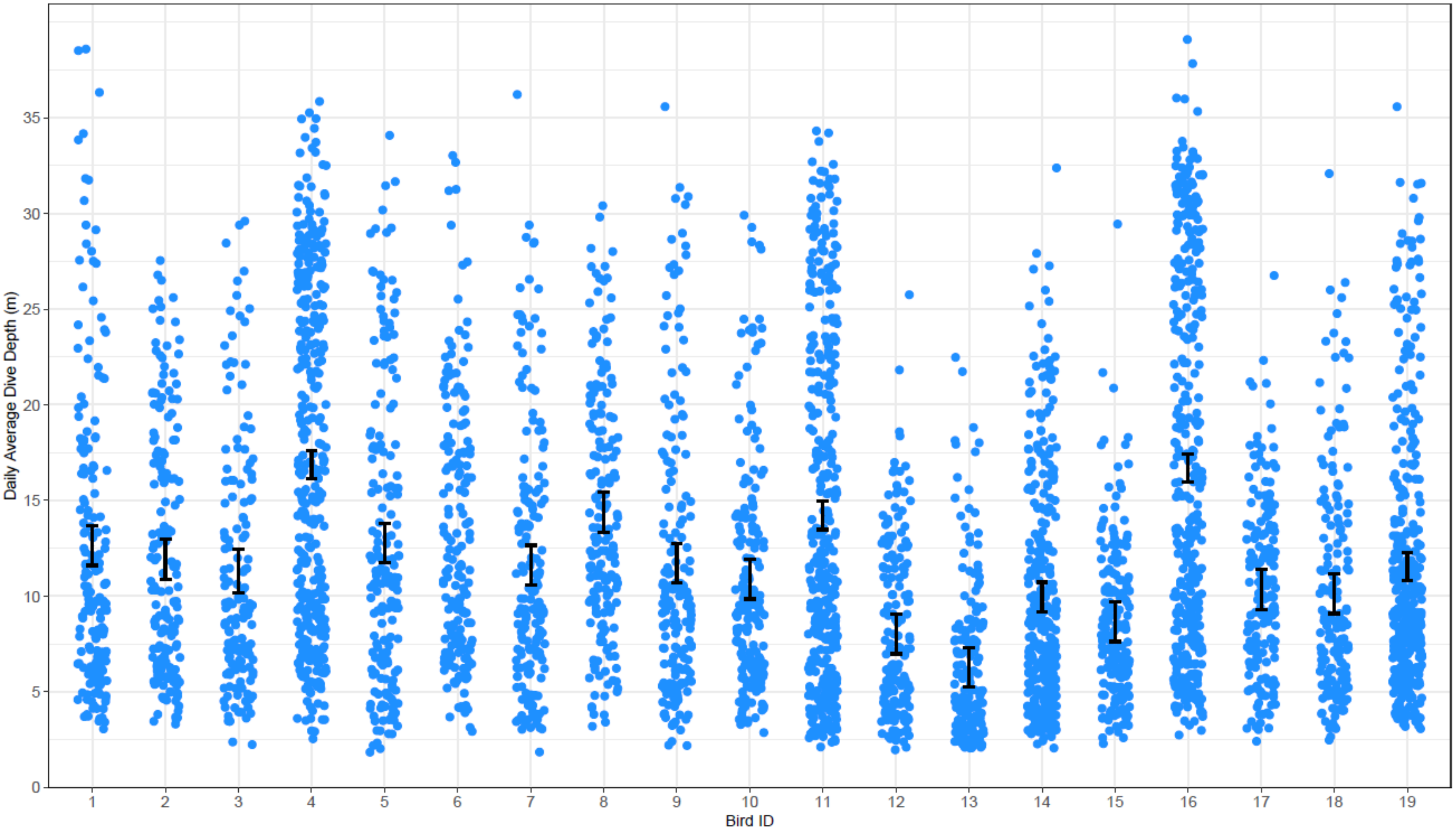

Figure 4. The daily average dive depth of each tagged razorbill collected with time-depth recorders (TDRs). Predicted depth values for each individual from a generalised linear model (GLM) are shown as error bars with 95% confidence intervals.

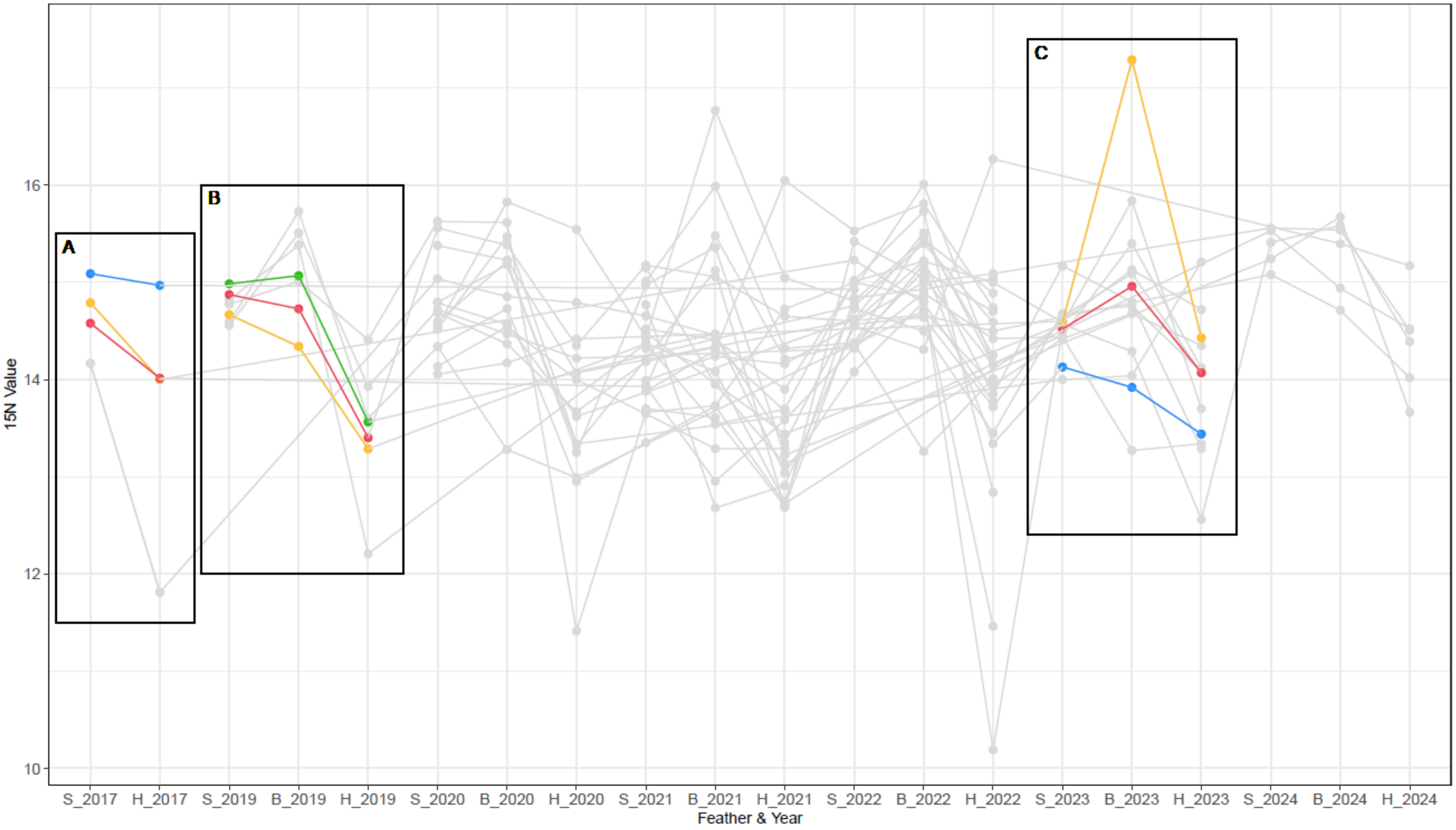

Figure 5. Stable isotope ratios of nitrogen ($\delta^{15}N$) for razorbill head, belly and secondary feathers. All individuals are shown in light grey and examples of consistent between individual differences in $\delta^{15}N$ value are shown in box **A** (2017), box **B** (2019) and box **C** (2023), with each individual shown in a different colour. Note, these are not the same individuals across all three boxes.

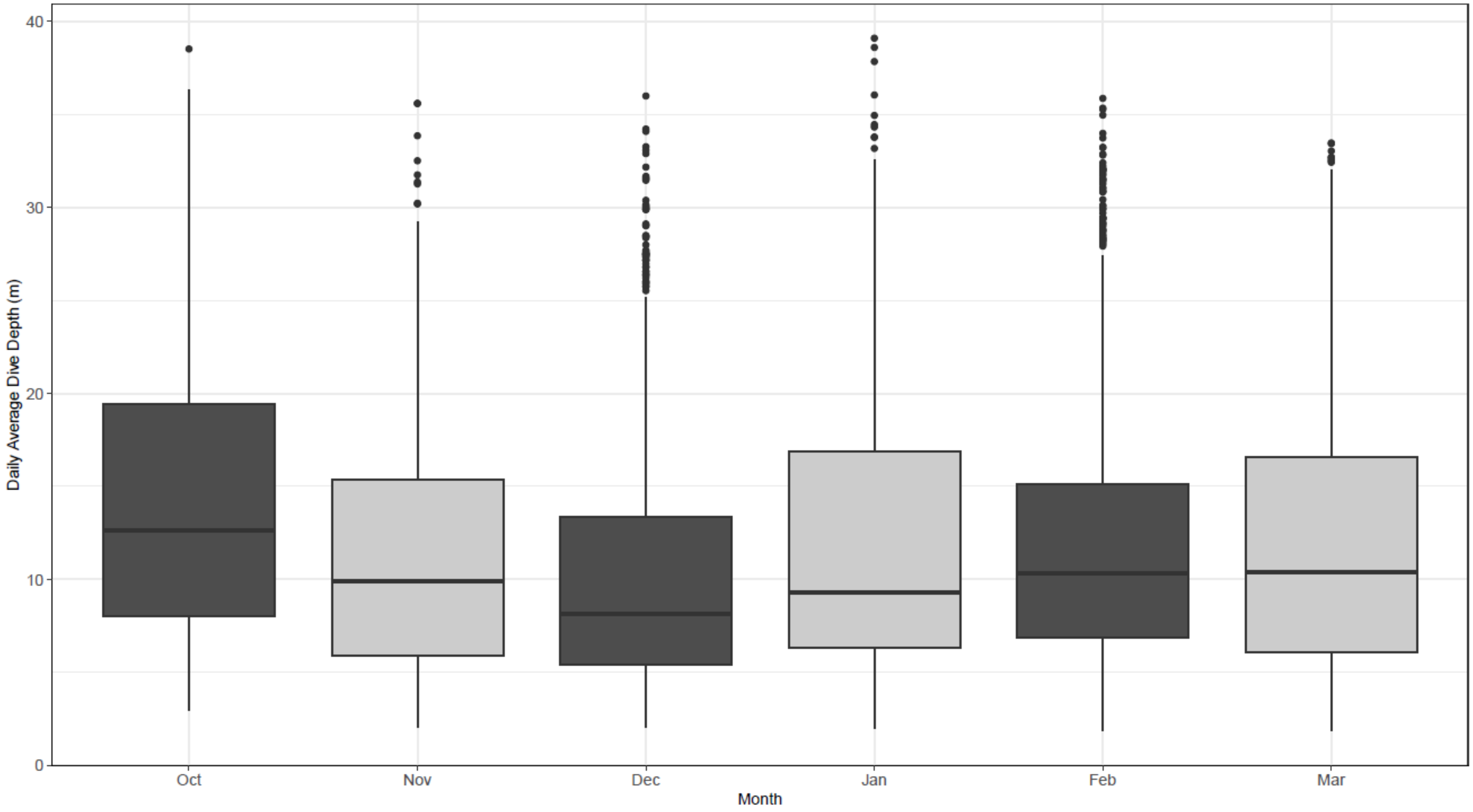

Figure S1. Average daily dive depth for all Time-Depth Recorder (TDR) tagged razorbills in each non-breeding month (October, November, December, January February, March).

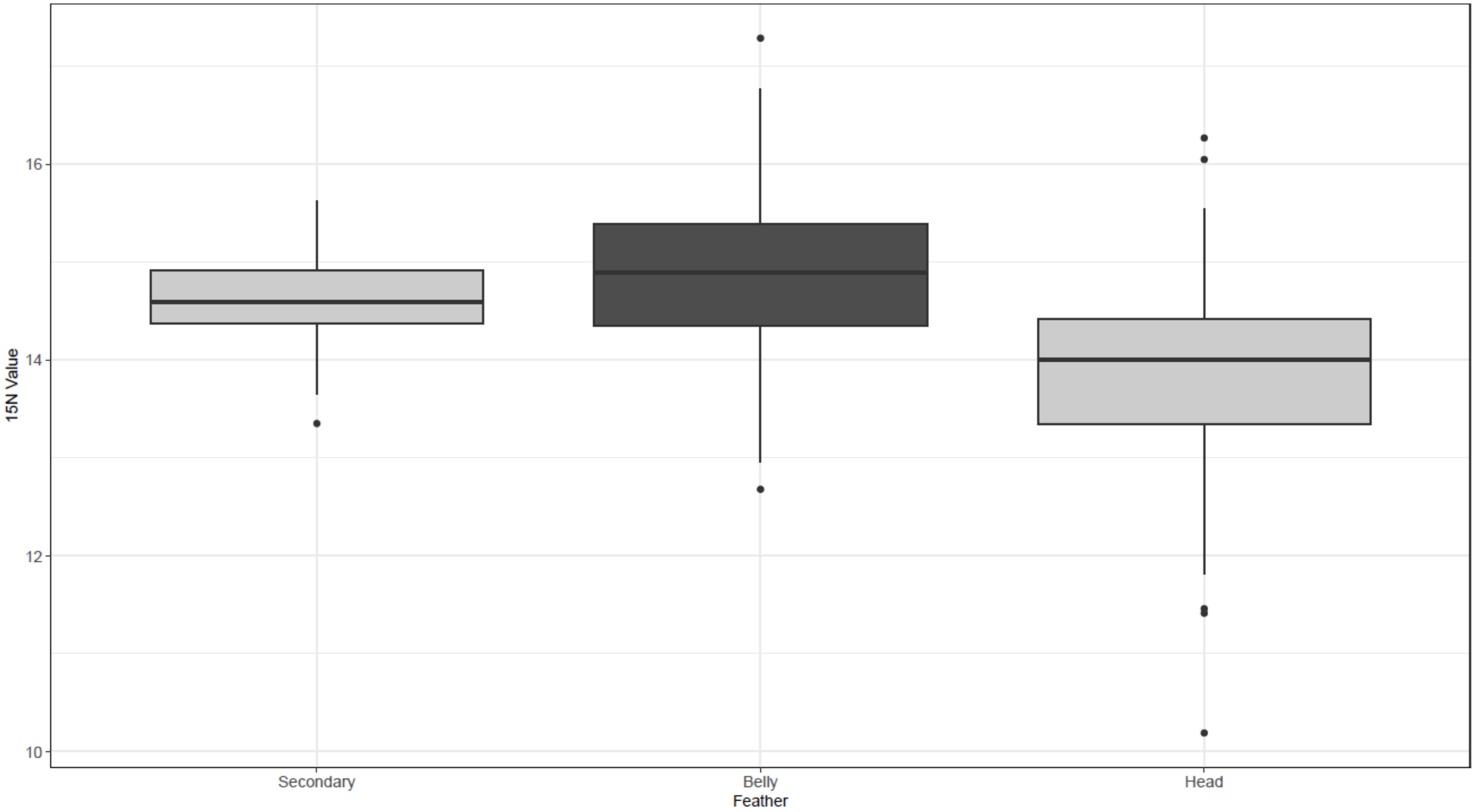

Figure S2. Razorbill δ^{15}N values from all sampled individuals across all years for the three different feather types (head, belly and secondary).

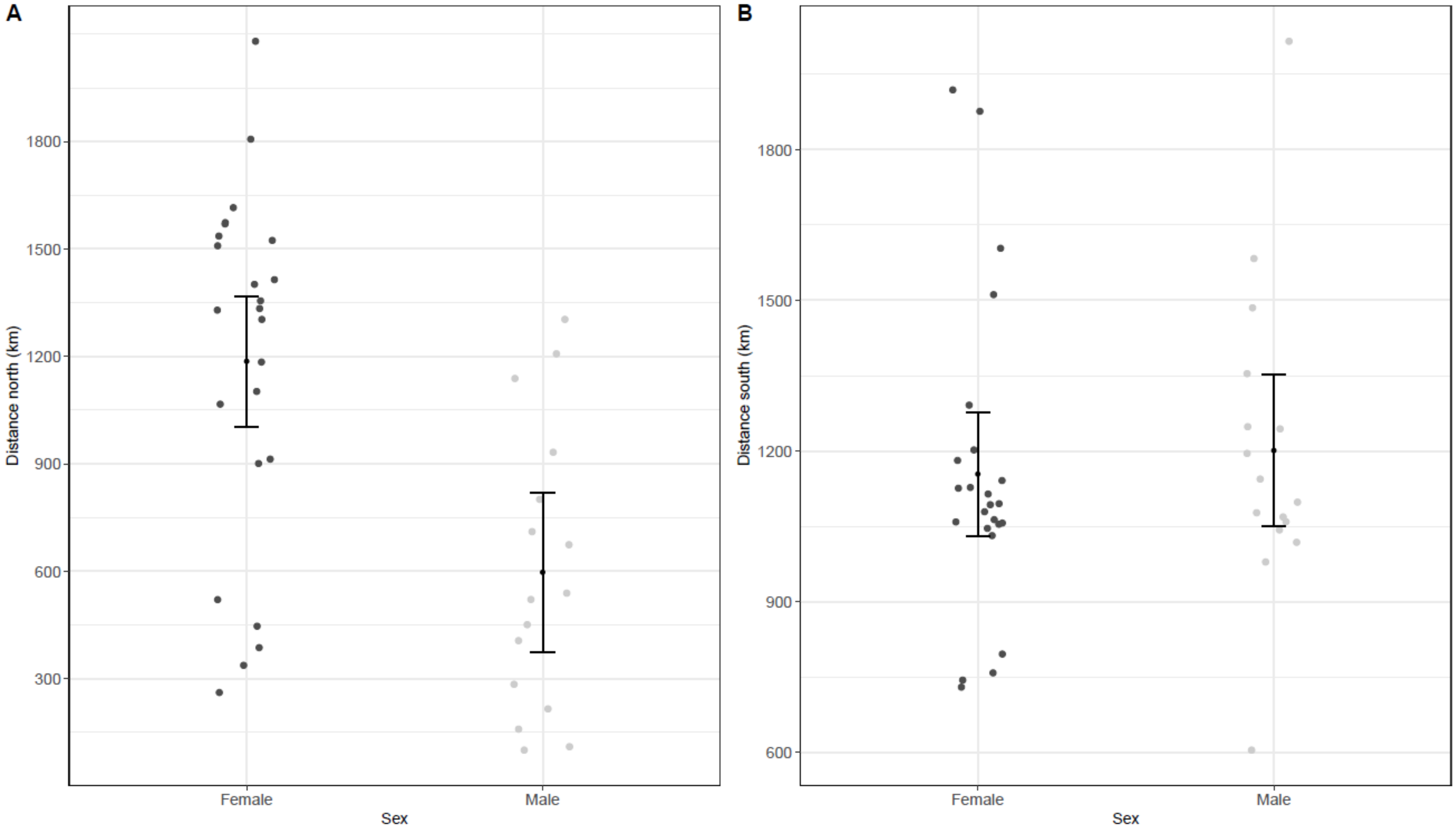

Figure S3. Distances (km) travelled north (**A**) and south (**B**) from the breeding colony by male and female tagged (Global Location Sensor; GLS) razorbills.

Chapter 3 - Supplementary Materials

Additional Details on *probGLS* Processing

One of the first parameters required by *probGLS* is to set a range of possible twilight solar angles that are appropriate for the whole duration of the deployment of the tags. The twilight solar angle is the angle below the horizon that the sun has to be to trigger a twilight event in the tag. This angle can be influenced by several factors including shading (vegetation, topography etc.) of the tag or geographical location. For example, a low solar angle (< -5°) would be typical of an environment with shading, while a high solar angle (> -5°) would be common in an environment with little shading. Many GLS processing manuals and protocols suggest either a two week 'rooftop' calibration or a calibration on the bird while it is still at the deployment site (both known locations) to then calculate an appropriate solar angle for the *probGLS* algorithm (Halpin et al., 2021; Lisovski et al., 2020). Instead, for this study, a small number (n=10) of previously deployed C330 GLS tags were attached to plastic common murre (*Uria aalge*) decoys and placed in the ocean close to James Island for 3-7 days. This imitated the location of the tag beneath a bird when floating on the water, a common behaviour during the non-breeding period, and was therefore believed to be a more appropriate representation of solar angle throughout the non-breeding period. Solar angles were calculated from these deployments using the *GeoLight* package (Lisovski and Hahn, 2013) generating values between-2.98° to -5.63° (-4.54° ± 0.82°) leading to a selection of -3° to -6° as the solar angle range in the *probGLS* algorithm.

ProbGLS also requires values for expected and maximum possible speeds (plus associated standard deviation) for when the tag is dry (bird presumed to be flying) and wet (bird on the water). Wet speeds were determined following identification of ocean current speeds for the North Atlantic and taken from the GLS processing manual produced by Lisovski et al (2020). The dry flight speeds used follow the methods of Buckingham et al, (2022), which was informed by a study on razorbills by Thaxter et al (2010) and another study by Pennycuick (1987) on the flight of several bird species.

The accuracy of *probGLS* location estimates is increased by the addition of SST data (Merkel et al., 2016). For C330 and MK3006 tags the raw SST data collected by the tag was used but as the sampling interval for Lat2800 tags was much more frequent (every 10 s) the temperature data recorded incorporates a lot of additional noise. For example, the temperature while diving at sea is recorded (often colder than SST) and leg tucking behaviour also influences the temperature recorded (warmer than SST and can reach up to 38°C). Therefore, R code from the *seabiRds* package (Patterson, 2023) was used to create an SST estimate for each 10 second interval. This R code uses other information collected by the tag (wet/dry sensor, depth data etc.) to help inform the SST estimate and remove the noise. This SST estimation method was validated following examination of SST data from two C330 tags and data from Lat1800 tags that were deployed concurrently on the same bird. These Lat1800 tags recorded the same data types (minus light data) at the same interval as the Lat2800 tags and were also processed using the *seabiRds* code to compare to the temperature profile from the C330 tag. These SST profiles throughout the tag deployment were found to be similar and therefore justified this method for Lat2800 tags.

Also concerning temperature, *probGLS* needs to be informed of the range around the tag-recorded SST that the algorithm can place a location based on supplementary satellite-recorded SST data. For example, if this value is set at 3°C and the tag temperature recording is 12° then the algorithm can select locations with satellite SST values of 9 to 15°C. A value of 2°C was selected for the processing of final tracks. This was selected following preliminary running of movement tracks where a value of 3°C produced tracks with unreasonable jumps in location between twilight events (>1500km). This was reduced to 2°C to constrain the algorithm and prevent these jumps while still allowing some freedom to produce a range of possible locations for each twilight and prevent SST from overriding the light data as the driving force behind location selection.

As the nature of the light sensors differed between tag types a different threshold value indicating sunset and sunrise was required for each: 0.9 (following log transformation), 135 and 2 for C330, Lat2800 and MK3006 tags, respectively. Additionally, as geolocation requires accurate twilight times, it is important light data are accompanied by accurate time information. C330 and MK3006 tags carried out automatic post-deployment time drift adjustments to account for any time drift in the clock of the tag during the deployment period. For Lat2800 tags, this had to be completed manually and was achieved using a linear adjustment (similar to the methods used by the other tag types) that assumed consistent time drift throughout the tag deployment. To do this, the difference between the time on the tag and the time on the computer when the tag was stopped for data download was noted. These two time points were put into a linear model with both time series starting at the known tag start time. The relationship between these two-time series (slope) was then used to inform the R function *predict* and adjust all known tag times accordingly. This resulted in times towards the end of the deployment being adjusted more than those at the beginning and therefore aligning with the assumption that the drift was consistent. Of the sixteen Lat2800 tags retrieved, 5 had time drift too large to be corrected accurately (> 8 hours, suggestion of inconsistent time drift), and, thus, had to be discarded from analysis. The remaining eleven were adjusted for use in analysis. Of these, 7 had unknown levels of drift, as the tag died before data download and prevented the identification of the difference between tag and computer time. The time drift of these 7 tags was estimated at 2 hrs (1 tag) or appeared minimal (<1 hour, 6 tags) following examination of light data in relation to known sunset/sunrise times at the study colony. The final 4 tags had low levels of known time drift (<1 hour).

Finally, before generating each movement track in *probGLS* the raw light data were subset based on the best estimate of the departure/arrival dates from/to the colony. For C330 and Lat2800 tags these estimates were calculated using the raw light data as it is possible to see nest attendance during the breeding season as dips in the light data during daylight hours. These lower light levels are not present at equivalent times during the day in the non-breeding period. Following data examination using histograms, a bimodal distribution in log transformed light data was observed with a peak at lower light levels indicating nest attendance and then a larger peak at high light levels indicating daylight hours. Due to the nature of razorbill rock crevice nests, shading is not always complete resulting in lower light levels above the twilight threshold of 0.9. Following examination of all razorbill data, a threshold light level of 3 was selected to indicate nest attendance when light dropped below this value. Daylight hours (08:00 – 19:00) were then examined starting on May 1 to identify the first date of nest attendance (arrival) and starting on June 15 to determine the last day of nest attendance (departure). Due to the nature of the light data collected by MK3006 tags (binary, yes or no light), these estimates were calculated using immersion data instead as it is possible to see colony attendance during the breeding season as continuous periods where the tag is dry. These long dry periods do not occur during the non-breeding period. Following data examination of all 4 tags of this type, a period of 6 hours continuously dry was chosen to indicate colony attendance, as dry periods of this length do not occur outside the breeding season. The first such period after May 1 was designated the arrival date and the last after June 15 was determined to be the departure date. Departure dates for all razorbills ranged between July 12 and September 14 (average: August 17 ± 18 days) while the range of arrival dates was May 1 to June 1 (average: May 10 ± 8 days).

References

Buckingham, L., Bogdanova, M., Green, J., Dunn, R., Wanless, S., Bennett, S., Bevan, R., Call, A., Canham, M., Corse, C., Harris, M., Heward, C., Jardine, D., Lennon, J., Parnaby, D., Redfern, C., Scott, L., Swann, R., Ward, R., … Daunt, F. (2022). Interspecific variation in non-breeding aggregation: a multi-colony tracking study of two sympatric seabirds. *Mar. Ecol. Prog. Ser.*, 684, 181–197. https://doi.org/10.3354/meps13960

Halpin, L. R., Ross, J. D., Ramos, R., Mott, R., Carlile, N., Golding, N., Reyes-González, J. M., Militão, T., De Felipe, F., Zajková, Z., Cruz-Flores, M., Saldanha, S., Morera-Pujol, V., Navarro-Herrero, L., Zango, L., González-Solís, J., & Clarke, R. H. (2021). Double-tagging scores of seabirds reveals that light-level geolocator accuracy is limited by species idiosyncrasies and equatorial solar profiles. *Methods Ecol. Evol.*, 21(11), 2243–2255. https://doi/10.1111/2041-210X.13698

Lisovski, S., Bauer, S., Briedis, M., Davidson, S. C., Dhanjal-Adams, K. L., Hallworth, M. T., Karagicheva, J., Meier, C. M., Merkel, B., Ouwehand, J., Pedersen, L., Rakhimberdiev, E., Roberto-Charron, A., Seavy, N. E., Sumner, M. D., Taylor, C. M., Wotherspoon, S. J., & Bridge, E. S. (2020). Light-level geolocator analyses: a user’s guide. *J. Anim. Ecol.*, 89(1), 221–236. https://doi.org/10.1111/1365-2656.13036

Lisovski, S., & Hahn, S. (2013). GeoLight - processing and analysing light-based geolocation in R. *Methods Ecol. Evol.*, 3, 1055–1059. https://doi.org/10.1111/j.2041-210X.2012.00248.x

Merkel, B., Phillips, R. A., Descamps, S., Yoccoz, N. G., Moe, B., & Strøm, H. (2016). A probabilistic algorithm to process geolocation data. *Mov. Ecol.*, 4(1). https://doi.org/10.1186/s40462-016-0091-8

Patterson, A. (2023). *seabiRds*: prepares biologging data for analysis and upload to the lab database (R package version 0.1.0).

Pennycuick, C. J. (1987). Flight of Auks (Alcidae) and other northern seabirds compared with southern procellariiformes: ornithodolite observations. *JEB*, 128, 335–347.

Thaxter, C. B., Wanless, S., Daunt, F., Harris, M. P., Benvenuti, S., Watanuki, Y., Grémillet, D., & Hamer, K. C. (2010). Influence of wing loading on the trade-off between pursuit-diving and flight in common guillemots and razorbills. *JEB*, 213(7), 1018–1025. https://doi.org/10.1242/jeb.037390

Link between Chapters 3 & 4

In Chapter 3, I found razorbills to be individually consistent in their behaviour (i.e. migratory location and distance, foraging dive depth and trophic level) during the non-breeding season. However, none of these behaviours were related to the aggressive-docile continuum, with only the distance travelled north from the colony influenced by an intrinsic factor (i.e., sex). In Chapter 4, I aimed to link individual migratory consistency with population-level migratory behavioural diversity across six seabird species, representing three seabird families (Alcidae, Laridae and Sulidae) breeding in the Atlantic Canada. Species with low or high behavioural diversity may be vulnerable or more resilient to environmental change, respectively. Therefore, it is important to identify these species to aid conservation and management decisions.

Chapter 4: Diversity in non-breeding distribution differs across seabird species in the northwest Atlantic.

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Abstract

Species-specific behavioural diversity (i.e., differences among individuals that are consistent across time) can influence population dynamics, with lower diversity resulting in a higher probability of population declines. In seabirds, non-breeding locations and migratory routes can be highly consistent within individuals but can vary among individuals within a species. We aimed to determine the level of behavioural diversity within several seabird species that breed in Atlantic Canada and overwinter in the northwest Atlantic. To do this, we collated non-breeding bird-borne tracking data from GPS and geolocator GLS tags from six species (Atlantic puffin, razorbill, northern gannet, thick-billed murre, glaucous gull and herring gull) representing three seabird families (Alcidae, Laridae and Sulidae) with a focus on datasets that had repeat non-breeding tracks within individuals. We used Earth Movers Distance (EMD) to compare non-breeding distributions within and among individuals in a colony/species. All species showed high levels of individual consistency in non-breeding locations. Behavioural diversity, observed as bimodal distributions of between-individual EMD values (i.e., distinct migratory routes), varied across and within colonies and species, with northern gannets and glaucous gulls showing the greatest diversity. Findings suggest that the lower behavioural diversity of species from the family Alcidae (puffins, razorbill, murres) make them more vulnerable to environmental change and anthropogenic threats (e.g., offshore wind farms). Identifying species and populations with lower behavioural diversity is valuable for seabird conservation and management due to their lower response diversity and greater likelihood to suffer from mass mortality related to a single local event (e.g., oil spill).

Introduction

Increasingly variable environmental conditions due to anthropogenic related disturbances (e.g., climate change) are resulting in population declines across the animal kingdom, with declines often being greater in specialist species (Clavel et al., 2011). Indeed, the behavioural diversity within a species (i.e., differences among individuals) can influence population dynamics, with greater diversity potentially resulting in increased stability (Sydeman et al., 2015) and lower diversity resulting in a higher probability of population change under variable environmental conditions (Gilroy et al., 2016; Wolf & Weissing, 2012). This higher vulnerability may increase if the individuals within a species are highly consistent (i.e., not behaviourally flexible), leading to potentially sub-optimal behaviour when environmental conditions (e.g., prey availability) change. Therefore, an understanding of the behavioural diversity both among and within populations will aid in understanding their ability to tolerate future environmental variation (Nussey et al., 2007).

Variation in migratory behaviour (e.g., differential migration) among individuals within a species or population (Dias et al., 2011; Gutowsky et al., 2020; Spencer et al., 2016) is an important example of behavioural diversity. Migration (i.e., movements between breeding and non-breeding areas that occur seasonally; Newton, 2008) is an adaptive trait that has evolved to maximize fitness under temporal and spatial variation in resource availability (McNamara & Dall, 2010). Therefore, migration occurs when winter survival is higher at one location, but reproduction is more successful at another location (Lack, 1954; Stearns, 1992). Diversity in migration locations may occur when there are multiple profitable wintering areas that can be reached by a population (Davis et al., 2016). Within species, individual site fidelity can increase familiarity with the conditions at a wintering area (e.g., resource availability; Fifield et al., 2014; McNamara & Dall, 2010; Newton, 2008) and is common across animal taxa (Bradshaw et al., 2004; Broderick et al., 2007; Phillips et al., 2017). The survival rates of sub-groups within a population may differ if individuals consistently migrate to different wintering locations, where they experience varying environmental conditions (Newton, 2004) and are exposed to different types and levels of anthropogenic change or threats (Baak et al., 2021b). Therefore, understanding the migratory locations of distinct sub-groups of a population is important to understand the risk and vulnerability of populations experiencing environmental change (Phillips et al., 2017; Wolf & Weissing, 2012). Indeed, tracking data frequently inform conservation and management decisions (Davies et al., 2021; Hays et al., 2019; Hindell et al., 2020). The non-breeding period, however, remains an understudied component of the annual cycle of animals (Bell et al., 2009) and this is particularly the case in seabirds (Dunn et al., 2019).

During the non-breeding period, many seabird species travel large distances to wintering areas (Daunt et al., 2014; Nelson, 2002), but species vary in migratory patterns (e.g., distance and location; Fort et al., 2013). For instance, some seabird species or populations exhibit variation in migratory routes and overwinter in several distinct locations (e.g., Fayet et al., 2016; Fifield et al., 2014; Gatt et al., 2021). Many seabird species also show individually consistent differences in migratory behaviour (e.g., timing, location; Baak et al., 2021b; Franklin et al., 2022). Technological advancements (e.g., smaller tracking devices) have reduced the challenges associated with studying migration across a wide range of seabird species (e.g., reduced tag effects in smaller species) and avoid biases of visual methods, such as at sea surveys or coastal band resights (Engler et al., 2017; Fort et al., 2012). During the non-breeding period, seabirds face a large range of threats (Gilroy et al., 2016) and many of these have significant spatial heterogeneity (Phillips et al., 2017), including offshore wind farms (Peschko et al., 2020), oil pollution (Montevecchi et al., 2011), fisheries (Thiers et al., 2014) and artificial lighting at night (Rodríguez et al., 2017).

Seabirds from the family Alcidae (hereafter 'alcid') are characterised by a high body mass to wing area ratio which enhances their diving capability but results in a high energetic cost of flight relative to other seabird families (Elliott et al., 2013). During the non-breeding period, alcid species in north America typically overwinter south of their breeding range (Baran et al., 2022; Patterson et al., 2021; Runnells et al., 2024). In contrast to alcids, members of the family Laridae (hereafter 'larid') are considered flight generalists using several flight modes (e.g., flapping, soaring, etc.) which result in reduced energetic restrictions (Hedenström, 2008). Additionally, many species are omnivorous generalists that consume many types of food (Pierotti & Annett, 1991; van Donk et al., 2017) and, thus, are found in a variety of habitats including terrestrial, marine and freshwater (Baak et al., 2021b). Subsequently, larids exhibit a diverse range of migratory strategies (e.g., migratory, resident; Baak et al., 2021a; Baak et al., 2021b; Weiser & Gilchrist, 2020; Weseloh et al., 2024). The seabird family Sulidae (hereafter 'sulid') is capable of strong, direct flight with minimal impact of high winds on energy expenditure (Mowbray, 2020), and northern hemisphere populations migrate south towards the equator during the non-breeding period (Fifield et al., 2014; Mowbray, 2020).

The primary objective of this study was to investigate diversity in non-breeding migratory behaviour (e.g., distance and location) among and within alcid, larid and sulid species breeding in Atlantic Canada using archived datasets (Table 1, Figure 1). The secondary objective was to investigate whether this diversity is persistent across years due to individual consistency in migratory routes. Therefore, the study populations included those having archived datasets with individuals that had been tracked for more than one year, allowing us to quantify both individual consistency and behavioural diversity, and how these metrics vary within and among species. We hypothesized that behavioural diversity in migratory location and distance vary among seabird families due to varying energetic costs of flight, but that all species will exhibit individual consistency. We predicted that larids and sulids (i.e., lower flight costs) will exhibit greater between-individual variation in migration location and distance than alcids (i.e., higher flight costs). As many previous studies on seabird migration have focused on single species (Brown et al., 2021), with few comparisons across species (Montevecchi et al., 2012; Ronconi et al., 2022), identifying species and populations with lower behavioural diversity will indicate groups of individuals that may be less resilient to environmental change (Clavel et al., 2011) and at greater risk from localised threats (e.g., offshore wind farms; Garthe et al., 2023; Peschko et al., 2020).

Methods

Seabirds typically show high nest site fidelity, allowing the deployment/retrieval of bird-borne archival tags and the tracking of individuals across multiple years. For this study, archived non-breeding tracking data were compiled from six species that breed across six different colonies in Atlantic Canada: Atlantic puffins (*Fratercula arctica*, hereafter 'puffin') and razorbills (*Alca torda*) from both James Island (JI) and Machias Seal Island (MSI), thick-billed murres (*Uria lomvia*, hereafter 'murre') and glaucous gulls (*Larus hyperboreus*) from Coats Island (CI), American herring gulls (*Larus smithsonianus*; hereafter 'herring gull') from Gull Island (GI), and northern gannets (*Morus bassanus*; hereafter 'gannet') from Bonaventure Island (BI) and Funk Island (FI;

Table 1, Figure 1). These species represent three seabird families; alcids: puffins, razorbills and murres; larids: glaucous and herring gulls; sulids: gannets.

Tracking data were collected using bird-borne global location sensor (GLS) and global positioning system (GPS) tags set to record data to either estimate locations (i.e., light; GLS) or directly collect locations (GPS). Full details on the deployment and retrieval methods for each species can be found in the references listed in Table 1. Processing of each tag and data type required its own methodology due to species behaviour or the parameters recorded by the tag (Table 1). GLS data required processing to establish location estimates. In brief, this involved using the ambient light data recorded by the tag to estimate geographical locations (± 200 km): latitude from day length and longitude from the timing of solar noon (Lisovski et al., 2020). These location estimates were then refined with the input of additional information when possible (e.g., sea surface temperature, species-specific flight speeds) using GLS processing methods: *probGLS* (Merkel et al., 2016) and MULTITRACE for Windows (Jensen Software Systems, Laboe, Germany). Although different GLS processing methods were used across species (see references listed in Table 1), the same methods were used within species to ensure track comparability among and within individuals. In comparison to GLS data, GPS data were quality checked but required minimal pre-processing because geographical locations are collected directly.

Statistical Analysis

All statistical analyses were carried out in R version 4.3.0 (R Core Team, 2023). For each species and colony within species (i.e., gannets, puffins, razorbills), between and within-individual differences in overwintering migration tracks were quantified as Earth Mover's Distance (EMD) values (km) using the *emd* function in the R package *move* (Kranstauber et al., 2021). EMD calculates the spatial proximity of two distributions, with each location in the first distribution measured to the closest location in the second, thus generating an average minimum distance (km) between the two distributions (Franklin et al., 2022; Kranstauber et al., 2017). EMD values resulting from pairwise comparisons of tracks within birds and between birds are on a continuous scale, with values increasing from zero (i.e., two identical distributions) with growing dissimilarity (Franklin et al., 2022). Geographical coordinates were used as the input and the Haversine function was applied to account for distributions that stretch over large distances to account for the spherical surface of the Earth (Franklin et al., 2022; Kranstauber et al., 2017). Different tags and processing methods provided varying numbers of location estimates each day. For example, GLS data and processing typically produces two locations per day (one for each twilight), while GPS tracks can have many locations per day depending on programming settings. Therefore, all movement tracks were subsampled to the first recorded location on each day throughout deployment to standardise comparisons across species. Following subsampling, an EMD value was then calculated for all possible between and within-individual track pairs for each species/colony. Across all species, the maximum distance travelled from the colony in each direction (north, south, east, west) was also quantified for each individual track (± 200 km for GLS tags, Merkel et al., 2016).

To quantify behavioural diversity for each species/colony, we examined the distribution of between-individual EMD values. This was achieved using Hartigan's dip test (Hartigan & Hartigan, 1985) using the R package *diptest* (Maechler, 2024). We used the resulting p value to classify distributions as having higher behavioural diversity (significantly bimodal, $p = < 0.05$), moderate behavioural diversity (moderately bimodal, *p* = 0.05 – 0.10) and lower behavioural diversity (unimodal/normally distributed, *p* = > 0.10; Freeman & Dale, 2013). To quantify the differences in magnitude of between-individual EMD values among families and between species/colonies, Kruskall-Wallis tests were carried out in combination with posthoc Dunn's tests.

Within species/colonies, the between- and within-individual EMD values were compared using generalised linear models (GLM) to determine whether migratory routes of individuals were spatially consistent across consecutive years (i.e., significantly higher between-individual compared to within-individual EMD values). All EMD values were non-negative and continuous, but distributions varied. Therefore, gaussian (razorbills, puffins, FI gannets, glaucous and herring gulls) and gamma (BI gannets, murres) error families with the identity link function were used. After data exploration showed bimodal distributions of EMD values in glaucous gulls and gannets from FI, we added migration direction (i.e. east or west) as another fixed factor to account for this distribution of EMD values. Finally, the predict function was used to generate a predicted value and 95% confidence intervals for between- and within-individual EMD values for each species/colony from the outputs of the GLMs. During analyses, model assumptions were confirmed in all cases following protocols outlined in (Zuur & Ieno, 2016).

Ethical Note

Efforts were made to reduce animal use, minimise the handling duration for each individual, and prevent disturbance to the seabird colonies. Additionally, all data collected has contributed to multiple scientific projects and objectives (Anderson et al., 2020; Baak et al., 2021b; Baran et al., 2022; Fifield et al., 2014; Patterson et al., 2021; Runnells et al., 2024). On James Island, the research was conducted under a Canadian Master Banding Permit (10873) and in agreement with the Canadian Council for Animal Care (Protocols F16-017, F20-017). Work on Machias Seal Island was approved by the Animal Care Committee at the University of New Brunswick (UNBF AUP No. 17005 and 18004; UNBSJ AUP no. 2017-2S-05, 2018-3I-01, and 2019-2S-04), the Canadian Wildlife Service (Permit No. ST2728 and MBS3001) and carried out under a Canadian Master Banding permit (10480). Access was granted to Gull Island in the Witless Bay Islands Ecological Reserve by the Newfoundland and Labrador Department of Parks and Natural Areas, had approval from Environment and Climate Change Canada Animal Care permits (EC-PN-08-026, 15GR01), and was carried out under a Canadian Banding Permit (10559G). Access to Funk Island was provided by the Newfoundland and Labrador Department of Parks and Natural Areas, and to Bonaventure Island by Parcs Quebec, and to both Islands by the Canadian Wildlife Service. Work at these islands was approved by the Animal Care Committee at Memorial University and carried out under a Canadian Master Banding Permit (10332). At Coats Island research was undertaken with approval of the Animal Care Committee at McGill University (2015-7599) the Canadian Wildlife Service (Permit No. NUN-01) and carried out under a Canadian Master Banding Permit (10892).

Results

The distribution of between-individual EMD values suggests differing levels of behavioural diversity among and within seabird families. All alcid populations had low behavioural diversity (dip test *p* values: MSI puffins = 0.452 and JI puffins = 0.141, MSI razorbills = 0.601 and JI razorbills = 0.992, and murres = 0.990; Figure 2). Puffins from JI, however, had the lowest *p* value relative to the other alcid populations, as indicated by subtly different migratory routes among tracked individuals (Figure 2) and high variation in distances travelled north, south and east (Figure 3d; Figure 4). In larids, herring gulls also had lower behavioural diversity (*p* = 0.736; Figure 2), especially in comparison to glaucous gulls that had higher behavioural diversity, indicated by a significant bimodal distribution (*p* = <0.001; Figure 2) and a distinct east or west migratory route from CI (Figure 3f; Figure 4). Within gannets, the BI population had lower behavioural diversity (*p* = 0.997) but the FI population had higher behavioural diversity (*p* = <0.001; Figure 2), as indicated by two distinct migratory routes and variation in the distance travelled south and east (Figure 3e; Figure 4).

Between-individual EMD values differed significantly among seabird families (H = 141.589, df = 2, *p* = < 0.001; Figure 3a, 3b, 3c). Between-individual EMD values were lower in alcids (46 - 1881 km) compared to larids (63 - 4895 km; z = -3.608, df = 2, *p* = <0.001) and sulids (69 - 5683 km; z = -11.682, df = 2, *p* = <0.001), indicating greater between-individual variation in these two families, but there was no difference between larids and sulids (z = -1.418; df = 2, *p* = 0.156). There was also variation in migratory behaviour within seabird families and species. In alcids, between-individual EMD values of puffins (280 ± 128 km) and razorbills (309 ± 176 km) from MSI were lower than JI puffins (817 ± 430 km) and razorbills (488 ± 202 km; Table 2; Figure 2). Overall, JI puffins had the highest average between-individual EMD values of the five alcid populations investigated (Table 2, Figure 2). Within larids, between-individual EMD values of glaucous gulls (2171 ± 1869 km) were both higher and had a greater range than herring gulls (516 ± 295 km). Within gannets, between-individual EMD values of birds from FI (1807 ± 1679 km) were higher and had a greater range relative to birds from BI (693 ± 421 km; Table 2; Figure 2).

When examining individual spatial consistency of migratory tracks within each species/colony, within-individual EMD values were significantly lower than between-individual EMD values in glaucous gulls, herring gulls, gannets and murres (Table 3, Figure 5), showing individual consistency in these species. Within-individual EMD values were also significantly lower than between-individual values in puffins and razorbills from JI (i.e., individual consistency); however, between- and within-individual EMD values did not differ significantly for these two species from MSI (Table 3, Figure 5).

Discussion

Our results partially align with our prediction that larids and sulids exhibit greater between-individual variation in migratory routes than alcids. Although the highest levels of behavioural diversity were observed in larids (i.e., glaucous gulls) and sulids (FI gannets), low behavioural diversity was also observed within these seabird families (i.e., herring gulls and BI gannets). Additionally, our results partly align with our prediction that all species display individual consistency. Indeed, individual consistency in overwintering locations was observed in seven of the nine populations studied, with only MSI puffins and razorbills lacking evidence of individual consistency. This lack of consistency, however, may be related to low sample sizes of individuals with repeat tracks in these populations relative to the other populations studied (Table 1). Overall, behavioural diversity in migratory routes varied among and within species and the differences in migratory routes were generally consistent within individuals, suggesting that some species (e.g., alcids) are more vulnerable to anthropogenic threats.

Behavioural Diversity

The species or populations with lower behavioural diversity identified in this study (alcids, BI gannets and herring gulls) are potentially at greater risk from regional or localised threats, while those with higher diversity (FI gannets and glaucous gulls) may be more resistant to change. To illustrate, if only part of a population over-winters in a location that is affected by regional changes in conditions (e.g., marine heatwaves; Wyatt et al., 2022) or the introduction of a new threat (e.g., an oil spill; Montevecchi et al., 2011), then only this part of the population will be affected rather than the entire population and, thus, the population is more likely to persist into the future. This is an important issue as marine environments are currently changing rapidly due to climate change (Steele et al., 2019; Weber et al., 2021). Indeed, marine heat waves are expected to increase in frequency (Wyatt et al., 2022) and some regions are warming faster than others (e.g., the Arctic; Rantanen et al., 2022). Furthermore, anthropogenic activities such as the rapid development of offshore wind infrastructure, also pose many threats to marine animals including seabirds (Williams et al., 2024).

The two gannet populations exhibited differing levels of behavioural diversity, showing that differences in behavioural variation exist within species. Among tagged gannets from FI, some had a trans-Atlantic strategy, while the remainder overwintered on the east coast of North America, an over-wintering location used by all tagged gannets from BI (Figure 3b, 3e). Gannets from other colonies also have distinct overwintering areas, such as those at Bass Rock (Kubetzki et al., 2009) and Skrúður (Garthe et al., 2016) in Scotland and Iceland, respectively. The BI gannets, therefore, are at greater risk of localised anthropogenic threats that occur along the east coast of North America. Indeed, the Deepwater Horizon oil spill during 2010 in the Gulf of

Mexico was a significant mortality event for gannets (Haney et al., 2014; Montevecchi et al., 2011). By contrast, gannets from FI may be buffered against such mortality events, as the birds that travel to northwest Africa would not have encountered the spill. It is important to note, however, that diversity in overwintering areas does not ensure the protection of a population against all threats. For example, gannets usually overwinter near the mouths of major river systems (Fifield et al., 2014) that are frequently the source of contaminants (Rattner & McGowan, 2007).

Like gannets from FI, high diversity in migratory routes was also observed in glaucous gulls from CI (Figure 3f), which contrasted with the low diversity in herring gulls from GI. Most of the tagged glaucous gulls migrated to the Labrador Sea, likely due to its high productivity (Davoren et al., 2002), but one travelled to the Sea of Okhotsk, another productive marine region (Mundo et al., 2024). This Atlantic-Pacific migratory spit has also been observed in another larid species (Sabine's gull, *Xema sabini*; Davis et al., 2016). As a result of this diversity, it is likely that this glaucous gull population will be more resistant to change than the herring gull's from GI that overwinter only on the northeast coast of North America. Indeed, although glaucous gulls visiting the Sea of Okhotsk will be at risk from regional productivity changes due to altering sea ice dynamics or from offshore oil and gas infrastructure around Sakhalin Island (Mundo et al., 2024), individuals overwintering in the Labrador Sea would avoid these threats.

In contrast to larids and sulids, behavioural diversity in alcids was consistently low across all species and populations, potentially making this seabird family more susceptible to environmental change and anthropogenic threats. Indeed, the murres investigated in this study overwintered in the highly productive Labrador Sea (Davoren et al., 2002), but all individuals used this area and this lack of diversity may be an issue as warming ocean temperatures result in northern range shifts that will lead to reduced daylight foraging time (Patterson et al., 2021). Additionally, low behavioural diversity was observed in puffins and razorbills from MSI, with most birds overwintering in the Gulf of Maine. This is the southern edge of the range for both these species (Lavers et al., 2020; Lowther et al., 2020), potentially constraining their distribution and explaining why these two populations have the lowest between-individual EMD values among the alcid species studied (Table 2; Figure 2). Furthermore, the southernly distribution of these populations means they are most likely to experience temperature related impacts (Hazen et al., 2013). In contrast, alcid populations breeding further north typically travel further from their colonies than those breeding at more southern colonies (Fayet et al., 2017), and this is the case for murres from CI along with puffins and razorbills from JI, with these puffins in particular exhibiting the highest diversity of the alcid populations studied (Figure 2).

There was overlap in the migratory routes of razorbills and puffins from both JI and MSI, with individuals from all four populations using the Gulf of Maine during non-breeding. Importantly, the Gulf of Maine is one of the fastest warming ocean regions (Pershing et al., 2015) and is experiencing changes in zooplankton and fish species composition (Pershing et al., 2021). Therefore, populations containing individuals that use the Gulf of Maine are at greater risk from these changes to food web dynamics, especially populations that predominantly use the Gulf of Maine (i.e., razorbills and puffins from MSI). The puffin population from JI, however, is less as risk from this regional warming in the Gulf of Maine as individuals also used waters in the mid-Atlantic and the Labrador Sea (Figure 3d). It is also important to consider that even when species or populations have overlap in migratory routes, there can still be variation in the level of spatial overlap with threats. For example, two murre species (thick-billed and common, *Uria aalge*) from Canadian colonies have high non-breeding range overlap, but common murres have greater spatial overlap with hydrocarbon infrastructure (e.g., extraction and shipping; McFarlane Tranquilla et al., 2014).

Individual Consistency

All species and populations, except razorbills and puffins populations from MSI, displayed individual spatial consistency in their overwintering migratory routes. These results align with the many studies that have shown site fidelity in the overwintering locations of seabirds (Ceia & Ramos, 2015; Phillips et al., 2017), including other populations of puffins (Guilford et al., 2011), gannets (Grecian et al., 2019) and herring gulls (Clark et al., 2016). This site fidelity may result from experiential learning before individuals reach maturity (i.e., the exploration-refinement hypothesis; Guilford et al., 2011). Indeed, juvenile seabirds display more explorative behaviour during the non-breeding period in comparison to adult birds (e.g., longer migrations, sinuous pathways; Péron & Grémillet, 2013; Ponti et al., 2024). Additionally, returning to the same locations where prey is annually persistent is more efficient than searching for new areas each year (McNamara & Dall, 2010). For example, static features (e.g., bathymetry) combine with changes in temperature and salinity to create oceanographic features (e.g., ocean fronts, coastal upwellings) that result in prey concentrations at predictable locations across multiple spatial and temporal scales (Phillips et al., 2017; Wakefield et al., 2009). Individual consistency is, however, expected to be greater at higher latitudes (e.g., temperate and polar regions) compared to lower latitudes (e.g., tropics) because seasonal shifts are less pronounced closer to the equator making prey aggregations less predictable (Weimerskirch, 2007). Additionally, tropical seabirds often rely on other marine predators (e.g., dolphin and tuna) to concentrate prey (Au & Pitman, 1986; Jaquemet et al., 2004), that are less predictable than static marine features.

Conclusion

Overall, the diversity in migratory routes observed in some species or populations, combined with the individual site fidelity to overwintering locations, shows that some or all individuals in the populations examined may be consistently exposed to the same threats or adverse conditions across years, with potential impacts on population dynamics. The lower migratory route diversity of alcids suggests that more individuals of these species are at risk from the same localized threats in their more limited overwintering distribution than larids and sulids. There are examples, however, of more vulnerable species or populations (i.e., low behavioural diversity) within all three families. Therefore, this study is an important step towards identifying species/populations that may be more as risk (i.e., low behavioural diversity) during their non-breeding season. Indeed, tracking data are commonly used to inform conservation and management of marine taxa (Davies et al., 2021; Hays et al., 2019; Hindell et al., 2020) because understanding spatial patterns can help identify areas that contribute to the persistence of species (Beal et al., 2021). However, as seabird research rarely compares across species (Brown et al., 2021), this study may aid in identifying conservation targets. Finally, understanding variation among individuals within a species/population also has benefits for understanding other aspects of seabird ecology, such as intra- and inter-specific competition (de Grissac et al., 2016; Phillips et al., 2004).

References

Anderson, C. M., Gilchrist, H. G., Ronconi, R. A., Shlepr, K. R., Clark, D. E., Fifield, D. A., Robertson, G. J., & Mallory, M. L. (2020). Both short and long distance migrants use energy-minimizing migration strategies in North American herring gulls. *Mov. Ecol.*, 8(1). https://doi.org/10.1186/s40462-020-00207-9

Au, D. W. K., & Pitman, R. L. (1986). Seabird interactions with dolphins and tuna in the eastern tropical Pacific. *Condor*, 88(3), 304–317.

Baak, J. E., Mallory, M. L., Anderson, C. M., Auger-Méthé, M., MacDonald, C. A., Janssen, M. H., Gilchrist, H. G., Provencher, J. F., & Gutowsky, S. E. (2021a). Inter-individual variation in the migratory behaviour of a generalist seabird, the herring gull (*Larus smithsoniansus*), from the Canadian Arctic. *Anim. Migr.*, 8(1), 144–155. https://doi.org/10.1515/ami-2020-0109

Baak, J. E., Patterson, A., Grant Gilchrist, H., & Elliott, K. H. (2021b). First evidence of diverging migration and overwintering strategies in glaucous gulls (*Larus hyperboreus*) from the Canadian Arctic. *Anim. Migr.*, 8(1), 98–109. https://doi.org/10.1515/ami-2020-0107

Baran, M. A., Kress, S. W., Shannon, P., Lyons, D. E., Major, H. L., & Diamond, A. W. (2022). Overwinter movement of Atlantic puffins (*Fratercula arctica*) breeding in the Gulf of Maine: inter- and intra-colony effects. *Waterbirds*, 45(1), 1–16. https://doi.org/10.1675/063.045.0103

Beal, M., Oppel, S., Handley, J., Pearmain, E. J., Morera-Pujol, V., Carneiro, A. P. B., Davies, T. E., Phillips, R. A., Taylor, P. R., Miller, M. G. R., Franco, A. M. A., Catry, I., Patrício, A. R., Regalla, A., Staniland, I., Boyd, C., Catry, P., & Dias, M. P. (2021). track2KBA: an R package for identifying important sites for biodiversity from tracking data. *Methods Ecol. Evol.*, 12(12), 2372–2378. https://doi.org/10.1111/2041-210X.13713

Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: a meta-analysis. *Anim. Behav.*, 77(4), 771–783. https://doi.org/10.1016/j.anbehav.2008.12.022

Bradshaw, C. J. A., Hindell, M. A., Sumner, M. D., & Michael, K. J. (2004). Loyalty pays: potential life history consequences of fidelity to marine foraging regions by southern elephant seals. *Anim. Behav.*, 68(6), 1349–1360. https://doi.org/10.1016/j.anbehav.2003.12.013

Broderick, A. C., Coyne, M. S., Fuller, W. J., Glen, F., & Godley, B. J. (2007). Fidelity and over-wintering of sea turtles. *Proc. R. Soc. B.*, 274(1617), 1533–1539. https://doi.org/10.1098/rspb.2007.0211

Brown, J. M., van Loon, E. E., Bouten, W., Camphuysen, K. C. J., Lens, L., Müller, W., Thaxter, C. B., & Shamoun-Baranes, J. (2021). Long-distance migrants vary migratory behaviour as much as short-distance migrants: An individual-level comparison from a seabird species with diverse migration strategies. *J. Anim. Ecol.*, 90(5), 1058–1070. https://doi.org/10.1111/1365-2656.13431

Ceia, F. R., & Ramos, J. A. (2015). Individual specialization in the foraging and feeding strategies of seabirds: a review. Mar. Biol., 162(10), 1923–1938. https://doi.org/10.1007/s00227-015-2735-4

Clark, D. E., Koenen, K. K. G., Whitney, J. J., Mackenzie, K. G., & Destefano, S. (2016). Fidelity and persistence of ring-billed (*Larus delawarensis*) and herring (*Larus argentatus*) gulls to wintering sites. *Waterbirds*, 39, 220–234. https://doi.org/10.1675/063.039.sp120

Clavel, J., Julliard, R., & Devictor, V. (2011). Worldwide decline of specialist species: toward a global functional homogenization? *Front. Ecol. Environ.*, 9(4), 222–228. https://doi.org/10.1890/080216

Daunt, F., Reed, T. E., Newell, M., Burthe, S., Phillips, R. A., Lewis, S., & Wanless, S. (2014). Longitudinal bio-logging reveals interplay between extrinsic and intrinsic carry-over effects in a long-lived vertebrate. *Ecology*, 95(8), 2077–2083. https://doi.org/10.1890/13-1797.1

Davies, T. E., Carneiro, A. P. B., Tarzia, M., Wakefield, E., Hennicke, J. C., Frederiksen, M., Hansen, E. S., Campos, B., Hazin, C., Lascelles, B., Anker-Nilssen, T., Arnardóttir, H., Barrett, R. T., Biscoito, M., Bollache, L., Boulinier, T., Catry, P., Ceia, F. R., Chastel, O., … Dias, M. P. (2021). Multispecies tracking reveals a major seabird hotspot in the North Atlantic. *Conserv. Lett.*, 14(5), 1–14. https://doi.org/10.1111/conl.12824

Davis, S. E., Maftei, M., & Mallory, M. L. (2016). Migratory connectivity at high latitudes: Sabine's gulls (*Xema sabini*) from a colony in the Canadian high arctic migrate to different oceans. *PLoS One*, 11(12), 1–12. https://doi.org/10.1371/journal.pone.0166043

Davoren, G. K., Montevecchi, W. A., & Anderson, J. T. (2002). Scale-dependent associations of predators and prey: constraints imposed by flightlessness of common murres. *Mar. Ecol. Prog. Ser.*, 245, 259–272. https://doi.org/10.3354/meps245259

de Grissac, S., Börger, L., Guitteaud, A., & Weimerskirch, H. (2016). Contrasting movement strategies among juvenile albatrosses and petrels. *Sci. Rep.*, 6, 1–12. https://doi.org/10.1038/srep26103

Dias, M. P., Granadeiro, J. P., Phillips, R. A., Alonso, H., & Catry, P. (2011). Breaking the routine: Individual Cory's shearwaters shift winter destinations between hemispheres and across Ocean basins. *Proc. R. Soc. B.*, 278(1713), 1786–1793. https://doi.org/10.1098/rspb.2010.2114

Dunn, R. E., Wanless, S., Green, J. A., Harris, M. P., & Daunt, F. (2019). Effects of body size, sex, parental care and moult strategies on auk diving behaviour outside the breeding season. *J. Avian Biol.*, 50(7), 1–14. https://doi.org/10.1111/jav.02012

Elliott, K. H., Ricklefs, R. E., Gaston, A. J., Hatch, S. A., Speakman, J. R., & Davoren, G. K. (2013). High flight costs, but low dive costs, in auks support the biomechanical hypothesis for flightlessness in penguins. *PNAS*, 110(23), 9380–9384. https://doi.org/10.1073/pnas.1304838110

Engler, J. O., Stiels, D., Schidelko, K., Strubbe, D., Quillfeldt, P., & Brambilla, M. (2017). Avian SDMs: current state, challenges, and opportunities. *J. Avian Biol.*, 48(12), 1483–1504. https://doi.org/10.1111/jav.01248

Fayet, A. L., Freeman, R., Anker-Nilssen, T., Diamond, A., Erikstad, K. E., Fifield, D., Fitzsimmons, M. G., Hansen, E. S., Harris, M. P., Jessopp, M., Kouwenberg, A. L., Kress, S., Mowat, S., Perrins, C. M., Petersen, A., Petersen, I. K., Reiertsen, T. K., Robertson, G. J., Shannon, P., … Guilford, T. (2017). Ocean-wide drivers of migration strategies and their influence on population breeding performance in a declining seabird. *Curr. Biol.*, 27(24), 3871–3873. https://doi.org/10.1016/j.cub.2017.11.009

Fayet, A. L., Freeman, R., Shoji, A., Boyle, D., Kirk, H. L., Dean, B. J., Perrins, C. M., & Guilford, T. (2016). Drivers and fitness consequences of dispersive migration in a pelagic seabird. *Behav. Ecol.*, 27(4), 1061–1072. https://doi.org/10.1093/beheco/arw013

Fifield, D. A., Montevecchi, W. A., Garthe, S., Robertson, G. J., Kubetzki, U., & Rail, J. F. (2014). Migratory tactics and wintering areas of northern gannets (morus bassanus) breeding in North America. Ornithol. Monogr., 79, 1–63. https://doi.org/10.1642/aoum.79-1

Fort, J., Pettex, E., Tremblay, Y., Lorentsen, S.-H., Garthe, S., Votier, S., Pons, J. B., Siorat, F., Furness, R. W., Grecian, J., Bearhop, S., Montevecchi, W. A., & Grémillet, D. (2012). Meta-population evidence of oriented chain migration in northern gannets (*Morus bassanus*). *Front. Ecol. Environ.*, 10(5), 237–242. https://doi.org/10.1890/l

Fort, J., Steen, H., Strøm, H., Tremblay, Y., Grønningsæter, E., Pettex, E., Porter, W. P., & Grémillet, D. (2013). Energetic consequences of contrasting winter migratory strategies in a sympatric Arctic seabird duet. *J. Avian Biol.*, 44(3), 255–262. https://doi.org/10.1111/j.1600-048X.2012.00128.x

Franklin, K. A., Norris, K., Gill, J. A., Ratcliffe, N., Bonnet-Lebrun, A.-S., Butler, S. J., Cole, N. C., Jones, C. G., Lisovski, S., Ruhomaun, K., Tatayah, V., & Nicoll, M. A. C. (2022). Individual consistency in migration strategies of a tropical seabird, the Round Island petrel. *Mov. Ecol.*, 10, 1–14. https://doi.org/10.1186/s40462-022-00311-y

Freeman, J. B., & Dale, R. (2013). Assessing bimodality to detect the presence of a dual cognitive process. *Behav. Res. Methods*, 45(1), 83–97. https://doi.org/10.3758/s13428-012-0225-x

Garthe, S., Hallgrimsson, G. T., Montevecchi, W. A., Fifield, D., & Furness, R. W. (2016). East or west? Migration routes and wintering sites of Northern Gannets *Morus bassanus* from south-eastern Iceland. *Mar. Biol.*, 163(7), 1–9. https://doi.org/10.1007/s00227-016-2918-7

Garthe, S., Schwemmer, H., Peschko, V., Markones, N., Müller, S., Schwemmer, P., & Mercker, M. (2023). Large-scale effects of offshore wind farms on seabirds of high conservation concern. *Sci. Rep.*, 13(1), 1–13. https://doi.org/10.1038/s41598-023-31601-z

Gatt, M. C., Granadeiro, J. P., & Catry, P. (2021). Migrants and residents of a long-lived seabird differ in their behavioural response to a stressor. *J. Avian Biol.*, 52(2), 1–8. https://doi.org/10.1111/jav.02589

Gilroy, J. J., Gill, J. A., Butchart, S. H. M., Jones, V. R., Aldina, &, & Franco, M. A. (2016). Migratory diversity predicts population declines in birds. *Ecol. Lett.*, 19(3), 308–317. https://doi.org/10.1111/ele.12569

Grecian, W. J., Williams, H. J., Votier, S. C., Bearhop, S., Cleasby, I. R., Grémillet, D., Hamer, K. C., Nuz, M. Le, Lescroël, A., Newton, J., Patrick, S. C., Phillips, R. A., Wakefield, E. D., & Bodey, T. W. (2019). Individual spatial consistency and dietary flexibility in the migratory behavior of northern gannets wintering in the northeast Atlantic. *Front. Ecol. Evol.*, 7, 1–11. https://doi.org/10.3389/fevo.2019.00214

Guilford, T., Freeman, R., Boyle, D., Dean, B., Kirk, H., Phillips, R., & Perrins, C. (2011). A dispersive migration in the atlantic Puffin and its implications for migratory navigation. *PLoS ONE*, 6(7), 1–8. https://doi.org/10.1371/journal.pone.0021336

Gutowsky, S. E., Hipfner, J. M., Maftei, M., Boyd, S., Auger-Méthé, M., Yurkowski, D. J., & Mallory, M. L. (2020). First insights into Thayer's gull *Larus glaucoides thayeri* migatory and overwinter patterns along the northwest Pacific coast. *Mar. Ornithol.*, 48, 9–16. http://doi.org/10.5038/2074-1235.48.1.1340

Haney, J. C., Geiger, H. J., & Short, J. W. (2014). Bird mortality from the Deepwater Horizon oil spill. II. Carcass sampling and exposure probability in the coastal Gulf of Mexico. *Mar. Ecol. Prog. Ser.*, 513, 239–252. https://doi.org/10.3354/meps10839

Hartigan, J. A., & Hartigan, P. M. (1985). The Dip Test of unimodality. *Ann. Stat.*, 13(1), 70.

Hays, G. C., Bailey, H., Bograd, S. J., Bowen, W. D., Campagna, C., Carmichael, R. H., Casale, P., Chiaradia, A., Costa, D. P., Cuevas, E., Nico de Bruyn, P. J., Dias, M. P., Duarte, C. M., Dunn, D. C., Dutton, P. H., Esteban, N., Friedlaender, A., Goetz, K. T., Godley, B. J., … Sequeira, A. M. M. (2019). Translating marine animal tracking data into conservation policy and management. *Trends Ecol. Evol.*, 34(5), 459–473. https://doi.org/10.1016/j.tree.2019.01.009

Hazen, E. L., Jorgensen, S., Rykaczewski, R. R., Bograd, S. J., Foley, D. G., Jonsen, I. D., Shaffer, S. A., Dunne, J. P., Costa, D. P., Crowder, L. B., & Block, B. A. (2013). Predicted habitat shifts of Pacific top predators in a changing climate. *Nature*, 3(3), 234–238. https://doi.org/10.1038/nclimate1686

Hedenström, A. (2008). Adaptations to migration in birds: Behavioural strategies, morphology and scaling effects. *Philo. Trans. R. Soc. B.*, 363(1490), 287–299. https://doi.org/10.1098/rstb.2007.2140

Hindell, M. A., Reisinger, R. R., Ropert-Coudert, Y., Hückstädt, L. A., Trathan, P. N., Bornemann, H., Charrassin, J. B., Chown, S. L., Costa, D. P., Danis, B., Lea, M. A., Thompson, D., Torres, L. G., Van de Putte, A. P., Alderman, R., Andrews-Goff, V., Arthur, B., Ballard, G., Bengtson, J., … Raymond, B. (2020). Tracking of marine predators to protect Southern Ocean ecosystems. *Nature*, 580(7801), 87–92. https://doi.org/10.1038/s41586-020-2126-y

Jaquemet, S., Le Corre, M., & Weimerskirch, H. (2004). Seabird community structure in a coastal tropical environment: importance of natural factors and fish aggregating devices (FADs). *Mar. Ecol. Prog. Ser.*, 268, 281–292. https://doi.org/10.3354/meps268281

Kranstauber, B., Smolla, M., & Safi, K. (2017). Similarity in spatial utilization distributions measured by the earth mover's distance. *Methods Ecol. Evol.*, 8(2), 155–160. https://doi.org/10.1111/2041-210X.12649

Kranstauber, B., Smolla, M., & Scharf, A. (2021). move: visualising and analysing animal track data (R package version 4.1.6.).

Kubetzki, U., Garthe, S., Fifield, D., Mendel, B., & Furness, R. W. (2009). Individual migratory schedules and wintering areas of northern gannets. *Mar. Ecol. Prog. Ser.*, 391, 257–265. https://doi.org/10.3354/meps08254

Lack, D. (1954). The natural regulation of animal numbers. Clarendon Press.

Lavers, J. L., Hipfner, M., & Chapdelaine, G. (2020). Razorbill (*Alca torda*). In Billerman SM (Ed.), Birds of the World (1.0). Cornell Lab of Ornithology.

Lisovski, S., Bauer, S., Briedis, M., Davidson, S. C., Dhanjal-Adams, K. L., Hallworth, M. T., Karagicheva, J., Meier, C. M., Merkel, B., Ouwehand, J., Pedersen, L., Rakhimberdiev, E., Roberto-Charron, A., Seavy, N. E., Sumner, M. D., Taylor, C. M., Wotherspoon, S. J., & Bridge, E. S. (2020). Light-level geolocator analyses: a user's guide. *J. Anim. Ecol.*, 89(1), 221–236. https://doi.org/10.1111/1365-2656.13036

Lowther, P., Diamond, A., Kress, S., Robertson, G., Russel, K., Nettleship, D., Kirwan, G., Christie, D., Sharpe, C., Garcia, E., & Boesman, P. (2020). Atlantic puffin (*Fratercula arctica*). In Billerman SM (Ed.), Birds of the World (1.0). Cornell Lab of Ornithology.

Maechler, M. (2024). diptest: Hartigan's Dip Test for unimodality - corrected (R Package Version 0.77.1).

McFarlane Tranquilla, L. A., Montevecchi, W. A., Fifield, D. A., Hedd, A., Gaston, A. J., Robertson, G. J., & Phillips, R. A. (2014). Individual winter movement strategies in two species of murre (Uria spp.) in the Northwest Atlantic. *PLoS ONE*, 9(4), 1–13. https://doi.org/10.1371/journal.pone.0090583

McNamara, J. M., & Dall, S. R. X. (2010). Information is a fitness enhancing resource. *Oikos*, 119(2), 231–236. https://doi.org/10.1111/j.1600-0706.2009.17509.x

Merkel, B., Phillips, R. A., Descamps, S., Yoccoz, N. G., Moe, B., & Strøm, H. (2016). A probabilistic algorithm to process geolocation data. *Mov. Ecol.*, 4(1). https://doi.org/10.1186/s40462-016-0091-8

Montevecchi, W. A., Hedd, A., McFarlane Tranquilla, L., Fifield, D. A., Burke, C. M., Regular, P. M., Davoren, G. K., Garthe, S., Robertson, G. J., & Phillips, R. A. (2012). Tracking seabirds to identify ecologically important and high risk marine areas in the western North Atlantic. *Biol. Conserv.*, 156, 62–71. https://doi.org/10.1016/j.biocon.2011.12.001

Montevecchi, W. A., Fifield, D., Burke, C., Garthe, S., Hedd, A., Rail, J. F., & Robertson, G. (2011). Tracking long-distance migration to assess marine pollution impact. *Biol. Lett.*, 8(2), 218–221. https://doi.org/10.1098/rsbl.2011.0880

Mowbray, T. (2020). Northern gannet (*Morus bassanus*). In Billerman SM (Ed.), Birds of the World (1.0). Cornell Lab of Ornithology.

Mundo, R., Matsunaka, T., Nakanowatari, T., Taniuchi, Y., Inoue, M., Kasai, H., Mashita, K., Mitsunushi, H., & Nagao, S. (2024). A review of the oceanographic structure and biological productivity in the southern Okhotsk Sea. *Prog. Oceanogr.*, 221, 1–22. https://doi.org/10.1016/j.pocean.2023.103194

Nelson, J. B. (2002). The Atlantic Gannet (2nd ed.). Fennix Books.

Newton, I. (2004). Population limitation in migrants. *Ibis*, 146(2), 197–226. https://doi.org/10.1111/j.1474-919X.2004.00293.x

Newton, I. (2008). The Migration Ecology of Birds. Academic Press.

Nussey, D. H., Wilson, A. J., & Brommer, J. E. (2007). The evolutionary ecology of individual phenotypic plasticity in wild populations. *J. Evol. Biol.*, 20(3), 831–844. https://doi.org/10.1111/j.1420-9101.2007.01300.x

Patterson, A., Gilchrist, H., Gaston, A., & Elliott, K. (2021). Northwest range shifts and shorter wintering period of an Arctic seabird in response to four decades of changing ocean climate. *Mar. Ecol. Prog. Ser.*, 679, 163–179. https://doi.org/10.3354/meps13890

Péron, C., & Grémillet, D. (2013). Tracking through life stages: adult, immature and juvenile autumn migration in a long-lived seabird. *PLoS ONE*, 8(8), 1–14. https://doi.org/10.1371/journal.pone.0072713

Pershing, A. J., Alexander, M. A., Brady, D. C., Brickman, D., Curchitser, E. N., Diamond, A. W., McClenachan, L., Mills, K. E., Nichols, O. C., Pendleton, D. E., Record, N. R., Scott, J. D., Staudinger, M. D., & Wang, Y. (2021). Climate impacts on the Gulf of Maine ecosystem: a review of observed and expected changes in 2050 from rising temperatures. *Elem. Sci. Anth.*, 9(1), 1–8. https://doi.org/10.1525/elementa.2020.00076

Pershing, A. J., Alexander, M. A., Hernandez, C. M., Kerr, L. A., Bris, A. L., Mills, K. E., Nye, J. A., Record, N. R., Scannell, H. A., Scott, J. D., Sherwood, G. D., & Thomas, A. C. (2015). Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. *Sci.*, 350(6262), 809–812. https://doi.org/10.1126/science.aac9819

Peschko, V., Mercker, M., & Garthe, S. (2020). Telemetry reveals strong effects of offshore wind farms on behaviour and habitat use of common guillemots (*Uria aalge*) during the breeding season. *Mar. Biol.*, 167(8), 1–3. https://doi.org/10.1007/s00227-020-03735-5

Phillips, R. A., Lewis, S., González-Solís, J., & Daunt, F. (2017). Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds. *Mar. Ecol. Prog. Ser.*, 578, 117–150. https://doi.org/10.3354/meps12217

Phillips, R. A., Silk, J. R. D., Phalan, B., Catry, P., & Croxall, J. P. (2004). Seasonal sexual segregation in two *Thalassarche* albatross species: competitive exclusion, reproductive role specializaion or foraging niche divergence? *Proc. R. Soc. B*., 271(1545), 1283–1291. https://doi.org/10.1098/rspb.2004.2718

Pierotti, R., & Annett, C. A. (1991). Diet choice in the herring gull: constraints imposed by reproductive and ecological factors. *Ecology*, 72(1), 319–328.

Ponti, R., Morera-Pujol, V., Sallent, Á., González-Solís, J., & Ramos, R. (2024). Age-related spatial ecology of Audouin's gull during the non-breeding season. *Endang. Species Res*., 55, 155–167. https://doi.org/10.3354/esr01370

R Core Team. (2023). R: a language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/

Rantanen, M., Karpechko, A. Y., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., Vihma, T., & Laaksonen, A. (2022). The Arctic has warmed nearly four times faster than the globe since 1979. *Commun. Earth Environ.*, 3(1). https://doi.org/10.1038/s43247-022-00498-3

Rattner, B. A., & McGowan, P. C. (2007). Potential hazards of environmental contaminants to avifauna residing in the Chesapeake Bay estuary. *Waterbirds*, 30, 63–81. https://doi.org/10.1675/1524-4695(2007)030[0063:PHOECT]2.0.CO;2

Rodríguez, A., Holmes, N. D., Ryan, P. G., Wilson, K.-J., Faulquier, L., Murillo, Y., Raine, A. F., Penniman, J. F., Neves, V., Rodríguez, B., Negro, J. J., Chiaradia, A., Dann, P., Anderson, T., Metzger, B., Shirai, M., Deppe, L., Wheeler, J., Hodum, P., … Couzi, F.-X. (2017). Society for Conservation Biology Seabird mortality induced by land-based artificial lights. *Conserv. Biol.*, 31(5), 986–1001.

Ronconi, R. A., Lieske, D. J., McFarlane Tranquilla, L. A., Abbott, S., Allard, K. A., Allen, B., Black, A. L., Bolduc, F., Davoren, G. K., Diamond, A. W., Fifield, D. A., Garthe, S., Gjerdrum, C., Hedd, A., Mallory, M. L., Mauck, R. A., McKnight, J., Montevecchi, W. A., Pollet, I. L., … Wilhelm, S. I. (2022). Predicting Seabird Foraging Habitat for Conservation Planning in Atlantic Canada: Integrating Telemetry and Survey Data Across Thousands of Colonies. *Front. Mar. Sci.*, 9, 1–18. https://doi.org/10.3389/fmars.2022.816794

Runnells, E., Montevecchi, W., & Davoren, G. (2024). Spatiotemporal and isotopic niche overlap among Atlantic puffins, razorbills, and common murres during the non-breeding season in the Northwest Atlantic. *Mar. Ecol. Prog. Ser.*, 739, 241–256. https://doi.org/10.3354/meps14614

Spencer, N. C., Gilchrist, H. G., Strøm, H., Allard, K. A., & Mallory, M. L. (2016). Key winter habitat of the ivory gull *Pagophila eburnea* in the Canadian Arctic. Endanger. *Species Res.*, 31(1), 33–45. https://doi.org/10.3354/esr00747

Stearns, S. (1992). The evolution of life histories. Oxford University Press.

Steele, J. H., Brink, K. H., & Scott, B. E. (2019). Comparison of marine and terrestrial ecosystems: suggestions of an evolutionary perspective influenced by environmental variation. *ICES J. Mar. Sci.*, 76(1), 50–59. https://doi.org/10.1093/icesjms/fsy149

Sydeman, W. J., Poloczanska, E., Reed, T. E., & Ann, S. (2015). Climate change and marine vertebrates. *Sci*., 350(6262), 772–777. https://doi.org/10.1126/science.aac9874

Thiers, L., Delord, K., Barbraund, C., Phillips, R. A., Pinaud, D., & Weimerskirch, H. (2014). Foraging zones of the two sibling species of giant petrels in the Indian Ocean throughout the annual cycle: implication for their conservation. *Mar. Ecol. Prog. Ser.*, 499, 233–248. https://doi.org/10.3354/meps10620

van Donk, S., Camphuysen, K. C. J., Shamoun-Baranes, J., & van der Meer, J. (2017). The most common diet results in low reproduction in a generalist seabird. *Ecol. Evol.*, 7(13), 4620–4629. https://doi.org/10.1002/ece3.3018

Wakefield, E. D., Phillips, R. A., & Matthiopoulos, J. (2009). Quantifying habitat use and preferences of pelagic seabirds using individual movement data: a review. *Mar. Ecol. Prog. Ser.*, 391, 165–182. https://doi.org/10.3354/meps08203

Weber, S. B., Richardson, A. J., Brown, J., Bolton, M., Clark, B. L., Godley, B. J., Leat, E., Oppel, S., Shearer, L., Soetaert, K. E. R., Weber, N., & Broderick, A. C. (2021). Direct evidence of a prey depletion “halo” surrounding a pelagic predator colony. *PNAS*, 118(28), 1–8. https://doi.org/10.1073/pnas.2101325118/-/DCSupplemental

Weimerskirch, H. (2007). Are seabirds foraging for unpredictable resources? *Deep-Sea Res. II: Top. Stud. Oceanogr.*, 54(3–4), 211–223. https://doi.org/10.1016/j.dsr2.2006.11.013

Weiser, E., & Gilchrist, G. H. (2020). Glaucous gull (*Larus hyperboreus*). In Billerman SM (Ed.), Birds of the World (1.0). Cornell Lab of Ornithology.

Weseloh, D. V., Heber, C. E., Mallory, M. L., Poole, A. F., Ellis, J. C., Pyle, P., & Patten, M. A. (2024). American herring gull (*Larus smithsonius*). In Billerman SM (Ed.), Birds of the World (1.0). Cornell Lab of Ornithology.

Williams, K. A., Gulka, J., Cook, A. S. C. P., Diehl, R. H., Farnsworth, A., Goyert, H., Hein, C., Loring, P., Mizrahi, D., Petersen, I. K., Peterson, T., Press, K. M. C., & Stenhouse, I. J. (2024). A framework for studying the effects of offshore wind energy development on birds and bats in the Eastern United States. *Front. Mar. Sci.*, 11, 1–18. https://doi.org/10.3389/fmars.2024.1274052

Wolf, M., & Weissing, F. J. (2012). Animal personalities: Consequences for ecology and evolution. *Trends Ecol. Evol.*, 27(8), 452–461. https://doi.org/10.1016/j.tree.2012.05.001

Wyatt, A. M., Resplandy, L., & Marchetti, A. (2022). Ecosystem impacts of marine heat waves in the northeast Pacific. *Biogeosciences*, 19(24), 5689–5705. https://doi.org/10.5194/bg-19-5689-2022

Zuur, A. F., & Ieno, E. N. (2016). A protocol for conducting and presenting results of regression-type analyses. *Methods Ecol. Evol.*, 7(6), 636–645. https://doi.org/10.1111/2041-210X.12577

Table 1. Summary of non-breeding distribution data from the six seabird species across the six colonies in the northwest Atlantic. The number of individuals including those with tracks in multiple years, tag type (GPS/GLS) and model are shown, along with the source for further information on deployment, retrieval and processing methods.

Species	Colony	Total Individuals	Repeat Individuals	Total Tracks	Tag Type and Model	Tagging Period	Details on Deployment and Processing Method
American herring gull (*Larus argentatus*)	Gull Island	7	6	13	**GPS** – Ecotone Harrier GPS-UHF	2015-2017	Anderson et al., 2020
glaucous gull (*Larus hyperboreus*)	Coats Island	6	3	9	**GLS** – Biotrack MK3005 **GPS** – Ecotone Sterna and Kite-M	2017-2019 2018-2019	Baak et al., 2021
northern gannet (*Morus bassanus*)	Bonaventure Island	25	11	36	**GLS** – Earth and Ocean Technologies Geo-LT and Lotek LTD2400	2004-2006	Fifield et al., 2014
	Funk Island	9	6	15		2005-2007	
Thick-billed murre (*Uria lomvia*)	Coats Island	12	7	19	**GLS** – Lotek Lat2800	2018-2020	Patterson et al., 2021
Atlantic puffin (*Fratercula arctica*)	James Island	16	8	24	**GLS** – Migrate Technology Ltd C65+ and C330	2019-2024	Runnells et al. (Thesis) & Legard et al. (Chapter 3)
	Machias Seal Island	23	2	25	**GLS** – Biotrack MK3005 and MK4093	2014-2017 & 2018-2019	Baran et al., 2022
razorbill (*Alca torda*)	James Island	28	13	42	**GLS** – Biotrack MK3006, Migrate Technology Ltd C330 and Lotek Lat2800	2017-2024	Legard et al. (Chapter 3)
	Machias Seal Island	17	2	19	**GLS** – Biotrack MK3006	2017-2019	Dodds (Thesis) & Legard et al. (Chapter 3)

Table 2. Summary of between-individual EMD value comparisons within each species within the three seabird families (Alcidae, Laridae, Sulidae): glaucous gulls (GLGU), American herring gulls (HERG), northern gannets (NOGA, split into Bonaventure Island and Funk Island), Atlantic puffin (ATPU, split into James Island and Machias Seal Island), razorbill (RAZO, split into James Island and Machias Seal Island) and thick-billed murre (TBMU). Z and *p* values from a post-hoc Dunn's test following a Kruskal-Wallis test are reported. Significant *p* values are shown in bold.

Family	Comparison	Z	*p*
Alcids	ATPU MSI - ATPU JI	**-20.513**	**<0.001**
	ATPU MSI - RAZO MSI	-1.584	0.324
	ATPU MSI - RAZO JI	**-13.049**	**<0.001**
	ATPU MSI - TBMU	**-8.588**	**<0.001**
	ATPU JI - RAZO MIS	**15.589**	**<0.001**
	ATPU JI - RAZO JI	**12.022**	**<0.001**
	ATPU JI - TBMU	**8.182**	**<0.001**
	RAZO MSI - RAZO JI	**-8.538**	**<0.001**
	RAZO MSI - TBMU	**-6.226**	**<0.001**
	RAZO JI - TBMU	0.347	0.808
Larids	GLGU - HERG	**4.547**	**<0.001**
Sulids	NOGA BI - NOGA FI	**-5.828**	**<0.001**

Table 3. Results of generalised linear models (GLMs) comparing EMD values within-individuals relative to between-individuals of American herring gull, glaucous gull, northern gannet, thick-billed murre, Atlantic puffin and razorbill at each colony where applicable. Significant differences between within-individuals and between-individuals are shown in bold.

Species	Colony	estimate ± SE	t value	*p* value
American herring gull (*Larus argentatus*)	Gull Island	**-404.5 ± 122.2**	**-3.311**	**0.001**
glaucous gull (*Larus hyperboreus*)	Coats Island	**-1476.7 ± 358.9**	**-4.115**	**<0.001**
northern gannet (*Morus bassanus*)	Bonaventure Island	**-433.7 ± 50.7**	**-8.550**	**<0.001**
	Funk Island	**-1245.1 ± 251.1**	**-4.959**	**<0.001**
thick-billed murre (*Uria lomvia*)	Coats Island	**-242.7 ± 51.7**	**-4.694**	**<0.001**
Atlantic puffin (*Fratercula arctica*)	James Island	**-578.6 ± 102.0**	**-5.675**	**<0.001**
	Machias Seal Island	61.7 ± 90.8	0.680	0.497
Razorbill (*Alca torda*)	James Island	**-163.6 ± 44.3**	**-3.695**	**<0.001**
	Machias Seal Island	-100.2 ± 125.2	-0.800	0.425

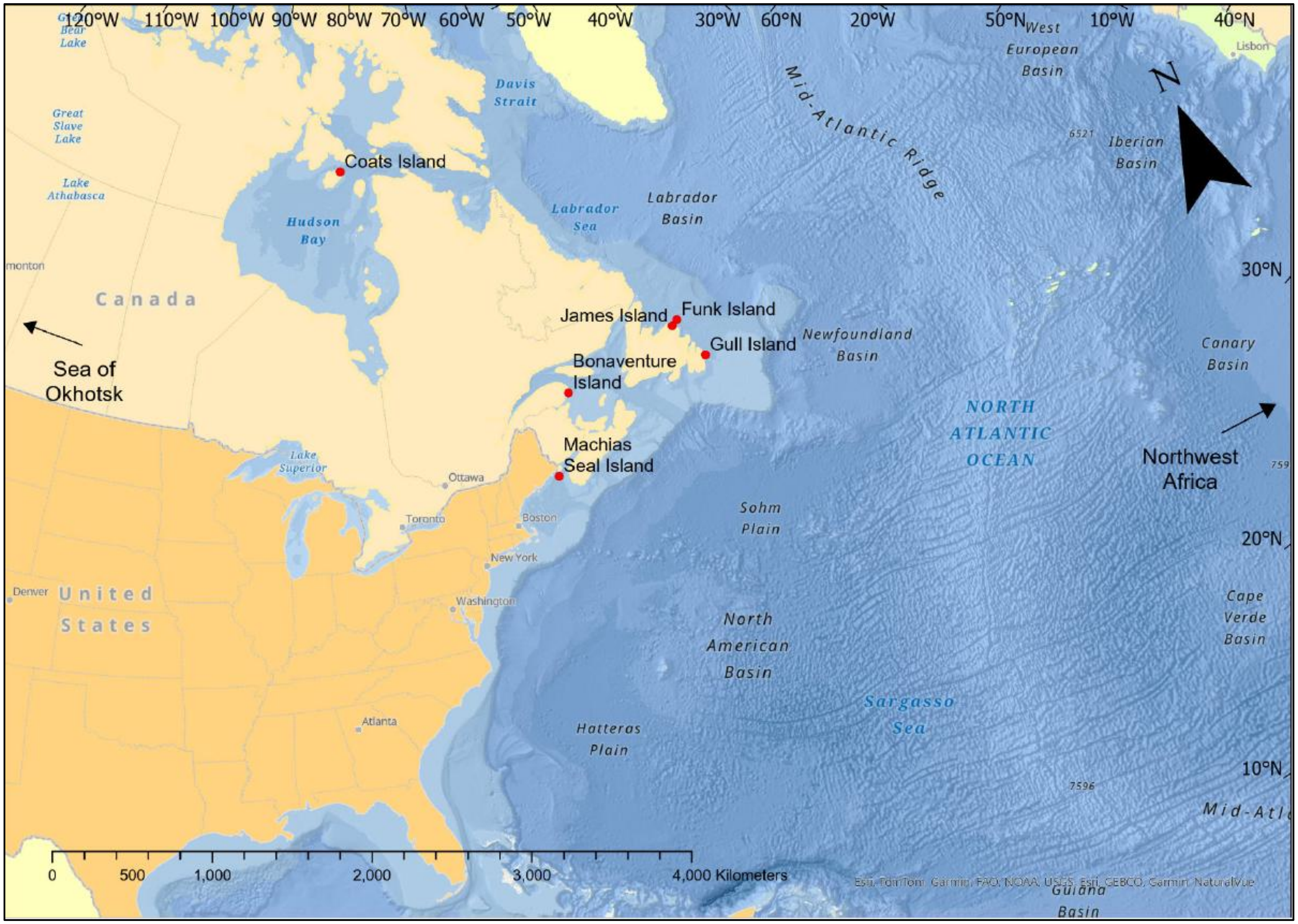

Figure 1. The location of the breeding colonies where data were collected for this study.

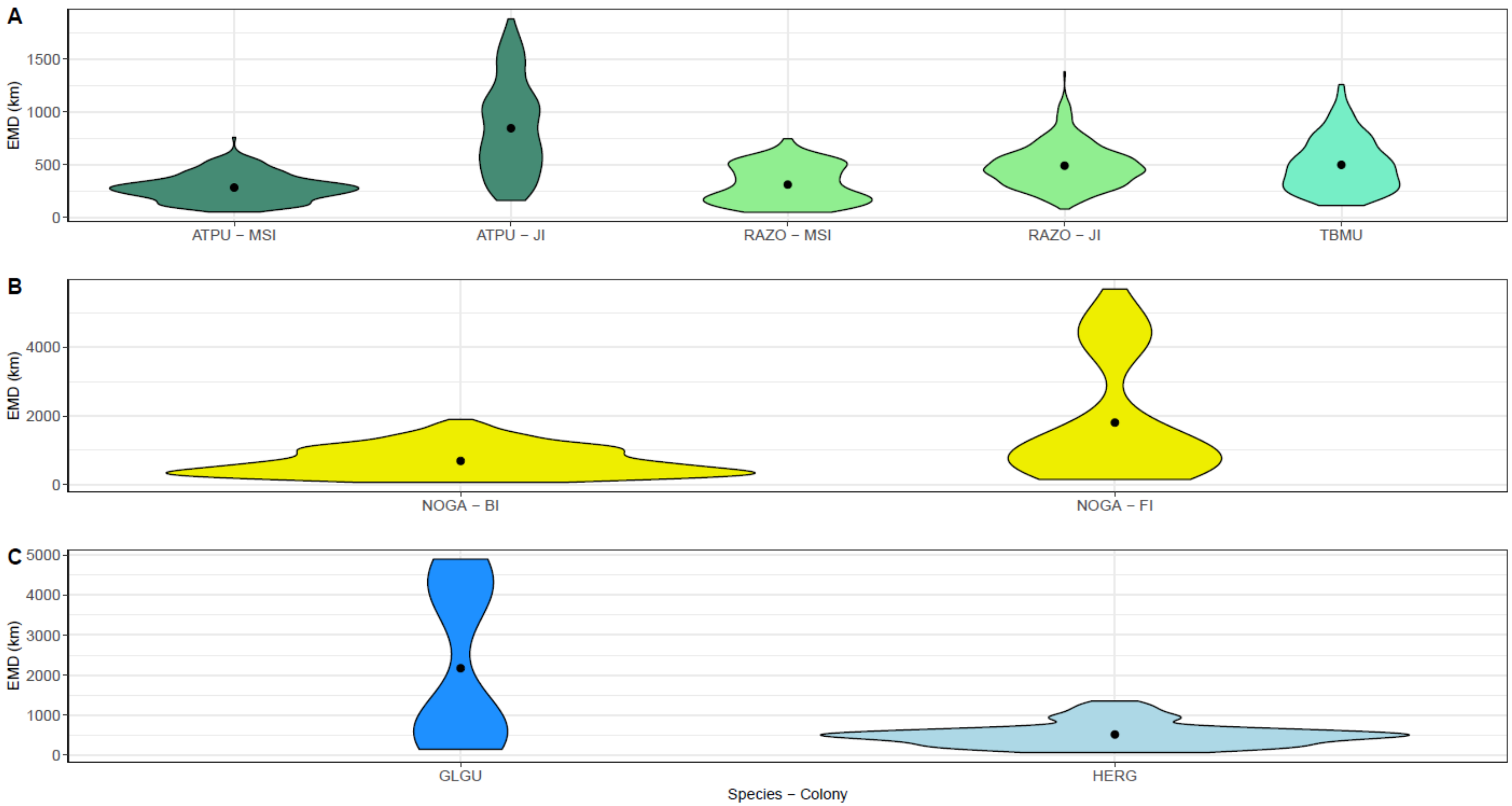

Figure 2. Distributions of between-individual Earth mover's distance (EMD values). Divided into seabird families: Alcidae (**A**), Atlantic puffin (ATPU, split into James Island and Machias Seal Island), razorbill (RAZO, split into James Island and Machias Seal Island) and thick-billed murre; Sulidae (**B**), northern gannet (NOGA, split into Bonaventure Island and Funk Island); and Laridae (**C**), glaucous gull (GLGU) and American herring gull (HERG). Mean EMD values are shown with black circles.

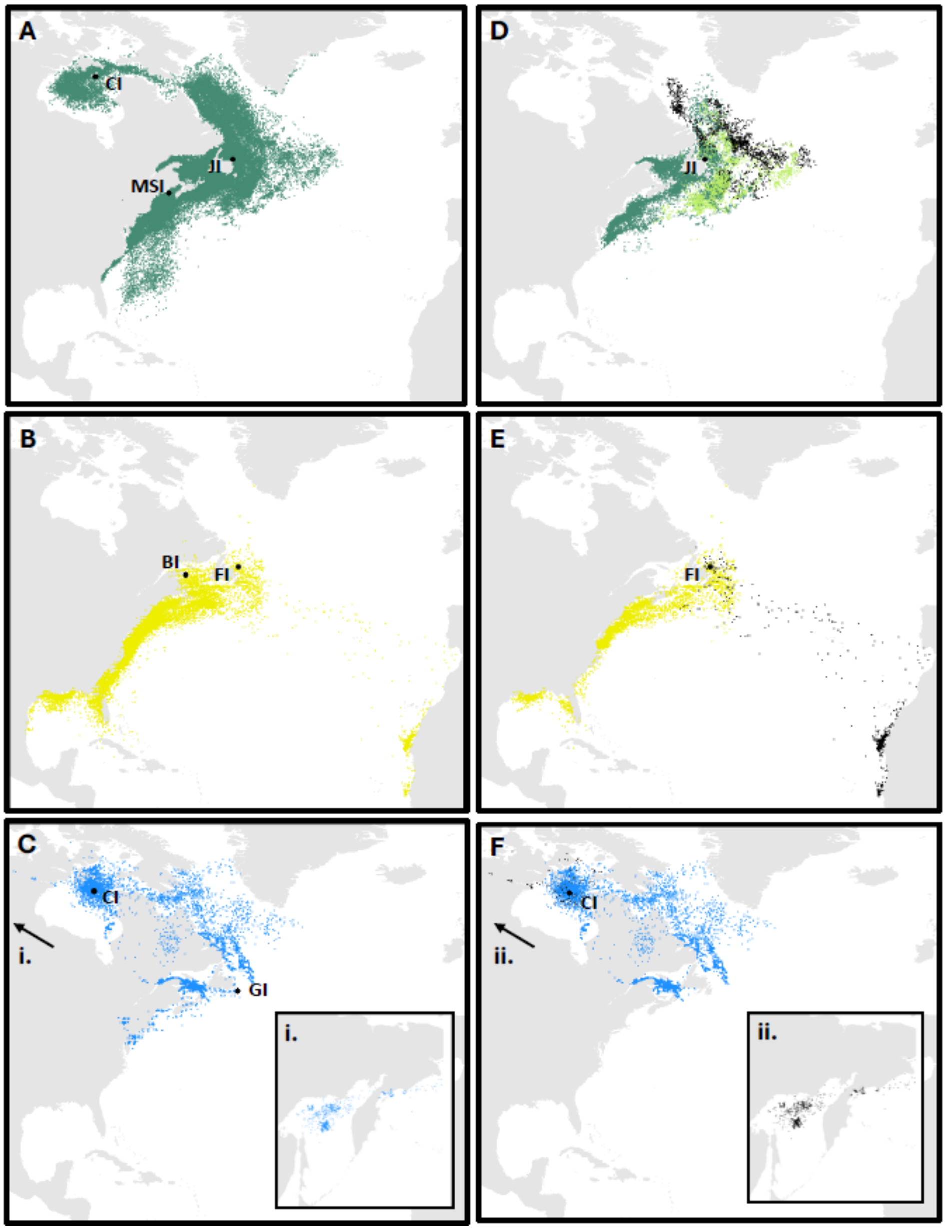

Figure 3. Combined overwintering migration tracks of alcids (Atlantic puffin, razorbill, thick-billed murre; **A**), sulids (northern gannets, **B**), and larids (American herring gulls and glaucous gulls, **C**). Breeding colonies (James Island, JI; Machias Seal Island, MSI; Coats Island, CI; Gull Island, GI; Funk Island, FI; Bonaventure Island, BI) are shown by black circles. Overwintering tracks of Atlantic puffins from James Island (**D**), northern gannets from Funk Island (**E**) and glaucous gulls from Coats Island (**F**). Colours indicate migratory routes used by each population: Atlantic puffins (north – black, east – light green, west – dark green), northern gannets (east – black, west – yellow) and glaucous gulls (east – blue, west – black). Inset boxes (**C i** and **F ii**) show the Sea of Okhotsk, used by one individual glaucous gull.

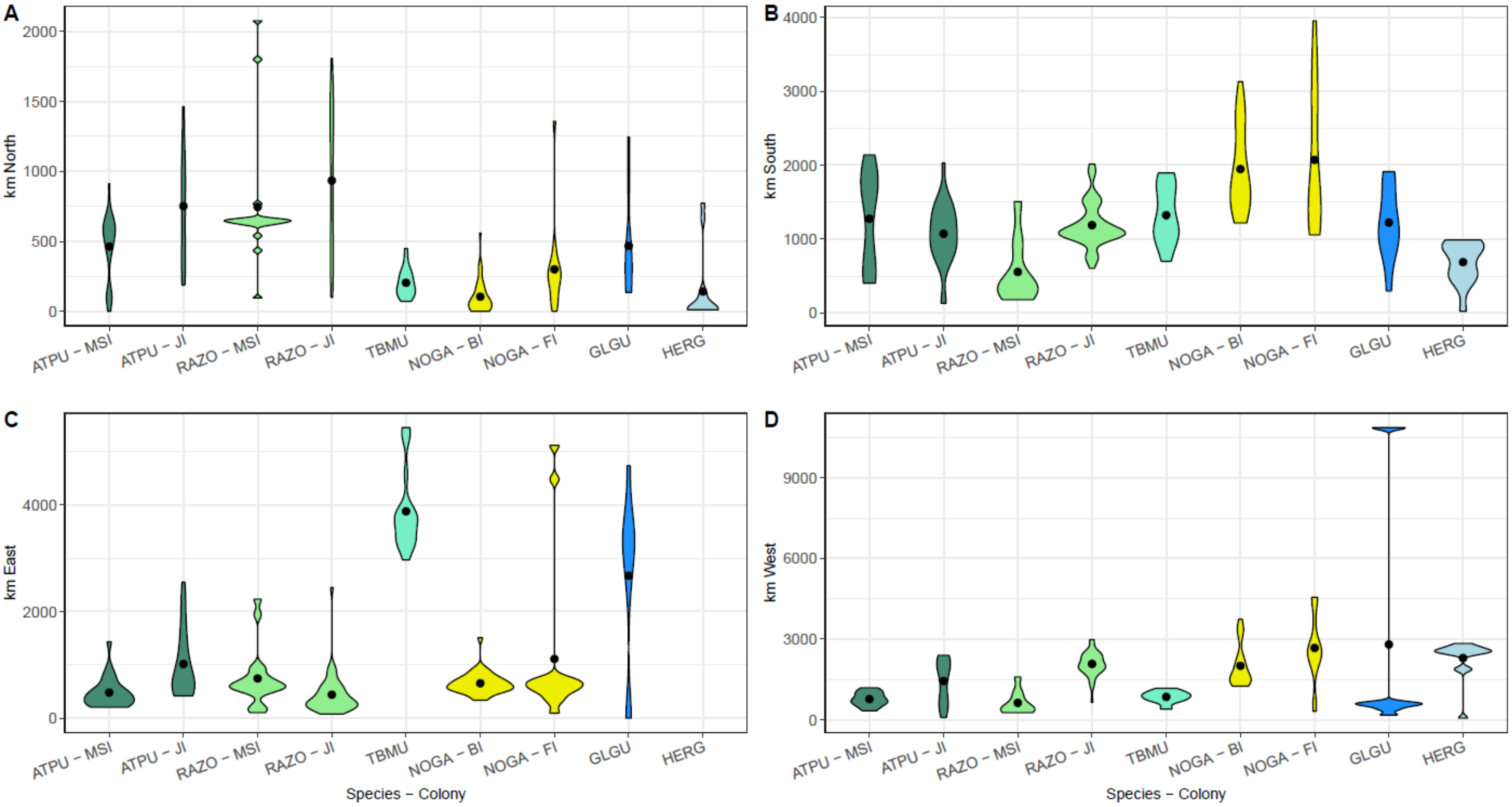

Figure 4. Distributions of the maximum distance (km) travelled north (**A**), south (**B**), east (**C**) and west (**D**) by each species: Atlantic puffin (ATPU, split into James Island and Machias Seal Island), razorbill (RAZO, split into James Island and Machias Seal Island), thick-billed murre (TBMU), northern gannet (NOGA, split into Bonaventure Island and Funk Island), glaucous gull (GLGU) and American herring gull (HERG). Mean values are shown with black circles.

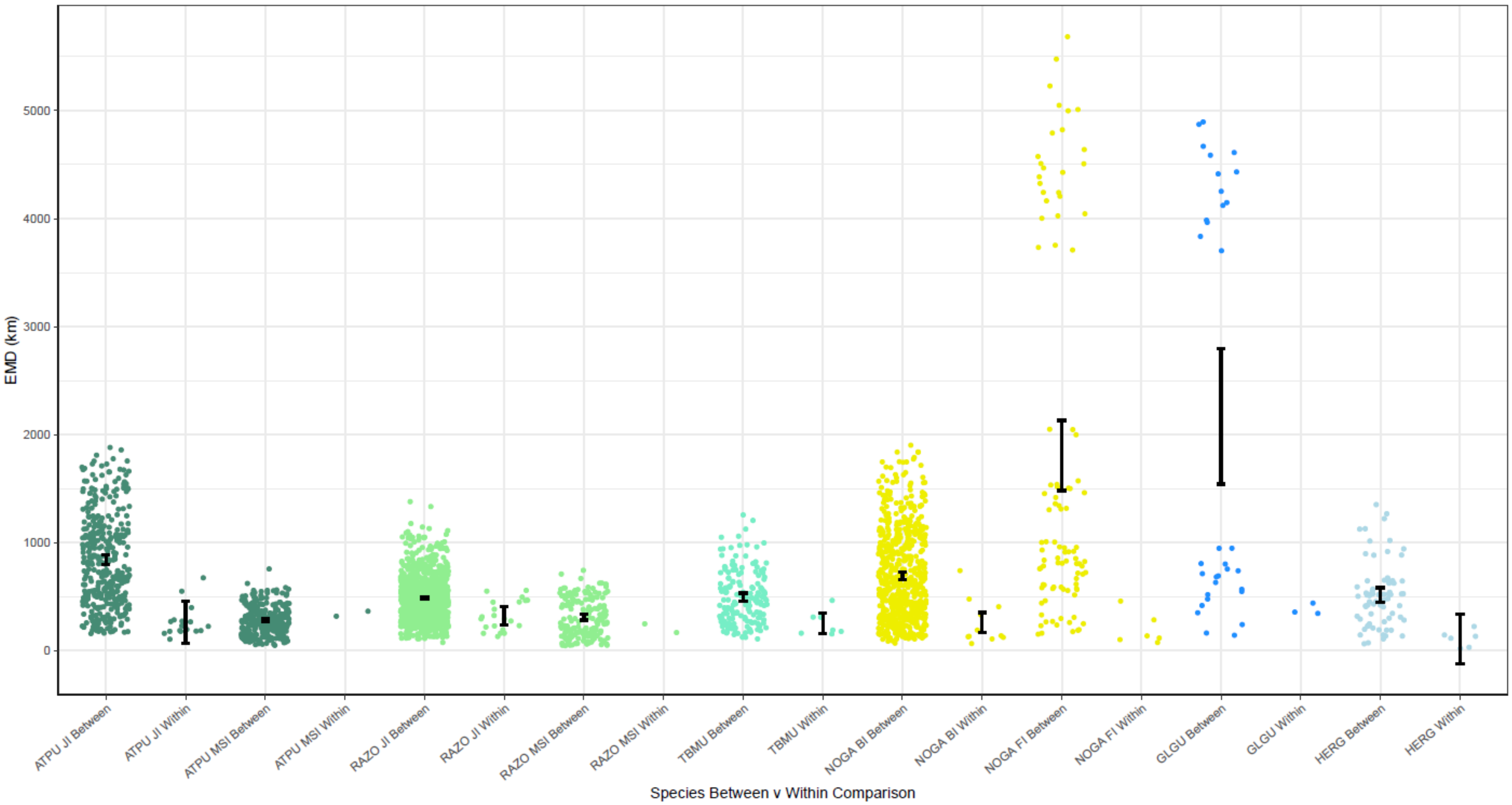

Figure 5. Earth mover's distance (EMD) values for between and within-individual differences in migratory track locations of non-breeding Atlantic puffin (ATPU, split into James Island and Machias Seal Island), razorbill (RAZO, split into James Island and Machias Seal Island), thick-billed murre (TBMU), northern gannet (NOGA, split into Bonaventure Island and Funk Island), glaucous gull (GLGU) and American herring gull (HERG). Predicted EMD values from generalised linear models (GLM) are shown as error bars with 95% confidence intervals. Error bars are omitted for some within-individual groups (ATPU MSI, RAZO MSI, GLGU, NOGA FI) due to low sample sizes (≤ 5).

General Discussion and Conclusions

The aim of the first chapter of this thesis was to determine an appropriate method for quantifying personality in a crevice nesting seabird (razorbill, *Alca torda*) by conducting three tests associated with the docility-aggression personality trait. Two tests used quantitative behavioural coding during standardised behavioural tests, while the other used qualitative observer ratings during routine handling. Observer ratings during routine handling had the highest repeatability compared to quantified scores from behavioural tests, which were difficult to standardise in this species. These findings suggest that observer ratings may be a good method to quantify personality traits in species that are hard to observe in the wild. Additionally, these results align with the other studies that have quantified personality traits in birds (van Oers and Naguib, 2013), and specifically, seabirds (e.g., Gatt et al., 2021; Harris et al., 2020; Patrick et al., 2017; Traisnel and Pichegru, 2018).

Using this personality metric, I investigated whether the docility trait in razorbills was linked to spatial consistency and other behaviours during the breeding and non-breeding periods in Chapters 2 and 3, respectively. In Chapter 2 we investigated foraging behaviour (e.g., foraging effort, location) and reproductive success (i.e., fledging success) as these are behaviours where relationships have been found with personality traits in other seabird species during the breeding period (e.g., Collins et al., 2019; Kruger et al., 2019). We were also able to incorporate annual biomass data of a key prey species (i.e., capelin, *Mallotus villosus;* Davoren, 2024) to investigate how these relationships were influenced by fluctuating prey availability. We found individual spatial consistency in razorbills to be related to prey availability rather than personality. Indeed, razorbill foraging locations were only spatially consistent under high prey availability. However, dive depth and foraging trip characteristics were not repeatable regardless of prey context. Additionally, these foraging behaviour metrics, along with fledging success were not related to personality, despite annually varying prey availability. Therefore, these results contrast with studies that have shown relationships between personality and reproductive success (e.g., Collins et al., 2019) or foraging behaviour (e.g., Harris et al., 2020) during the breeding season in seabirds. However, these results do align with studies that have shown no relationships between personality and reproductive success in seabirds (e.g., van de Walle et al., 2024). Our findings therefore show that prey availability should be incorporated, if possible, when investigating seabird behavioural consistency.

In Chapter 3, we investigated spatial consistency in migratory behaviour (e.g., location and distance) and relationships between personality and behaviour. Individual consistency in seabird migratory behaviour is common and well-studied (Phillips et al., 2017), but rarely investigated in relation to personality traits. Indeed, relationships between personality and migration have only been shown in one other seabird species (Cory's shearwater, *Calonectris borealis*; Gatt et al., 2021). In addition to migratory behaviour, we also investigated foraging behaviour (e.g., dive depth and trophic level) in relation to personality. During their migrations, razorbills had high spatial consistency and were highly repeatable in the distances travelled north and south from the colony. Additionally, average daily dive depth and $\delta^{15}N$ (i.e., trophic level) were also repeatable. However, spatial consistency of migrations and foraging behaviours were not related to personality, and these results therefore contrast with those of Gatt et al (2021). Overall, a consistent finding across the first three chapters is individual consistency in razorbill behaviour.

Finally, in the fourth chapter, the aim was to determine the level of behavioural diversity (i.e., differences among individuals) within several seabird species that breed in Atlantic Canada and overwinter in the northwest Atlantic. Behavioural diversity within species, especially when behaviour is highly consistent at the individual level, can influence population dynamics, with lower diversity resulting in a higher probability of population declines (Clavel et al., 2011). In seabirds, non-breeding locations and migratory routes vary among individuals within a species (e.g., Fifield et al., 2014) but can be highly consistent within individuals (e.g., Franklin et al., 2022). We found high levels of individual consistency in the non-breeding locations of all species investigated. However, behavioural diversity varied across and within colonies and species. These findings suggest that the species with lower behavioural diversity identified in this study may be more vulnerable to anthropogenic threats (e.g., offshore wind farms) and environmental change (Baak et al., 2022).

Significance

Standardised, independent observer ratings were found to be the best method for quantifying repeatable behavioural responses in razorbills. This result is significant because it highlights the value of observer ratings when carrying out investigations of personality in other wild animals that are hard to study with commonly used personality tests (e.g., novel items). Additionally, if animal handling is necessary for other scientific objectives (e.g., deployment and retrieval of tracking devices, banding), observer ratings may provide a time-efficient, non-invasive and low-cost method to test for personality (Ebenau et al., 2020), that also potentially facilitate larger sample sizes. As observer ratings are most commonly used in studies of captive animals (e.g., Powell & Svoke, 2008; Torgerson-White, 2014), showing this method to be suitable in non-captive animals provides a potential simple method for researchers to quantify personality across species.

Although relationships between personality (i.e., docility) and breeding or non-breeding behaviour were not observed in our studies, other studies have observed these relationships and subsequently linked personality to conservation and management (Collins et al, 2022). Indeed, personality traits in animals can both directly and indirectly influence fitness, due to their correlations with foraging and movement decisions (Smith & Blumstein, 2008). Therefore, identifying personality and between-individual differences within a species is vital to understand species-specific tolerances to increasing anthropogenic threats (Dingemanse & Wolf, 2013). Indeed, there are increasing changes in marine ecosystems that result in multiple simultaneous threats (Dias et al. 2019). Consequently, studying personality is important to help develop strategies that may protect larger proportions of populations (MacKinlay & Shaw 2023), such as informing the locations of marine protected areas (Davies et al., 2021; Hanson et al., 2020; Hindell et al., 2020) that can contribute to the persistence of species (Beal et al., 2023). For example, seabird populations have been predicted to become less diverse with a greater proportion of shyer individuals as they likely have higher success in more variable, poorer conditions (Jeffries et al. 2021). Therefore, ensuring conditions are suitable for all individuals will help maintain diversity in populations, which in turn will aid in their future persistence (Clavel et al., 2011).

There are a number of potential reasons why no relationships were found between personality and breeding and non-breeding behaviours in razorbills. For instance, maybe the data collection methods were not appropriate for identifying links between personality and behaviour in this species. For example, maybe a relationship between personality and foraging behaviour in the breeding season would have been found if it had been possible to track individuals across prey availability periods or across years. Similarly, it is possible that links between personality and migratory behaviour in the non-breeding season would have been identified if it had been possible to track razorbill migrations without the error associated with geolocator tags (± 200 km, Halpin et al., 2021). Indeed, personality traits (i.e., boldness) have been linked to the exploitation-exploration continuum in seabirds (Patrick et al., 2017). Therefore, if migratory routes in razorbills could be tracked at a finer scale (e.g., GPS tags), then it may be possible to observe differences in exploratory behaviour (i.e., more/less sinuous tracks) during migration related to docility. Finally, the ecosystem surrounding the razorbill colony (James Island) in the summer may not promote significant differences in behaviour related to personality. The transition between two prey availability periods (i.e., low prior to capelin spawning, to high, in dense localised aggregations, during spawning; Davoren, 2024) may mean personality does not have a significant role in promoting intra-specific niche partitioning, as observed in other seabird species where prey availability is more homogenous throughout the breeding season (e.g., Harris et al., 2020; Kruger et al., 2019). Indeed, prey may be sufficiently available at predictable hotspots in our study area after capelin spawning that differences in foraging location or effort related to personality are not beneficial.

Similar to the importance of identifying between-individual variation within species, identifying species and populations with lower diversity in their behaviour is valuable for seabird management and conservation since lower diversity (e.g., fewer migratory locations) results in a greater likelihood of mass mortality related to a single local event (e.g., oil spill). However, as seabird research rarely compares across species (Brown et al., 2021), this study is significant as it will aid in identifying conservation target species. Indeed, tracking data are commonly used to inform conservation and management (Davies et al., 2021) because understanding spatial patterns can help identify important areas for species (Beal et al., 2021). For example, as species with more specialised behaviour have higher likelihoods of population declines (Clavel et al., 2011), populations that have a distinct migratory location will be of particular conservation interest.

Future Directions

There are several possible future directions of this work. Further investigation of the observer rating method across other wild species, and not only seabirds or those that are hard to test with the common assessment methods (i.e., novel items), will help confirm whether this method can be used more frequently in the assessment of personality traits in non-captive animals. In razorbills there may be relationships between docility and other, not investigated behaviours. For example, although fledging success was not influenced by docility, it is possible docility is related to other aspects of the reproductive cycle in razorbills, such as the likelihood an individual will skip a breeding season or return to the colony to breed, as seen in wandering albatross (*Diomedea exulans*, van de Walle et al., 2024). Additionally, links between the personality composition of a breeding pair and reproductive success have also been shown in wandering albatross (McCully et al., 2022). Therefore, expanding the docility assessments to both adult birds when assessing fledging success is also an avenue worthy of investigation to increase understanding of how or if docility influences reproductive success in razorbills. The investigation into seabird migratory behavioural diversity could be expanded to include a wider range of species and colonies from across Atlantic Canada, potentially including data sets on seabird migration that do not include repeat tracks of individuals, due to the high individual consistency of seabird migratory routes seen across many studied species (Phillips et al, 2017). This would allow the identification of other species or colonies where conservation work may be prioritised and provide the groundwork for the identification of ocean regions important for the persistence of species identified to be most at risk (i.e., low behavioural diversity).

References

Baak, J. E., Patterson, A., Grant Gilchrist, H., & Elliott, K. H. (2021). First evidence of diverging migration and overwintering strategies in glaucous gulls (*Larus hyperboreus*) from the Canadian Arctic. *Anim. Migr.*, 8(1), 98–109. https://doi.org/10.1515/ami-2020-0107

Beal, M., Catry, P., Phillips, R. A., Oppel, S., Arnould, J. P. Y., Bogdanova, M. I., Bolton, M., Carneiro, A. P. B., Clatterbuck, C., Conners, M., Daunt, F., Delord, K., Elliott, K., Fromant, A., Granadeiro, J. P., Green, J. A., Halsey, L., Hamer, K. C., Ito, M., … Dias, M. P. (2023). Quantifying annual spatial consistency in chick-rearing seabirds to inform important site identification. *Biol. Conserv.*, 281, 1–14. https://doi.org/10.1016/j.biocon.2023.109994

Beal, M., Oppel, S., Handley, J., Pearmain, E. J., Morera-Pujol, V., Carneiro, A. P. B., Davies, T. E., Phillips, R. A., Taylor, P. R., Miller, M. G. R., Franco, A. M. A., Catry, I., Patrício, A. R., Regalla, A., Staniland, I., Boyd, C., Catry, P., & Dias, M. P. (2021). track2KBA: an R package for identifying important sites for biodiversity from tracking data. *Methods Ecol. Evol.*, 12(12), 2372–2378. https://doi.org/10.1111/2041-210X.13713

Brown, J. M., van Loon, E. E., Bouten, W., Camphuysen, K. C. J., Lens, L., Müller, W., Thaxter, C. B., & Shamoun-Baranes, J. (2021). Long-distance migrants vary migratory behaviour as much as short-distance migrants: An individual-level comparison from a seabird species with diverse migration strategies. *J. Anim. Ecol.*, 90(5), 1058–1070. https://doi.org/10.1111/1365-2656.13431

Clavel, J., Julliard, R., & Devictor, V. (2011). Worldwide decline of specialist species: toward a global functional homogenization? *Front. Ecol. Environ.*, 9(4), 222–228. https://doi.org/10.1890/080216

Collins, S. M., Hatch, S. A., Elliott, K. H., & Jacobs, S. R. (2019). Boldness, mate choice and reproductive success in *Rissa tridactyla*. *Anim. Behav.*, 154, 67–74. https://doi.org/10.1016/j.anbehav.2019.06.007

Collins, S. M., Hendrix, J. G., Webber, Q. M. R., Boyle, S. P., Kingdon, K. A., Blackmore, R. J., d'Entremont, K. J. N., Hogg, J., Ibáñez, J. P., Kennah, J. L., Lamarre, J., Mejías, M., Newediuk, L., Richards, C., Schwedak, K., Wijekulathilake, C., & Turner, J. W. (2022). Bibliometric investigation of the integration of animal personality in conservation contexts. *Conserv. Biol*., 1–13. https://doi.org/10.1111/cobi.14021

Davies, T. E., Carneiro, A. P. B., Tarzia, M., Wakefield, E., Hennicke, J. C., Frederiksen, M., Hansen, E. S., Campos, B., Hazin, C., Lascelles, B., Anker-Nilssen, T., Arnardóttir, H., Barrett, R. T., Biscoito, M., Bollache, L., Boulinier, T., Catry, P., Ceia, F. R., Chastel, O., … Dias, M. P. (2021). Multispecies tracking reveals a major seabird hotspot in the North Atlantic. *Conserv. Lett.*, 14(5), 1–14. https://doi.org/10.1111/conl.12824

Davoren, G. K. (2024). Variable forage fish biomass and phenology influence marine predator diet, foraging behavior, and species interactions in coastal Newfoundland, Canada. *ICES J. Mar. Sci.*, 1–14. https://doi.org/10.1093/icesjms/fsae021

Dias, M. P., Martin, R., Pearmain, E. J., Burfield, I. J., Small, C., Phillips, R. A. 4, Yates, O., Lascelles, B., Borboroglu, P. G., & Croxall, J. P. (2019). Threats to seabirds: a global assessment. *Biol. Conserv.*, 237, 525–537. https://doi.org/10.1016/j.biocon.2019.06.033

Dingemanse, N. J., & Wolf, M. (2013). Between-individual differences in behavioural plasticity within populations: causes and consequences. *Anim. Behav.*, 85(5), 1031–1039. https://doi.org/10.1016/j.anbehav.2012.12.032

Ebenau, A., von Borell, C., Penke, L., Ostner, J., & Schulke, O. (2020). Supplemental material for integrative personality assessment in wild Assamese macaques (*Macaca assamensis*). *J. Comp. Psychol.*, 134(1), 27–41. https://doi.org/10.1037/com0000190.supp

Fifield, D. A., Montevecchi, W. A., Garthe, S., Robertson, G. J., Kubetzki, U., & Rail, JF. (2014). Migratory tactics and wintering areas of northern gannets (*Morus bassanus*) breeding in North America. *Ornithol. Monogr.*, 79, 1–63. https://doi:10.1642/aoum.79-1.

Franklin, K. A., Norris, K., Gill, J. A., Ratcliffe, N., Bonnet-Lebrun, A.-S., Butler, S. J., Cole, N. C., Jones, C. G., Lisovski, S., Ruhomaun, K., Tatayah, V., & Nicoll, M. A. C. (2022). Individual consistency in migration strategies of a tropical seabird, the Round Island petrel. *Mov. Ecol.*, 10, 1–14. https://doi.org/10.1186/s40462-022-00311-y

Gatt, M. C., Granadeiro, J. P., & Catry, P. (2021). Migrants and residents of a long-lived seabird differ in their behavioural response to a stressor. *J. Avian Biol.*, 52(2), 1–8. https://doi.org/10.1111/jav.02589

Halpin, L. R., Ross, J. D., Ramos, R., Mott, R., Carlile, N., Golding, N., Reyes-González, J. M., Militão, T., De Felipe, F., Zajková, Z., Cruz-Flores, M., Saldanha, S., Morera-Pujol, V., Navarro-Herrero, L., Zango, L., González-Solís, J., & Clarke, R. H. (2021). Double-tagging scores of seabirds reveals that light-level geolocator accuracy is limited by species idiosyncrasies and equatorial solar profiles. *Methods Ecol. Evol.*, 21(11), 2243–2255. https://doi/10.1111/2041-210X.13698

Hanson, J. O., Rhodes, J. R., Butchart, S. H. M., Buchanan, G. M., Rondinini, C., Ficetola, G. F., & Fuller, R. A. (2020). Global conservation of species' niches. *Nature*, 580, 232–234. https://doi.org/10.1038/s41586-020-2138-7

Harris, S. M., Descamps, S., Sneddon, L. U., Bertrand, P., Chastel, O., & Patrick, S. C. (2020). Personality predicts foraging site fidelity and trip repeatability in a marine predator. *J. Anim. Ecol.*, 89(1), 68–79. https://doi.org/10.1111/1365-2656.13106

Hindell, M. A., Reisinger, R. R., Ropert-Coudert, Y., Hückstädt, L. A., Trathan, P. N., Bornemann, H., Charrassin, J. B., Chown, S. L., Costa, D. P., Danis, B., Lea, M. A., Thompson, D., Torres, L. G., Van de Putte, A. P., Alderman, R., Andrews-Goff, V., Arthur, B., Ballard, G., Bengtson, J., … Raymond, B. (2020). Tracking of marine predators to protect Southern Ocean ecosystems. *Nature*, 580(7801), 87–92. https://doi.org/10.1038/s41586-020-2126-y

Jeffries, P. M., Patrick, S. C., & Potts, J. R. (2021). Be different to be better: the effect of personality on optimal foraging with incomplete knowledge. *Theor. Ecol.*, 1–13. https://doi.org/10.1007/s12080-021-00517-7

Krüger, L., Pereira, J. M., Paiva, V. H., & Ramos, J. A. (2019). Personality influences foraging of a seabird under contrasting environmental conditions. *JEMBE*, 516, 123–131. https://doi.org/10.1016/j.jembe.2019.04.003

MacKinlay, R. D., & Shaw, R. C. (2023). A systematic review of animal personality in conservation science. *Conserv. Biol.*, 37(1), 1–16. https://doi.org/10.1111/cobi.13935

McCully, F. R., Weimerskirch, H., Cornell, S. J., Hatchwell, B. J., Cairo, M., & Patrick, S. C. (2022). Partner intrinsic characteristics influence foraging trip duration, but not coordination of care in wandering albatrosses *Diomedea exulans*. *Ecol. Evol.*, 12, 1–13. https://doi.org/10.1002/ece3.9621

Patrick, S. C., Pinaud, D., & Weimerskirch, H. (2017). Boldness predicts an individual's position along an exploration–exploitation foraging trade-off. *J. Anim. Ecol.*, 86(5), 1257–1268. https://doi.org/10.1111/1365-2656.12724

Phillips, R. A., Lewis, S., González-Solís, J., & Daunt, F. (2017). Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds. *Mar. Ecol. Prog. Ser.*, 578, 117–150. https://doi.org/10.3354/meps12217

Powell, D. M., & Svoke, J. T. (2008). Novel environmental enrichment may provide a tool for rapid assessment of animal personality: a case study with giant pandas (*Ailuropoda melanoleuca*). *J. Appl. Anim. Welf. Sci.*, 11(4), 301–318. https://doi.org/10.1080/10888700802329673

Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: a meta-analysis. *Behav. Ecol.*, 19(2), 448–455. https://doi.org/10.1093/beheco/arm144

Torgerson-White, L. L. (2014). Rating methodology, personality axes, and behavioural plasticity: a case study in African lions. *Anim. Behav. Cogn.*, 1(3), 230–248. https://doi.org/10.12966/abc.08.02.2014

Traisnel, G., & Pichegru, L. (2018). Does it always pay to defend one's nest? A case study in African penguin. *J. Ethol.*, 124(1), 74–83. https://doi.org/10.1111/eth.12704

van de Walle, J., Sun, R., Fay, R., Patrick, S. C., Barbraud, C., Delord, K., Weimerkirch, H., & Jenouvrier, S. (2024). The impact of boldness on demographic rates and life-history outcomes in the wandering albatross. *J. Anim. Ecol.*, 93, 676–690. https://doi.org/10.1111/1365-2656.14077

van Oers, K., & Naguib, M. (2013). Avian Personality. In C. Carere & D. Maestripieri (Eds.), Animal Personalities: Behaviour, Physiology and Evolution (pp. 66–95). University of Chicago Press.