A Hidden Markov Modelling Approach to Understanding Ancient Murrelet Behaviour and Foraging Habitat

By

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Abstract

Seabird species are increasingly threatened around the world due to a range of anthropogenic impacts affecting at-sea and breeding habitat. One such species is the Ancient Murrelet, an Alcid species nesting on the Pacific Coast of Canada. Ancient Murrelets are an important species in Canadian waters as approximately 50 % of the world's breeding population nest in a small region of the British Columbia coast. Ancient Murrelets are listed as a species of *Special Concern*, due to threats in their breeding colonies; threats to their at-sea habitat, such as disturbance from shipping traffic, oil pollution, and fisheries bycatch, are currently poorly-documented due to the challenges associated with studying seabirds in their offshore environments. Conservation efforts to protect this species require information on movements and habitat use at sea. Therefore, there exists a critical need for research that provides new knowledge on where murrelets are travelling and the habitats in which they are foraging.

The objective of this thesis research is to investigate movement behaviour and at-sea habitat of Ancient Murrelets during breeding season foraging trips. Movement modelling using hidden Markov models differentiated the tracks into behaviour states, and identified foraging locations at sea. Foraging locations were used in regression modelling to investigate the degree to which variability in Ancient Murrelet foraging locations could be explained by seafloor depth, slope and tidal current, and spatial measures such as distance from the breeding colony. From characteristics of movement paths, hidden Markov models identified three movement behaviour states, which were interpreted as transit, resting, and foraging behaviours. Logistic regression models suggested that depth, seafloor slope, tidal speed, and distance from the colony exhibited a negative influence on locations where birds chose to forage. Nevertheless, of the locations where foraging took place, foraging intensity was found to be higher in deeper areas suggesting Ancient

Murrelets may be focusing efforts in areas of higher prey abundance. The combination of individual movement analysis and habitat analysis provides an important first step in gaining a greater understanding of Ancient Murrelet behaviour and foraging habitat at sea. These findings can inform marine management planning in this region and conservation of this vulnerable species.

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Chapter 1. Introduction

1.1 Overview

Seabird populations are being globally impacted by many anthropogenic threats, from climate change, to habitat degradation, to pollution (Dias et al., 2019). Terrestrial threats to seabirds, such as predation by introduced species, have been well-documented (reviewed in Boersma et al., 2002), in part because land-based research provides more opportunities for observation than research at sea. However, recent research has shown that seabirds face several threats at sea, for which mitigation measures must be considered in conjunction with terrestrial protections in order to establish successful seabird conservation efforts (Dias et al., 2019). Seabirds are long-lived and spend a large part of their lives at sea (Gaston, 2004); therefore, populations are sensitive to adult mortality experienced at sea from threats such as bycatch in fisheries (Dias et al., 2019). Management measures such as marine protected areas can be implemented in order to help protect seabirds in the marine environment. The first step to managing this dynamic habitat is understanding where and how seabirds use their habitat (Chivers et al., 2013; Thaxter et al., 2012). Movement data based on individual animal tracking is one way to gain a better understanding of the specifics of habitat use of seabirds at sea (Hays et al., 2016). By understanding detailed movement patterns over space and time, managers can incorporate these details into management planning with the aim of mitigating negative human-seabird interactions (Allen and Singh, 2016; Ogburn et al., 2017).

Movement ecology is a rapidly growing field in wildlife research that combines tracking of individual animals and methods for modelling movement characteristics used to infer animal behaviour (Gurarie et al., 2016). Animal tracking and movement modelling can inform us about factors such as location and size of home ranges (Soanes et al., 2013), human-wildlife interactions (McGowan et al., 2017), and foraging site fidelity (Grecian et al., 2018), amongst others. Locations and behaviour derived from movement paths can be related to the environment animals are using with habitat use models (Aarts et al., 2008). Here, the term ‘habitat’ is used to indicate the environmental characteristics of the area a seabird is using, and ‘habitat use’ is the time spent using an area that exhibits these environmental conditions (Wakefield et al., 2009). At-sea habitat use is an especially important gap in seabird research, as marine birds are highly vulnerable to threats on the water such as oil spills (Fox et al., 2016). This knowledge gap can be addressed using movement data. Particularly critical is understanding foraging locations and foraging habitat during the breeding season, in order to help preserve this critical habitat and protect seabirds during an energetically costly stage of their life (Chivers et al., 2013; Lennox et al., 2019).

Seabirds, by definition, are tied to the ocean, and many spend the majority of their life at sea, other than brief periods during the breeding season when they must nest on land (Ballance et al., 2001). Other than a few generalist species (e.g. some gulls), seabirds rely entirely on the ocean for their food supply (Gaston, 2004). To date, the majority of research on where and how seabirds use the marine environment has been based on data from at-sea surveys from vessels (Pinaud and Weimerskirch, 2005; Tremblay et al., 2009). At-sea surveys provide essential information about densities, species interactions, population estimates, and habitat use, but inferences are inherently at a population-level (Watanuki et al., 2016). Identification of important areas, typically equated with foraging areas, is often accomplished by looking for locations of high seabird densities; however, some authors suggest that high densities of birds cannot simply be equated to ecologically important areas (Camphuysen et al., 2012). This is where tracking of individual birds and modelling to infer behaviour can be especially useful (Thaxter et al., 2012).

In the past few decades, rapid development of tracking technologies is allowing researchers to mount varied types of devices on individuals of an increasing number of species (Wilson et al., 2002), which in turn allows for answering more detailed questions about animal movement regarding space-use, movement behaviour, and movement-habitat interactions (Hays et al., 2016; Nathan et al., 2008). Since the early 1990s, satellite tagging has been an option for seabird tracking (Wakefield et al., 2009). As technology has improved, the decrease in size of tracking devices has allowed smaller birds to be tagged while an increase in quality and accuracy of data is facilitating detailed behavioural inferences from bird tracks (Cooke et al., 2004). Previously, seabird data were mostly from ship-based population-level surveys. Now, with the addition of movement data from tagging and tracking of individuals, additional analytical techniques are required (Demšar et al., 2015; Nathan et al., 2008). Population-level survey data, known as Eulerian data, is often used to investigate distribution and density of birds, and regression analysis is often used with these data to investigate the relationship between seabird presence and habitat characteristics (Tremblay et al., 2009). Individual-based data from tracking (Lagrangian data; Tremblay et al., 2009), represent temporally autocorrelated point data, and analysis of these data requires consideration of alternative or additional methods, such as path segmentation and times-series analysis (Bennison et al., 2018; Schick et al., 2008). Although there are challenges presented by these data, such as spatial and temporal autocorrelation (Patterson et al., 2008), small sample sizes (Sequeira et al., 2019), and potential for tag-influence on behaviour of tracked birds (Vandenabeele et al., 2014), the benefits are numerous. Specifically, tracking individuals produces data from a known population at specific life stages and from specific colonies (Grecian et al., 2012; Lascelles et al., 2016; Soanes et al., 2013). Movement analysis can be employed to classify seabird movement paths into different movement behaviours, allowing for investigation of environmental influences on seabird movements (Grecian et al., 2018). Tracking and movement analysis also produces a greater degree of confidence that locations where birds are foraging have been identified, allowing incorporation of only foraging locations into habitat analysis (Camphuysen et al., 2012).

1.2 Study species

The Ancient Murrelet (*Synthliboramphus antiquus*) is a vulnerable seabird species nesting on the islands along the coast of British Columbia, Canada. This species is listed as *Special Concern* by the Canadian federal government's Committee on the Status of Endangered Wildlife in Canada (COSEWIC), and the federal government has a responsibility to manage the species to stabilize or reduce population declines of these birds in Canada (Environment Canada, 2015). The Canadian population of Ancient Murrelets makes up approximately half of the world's breeding population (Gaston, 1992), therefore it is essential that we understand and mitigate threats in Canadian waters. Previously, most research on Ancient Murrelet population declines has been focused in terrestrial breeding colonies and most threats, such as invasive mammalian predators, were identified on land (Gaston, 1992). This is in part due to the challenges of studying seabirds at sea rather than an absence of at-sea threats for this species. Fisheries bycatch due to gill-net fisheries of salmon near Ancient Murrelet breeding colonies in the 1960s has been suggested as a possible reason for population declines at one of the largest colonies in Canada (Bertram, 1995). Fisheries bycatch is a growing concern worldwide for many seabird species (Dias et al., 2019), and is a likely threat to Ancient Murrelets, yet remains poorly documented (Environment Canada, 2015). Ancient Murrelets in Canadian waters could also become increasingly impacted by shipping traffic (Gaston et al., 2017), as vessel traffic increases in areas where they are foraging during breeding. Along with increased vessel traffic could come increased oil spills (Fox et al., 2016), as well as increased vessel interactions and disturbance. Only recently was there confirmation about where Ancient Murrelets were travelling in the nonbreeding season (Gaston et al., 2017), emphasizing the fact that we are really only starting to acquire the detailed information on at-sea habitat use that is necessary to address many anthropogenic threats.

1.3 Research objectives

In the following thesis, I have addressed several questions about Ancient Murrelet movement and habitat use, utilizing individual movement data from GPS tracking devices and statistical modelling. I have used two steps to addressing these questions:

(1) Individual-level movement modelling using hidden Markov models based on data from GPS tracks to investigate characteristics of Ancient Murrelet movement behaviour at sea. This step focuses on identifying foraging behaviour and defining locations where Ancient Murrelets forage.

(2) Regression models to address two questions regarding the relationship between foraging and habitat characteristics, using foraging locations as defined from movement models: (a) Do certain physical characteristics of the environment explain where Ancient Murrelets preferentially foraged along their movement path? And (b) in locations where Ancient Murrelets were found foraging, is the length of time spent foraging explained by characteristics of the habitat?

1.4 Thesis structure

This thesis is formatted as two stand-alone papers (Chapter 2 and 3) that will be submitted for publication as separate manuscripts to peer-reviewed journals. As a result of this structure, there is some repetition of background concepts in each chapter. Chapter 2 addresses movement modelling and how it can be applied to understanding at-sea movements, behaviours, and foraging locations of Ancient Murrelets. Chapter 3 utilizes the foraging locations identified in Chapter 2 in combination with characteristics of the physical environment to investigate Ancient Murrelet relative foraging habitat quality. Finally, Chapter 4 is a conclusion that summarizes the finding from the two papers, and suggests future directions and research potential from this project.

1.5 References

Aarts, G., MacKenzie, M., McConnell, B., Fedak, M., Matthiopoulos, J., 2008. Estimating space-use and habitat preference from wildlife telemetry data. Ecography 31, 140–160. https://doi.org/10.1111/j.2007.0906-7590.05236.x

Allen, A.M., Singh, N.J., 2016. Linking movement ecology with wildlife management and conservation. Front. Ecol. Evol. 3. https://doi.org/10.3389/fevo.2015.00155

Ballance, L., Ainley, D.G., Hunt, G.L., 2001. Seabird foraging ecology, in: Encyclopedia of Ocean Sciences, Volume 5. Elsevier Ltd., pp. 227–235.

Bennison, A., Bearhop, S., Bodey, T.W., Votier, S.C., Grecian, W.J., Wakefield, E.D., Hamer, K.C., Jessopp, M., 2018. Search and foraging behaviors from movement data: A comparison of methods. Ecol. Evol. 8. https://doi.org/10.1002/ece3.3593

Bertram, D.F., 1995. The roles of introduced rats and commercial fishing in the decline of Ancient Murrelets on Langara Island, British Columbia. Conserv. Biol. 9, 865–872. https://doi.org/10.1046/j.1523-1739.1995.09040865.x

Boersma, P.D., Clark, J.A., Hillgarth, N., 2002. Seabird Conservation, in: Schreiber, E.A., Burger, J. (Eds.), Biology of Marine Birds. CRC Press, Boca Raton, pp. 559–580.

Camphuysen, K.C.J., Shamoun-Baranes, J., Bouten, W., Garthe, S., 2012. Identifying ecologically important marine areas for seabirds using behavioural information in combination with distribution patterns. Biol. Conserv. 156, 22–29. https://doi.org/10.1016/j.biocon.2011.12.024

Environment Canada, 2015. Management plan for the Ancient Murrelet (*Synthliboramphus antiquus*) in Canada, in: Speices at Risk Act: Management Plan Series. Environment Canada, Ottawa.

Chivers, L.S., Lundy, M.G., Colhoun, K., Newton, S.F., Houghton, J.D.R., Reid, N., 2013. Identifying optimal feeding habitat and proposed Marine Protected Areas (pMPAs) for the black-legged kittiwake (*Rissa tridactyla*) suggests a need for complementary management approaches. Biol. Conserv. 164, 73–81. https://doi.org/10.1016/j.biocon.2013.04.022

Cooke, S.J., Hinch, S.G., Wikelski, M., Andrews, R.D., Kuchel, L.J., Wolcott, T.G., Butler, P.J., 2004. Biotelemetry: A mechanistic approach to ecology. Trends Ecol. Evol. 19, 334–343. https://doi.org/10.1016/j.tree.2004.04.003

Demšar, U., Buchin, K., Cagnacci, F., Safi, K., Speckmann, B., Van de Weghe, N., Weiskopf, D., Weibel, R., 2015. Analysis and visualisation of movement: an interdisciplinary review. Mov. Ecol. 3, 1–24. https://doi.org/10.1186/s40462-015-0032-y

Dias, M.P., Martin, R., Pearmain, E.J., Burfield, I.J., Small, C., Phillips, R.A., 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

Fox, C.H., Hara, P.D.O., Bertazzon, S., Morgan, K., Underwood, F.E., Paquet, P.C., 2016. A preliminary spatial assessment of risk: Marine birds and chronic oil pollution on Canada’s Pacific coast. Sci. Total Environ. 573, 799–809.

https://doi.org/10.1016/j.scitotenv.2016.08.145

Gaston, A.J., 2004. Seabirds: a Natural History. Yale Univeristy Press, New Haven.

Gaston, A.J., 1992. The Ancient Murrelet: a Natural History in the Queen Charlotte Islands. T & AD Poyser, London.

Gaston, A.J., Hashimoto, Y., Wilson, L., 2017. Post-breeding movements of Ancient Murrelet *Synthliboramphus antiquus* family groups, subsequent migration of adults and implications for management. PLoS One 12, e0171726. https://doi.org/10.1371/journal.pone.0171726

Grecian, W.J., Lane, J. V, Michelot, T., Wade, H.M., Hamer, K.C., 2018. Understanding the ontogeny of foraging behaviour: insights from combining marine predator bio-logging with satellite-derived oceanography in hidden Markov models. J. R. Soc. Interface 15. https://doi.org/10.1098/rsif.2018.0084

Grecian, W.J., Witt, M.J., Attrill, M.J., Bearhop, S., Godley, B.J., Grémillet, D., Hamer, K.C., Votier, S.C., 2012. A novel projection technique to identify important at-sea areas for seabird conservation: An example using Northern gannets breeding in the North East Atlantic. Biol. Conserv. 156, 43–52. https://doi.org/10.1016/j.biocon.2011.12.010

Gurarie, E., Bracis, C., Delgado, M., Meckley, T.D., Kojola, I., Wagner, C.M., 2016. What is the animal doing? Tools for exploring behavioural structure in animal movements. J. Anim. Ecol. 85, 69–84. https://doi.org/10.1111/1365-2656.12379

Hays, G.C., Ferreira, L.C., Sequeira, A.M.M., Meekan, M.G., Duarte, C.M., Bailey, H., Bailleul, F., Bowen, W.D., Caley, M.J., Costa, D.P., Eguíluz, V.M., Fossette, S., Friedlaender, A.S., Gales, N., Gleiss, A.C., Gunn, J., Harcourt, R., Hazen, E.L., Heithaus, M.R., Heupel, M., …Thums, M., 2016. Key questions in marine megafauna movement ecology. Trends Ecol. Evol. 31, 463–475. https://doi.org/10.1016/j.tree.2016.02.015

Lascelles, B.G., Taylor, P.R., Miller, M.G.R., Dias, M.P., Oppel, S., Torres, L., Hedd, A., Le Corre, M., Phillips, R.A., Shaffer, S.A., Weimerskirch, H., Small, C., 2016. Applying global criteria to tracking data to define important areas for marine conservation. Divers. Distrib. 22, 422–431. https://doi.org/10.1111/ddi.12411

Lennox, R.J., Engler-Palma, C., Kowarski, K., Filous, A., Whitlock, R., Cooke, S.J., Auger-Méthé, M., 2019. Optimizing marine spatial plans with animal tracking data. Can. J. Fish. Aquat. Sci. 76, 497–509. https://doi.org/10.1139/cjfas-2017-0495

McGowan, J., Beger, M., Lewison, R.L., Harcourt, R., Campbell, H., Priest, M., Dwyer, R.G., Lin, H.Y., Lentini, P., Dudgeon, C., McMahon, C., Watts, M., Possingham, H.P., 2017. Integrating research using animal-borne telemetry with the needs of conservation management. J. Appl. Ecol. 54, 423–429. https://doi.org/10.1111/1365-2664.12755

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., Smouse, P.E., 2008. A movement ecology paradigm for unifying organismal movement research. Proc. Natl. Acad. Sci. 105, 19052–19059. https://doi.org/10.1073/pnas.0800375105

Ogburn, M.B., Harrison, A.-L., Whoriskey, F.G., Cooke, S.J., Mills Flemming, J.E., Torres, L.G., 2017. Addressing challenges in the application of animal movement ecology to aquatic conservation and management. Front. Mar. Sci. 4. https://doi.org/10.3389/fmars.2017.00070

Patterson, T.A., Thomas, L., Wilcox, C., Ovaskainen, O., Matthiopoulos, J., 2008. State-space models of individual animal movement. Trends Ecol. Evol. 23, 87–94. https://doi.org/10.1016/j.tree.2007.10.009

Pinaud, D., Weimerskirch, H., 2005. Scale-dependent habitat use in a long-ranging central place predator. J. Anim. Ecol. 74, 852–863. https://doi.org/10.1111/j.1365-2656.2005.00984.x

Schick, R.S., Loarie, S.R., Colchero, F., Best, B.D., Boustany, A., Conde, D.A., Halpin, P.N., Joppa, L.N., McClellan, C.M., Clark, J.S., 2008. Understanding movement data and movement processes: Current and emerging directions. Ecol. Lett. 11, 1338–1350. https://doi.org/10.1111/j.1461-0248.2008.01249.x

Sequeira, A.M.M., Heupel, M.R., Lea, M.A., Eguíluz, V.M., Duarte, C.M., Meekan, M.G., Thums, M., Calich, H.J., Carmichael, R.H., Costa, D.P., Ferreira, L.C., Fernandéz-Gracia, J., Harcourt, R., Harrison, A.L., Jonsen, I., McMahon, C.R., Sims, D.W., Wilson, R.P., Hays, G.C., 2019. The importance of sample size in marine megafauna tagging studies. Ecol. Appl. 29, 1344–1360. https://doi.org/10.1002/eap.1947

Soanes, L.M., Arnould, J.P.Y., Dodd, S.G., Sumner, M.D., Green, J.A., 2013. How many seabirds do we need to track to define home-range area? J. Appl. Ecol. 50, 671–679. https://doi.org/10.1111/1365-2664.12069

Thaxter, C.B., Lascelles, B., Sugar, K., Cook, A.S.C.P., Roos, S., Bolton, M., Langston, R.H.W., Burton, N.H.K., 2012. Seabird foraging ranges as a preliminary tool for identifying candidate Marine Protected Areas. Biol. Conserv. 156, 53–61. https://doi.org/10.1016/j.biocon.2011.12.009

Tremblay, Y., Bertrand, S., Henry, R.W., Kappes, M.A., Costa, D.P., Shaffer, S.A., 2009. Analytical approaches to investigating seabird-environment interactions: A review. Mar. Ecol. Prog. Ser. 391, 153–163. https://doi.org/10.3354/meps08146

Vandenabeele, S.P., Grundy, E., Friswell, M.I., Grogan, A., Votier, S.C., Wilson, R.P., 2014. Excess baggage for birds: Inappropriate placement of tags on gannets changes flight patterns. PLoS One 9. https://doi.org/10.1371/journal.pone.0092657

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

Watanuki, Y., Suryan, R.M., Sasaki, H., Yamamoto, T., Hazen, E.L., Renner, M., Santora, J.A., O’Hara, P.D., Sydeman, W.J., 2016. Spatial ecology of marine top predators in the North Pacific : tools for integrating across datasets and identifying high use areas. PICES Sci. Rep. 50, 55.

Wilson, R., Grémillet, D., Syder, J., Kierspel, M., Garthe, S., Weimerskirch, H., Schäfer-Neth, C., Scolaro, J., Bost, C., Plötz, J., Nel, D., 2002. Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. Mar. Ecol. Prog. Ser. 228, 241–261. https://doi.org/10.3354/meps228241

Chapter 2. Investigating characteristics of Ancient Murrelet behaviour during breeding-season foraging trips using hidden Markov models

2.1 Introduction

Efforts to protect oceanic habitats for highly mobile top predators such as seabirds have increased in recent years due to heightened awareness of anthropogenic impacts on the ocean. Seabirds are susceptible to many anthropogenic threats at sea, such as oil spills, plastic pollution, fisheries bycatch, decreased prey availability, and climate change (Croxall et al., 2012; Dias et al., 2019; Turley et al., 2013). In order to mitigate negative interactions and protect the foraging habitat upon which seabirds depend, an understanding of their oceanic habitat needs to be established. However, seabirds spend a large amount of their lives in the open ocean far from human observers, thus posing a challenge for researchers interested in understanding at-sea behaviour and habitat use of this group. Therefore, a first step to identifying important foraging habitat and informing seabird habitat protection can involve movement behaviour analysis using data from tracking studies (Tremblay et al., 2009).

A seabird species for which at-sea behaviour and critical at-sea habitat is still poorly understood is the Ancient Murrelet (*Synthliboramphus antiquus*), a species that breeds on islands throughout the north Pacific Ocean. Canada hosts approximately 50 % of the world's breeding population (Gaston, 1992), which makes the country's efforts to manage this species an important part of global efforts to prevent further population declines (Environment Canada, 2015). Ancient Murrelets are listed as a species of *Special Concern* by the Committee on the Status of Endangered Wildlife in Canada due to population declines in terrestrial breeding colonies (Rodway and Lemon, 2011). There is also concern that this species is being negatively impacted by at-sea threats to populations and habitat, such as fisheries bycatch and vessel interactions, but these threats to date have been poorly documented (Environment Canada, 2015). At-sea vessel-based surveys have shown that Ancient Murrelets are distributed widely along the coast of British Columbia (BC) during the breeding season (Fox et al., 2017), but detailed information on localized movement and behaviour of individuals on foraging trips is not well-understood.

As technology develops and tracking devices become smaller, collecting detailed movement data from devices mounted on adult Ancient Murrelets has become an option for studying at-sea behaviour (Breed et al., 2011; Tremblay et al., 2009; Wilson et al., 2002). In the last several decades, tracking devices have provided a way for seabird researchers to collect information on seabird movement away from their terrestrial habitats (Soanes et al., 2013; Tremblay et al., 2009). Ancient Murrelets are limited in the locations they are able to access during the breeding season when they are nesting on land and acting as central-place foragers, transiting between their nest-site and foraging areas (Hamilton and Watt, 1970; Matthiopoulos, 2003; Orians and Pearson, 1979). Tracking of individuals from breeding colonies provides insight not only into the locations of foraging areas they are able to access, but also into detailed characteristics of their movement patterns. Often, locations where foraging behaviour takes place are of the most interest, because successful foraging is essential for survival of both the adults and offspring. During foraging, seabirds are sensitive to disturbance and susceptible to threats such as entanglement in fishing gear while diving (Bertram, 1995). Foraging locations, once identified, can then be prioritized in management plans and marine protected area planning (Thaxter et al., 2012).

Ancient Murrelets act as central-place foragers for shorter periods of time than many other seabird species. The Ancient Murrelet belongs to a group of Alcids, the *Synthliboramphus* murrelets, which share a unique chick-rearing strategy (Springer et al., 1993). The highly precocial chicks of these species are never fed at the nest site, but instead go to sea within several days of hatching (Gaston, 1990). This strategy makes this group of murrelets more susceptible than other Alcids to anthropogenic threats at sea (Sealy et al., 2013), and generates challenges in working with this species. Unlike other seabirds that can be tracked throughout a much longer breeding season, tracking devices must be placed on adult Ancient Murrelet during the 32-day incubation period (Gaston and Powell, 1989). Also, for data loggers that must be recovered in order to download the data, the devices must be retrieved during the time prior to chicks hatching and departing the nest site. During this time period, adults are undertaking self-provisioning foraging trips that range from one to six days in length (Shoji et al., 2012) to feed on larval fish and zooplankton (Sealy, 1975; Vermeer et al., 1985). Observational studies have provided some details on foraging behaviour and locations (Gaston, 1992), but due to this species' small size (average 220 g; Sealy, 1976) and the challenges associated with their chick-rearing strategy, there have been limited studies using devices mounted on individual Ancient Murrelets. Researchers have previously used light-level geolocation (GLS) devices to identify ocean-basin scale migration patterns of breeding Ancient Murrelets (Gaston et al., 2015; Gaston et al., 2017a), and time-depth loggers have produced details on diving characteristics, but not foraging locations (Elliott et al., 2010; Shoji et al., 2011). To date, there have been no studies using Global Positioning System (GPS) tracking of Ancient Murrelets and subsequent movement modelling, to investigate details of at-sea behaviour on foraging trips.

As tracking technology develops and devices become more readily available, a proliferation of modelling approaches has emerged that examine animal movement and inform animal behaviour research (Demšar et al., 2015; Schick et al., 2008). These methods are varied, and include spatial statistics methods, clustering methods, and time-series analysis. State-space models are a time-series analysis method that have proved extremely useful for identifying behaviour from animal movement data, including seabird tracking studies (Patterson et al., 2008). Complex state-space models are often implemented to correct for high positional error in tracking data, but when tracking data are collected with high spatial resolution, such as from GPS devices, hidden Markov models (HMMs) can be used to classify animal movement along a track (Jonsen et al., 2013; Patterson et al., 2017). Researchers are more frequently implementing time-series analysis methods such as these because, unlike methods which are based on clustering of similar movement path characteristics, HMMs take into account the inherent temporal autocorrelation present in animal movement datasets (Breed et al., 2011; Dray et al., 2010). The state process in the model (i.e. the process modelled as the driver of the characteristics of the animal's movement) satisfies the Markov property that the behaviour state at a given time depends on the state at the previous time (Langrock et al., 2012). Similar to clustering methods, behaviours states are defined by grouping movements with differing speeds and turning angles, and then interpreting those states as biological behaviours. For example, directed, fast movement is often interpreted as commuting or transit behaviour, while slow movement with a greater amount of turning could be interpreted as area-restricted search (ARS; Kareiva and Odell, 1987; Morales et al., 2004).

The benefit of conducting movement analysis in the framework of state-space modelling is that it provides the ability to investigate the underlying processes driving the observations, rather than simply a description of track characteristics and locations where an animal has travelled (Barraquand and Benhamou, 2008; Edelhoff et al., 2016). State-space models not only produce an estimate of the characteristics of each state, such as mean velocities, but also estimates of the probabilities of switching between behaviour states (Patterson et al., 2008). With the inclusion of covariates, it is possible to estimate the degree to which state transitions are explained by environmental factors external to the animal, such as temperature, or biological factors inherent to the animal, such as sex (Langrock et al., 2014; Michelot et al., 2017). When location observations are collected with minimal positional error and at regular time intervals, such as from GPS devices, HMMs are an efficient method for classifying points along a track into different states (Michelot et al., 2017; Whoriskey et al., 2017), which can then be interpreted as behaviours. HMMs have proved to be a useful and practical analysis tool for understanding where seabirds are foraging, as demonstrated by many recent seabird studies (Bennison et al., 2018; Dean et al., 2013; Grecian et al., 2018; Zhang et al., 2019). Foraging behaviour can be identified from movement by looking for characteristics of ARS, such as a slowing of movement and an increase in turning frequency when birds encounter certain prey (Kareiva and Odell, 1987), or when they encounter habitat where prey is likely to be present (Weimerskirch, 2007). Although HMMs can be complex and challenging to implement for ecological practitioners without a background in state-space modelling, HMM analysis is becoming more accessible due to the development of several well-documented R packages (Joo et al., 2020).

In this study, we take the first steps to quantifying Ancient Murrelet foraging habitat by investigating movement behaviour characteristics and inferring foraging locations. Although previous studies have used radio tagging to track and estimate foraging ranges of similar closely related species (Hamilton et al., 2011; Whitworth et al., 2000), this is the first study that we are aware of to use GPS tracking and hidden Markov models to investigate foraging trip characteristics and movement patterns of any of the *Synthliboramphus* murrelets. We collected

GPS locations from two Ancient Murrelet colonies along the BC coast by tagging adult birds that were undertaking self-provisioning foraging trips during the incubation period. We developed HMMs based on these tracks to better understand movement patterns of Ancient Murrelets at sea, and to identify locations where foraging took place. We validated modelled foraging behaviour classification with immersion data recorded from the same GPS tracking devices. Outputs from the models were used to answer the following questions: Are we able to differentiate between slow-moving behaviour states such as foraging versus resting from Ancient Murrelet tracks? Where are breeding Ancient Murrelets exhibiting movement patterns that suggest foraging behaviour? What proportion of time are Ancient Murrelets spending in each behaviour state identified from the HMMs? To what degree do sex, time of day, and tag immersion explain the probability of transitioning between behaviour states?

2.2 Methods

2.2.1 Study sites

GPS tagging of Ancient Murrelets was conducted over two consecutive years (2018 and 2019) at two field sites in Haida Gwaii, BC, Canada. Haida Gwaii is an archipelago approximately 100 km west of the mainland coast of BC, and is made up of two large and many smaller islands. The two study sites were located along the south-eastern coast of Haida Gwaii, adjacent to Hecate Strait, the body of water separating the archipelago from the mainland (Figure 2-1). Tagging took place on Ramsay Island in 2018 and on George Island in 2019. Ramsay Island has an area of 4557 ha, with an estimated Ancient Murrelet population of approximately 18000 breeding pairs (Harfenist, 2003; Rodway et al., 1988). George Island is much smaller, at 42 ha, but the Ancient Murrelet population is similar, estimated to be approximately 17000 breeding pairs (Harfenist, 2003; Rodway et al., 1988). Both islands are forested, with old-growth Sitka spruce (*Picea sitchensis*), western red cedar (*Thuja plicata*), and western hemlock (*Tsuga heterophylla*) as the dominant canopy species. Ancient Murrelets nest in burrows that range from the shoreline up to several hundred meters from shore, and are generally dug into mossy banks, under rocks and under tree roots (Sealy, 1976). Due to the low density of accessible burrows on Ramsay Island, tagging was spread out along the northwest shoreline of the island, centred at approximately 52.56648˚ N, 131.426071˚ W. On George Island, accessible burrows were closer together, and tagging took place in two distinct areas. Plot 1 was located on the west coast of the island (52.34972˚ N, 131.21326˚ W), and Plot 2 was approximately 500 m away, on the east coast of the island (52.34909˚ N, 131.20529˚ W).

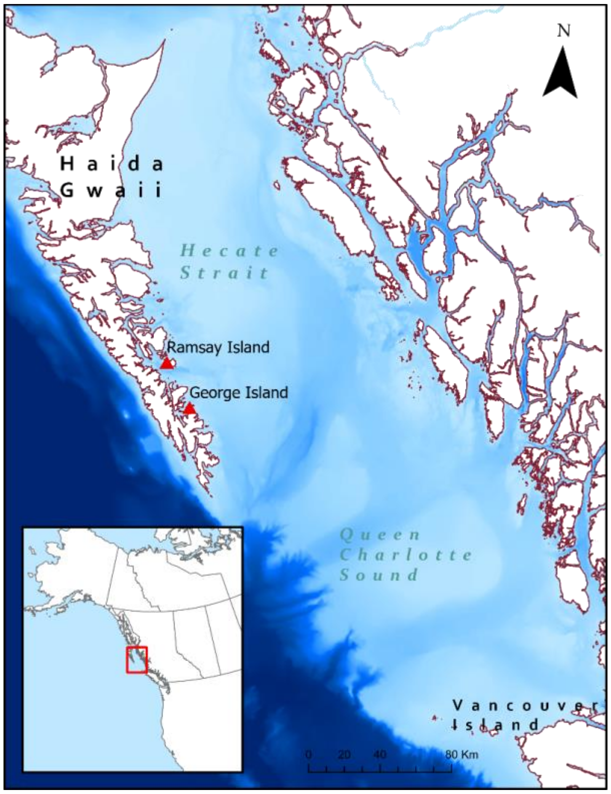


Figure 2-1. Map of British Columbia coastline showing Haida Gwaii and the adjacent bodies of water and surrounding bathymetry. Ancient Murrelet colonies where tagging took place during this study are shown as red triangles.

2.2.2 Field methods and data collection

GPS tags were deployed on one incubating bird per nest site, during the day, between late April and mid-May each year. Burrows can be greater than a meter long, therefore the nest cup was often accessed via a hatch dug into the ground and subsequently covered by a cedar shingle and soil to camouflage the access hatch. Ancient Murrelets only leave and return to their burrows at night (Gaston, 1992). Burrows were monitored using infrared wildlife cameras, knockdown sticks (Shoji and Gaston, 2010), and manual checks when necessary. Daily monitoring was crucial to determine which night the tagged bird left the burrow and when it returned in order to recover the tag after at least one full foraging trip. Mates were not tagged so that the tagged bird could be easily identified when it returned to the burrow, and to reduce disturbance to any one breeding pair. Ancient Murrelets were tagged with NanoFix GEO tags (Pathtrack Limited, Otley, UK) and also had a federally issued metal band placed on the right leg. The GPS tag was attached by using several thin strips of marine-grade cloth Tesa tape wrapped around the tag and several clumps of feathers on the mantle, between the shoulder blades towards the rump (following similar methods to Domalik et al., 2018). The tags were designed to be waterproof and pressure-proof to a depth of 40 m, and weighed on average 3.8 g. The total weight mounted on each bird, including tape and the metal band, was approximately 5.5 g, which does not exceed the acceptable recommendation of no more than 3 % of the species' average bodyweight (Kenward, 2001). Because Ancient Murrelets cannot be reliably sexed using morphological features, it was unknown whether tags were deployed on a male or female bird at the time of deployment, but blood samples for sex determination were taken when tags were recovered.

Birds were handled for an average of 11 minutes on deployment and an average of 14 minutes on retrieval. All procedures were carried out under the Environment and Climate Change Canada Animal Care Permits 18LW05 and 19LW05.

Tag settings were set to balance battery life and data resolution. There were several conditions that drain batteries at an unknown rate, such as a bird staying in the burrow after tagging and diving while at sea. Ancient Murrelet foraging trips can vary greatly in length; therefore, we were conservative with our settings as we wanted to maintain battery life for a sufficient period to collect locations from each individual throughout at least one foraging trip. Over the two-year study, several settings were tested: in 2018, tags were set to record one GPS location every 30 minutes, while in 2019 they were set to record one location every 20 minutes, except for two tags. These two tags recorded a location every 10 minutes, to test if the batteries would last with a higher-frequency sampling regime. In 2019, tags were also set to log data from internal immersion sensors that recorded a binary value indicating the immersion state of the tag (0 = wet, 1 = dry) every 5 seconds while the tag was enabled.

2.2.3 Data processing

Data on Ancient Murrelet locations were projected using the BC Albers coordinate reference system, and any locations on land were removed, including any time intervals when birds were underground. Tags that recorded multiple foraging trips were identified and the trips were separated. An individual foraging trip was defined as a time period of more than one day (~ 24 hours) at sea. The second set of locations was defined as a second foraging trip from the same individual if a track was broken up by a period of more than one night in the burrow. Multiple trips from the same individual were treated as separate tracks in the movement analysis. The two tracks that had a resolution of one location every 10 minutes were subsampled to select every other location in order to match the 20-minute resolution of the majority of the 2019 tracks. One track with only 27 locations was removed from the analysis.

To prepare the location data for inclusion in movement models, missing locations at sea were imputed using nonlinear interpolation, which, for animals in the marine environment, provides a more realistic estimate of track characteristics than simple linear interpolation (Tremblay et al., 2006). Missing GPS position fixes were present sporadically throughout the tracks when coordinates were not obtained at the scheduled time interval. One of the main reasons for missing position fixes in this study was because the tags cannot receive positions from satellites while underwater. As a means to preserve battery life, the tags are designed to turn off while underwater. Position fixes will also not be obtained if there are fewer than four satellites within range at the time of the attempted position fix. Although imputing some missing locations is not problematic for movement analysis using HMMs (Langrock et al., 2012), it could be problematic if imputed locations are consistently associated with a certain type of behaviour (Graves and Waller, 2006), therefore this possible bias must be considered before imputation. To reduce this bias we removed the two tracks with greater than 50 % of locations missing. We also visually inspected tracks with and without imputed locations, to investigate whether missing data might be highly associated with a single behaviour (for example, when birds are foraging and diving more often).

Missing locations were imputed using the ‘crawlWrap’ function in the R package *momentuHMM*, following the workflow presented by McClintock and Michelot (2018a). Because GPS locations generally have relatively low positional error, we used single imputation versus the multiple imputation technique suggested for tracking data with high positional error

(McClintock and Michelot, 2018a; Zhang et al., 2019). The ‘crawlWrap’ function estimates missing locations by fitting a single-state movement model to each track using a Kalman filter approach (McClintock, 2017). Kalman filtering is a method of fitting a continuous-time state-space model to temporally autocorrelated data, and similar to an HMM, estimates the state process driving characteristics of the location observations (Hooten et al., 2017; Patterson et al., 2017). The Kalman filter model formulation can accommodate missing location observations in a time series, and therefore can be used as a data processing step to impute missing locations at equal time intervals (Johnson et al., 2008; McClintock and Michelot, 2018a).

Other variables used in the movement modelling were sex of the tagged bird and a summary of the immersion log from each tag in 2019. Sex of one individual in 2019 was not obtained, and this individual was included as a male so that the track could still be incorporated into the behaviour models. There were many more males than females, therefore we included this individual as male as it was assumed it would have a lower influence on the results. A mean immersion value, referred to as the immersion index, was calculated in order to scale the immersion data to the same temporal resolution as the location data. The immersion index assigned to each location was the mean of all zeros (wet) and ones (dry) recorded over the previous 20-minute time interval. The immersion index was therefore the proportion of time that the logger was dry over each 20-minute time interval prior to the location to which it was assigned, as this reflects the resolution of the movement characteristics used in the HMMs.

2.2.4 Movement analysis using hidden Markov models

2.2.4.1 Hidden Markov model background

We used hidden Markov models (HMMs) to classify at-sea behaviour of Ancient

Murrelets into discrete behaviour states, based on track characteristics. An HMM consists of a time-series of observations, and the underlying process that produced the observations. The series of observations is referred to as the state-dependent process, or the observation process (X), which in animal movement analysis is the series of observed animal relocations at each time step t (Figure 2-2). The observation process is often multivariate, as there can be multiple movement path characteristics derived from each relocation. In the case of animal movement models, these two path characteristics are often step length (X_s) and turning angle (X_a; Morales et al., 2004). Step length is the distance between location X_{t-1} and location X_t, and turning angle is the change in direction of travel from location X_{t-1} to location X_t (Michelot et al., 2016). These two series of characteristics are assumed to have contemporaneous conditional independence: within any given state, observations are assumed to be independent (Patterson et al., 2017; Pohle et al., 2017). The unobserved underlying state process (S) is the driver of the observations X at each time step (Figure 2-2). S is the 'hidden' part of the model, and is what we are interested in estimating. In animal movement analysis S is often equated to behaviour; for example, in a two-state model, the two states could be interpreted as 'exploratory' and 'encamped' (Morales et al., 2004), or for marine central-place foragers, 'transit' and 'area-restricted search'. The goals of hidden Markov modelling of animal movement are determining the number of biologically meaningful states, N, represented in the observed data, estimating the parameters of the probability distributions that define each state, and estimating the probability of transitioning between states.

HMMs are non-independent mixture models that use the Markov property to take into account temporal autocorrelation. The Markov property defines the relationship between sequential points such that the future state (S_{t+1}) depends on the current state (S_t). Each set of observations (here, X_s and X_a at time t) is assumed to be generated by a temporally dependent mixture of probability distributions (the state process), each state usually being modelled as a correlated random walk (CRW; Michelot et al., 2017; Patterson et al., 2017). The mixture of N distributions represents the different states (the different CRWs) that are driving the characteristics of an animal's movement path. Many animal movement studies assume there are two states generating the observations, in which case the characteristics between each observed location, the step length and turning angle, could be produced by one of two CRW models that differ in their distribution parameters (Patterson et al., 2017). The parameters of these distributions are estimated using the HMM, as well as the transition probability matrix (TPM) representing the probabilities of transitioning between states. Possible distributions that are often used to model step length are gamma or Weibull (positive continuous distributions), while the von Mises and wrapped Cauchy distributions (circular distributions) are used for modelling turning angle. Parameter estimates from HMMs can be found using numerical maximization of the likelihood, by the forward algorithm (Patterson et al., 2017). The most probable sequence of states for the time series of observations is then classified using the Viterbi algorithm (Michelot et al., 2017; Zucchini et al., 2017).

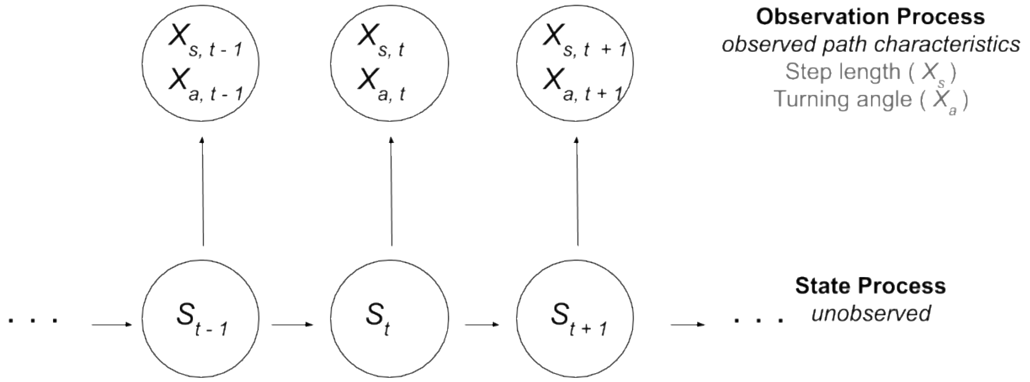


Figure 2-2. Schematic representation of the dependence structure of a hidden Markov model. The unobserved state process is the driver of the characteristics observed in the observation process, which can be multivariate. The state at time *t* is dependent on the previous state.

2.2.4.2 Model formulation and model selection

HMMs can be fit using various probability distributions and be based on observations from individual animals or from many animals. They can also include covariates, in either the state process or the observation process (McClintock and Michelot, 2018a). Here we formulated separate models for each year. We pooled individuals from each colony, used several covariates in the state process, and several different numbers of states. We used all combinations of the available covariates for each year: in 2019, time of day (in decimal hours between 0 and 24), immersion index, and sex of the individual birds; and in 2018 time of day and sex (see below for details). Only main effects were investigated with no interactions. We chose probability distributions that are commonly applied to the animal track characteristics of step length and turning angle (Michelot et al., 2016). To model step length, we used the gamma distribution, which has defining parameters of alpha and beta, which were converted to mean and standard deviation for interpretation purposes. We used the von Mises distribution to model turning angle, which has defining parameters of mean and concentration (κ). A low value of κ indicates highly variable angles, while a high value indicates angles concentrated around the mean. The gamma distribution is flexible and accommodates the right-skew that is often observed in step length data (Beyer et al., 2013) and the von Mises distribution is often considered a good choice for circular data centred around zero (Zucchini et al., 2017). To aid with the selection of the appropriate number of states, we explored the change in maximum likelihood estimates with the addition of states, using models with two to eight states, following Dean et al. (2013). HMMs were fit using the *momentuHMM* package (McClintock and Michelot, 2018b) in R (R Core Team, 2019).

We pooled tracks from all individuals in the HMMs in order to investigate population level characteristics of Ancient Murrelet foraging behaviour. Using complete pooling there is an assumption that individuals are independent and that the observations for each individual are generated by the same state process (the parameter estimates will be the same for all individuals). This is a simplification, as the model will be unable to recognize variability between individuals (Zucchini et al., 2017) but is the most straightforward way to scale up to population level inferences. Complete pooling can be appropriate if the goal is to identify locations where certain population-level behaviours are taking place (i.e., important foraging areas), rather than understanding the details of individual variability in behaviour (Jonsen, 2016; McClintock et al., 2013).

Choosing the number of states to use in an HMM has been shown to be a challenging task (Celeux and Durand, 2008; Pohle et al., 2017). Typical model selection criterion such as AIC or BIC are often not useful because adding more states almost always lowers the AIC or

BIC (Pohle et al., 2017). Movement data are complex, and the more states that are added, the more variation is accounted for (variation that could actually be due to model misspecification), and as a result the model will appear to fit the data better whether the additional states are biologically relevant or not (Li and Bolker, 2017). The number of states must therefore be chosen based on a combination of an understanding of the biology of the study species and the data resolution and by using an iterative process of fitting multiple models and comparing model performance. Two or three states are often the maximum number that can be reasonably identified and attributed to different biologically meaningful behaviour states if the dataset includes no covariates and only two movement path characteristics (step length and turning angle; Hooten et al., 2017). We decided on the number of states to be defined by our movement data by following procedures suggested by Pohle et al. (2017), and fit sets of models with two, three, and four states. Each set of models included a model with no covariates and models with combinations of all available covariates.

Finding appropriate starting parameters when fitting HMMs is also a well-documented challenge (McClintock and Michelot, 2018a), as specifying inappropriate starting parameters can easily lead to model convergence at local maxima during optimization, thus missing the true global maximum (Michelot et al., 2016). To address this issue, we followed procedures suggested by Michelot and Langrock (2019). We used a loop to sample random starting parameters, and between 20 and 50 models were run using these randomly chosen starting parameters. The model with the highest maximum log likelihood, which is most likely to be the global maximum, was chosen as the final model. For each set of models with *N* number of states, the global maximum was first determined from the model with no covariates, then the starting parameters were taken from this model to use as initial starting parameters for the models with all covariates. Next, the starting parameter space was explored using the ‘retryFits’ argument included in the model fitting function. This argument runs multiple models with different starting parameters so that we could be more certain that the global maximum likelihood was identified. Once a model was fit with all covariates, starting parameters for the following models with other combinations of covariates were taken from the model with all covariates, and again, ‘retryFits’ was used to explore the starting parameter space.

Covariates were incorporated into the state process once models were developed that appeared to converge at a global maximum likelihood for $N = 2$, 3, and 4 states. Covariates in the state process attempt to explain variability in the transition probabilities between states, and define factors that may be driving corresponding changes in movement behaviour (Michelot et al., 2017; Hooten et al. 2017). Covariates do not influence the classification of the points into different states or the parameter estimates of the states, but instead explain transitions between states, and therefore influence the transition probability matrix estimated from the model. Each element of the transition probability matrix becomes a function of the covariates. Our models included immersion index of the previous time step (2019 only), time of day, and sex of the individual Ancient Murrelet as covariates. Sex was included as a categorical variable, and hour of the day was included as a sinusoidal function, as per Li and Bolker (2017). The influence of each covariate on the transition probabilities was summarized and visualized using plots of the stationary state probabilities at certain fixed values of the other covariate (e.g. Leos-Barajas et al., 2017; Patterson et al., 2009).

Goodness-of-fit of models was investigated using a combination of AIC and pseudo-residual plots (Michelot et al., 2016). AIC was used as a measure of relative goodness-of-fit of models with different combinations of covariates, within each set of models with $N = 2$, 3, or 4 states. Within each set, the one with the lowest AIC was chosen as the model that best fit the data. In addition, pseudo-residuals were used as a measure of absolute goodness-of-fit as detailed in previous research (Langrock et al., 2012). In general, step length pseudo-residuals are easier to interpret than those for turning angle (Langrock et al., 2012; Pohle et al., 2017), therefore we focused on step length pseudo-residuals. Similar to standard model checking procedures with residuals, quantile-quantile (Q-Q) plots of the theoretical versus observed pseudo-residuals were plotted to observe if they follow a normal distribution. Autocorrelation function plots of the pseudo-residuals were also used to determine if there was unaccounted for temporal autocorrelation of observations. In summary, the final model was chosen based on these model diagnostics: which covariates to include was chosen based on AIC, and the number of states were chosen based on what was biologically reasonable with knowledge of the dataset and species, and on the pseudo-residual plots.

2.2.4.3 Model validation

Model validation was accomplished by performing a visual inspection of individual tracks from 2019, which were mapped with each location classified into the behaviour states as estimated by the HMM. These maps were compared to maps of (a) each location classified into day or night, and (b) the amount of diving at each location, as estimated by the immersion index. By visual inspection, areas where a relatively high amount of diving took place, but were not classified as foraging, could be identified. Visual comparison of these maps also helped to understand how well the model classified transit and resting behaviour. Transit towards and away from the colony is most likely at night, because Ancient Murrelets only enter or leave the colony at night. We used the proportion of night-time locations classified as the foraging behaviour state as an estimate of error, because Ancient Murrelets are not known to forage at night (Elliott et al., 2010).

2.3 Results

2.3.1 General track characteristics

A total of 46 complete foraging trips were collected over two years of field work at two colonies in Haida Gwaii (Table 2-1). Six tracks were collected from 6 different individuals nesting at the Ramsay Island colony in 2018, between April 29 and May 14. These tags recorded one GPS location every 30 minutes, and did not record tag immersion. From the George Island colony, tracks were collected from 36 individuals between April 28 and May 15, 2019. These tags recorded one location every 20 minutes, and also recorded an immersion value every 5 seconds. In 2019, four tags recorded multiple foraging trips, therefore there were 40 complete foraging trips collected. Tracks consisted of a mean of 226 locations per track, with a large range in number of locations per track (minimum 33 locations, maximum 560 locations) due to varied durations of foraging trips. Ancient Murrelets travelled hundreds of kilometers during single foraging trips (Table 2-1). Trips were generally in an easterly direction into Hecate Strait, and followed a variety of path types (Figure 2-3). Some tracks formed large loops in which the individual took very different incoming and outgoing paths, and other birds followed a similar path when departing and returning to the colony, referred to as ‘commuting’ trips (Weimerskirch, 2007). Direction of travel varied between individuals in both years. Some undertook trips in an overall counter-clockwise direction and others clockwise.

Table 2-1. Summary of Ancient Murrelet foraging trips from two years and two colonies, recorded by GPS devices. SD = standard deviation. ‘Range’ is the maximum distance between the colony and the farthest location recorded on the foraging trip.

Year	Number of individuals tagged	Number of foraging tracks	Sex	GPS resolution	Mean duration in days (SD)	Mean trip length in km (SD)	Mean range in km (SD)
2018	6	6	3 female 3 male	30 min.	4.3 (1.8)	453.1 (228.8)	107.9 (37.2)
2019	36	40	9 female 26 male 1 unknown	20 min.	3.0 (1.2)	263.8 (98.3)	81.3 (25.7)

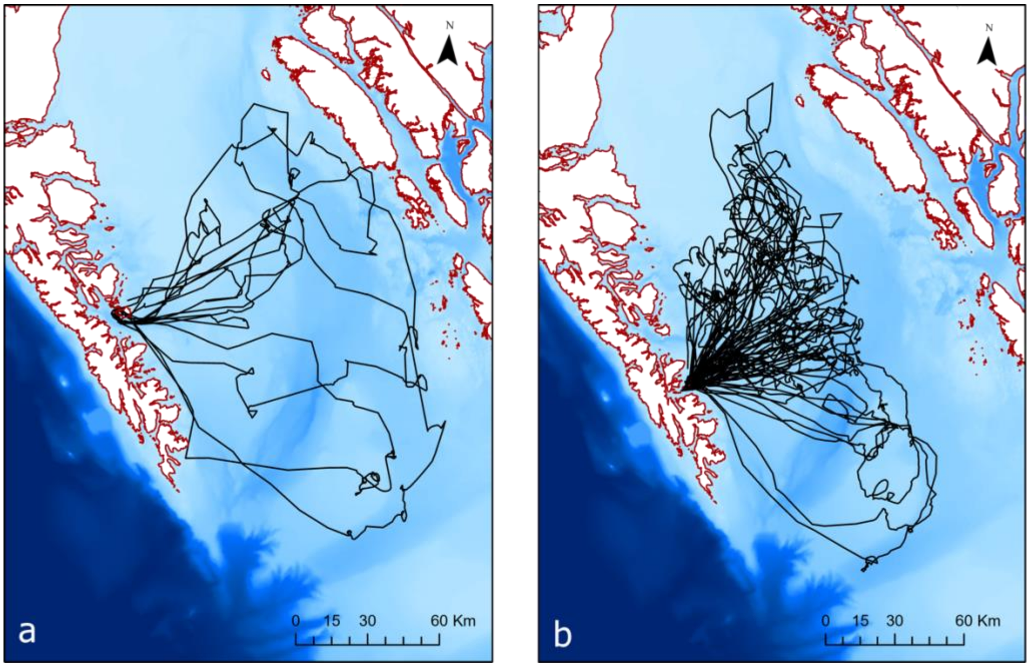


Figure 2-3. All GPS tracks from the two Ancient Murrelet colonies. (a) Ramsay Island, 2018. (b) George Island, 2019.

2.3.2 Immersion data and missing locations

For seabirds, the most likely reasons for missing location fixes from GPS devices are due to tag immersion while the bird is diving or while the bird is preening and splashing, or because of a lack of sufficient satellites overhead at the scheduled time of a required location fix. Based on immersion data from the tags, most missing locations coincided with the tag registering as wet. Few locations were missing when the tag was dry, indicating high tag success in acquiring position fixes. Over both years, the mean proportion of position fixes that were unsuccessful was 16 % (SD = 13.5 %), and we removed the two tracks from movement analyses that had greater than 35 % of locations missing. After imputing missing locations, a visual inspection of where imputed points were located along the tracks showed that missing locations were present during both fast-moving and slow-moving periods of activity, which suggested that missing location fixes would not necessarily bias the designation of behaviour states. Understanding this allowed us to more confidently use imputed points to account for missing locations.

Immersion data from the GPS tags showed that diving almost exclusively took place during the day (Figure 2-4), which is consistent with past research (Elliott et al., 2010). The immersion index was used as a proxy for diving, and showed the proportion of each 20-minute interval in which the tag was dry. An immersion index of 1 indicates the tag was dry for the entire 20 minutes prior to the location fix, while an immersion index of 0.5 indicates the tag was wet for 10 minutes (not necessarily consecutive) out of the 20-minute interval. Figure 2-4 shows that during nighttime (between ~ 21:30 and 06:00), almost all 20-minute intervals had an immersion index of 1 or close to 1, indicating very little tag immersion at night, and hence very little diving at night.

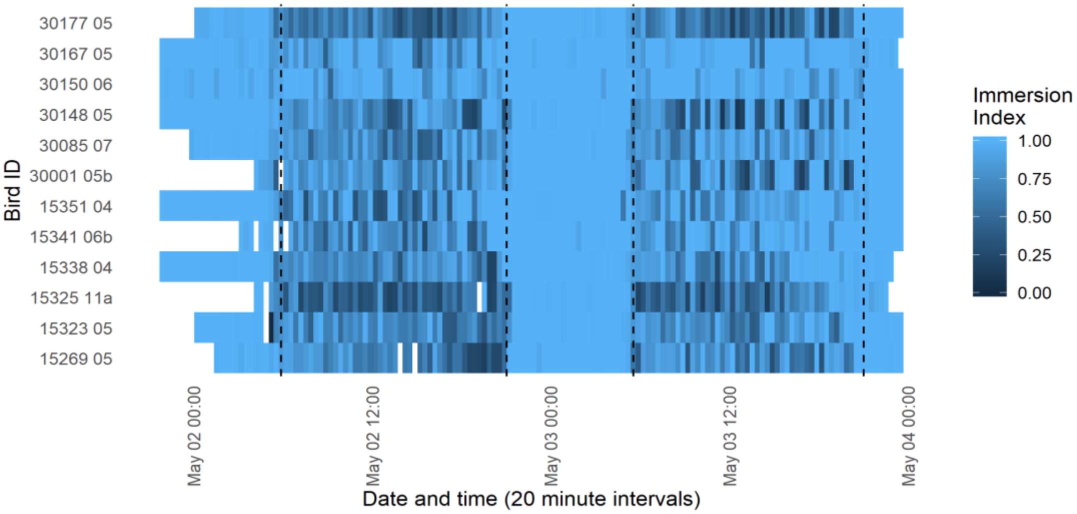


Figure 2-4. Summary of immersion data over a two-day period for a subset of 12 Ancient Murrelets, chosen because they contain data over the same time period. An immersion index of 1 means the tag was consistently dry for the previous 20-minute interval, while 0 means the tag was wet for the full 20-minute interval. Time intervals when the birds were on land have been removed. Sunrise (~ 06:00) and sunset (~ 21:30) are shown on the figure as dashed lines.

2.3.3 HMM movement behaviour analysis

2.3.3.1 Model fitting and selection

For initial movement modelling, we used the tracks from 2019 foraging trips. In total, there were 38 tracks, due to removal of the two tracks with greater than 50 % missing locations. A plot of maximum log-likelihood (MLL) output from models, with the addition of states, showed that the most dramatic increase in MLL was in going from a two-state to a three-state model (Figure 2-5). This suggests that a model with three states is a good compromise between model complexity and explanatory ability (Dean et al., 2013). Within each set of models (two, three, or four states) AIC was compared between models with the various combinations of covariates (Table 2-2). The best-fitting models within each set were those that included time of day (hour) and diving (immersion index) as covariates in the state process.

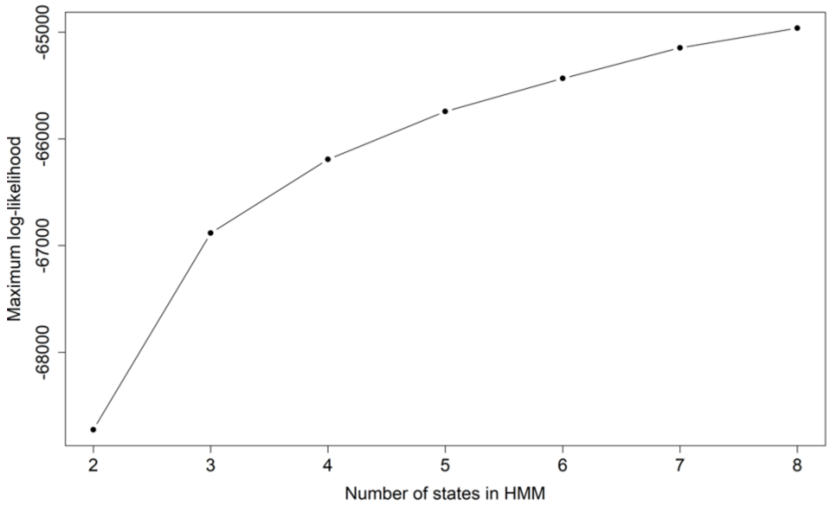


Figure 2-5. Maximum log-likelihood by number of states from HMMs with no covariates. The connecting lines are for visualization only and do not represent a model fit.

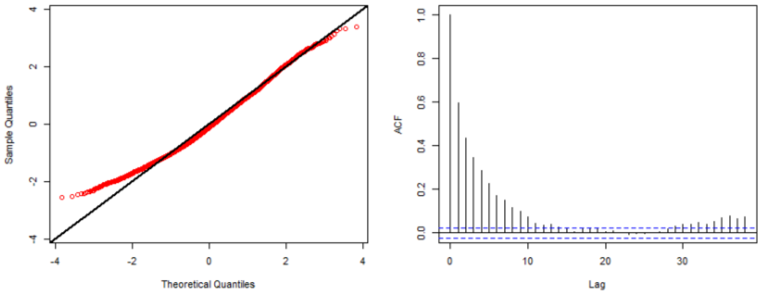
Table 2-2. Model selection results from the 2019 tracks, for each set of models with two, three, or four states. Each set included models with no covariates, and combinations of all covariates.

Number of states	Model	Maximum log likelihood	Number of estimated parameters	AIC	Δ AIC	AIC weights
2	hour + dive	-68696.12	15	137426.2	0.00	0.573
	hour	-68698.83	13	137427.7	1.41	0.282
	hour + dive + sex	-68695.94	17	137429.9	3.62	0.094
	hour + sex	-68698.53	15	137431.1	4.81	0.052
	dive	-68723.54	11	137473.1	46.84	0.000
	no covariates	-68726.44	8	137474.9	48.62	0.000
	dive + sex	-68723.25	13	137476.5	50.25	0.000
	sex	-68726.01	11	137478.0	51.77	0.000
3	hour + dive	-66784.33	35	133644.7	0.00	0.905
	hour + dive + sex	-66780.59	41	133649.2	4.51	0.095
	hour	-66819.65	29	133703.3	58.64	0.000
	hour + sex	-66816.66	35	133709.3	64.66	0.000
	dive	-66844.86	23	133741.7	97.05	0.000
	dive + sex	-66841.44	29	133746.9	102.22	0.000
	no covariates	-66882.88	15	133805.8	161.10	0.000
	sex	-66880.23	23	133812.5	167.79	0.000

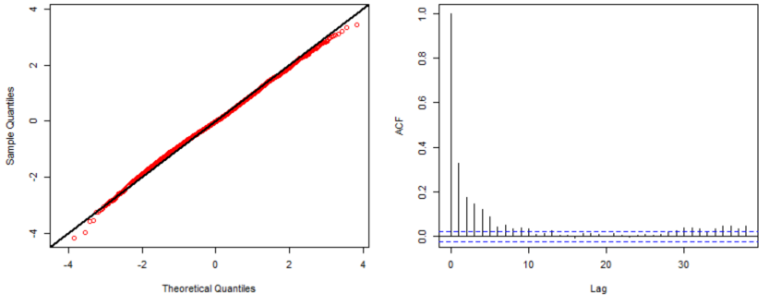
4	hour + dive	-66055.48	63	132245.0	0.00	0.998
	hour + dive + sex	-66049.76	75	132257.5	12.56	0.002
	dive	-66138.13	39	132362.3	117.3	0.000
	hour	-66127.94	51	132365.9	120.93	0.000
	dive + sex	-66131.73	51	132373.5	128.49	0.000
	hour + sex	-66138.97	63	132411.9	166.98	0.000
	no covariates	-66192.19	24	132446.4	201.41	0.000
	sex	-66220.70	39	132527.4	282.44	0.000

For the final models that included the covariates hour and immersion, pseudo-residual Q-Q plots of step length showed that there was a lack of fit in the shorter step lengths in the two-state model (Figure 2-6a). This lack of fit was reduced with the addition of more states (Figure 2-6b and 2-6c). The autocorrelation over time seen in the ACF plot of the two-state model was also reduced by the addition of states. The pseudo-residual Q-Q and ACF plots for the model with no covariates looked very similar to these, suggesting that the added covariates do not explain much more variability in the data. Although the three-state and four-state models both appeared to fit the data well based on pseudo-residual plots, the three-state model was chosen as the final model, as models with more than two or three states become much harder to interpret biologically without using additional path characteristics to define the states, such as acceleration or number of dives (McClintock et al., 2014), or without additional covariates (Michelot et al., 2017).

a. two-state model



b. three-state model



c. four-state model

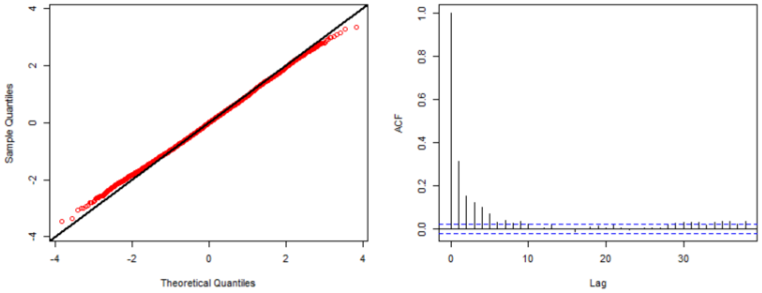


Figure 2-6. Pseudo-residual Q-Q plots (left column) and autocorrelation function plots (ACF; right column) of step length, for models including hour and immersion as covariates. Each time lag in the ACF is 20 minutes.

2.3.3.2 Model results

Parameter estimates from the final three-state model from the 2019 tracks indicated there was one behaviour state in which the Ancient Murrelets were moving relatively quickly, and two slower-moving behaviour states (Figure 2-7 and Appendix A Figure A-1). State 1 included the longest step lengths, indicating fast movement, and had variable turning angles, indicated by a low value of kappa (Table 2-3). This state was interpreted as transit behaviour, and was seen along tracks when birds were leaving and returning to the colony and when moving between foraging patches (Figure 2-8). The two slow-moving states were seen at the maximum extent of the trips, or in concentrated areas along the looping tracks (Figure 2-8). Although the mean step lengths of these two states were fairly similar, state 2 had much more variable step lengths (the ratio of standard deviation to mean for state 2 was 0.6, while for state 3 it was 0.36). The turning angle concentrations for these two states were also dramatically different: State 2 turning angles were varied, similar to state 1 (transit), while state 3 demonstrated turning angles that were highly concentrated around the mean of zero (κ = 16; Figure 2-7), indicating directed movement.

Table 2-3. Parameter estimates from the 2019 and 2018 movement models.

	2019				**2018**			
	Mean step length (m)	**Step standard deviation (m)**	**Turning angle concentration (κ)**	**Standard error of κ**	**Mean step length (m)**	**Step standard deviation (m)**	**Turning angle concentration (κ)**	**Standard error of κ**
State 1 'transit'	3539	3363	2.05	0.07	6417	5230	2.33	0.32
State 2 'foraging'	264	159	1.23	0.04	513	406	0.73	0.12
State 3 'resting'	535	190	16.00	0.76	703	331	11.52	1.53

Although the addition of hour and immersion as covariates in the models did not substantially change the fit of the models based on AIC and pseudo-residual plots, immersion was essential for differentiating and associating biological behaviour with the two slower-moving states. Furthermore, the inclusion of the hour covariate allowed us to investigate changes in probability of being in each state at different times of the day. The two slow-moving states (state 2 and state 3) were inferred to be foraging and resting. By including immersion as a proxy for diving activity, we were able to identify which of these two states represented foraging behaviour and which represented resting. Plots of the probability of being in each state at different immersion indices showed that at midday, when Ancient Murrelets are most likely to be foraging, and when there was a high proportion of diving activity (immersion index closer to 0), the probability of being in state 2 was much greater than the probability of being in state 3 (hour = 12 in Figure 2-9). State 2 is therefore much more likely to represent foraging behaviour (the slowest movement, with varied turning angles and high diving activity during the day), and state 3 is likely to be a state including all other slow movement, which we referred to as resting (slow speed movement with more consistent step lengths and more directed turning angles, and a lower proportion of diving activity). When the tag was dry (immersion index closer to 1) during the night (hour = 0 and hour = 22 in Figure 2-9), the model indicated there was a near-equal probability of being in either of the two slow-moving states.

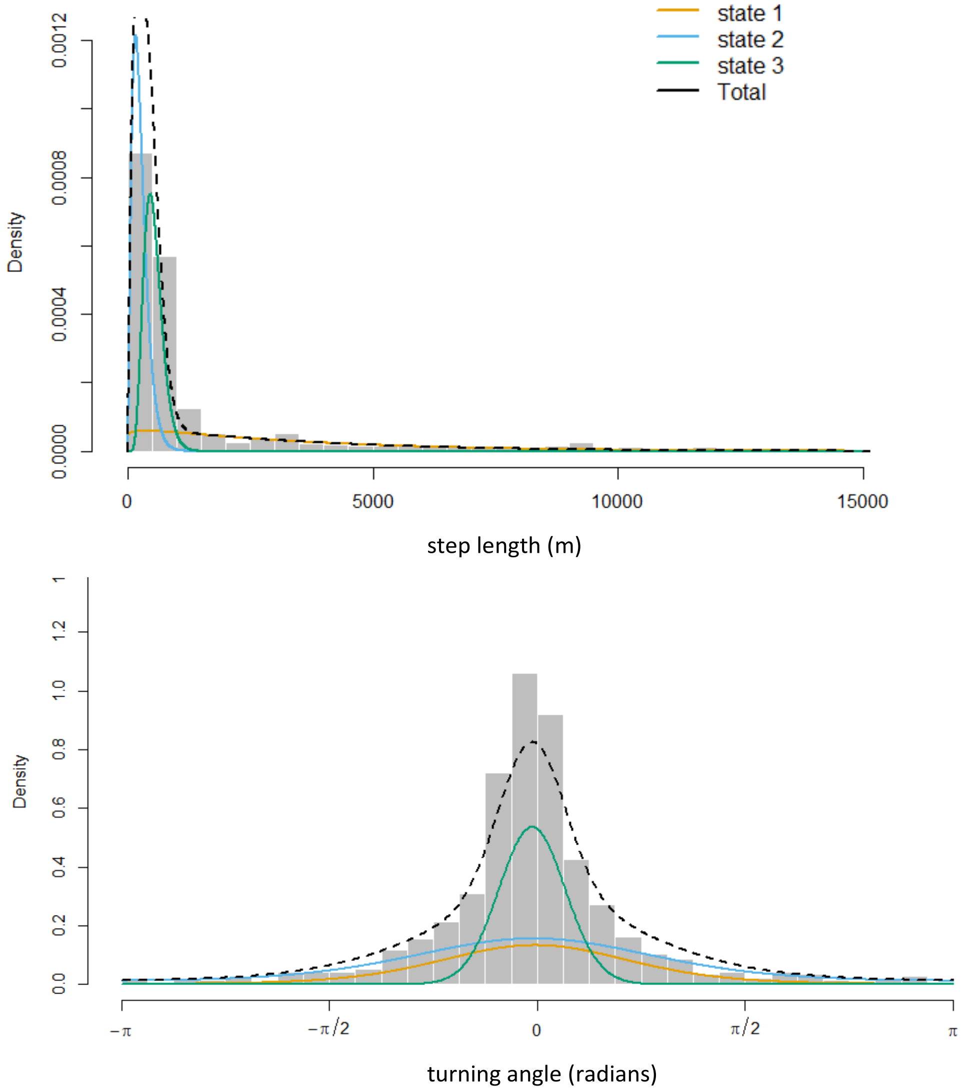


Figure 2-7. Probability density plots of step lengths (top) and turning angles (bottom) defining the three behaviour states estimated from the final HMM. Distribution are gamma (step length) and von Mises (turning angle). State 1 is interpreted as ‘transit’, state 2 as ‘foraging’ and state 3 as ‘resting’.

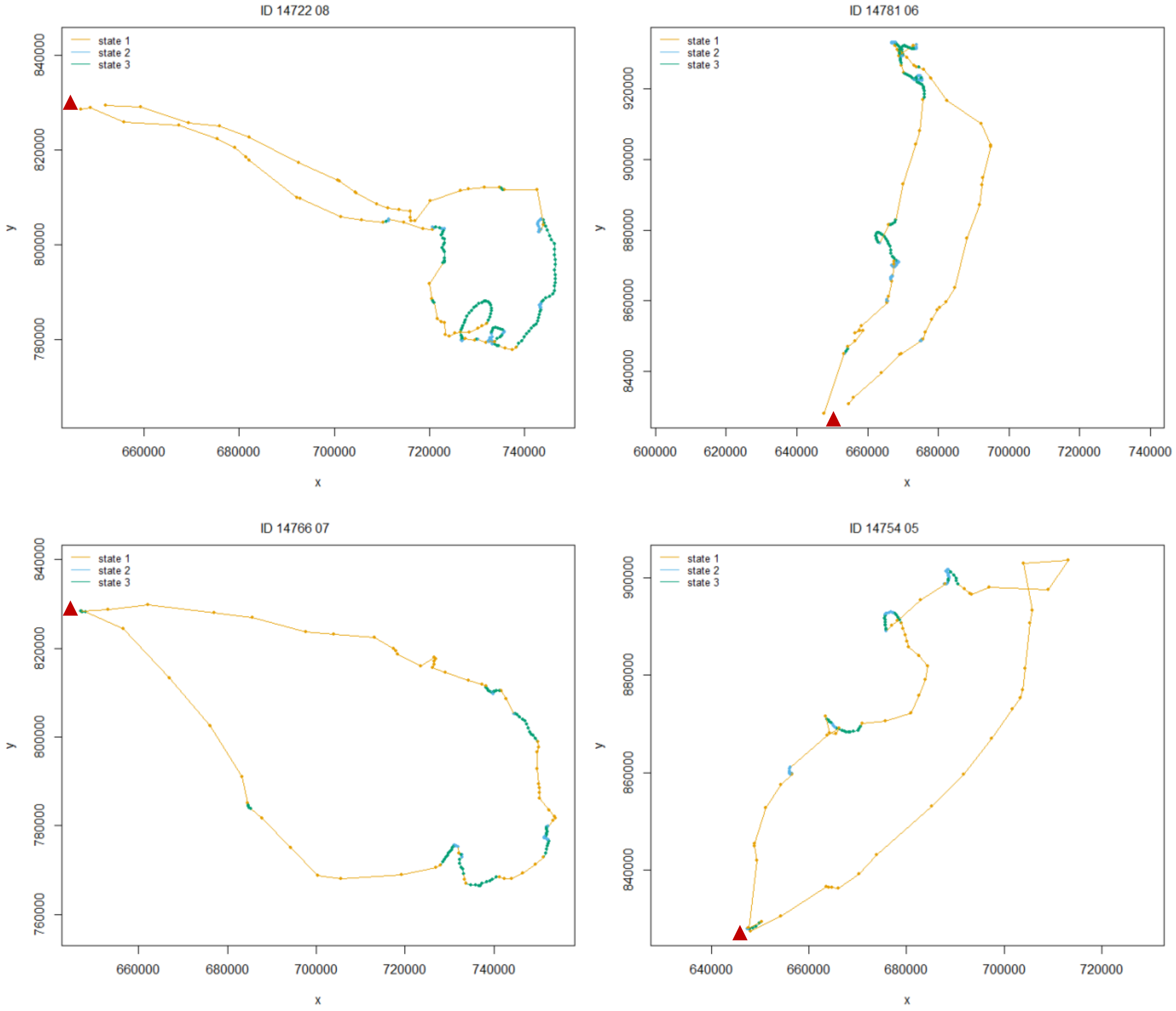


Figure 2-8. Four example tracks with track segments colour-coded by state, based on the final three-state HMM. State 1 is interpreted as 'transit', state 2 as 'foraging' and state 3 as 'resting'. The location of the colony is shown as a red triangle.

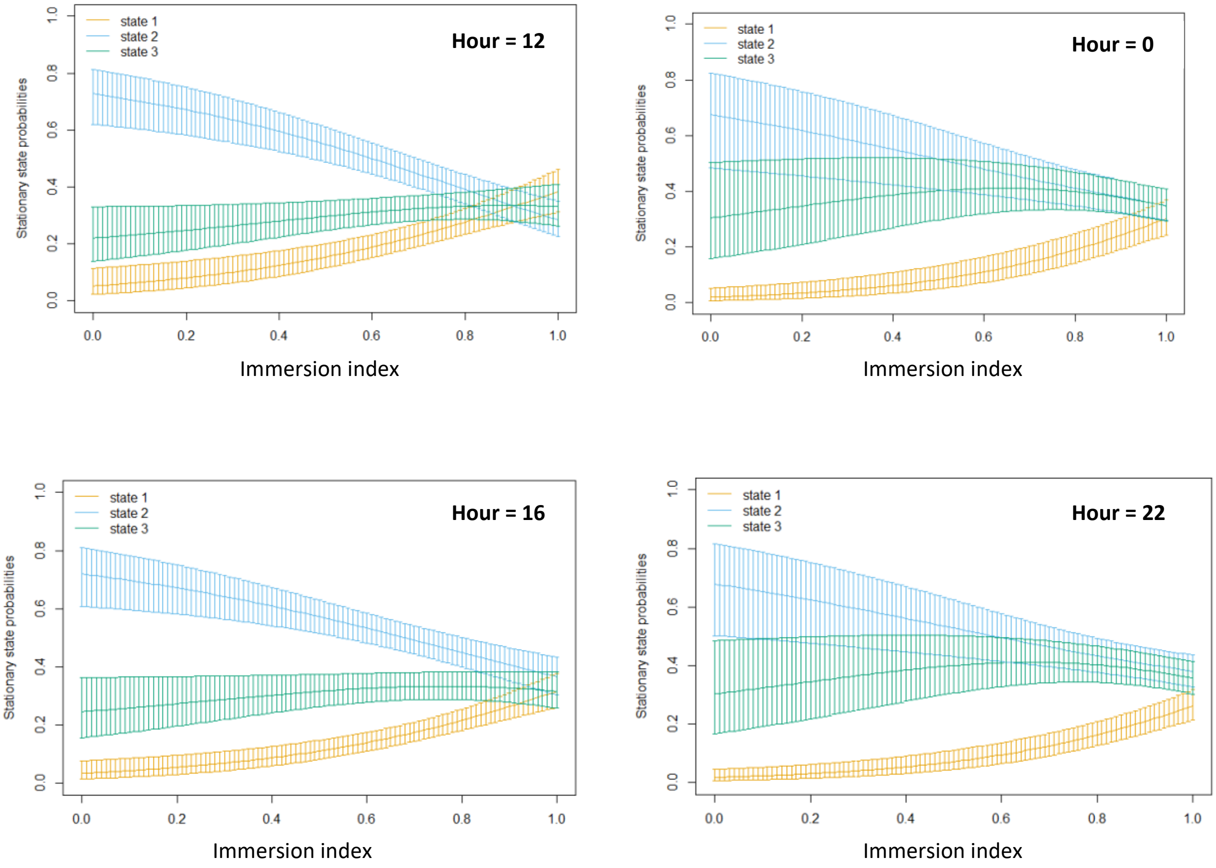


Figure 2-9. Stationary state probabilities, with 95 % confidence intervals, showing the probability of being in each state over the full range of immersion index values, at several times of the day (0 = midnight, 12 = noon). Immersion index of 0 means the tag was immersed 100 % of the time over the previous 20-minute interval, and an immersion index of 1 means the tag was dry 100 % of the time over the previous 20-minute interval.

The addition of time of day as a covariate allowed us to investigate when different states were more likely throughout the day. When there was a higher amount of diving activity (Figure 2-10, immersion = 0 and immersion = 0.5), it was much more likely for birds to exhibit foraging behaviour (state 2) between sunrise and sunset than resting or transit. When there was low or no diving activity (Figure 2-10, immersion = 0.8 and immersion = 1), there was less stability and more switching between states throughout the whole 24-hour period, although in the early morning it was slightly more likely for birds to be in state 1 (transit) and in the evening less likely to be in the transit state. Sex was also included as a covariate in the models, but state transition probabilities did not vary between male and female birds. Detailed plots of transition probabilities between all states for each covariate are provided in Appendix A.

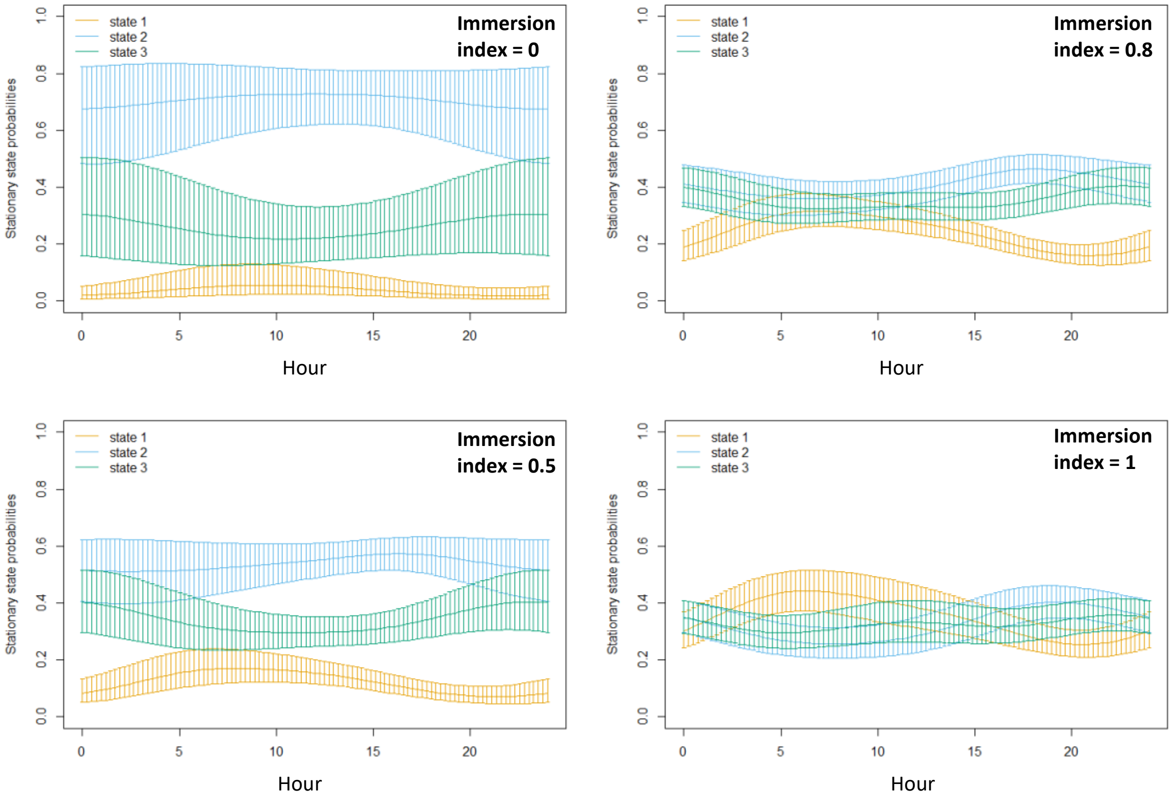


Figure 2-10. Stationary state probabilities throughout the day (0 = midnight, 12 = noon) at four different values of the immersion index (with 95 % confidence intervals). Immersion index close to 0 indicates high diving activity, and immersion index close to 1 indicates low or no diving activity.

Based on the knowledge gained by including the immersion index as a covariate in models of the 2019 movement data, we repeated the same HMM fitting procedure using the six tracks collected in 2018. Although we did not have immersion data from 2018, we were able to differentiate the same biological behaviours associated with three states identified from these tracks, based on the understanding that the slow-moving state with a highly concentrated turning angle and less variable step length (directed, slow movement) is likely resting, while the slow-moving state with varied turning angles and the lowest step length is most likely the foraging state. Parameter estimates for the three states from the 2018 data followed a similar pattern to those from 2019, although values of step lengths were higher because the temporal resolution of the data differed (30-minute intervals in 2018 versus 20-minute intervals in 2019). In 2018, the transit state exhibited a high mean step length and varied turning angles, the foraging state showed a low mean step length and varied turning angles, and the resting state had a low mean step length and turning angles concentrated around zero (Table 2-3). In both years, the foraging and resting states have a much lower step length than the transit states, and of the two, foraging has the shortest mean step length. For both years, locations were classified into each state using the Viterbi algorithm. The percentage of locations classified into each state for 2019 was 26 % transit, 41 % foraging, and 33 % resting. In 2018, 29 % of locations were transit, 35 % resting, and 36 % foraging. In 2018 there was a slightly higher proportion of time spent in the transit state and slightly lower proportion of time spent in the foraging state, compared to 2019, likely due to the small sample size in 2018 and several very long trips in that year having a disproportionate influence.

2.3.3.3 Model validation

Model validation through visual inspection showed that the HMM successfully differentiated behaviours at the scale of single foraging trips (10s to 100s of km), and captured much of the foraging activity taking place, although there appeared to be some diving activity that was not attributed to the foraging state. Based on the immersion log, diving was present along some sections of the track that were classified as transit behaviour. For example, in Figure 2-11, locations along the most northerly part of the track are classified as the transit state, although there are intervals with a lower immersion index along that section of the path, suggesting a higher proportion of diving activity in that area. This could represent immersion due to sporadic foraging, or possibly another behaviour causing the tag to register as wet, such as preening. Foraging behaviour also seemed to be misclassified as resting if it took place along a directed path (i.e. the bird was moving in a consistent direction). For example, in Figure 2-12, the most easterly part of the track is classified as resting behaviour, although it contains a high proportion of diving activity. As another validation, resting behaviour was investigated during the night. The HMM consistently classified slow-moving night-time locations into the resting state, which is consistent with Ancient Murrelets not foraging at night. In Figure 2-12, the loop in the southern part of the track is classified as resting (left panel), there is no diving (top right panel), and it is during the night (bottom right panel), all consistent with this representing resting behaviour. Finally, when locations classified as foraging were differentiated into day and night, 33 % of locations classified by the HMM into the foraging state were at night (Figure 2-13). Night was defined as one hour after sunset to one hour before sunrise, based on when Ancient Murrelets were found to be foraging by Elliott et al. (2010). Locations close to the colony that were classified as foraging (Figure 2-13 inset) were likely misclassified because there are behaviours that take place close to land, such as socializing and rafting before entering the colony, that were not accounted for in the three-state model.

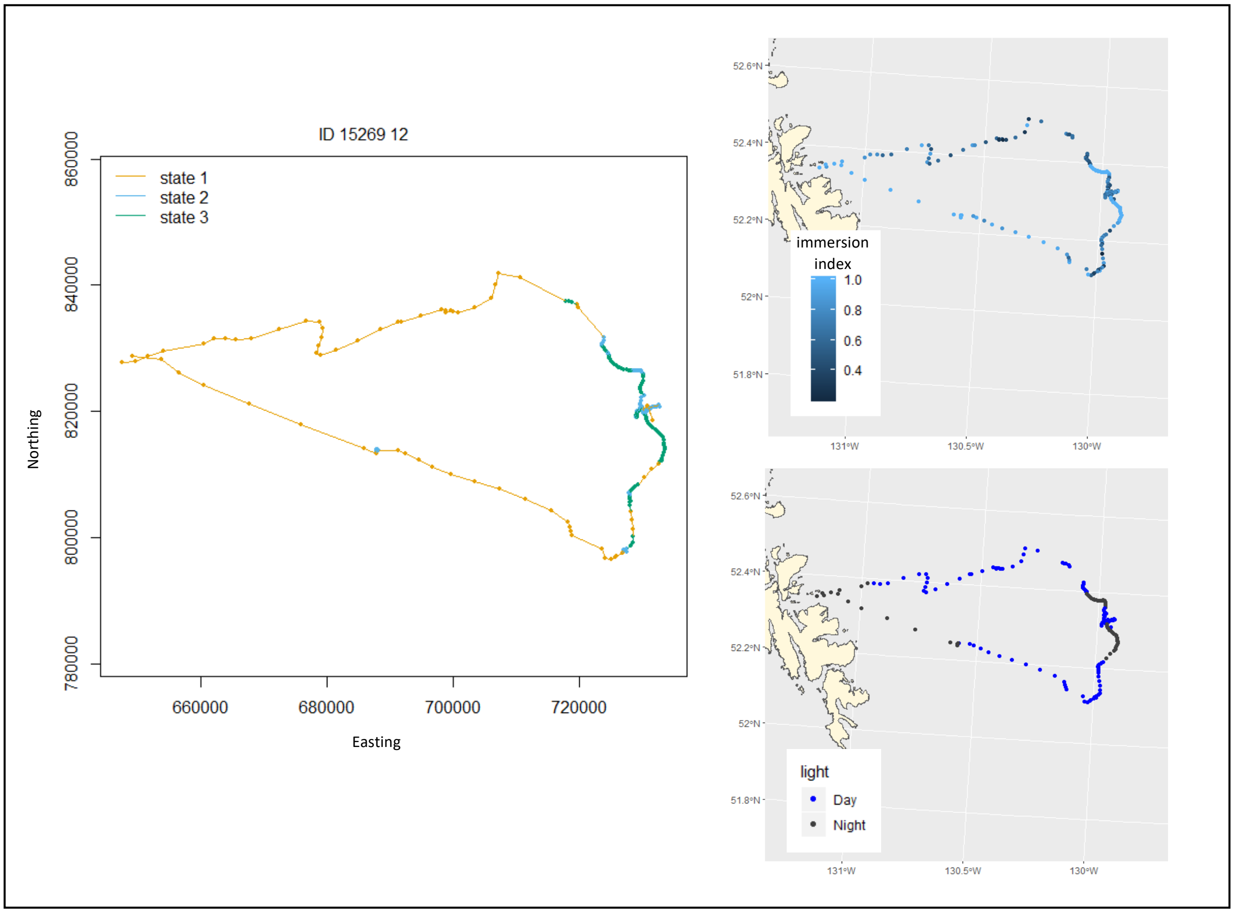


Figure 2-11. Example of looping style track used for model validation. HMM output (left) with locations along the track classified as transit (state 1), resting (state 3), or foraging (state 2). Immersion index along the track (top right; low index = more diving). Locations along the track differentiated into day and night (bottom right).

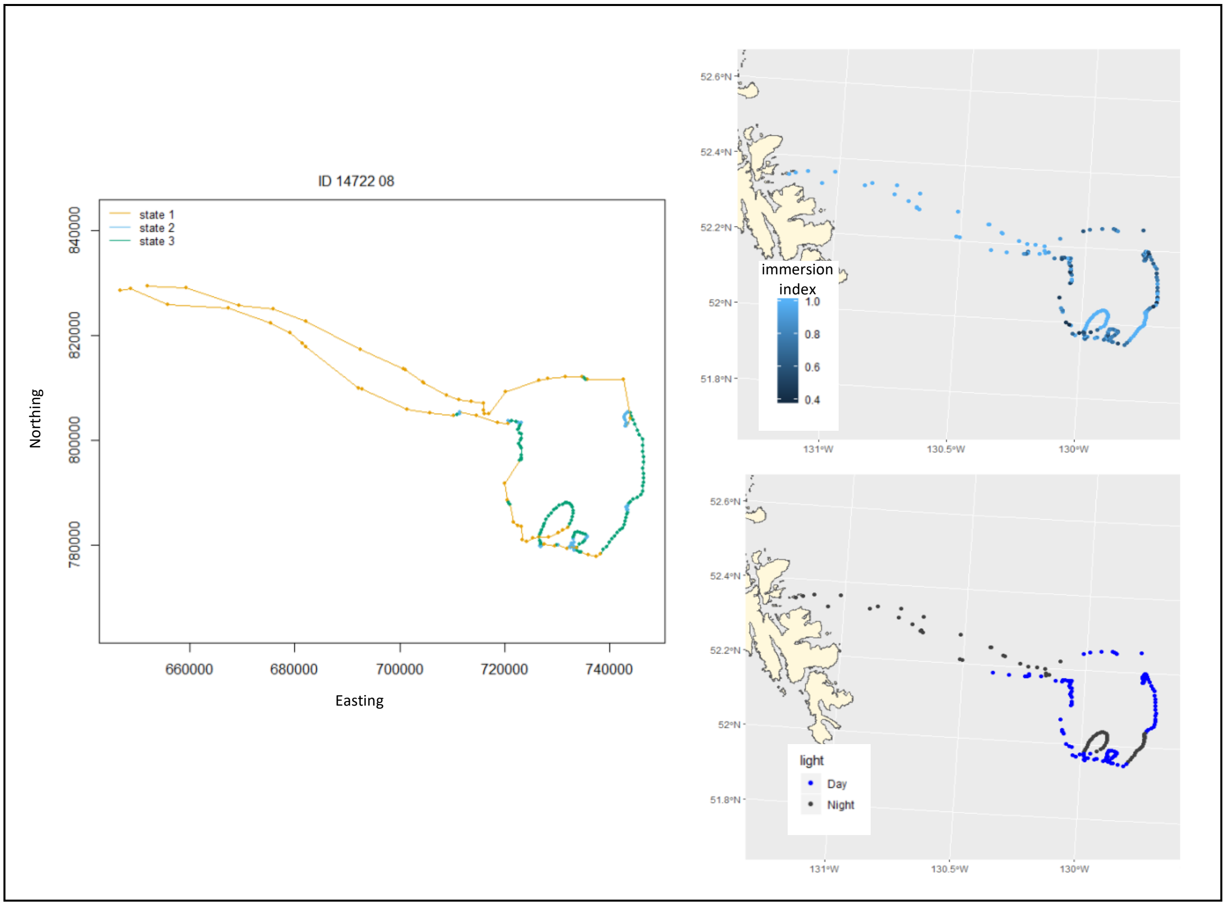


Figure 2-12. Example of commuting style track used for model validation. HMM output (left) with locations along the track classified as transit (state 1), resting (state 3), or foraging (state 2). Immersion index along the track (top right; low index = more diving). Locations along the track differentiated into day and night (bottom right).

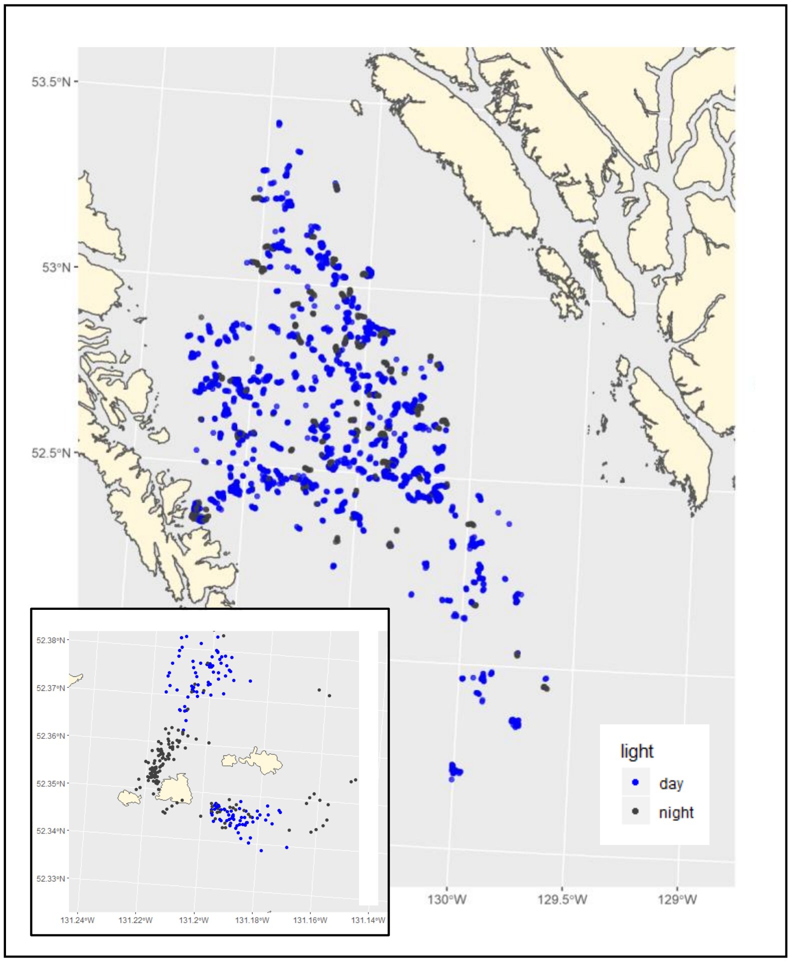


Figure 2-13. Foraging locations from 2019, differentiated into day and night. Day is defined as one hour before sunrise to one hour after sunset.

2.4 Discussion

This study utilized GPS tracking data and hidden Markov modelling to investigate the movement patterns and movement behaviour of individual Ancient Murrelets from two colonies along the southeast coast of Haida Gwaii. By tracking individuals during the nesting period, we determined that Ancient Murrelets in our study site travelled long distances on a single trip, up to on average 84 km away from the colony, which is consistent with previous estimates of maximum foraging ranges for this species based on flight speeds (Elliott et al., 2010; Shoji et al., 2012). Trips were seen in the form of both ‘looping’ and ‘commuting’ style trips, as defined by Weimerskirch (2007), which suggests varied strategies for finding food, giving an indication of predictability of prey patches and predictability of foraging locations. The more directed ‘commuting’ trips suggest these birds know where to find food, and the larger ‘looping’ tracks is an indication of birds that are sporadically searching for food throughout the whole trip.

Using hidden Markov modelling, we were able to identify three distinct states based on movement characteristics, and we inferred behaviours that Ancient Murrelets exhibited based on these states: transiting, resting, and foraging (similar to Grecian et al., 2018). Tag immersion data were essential for differentiating the two slow-moving behaviour states (foraging and resting) by including these data as a covariate in the 2019 HMMs. Once the movement characteristics of each of these states were quantified, we could use similar procedures to classify tracks from 2018, despite the lack of immersion data that year. The pattern was similar for both years, with one slow-moving state having a slightly higher mean step length, and a much more concentrated turning angle. The concentrated turning angle indicates persistent movement in one direction over time. This movement behaviour was interpreted as resting, as it often took place throughout a whole night at sea. Evenly spaced locations following smooth curved paths over tens of kilometers suggested birds could be floating on the water and moving with currents or wind. The other slow-moving state generally corresponded with a higher proportion of tag immersion and more variable turning, indicating birds were searching for prey (ARS) and diving. In both years, transit was easily identified as the state in which birds were moving more quickly, often away from or towards the colony. Transit could take place during the night, when birds were leaving or returning to the colony, or during the day. During the day short bouts of transit could indicate movement between prey patches. In both years, birds spent approximately one-third of their foraging trip in each behaviour state, although in 2019, time spent in the transit state was slightly lower than one-third, and time spent in the foraging state was slightly higher. There were more trips that were shorter distance and duration in 2019 than in 2018, which explains the lower proportion of transit in 2019. Year-to-year fluctuations in prey location and availability, due to oceanographic conditions, could also be influencing how far birds must travel, resulting in variability between years in time spent transiting versus foraging (Shoji et al., 2012).

We visualized the change in transition probabilities throughout the day by plotting the probability of being in each of the three states over 24 hours, at different values of immersion. Although stationary state plots do not show the details of transition probabilities, they are a useful summary tool (Patterson et al., 2009). Here, these plots demonstrated that differentiating the two slow-moving states was easier when there was more diving activity (based on tag immersion data) and easier during the day. During the day, there was a much higher probability of a bird being in the foraging state than the other two states, showing that the model was generally classifying foraging behaviour well. At night, and although the tag was mostly dry, the slow-moving states were more difficult to differentiate as there was equal probability of being in either the resting or foraging state. Given that Ancient Murrelets do not forage at night (Elliott et al., 2010), the equal probabilities of a bird being in either the foraging or resting state at night suggests our model could not distinctly differentiate night-time slow-moving behaviour states.

We included sex as a covariate and found that the probability of switching between states did not vary between male and female birds, suggesting their movement behaviour at sea was similar. This finding confirms results from other studies suggesting that male and female Ancient Murrelets undertake foraging trips with similar characteristics, such as similar trip lengths

(Gaston et al., 2017b; Shoji et al., 2011). Finding no difference in movement behaviour between sexes in this species is not surprising given that Ancient Murrelets are sexually monomorphic (physically indistinguishable), and foraging behaviour differences between sexes in birds is often attributed to sexual size-dimorphism (Lewis et al., 2002). Another sexually monomorphic seabird, the Northern Gannet, was also found to exhibit similar foraging trip characteristics between sexes, such as foraging trip length and duration, and variation in behaviour between sexes was only seen in finer-scale foraging behaviour characteristics such as diving duration (Lewis et al., 2002).

Interpretation of behaviour states from HMMs is dependent on a knowledge of the biology of the species of interest, but the temporal resolution of the movement data also plays a significant role in the interpretation of the results. Using movement analysis, it is only possible to capture and identify behaviours that take place at a greater temporal scale than the location sampling interval (Beyer et al., 2013; Jonsen, 2016). In our study, the data were at a relatively low temporal resolution compared to many other seabird tracking studies, which often record locations at a resolution of minutes (e.g. Domalik et al., 2018; Zhang et al., 2019) or even seconds (Mendez et al., 2017); however, longer interval data, as those used here, have some advantages. By using lower resolution movement data with more time between location fixes, we were observing movement patterns at a scale that included the entire foraging trip. Although we were not able to differentiate very short-term behaviour changes such as transitions between specific dives, we were able to gain an understanding of temporally and spatially larger-scale behavioural changes (McClintock et al., 2014) such as switching from transiting to foraging and vice-versa. We identified behavioural changes that were taking place over minutes or hours, rather than seconds or minutes, and over the kilometers to hundreds of kilometers over which the

Ancient Murrelets were foraging. Foraging locations were inferred from states where birds are exhibiting the slowest movement with a high frequency of turns, and where there is a much higher probability of diving taking place. Therefore, we have identified a movement pattern that appears to be ARS or a combination of searching for prey and diving, but we cannot actually differentiate the foraging dives, per se. For this study, this is not a problem as we are interested in a broader understanding of foraging areas, versus detailed movement patterns and understanding the behavioural biology behind these movement, in which case higher temporal resolution data and more elaborate models would be necessary.

Model validation was possible using the immersion data to independently identify segments of tracks where diving was likely occurring, and comparing these areas to locations classified by the HMM as the inferred foraging state. We were able to use immersion data both for validation of model output and as a covariate in the model because when included in the state process of an HMM, covariates do not influence the classification of locations into different states. From immersion loggers, we could see that diving almost exclusively took place during the day. This is consistent with previous studies that concluded that Ancient Murrelets do not forage at night. Elliott et al. (2010) found that Ancient Murrelets undertook foraging dives (greater than 2 m in depth) only between one hour before sunrise and one hour after sunset, which for our study period and latitude was approximately 05:30 to 22:00 hrs. Thirty-three percent of locations classified as foraging from 2019 were at night, which suggests that the inferred foraging state did also include some behaviour that was not foraging. It is likely that these locations were actually resting, versus transit, because they were often located close together (Figure 2-12), representing slow movement. This means that, although they have been misclassified, they do represent a slow-moving behaviour indicating an area of high use. There could be several reasons that some night-time locations were identified as foraging. For one, birds could be socializing, which is a state that is not accounted for in this three-state behaviour model. Socializing near the colony has been observed and involves short flights and some diving (Gaston, 1992; Sealy, 1976), which in our movement data would likely appear similar to foraging (short step lengths and varied turning angles).

Additionally, the locations at night close to the colony that have been classified as foraging could be when birds were rafting near the colony, waiting to enter the forest, and socializing. Ancient Murrelets stage on the water in defined areas prior to entering the colony. Staging areas are usually within 4 km of the colony (Jones et al., 1990; Vermeer et al., 1985) and birds have been observed spending up to four hours in these areas before entering the colony (Sealy, 1976). At the George Island colony, the staging area appears to be located to the south and east of the island (Rodway et al., 1988). Staging areas would account for many GPS locations concentrated on the water near the colony, although it is unknown whether the Ancient Murrelets using these defined staging areas are breeders or non-breeders (Gaston, 1992). It is unlikely these locations are actually foraging, as the model indicates, as Ancient Murrelets have not been observed foraging in staging areas (Sealy, 1976).

There also may be environmental reasons explaining why our HMMs classify locations as foraging states during the night. For example, if there are strong winds and waves when birds are resting on the water, the path between points could be displaying more varied turning angles than we would expect for resting movement (the defining feature of the resting state seems to be the highly directed movement). If movement is less directed, due to winds or waves buffeting the birds, it may be classified into the foraging state. One way this could be taken into account is by including the immersion data as another defining characteristic of the movement track when formulating the HMM (i.e. formulating an HMM with the observation process defined by step length, turning angle, and immersion). McClintock et al. (2013) found that including dive data as an additional movement path characteristic to define the observation process for Harbour Seal movement helped to differentiate foraging, transit, and resting.

As with all studies involving tagging, this study was subject to potential issues related to mounting a device directly onto a bird with a possible consequential influence on their behaviour. Devices can alter how and when seabirds dive, especially for pursuit-diving foragers (Ballard et al., 2001). In this study, we assume the influence of the device on the overall findings to be minimal as we were investigating behaviour over relatively large areas, with some tagged birds undertaking extensive multi-day trips, and returning to incubate as normal. However, future research is required to confirm this assumption. Another limitation of this study is that we were at most able to collect two foraging trips after the device was mounted on the bird; using only the first foraging trip can be unrepresentative of subsequent foraging trips (Soanes et al., 2013). Previous research on Ancient Murrelets showed that after mounting a geolocator tracking device on incubating birds, for some birds the first trip was much longer than future foraging trips (Gaston et al., 2017b), while for other seabird species the first trip was shorter than subsequent trips (Soanes et al., 2013). This could be an issue when drawing conclusions about distances of foraging trips. In our study, four birds did undertake multiple complete trips, and the second trips appear to encompass a larger area with travel extending farther from the colony, which is inconsistent with the findings of Gaston et al. (2017b). Because trip duration can be highly variable for this species, it is hard to predict whether birds without a device would have completed multiple short trips, or a single longer trip. Overall, this bias in the data is challenging to account for as leaving the devices on Ancient Murrelets for multiple foraging trips might not be logistically or ethically feasible (Sequeira et al., 2019); the devices can easily fall off over time, there is a short window of opportunity to tag adults before the chicks hatch, and this species is quite susceptible to disturbance (Gaston et al., 1988).

New information resulting from our analyses of movement data has provided a better understanding of Ancient Murrelet movements and behaviours at sea. Mapping of foraging trips from birds at both colonies demonstrated that individuals from the two colonies utilized large areas on foraging trips, and has shown us the distances and directions that birds from the two colonies are travelling to find prey during self-provisioning foraging trips. More detailed analysis of locations near the colony could help understand characteristics of behaviour near the colony, as well as help to determine if there is another behaviour (socializing) that is not being captured by the three-state HMM. Most importantly, the habitat characteristics of the foraging locations from both years can be investigated in the future to help understand why Ancient Murrelets are foraging where they are, and ideally help to predict high-quality foraging habitat that can be incorporated into conservation planning for this species. Additionally, studies such as this are important for understanding the applicability of HMMs to other species and datasets. It is important to evaluate lower-resolution data, and data from fewer birds, because often these are the data available. Managers and researchers often have limited resources to deploy tags, ethics permits may require that few birds are tagged, and smaller birds require smaller tags, which often equates to lower battery power and data at a lower temporal resolution. This study has helped us to understand that, given such constraints, HMMs can be useful in identifying seabird foraging locations at sea, and allows us to gain an understanding of behaviour with the use of available data.

2.5 References

Ballard, G., Ainley, D.G., Ribic, C.A., Barton, K.R., 2001. Effect of instrument attachment and other factors on foraging trip duration and nesting success of Adélie Penguins. Condor 103, 481–490. https://doi.org/https://doi.org/10.1093/condor/103.3.481

Barraquand, F., Benhamou, S., 2008. Animal movements in heterogeneous landscapes: identifying profitable places and homogeneous movement bouts. Ecology 89, 3336–3348. https://doi.org/10.1890/08-0162.1

Bennison, A., Bearhop, S., Bodey, T.W., Votier, S.C., Grecian, W.J., Wakefield, E.D., Hamer, K.C., Jessopp, M., 2018. Search and foraging behaviors from movement data: A comparison of methods. Ecol. Evol. 8. https://doi.org/10.1002/ece3.3593

Bertram, D.F., 1995. The roles of introduced rats and commercial fishing in the decline of Ancient Murrelets on Langara Island, British Columbia. Conserv. Biol. 9, 865–872. https://doi.org/10.1046/j.1523-1739.1995.09040865.x

Beyer, H.L., Morales, J.M., Murray, D., Fortin, M.J., 2013. The effectiveness of Bayesian state-space models for estimating behavioural states from movement paths. Methods Ecol. Evol. 4, 433–441. https://doi.org/10.1111/2041-210X.12026

Breed, G.A., Costa, D.P., Goebel, M.E., Robinson, P.W., 2011. Electronic tracking tag programming is critical to data collection for behavioral time-series analysis. Ecosphere 2, 1–12. https://doi.org/10.1890/ES10-00021.1

Environment Canada, 2015. Management plan for the Ancient Murrelet (*Synthliboramphus antiquus*) in Canada, in: Speices at Risk Act: Management Plan Series. Environment Canada, Ottawa.

Celeux, G., Durand, J.-B., 2008. Selecting hidden Markov model state number with cross-validated likelihood. Comput Stat 23, 541–564. https://doi.org/10.1007/s00180-007-0097-1

Croxall, J.P., Butchart, S.H.M., Lascelles, B., Stattersfield, A.J., Sullivan, B., Symes, A., Taylor, P., 2012. Seabird conservation status, threats and priority actions: a global assessment. Bird Conserv. Int. 22, 1–34. https://doi.org/10.1017/S0959270912000020

Dean, B., Guilford, T., Freeman, R., Kirk, H., Leonard, K., Phillips, R.A., Perrins, C.M., 2013. Behavioural mapping of a pelagic seabird: combining multiple sensors and a hidden Markov model reveals the distribution of at-sea behaviour. J. R. Soc. Interface 10. https://doi.org/10.1098/rsif.2012.0570

Demšar, U., Buchin, K., Cagnacci, F., Safi, K., Speckmann, B., Van de Weghe, N., Weiskopf, D., Weibel, R., 2015. Analysis and visualisation of movement: an interdisciplinary review. Mov. Ecol. 3, 1–24. https://doi.org/10.1186/s40462-015-0032-y

Dias, M.P., Martin, R., Pearmain, E.J., Burfield, I.J., Small, C., Phillips, R.A., 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

Domalik, A.D., Hipfner, J.M., Studholme, K.R., Crossin, G.T., Green, D.J., 2018. At-sea distribution and fine-scale habitat use patterns of zooplanktivorous Cassin's auklets during the chick-rearing period. Mar. Biol. 165, 177. https://doi.org/10.1007/s00227-018-3434-8

Dray, S., Royer-Carenzi, M., Calenge, C., 2010. The exploratory analysis of autocorrelation in animal-movement studies. Ecol. Res. 25, 673–681. https://doi.org/10.1007/s11284-010-0701-7

Edelhoff, H., Signer, J., Balkenhol, N., 2016. Path segmentation for beginners: An overview of current methods for detecting changes in animal movement patterns. Mov. Ecol. 4. https://doi.org/10.1186/s40462-016-0086-5

Elliott, K.H., Shoji, A., Campbell, K.L., Gaston, A.J., 2010. Oxygen stores and foraging behavior of two sympatric, planktivorous alcids. Aquat. Biol. 8, 221–235. https://doi.org/10.3354/ab00236

Fox, C.H., Huettmann, F.H., Harvey, G.K.A., Morgan, K.H., Robinson, J., Williams, R., Paquet, P.C., 2017. Predictions from machine learning ensembles: marine bird distribution and density on Canada's Pacific coast. Mar. Ecol. Prog. Ser. 566, 199–216. https://doi.org/10.3354/meps12030

Gaston, A.J., 1992. The Ancient Murrelet: a Natural History in the Queen Charlotte Islands. T & AD Poyser, London.

Gaston, A.J., 1990. Population Parameters of the Ancient Murrelet. Condor 92, 998–1011.

Gaston, A.J., Carter, H.R., Sealy, S.G., 1993. Winter ecology and diet of Ancient Murrelets off Victoria, British Columbia. Can. J. Zool. 71, 64–70. https://doi.org/10.1139/z93-010

Gaston, A.J., Hashimoto, Y., Wilson, L., 2017a. Post-breeding movements of Ancient Murrelet *Synthliboramphus antiquus* family groups, subsequent migration of adults and implications for management. PLoS One 12, e0171726. https://doi.org/10.1371/journal.pone.0171726

Gaston, A.J., Hashimoto, Y., Wilson, L., 2017b. Geographical variation in incubation shift length of Ancient Murrelets *Synthliboramphus antiquus* determined from geolocator devices. Mar. Ornithol. 45, 217–221.

Gaston, A.J., Hashimoto, Y., Wilson, L., 2015. First evidence of east-west migration across the North Pacific in a marine bird. Ibis. 157, 877–882. https://doi.org/10.1111/ibi.12300

Gaston, A.J., Jones, I.L., Noble, D.G., 1988. Monitoring Ancient Murrelet breeding populations. Colon. Waterbirds 11, 58–66.

Gaston, A.J., Powell, D.W., 1989. Natural incubation, egg neglect, and hatchability in the

Ancient Murrelet. Auk 106, 433–438.

Graves, T.A., Waller, J.S., 2006. Understanding the causes of missed Global Positioning System telemetry fixes. J. Wildl. Manage. 70, 844–851.

Grecian, W.J., Lane, J. V, Michelot, T., Wade, H.M., Hamer, K.C., 2018. Understanding the ontogeny of foraging behaviour: insights from combining marine predator bio-logging with satellite-derived oceanography in hidden Markov models. J. R. Soc. Interface 15. https://doi.org/10.1098/rsif.2018.0084

Hamilton, C.D., Golightly, R.T., Takekawa, J.Y., 2011. Relationships between breeding status, social-congregation attendance, and foraging distance of Xantus's Murrelets. Condor 113, 140–149. https://doi.org/10.1525/cond.2011.100040

Hamilton, W.J., Watt, K.E.., 1970. Refuging. Annu. Rev. Ecol. Syst. 1, 263–286.

Harfenist, A., 2003. Seabird colonies background report for the Haida Gwaii/Queen Charlotte Islands land use plan. British Columbia Ministry of Water, Land and Air Protection: Queen Charlotte.

Hooten, M.B., Johnson, D.S., McClintock, B.T., Morales, J.M., 2017. Animal movement: Statistical models for telemetry data, 1st ed. CRC Press, Boca Raton. https://doi.org/10.1201/9781315117744

Johnson, D.S., London, J.M., Lea, M.-A., Durban, J.W., 2008. Continuous-time correlated random walk model for animal telemetry data. Ecology 89, 1208–1215. https://doi.org/https://doi.org/10.1890/07-1032.1

Jones, I.L., Gaston, A.J., Falls, J.B., 1990. Factors affecting colony attendance by Ancient Murrelets (*Synthliboramphus antiquus*). Can. J. Zool. 68, 433–441. https://doi.org/10.1139/z90-064

Jonsen, I., 2016. Joint estimation over multiple individuals improves behavioural state inference from animal movement data. Sci. Rep. 6. https://doi.org/10.1038/srep20625

Jonsen, I.D., Basson, M., Bestley, S., Bravington, M. V, Patterson, T.A., Pedersen, M.W., Thomson, R., Thygesen, U.H., Wotherspoon, S.J., 2013. State-space models for bio-loggers: A methodological road map. Deep. Res. II 88–89, 34–46. https://doi.org/10.1016/j.dsr2.2012.07.008

Joo, R., Boone, M.E., Clay, T.A., Patrick, S.C., Clusella-Trullas, S., Basille, M., 2020. Navigating through the R packages for movement. J. Anim. Ecol. 89, 248–267. https://doi.org/10.1111/1365-2656.13116

Kareiva, P., Odell, G., 1987. Swarms of predators exhibit "preytaxis" if individual predators use area-restricted search. Am. Nat. 130, 233–270. https://doi.org/http://dx.doi.org/10.1086/284707

Kenward, R., 2001. A Manual for Wildlife Radio Tagging. Academic Press, San Diego.

Langrock, R., Hopcraft, J.G.C., Blackwell, P.G., Goodall, V., King, R., Niu, M., Patterson, T.A., Pedersen, M.W., Skarin, A., Schick, R.S., 2014. Modelling group dynamic animal movement. Methods Ecol. Evol. 5, 190–199. https://doi.org/10.1111/2041-210X.12155

Langrock, R., King, R., Matthiopoulos, J., Thomas, L., Fortin, D., Morales, J.M., 2012. Flexible and practical modeling of animal telemetry data: hidden Markov models and extensions. Ecology 93, 2336–2342. https://doi.org/10.1890/11-2241.1

Leos-Barajas, V., Photopoulou, T., Langrock, R., Patterson, T.A., Watanabe, Y.Y., Murgatroyd, M., Papastamatiou, Y.P., 2017. Analysis of animal accelerometer data using hidden Markov models. Methods Ecol. Evol. 8, 161–173. https://doi.org/10.1111/2041-210X.12657

Lewis, S., Benvenuti, S., Dall'antonia, L., Griffiths, R., Money, L., Sherratt, T.N., Wanless, S., Hamer, K.C., 2002. Sex-specific foraging behaviour in a monomorphic seabird. https://doi.org/10.1098/rspb.2002.2083

Li, M., Bolker, B.M., 2017. Incorporating periodic variability in hidden Markov models for animal movement. Mov. Ecol. 5. https://doi.org/10.1186/s40462-016-0093-6

Matthiopoulos, J., 2003. The use of space by animals as a function of accessibility and preference. Ecol. Modell. 159, 239–268. https://doi.org/10.1016/S0304-3800(02)00293-4

McClintock, B.T., 2017. Incorporating telemetry error into hidden Markov models of animal movement using multiple imputation. J. Agric. Biol. Environ. Stat. 22, 249–269. https://doi.org/10.1007/s13253-017-0285-6

McClintock, B.T., Johnson, D.S., Hooten, M.B., Ver Hoef, J.M., Morales, J.M., 2014. When to be discrete: the importance of time formulation in understanding animal movement. Mov. Ecol. 2. https://doi.org/10.1186/s40462-014-0021-6

McClintock, B.T., Michelot, T., 2018a. momentuHMM : R package for generalized hidden Markov models of animal movement. Methods Ecol. Evol. 9, 1518–1530. https://doi.org/10.1111/2041-210X.12995

McClintock, B.T., Michelot, T., 2018b. momentuHMM: R package for analysis of telemetry data using generalized multivariate hidden Markov models of animal movement. URL https://cran.r-project.org/web/packages/momentuHMM/vignettes/momentuHMM.pdf (accessed 2018-12-05)

McClintock, B.T., Russell, D.J.F., Matthiopoulos, J., King, R., 2013. Combining individual animal movement and ancillary biotelemetry data to investigate population-level activity budgets. Ecology 94, 838–849. https://doi.org/10.1890/12-0954.1

Mendez, L., Borsa, P., Cruz, S., De Grissac, S., Hennicke, J., Lallemand, J., Prudor, A., Weimerskirch, H., 2017. Geographical variation in the foraging behaviour of the pantropical red-footed booby. Mar. Ecol. Prog. Ser. 568, 217–230.

https://doi.org/10.3354/meps12052

Michelot, T., Langrock, R., 2019. A short guide to choosing initial parameter values for the estimation in moveHMM. URL https://cran.rproject.org/web/packages/moveHMM/ vignettes/moveHMM-starting-values.pdf (accessed 2020-02-01)

Michelot, T., Langrock, R., Bestley, S., Jonsen, I.D., Photopoulou, T., Patterson, T.A., 2017. Estimation and simulation of foraging trips in land-based marine predators. Ecology 98, 1932–1944. https://doi.org/10.1002/ecy.1880

Michelot, T., Langrock, R., Patterson, T.A., 2016. moveHMM: an R package for the statistical modelling of animal movement data using hidden Markov models. Methods Ecol. Evol. 7, 1308–1315. https://doi.org/10.1111/2041-210X.12578

Morales, J.M., Haydon, D.T., Frair, J., Holsinger, K.E., Fryxell, J.M., 2004. Extracting more out of relocation data : building movement models as mixtures of random walks. Ecology 85, 2436–2445.

Orians, G.H., Pearson, N.E., 1979. On the theory of central place foraging., in: Horn, D.J., Stairs, G.R., Mitchelle, R.G. (Eds.), Analysis of Ecological Systems. Ohio State Univeristy Press, Columbus, pp. 155–177.

Patterson, T.A., Basson, M., Bravington, M. V, Gunn, J.S., 2009. Classifying movement behaviour in relation to environmental conditions using hidden Markov models. J. Anim. Ecol. 78, 1113–1123.

Patterson, T.A., Parton, A., Langrock, R., Blackwell, P.G., Thomas, L., King, R., 2017. Statistical modelling of individual animal movement: an overview of key methods and a discussion of practical challenges. Adv. Stat. Anal. 101, 399–438. https://doi.org/10.1007/s10182-017-0302-7

Patterson, T.A., Thomas, L., Wilcox, C., Ovaskainen, O., Matthiopoulos, J., 2008. State-space models of individual animal movement. Trends Ecol. Evol. 23, 87–94. https://doi.org/10.1016/j.tree.2007.10.009

Pohle, J., Langrock, R., van Beest, F.M., Schmidt, N.M., 2017. Selecting the number of states in hidden Markov models: pragmatic solutions illustrated using animal movement. J. Agric. Biol. Environ. Stat. 22, 270–293. https://doi.org/10.1007/s13253-017-0283-8

R Core Team, 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Rodway, M.S., Lemon, M.J.F., 2011. Use of permanent plots to monitor trends in burrow-nesting seabird populations in British Columbia. Mar. Ornithol. 39, 243–253.

Rodway, M.S., Lemon, M.J.F., Kaiser, G.W., 1988. British Columbia seabird colony inventory: report # 1 - east coast Moresby Island, Technical Report Series No. 50. Canadian Wildlife Service, Delta.

Schick, R.S., Loarie, S.R., Colchero, F., Best, B.D., Boustany, A., Conde, D.A., Halpin, P.N., Joppa, L.N., McClellan, C.M., Clark, J.S., 2008. Understanding movement data and movement processes: Current and emerging directions. Ecol. Lett. 11, 1338–1350. https://doi.org/10.1111/j.1461-0248.2008.01249.x

Sealy, S.G., 1976. Biology of nesting Ancient Murrelets. Condor 78, 294–306.

Sealy, S.G., 1975. Feeding ecology and the ancient and marbled murrelets near Langara Island, British Columbia. Can. J. Zool. 53, 418–433.

Sealy, S.G., Carter, H.R., Thomson, R.E., Morgan, K.H., 2013. Movement of Ancient Murrelet family groups to northern Vancouver Island, British Columbia. Northwest. Nat. 94, 209–226.

Sequeira, A.M.M., Heupel, M.R., Lea, M.A., Eguíluz, V.M., Duarte, C.M., Meekan, M.G., Thums, M., Calich, H.J., Carmichael, R.H., Costa, D.P., Ferreira, L.C., Fernandéz-Gracia, J., Harcourt, R., Harrison, A.L., Jonsen, I., McMahon, C.R., Sims, D.W., Wilson, R.P., Hays, G.C., 2019. The importance of sample size in marine megafauna tagging studies. Ecol. Appl. 29, 1344–1360. https://doi.org/10.1002/eap.1947

Shoji, A., Elliott, K.H., Aris-Brosou, S., Crump, D., Gaston, A.J., 2011. Incubation patterns in a central-place forager affect lifetime reproductive success: Scaling of patterns from a foraging bout to a lifetime. PLoS One 6, 1–10. https://doi.org/10.1371/journal.pone.0017760

Shoji, A., Yoneda, M., Gaston, A.J., 2012. Ocean climate variability links incubation behaviour and fitness in Ancient Murrelets (*Synthliboramphus antiquus*). Can. J. Zool. 90, 361–367. https://doi.org/10.1139/Z2012-006

Shoji, A.M., Gaston, A.J., 2010. Comparing methods for monitoring nest attendance in Ancient Murrelets. Waterbirds Int. J. Waterbird Biol. 33, 260–263.

Soanes, L.M., Arnould, J.P.Y., Dodd, S.G., Sumner, M.D., Green, J.A., 2013. How many seabirds do we need to track to define home-range area? J. Appl. Ecol. 50, 671–679. https://doi.org/10.1111/1365-2664.12069

Springer, A.M., Kondratyev, A.Y., Ogi, J., Shlbaev, Y.V., van Vliet, G.B., 1993. Status, ecology, and conservation of *Synthliboramphus* murrelets and auklets, in: Vermeer, K., Briggs, K.T., Morgan, K.H., Siegel-Causey, D. (Eds.), The Status, Ecology, and Conservation of Marine Birds of the North Pacific. Canadian Wildlife Service Special Publications, Ottawa.

Thaxter, C.B., Lascelles, B., Sugar, K., Cook, A.S.C.P., Roos, S., Bolton, M., Langston, R.H.W., Burton, N.H.K., 2012. Seabird foraging ranges as a preliminary tool for identifying candidate Marine Protected Areas. Biol. Conserv. 156, 53–61. https://doi.org/10.1016/j.biocon.2011.12.009

Tremblay, Y., Bertrand, S., Henry, R.W., Kappes, M.A., Costa, D.P., Shaffer, S.A., 2009. Analytical approaches to investigating seabird-environment interactions: A review. Mar.

Ecol. Prog. Ser. 391, 153–163. https://doi.org/10.3354/meps08146

Tremblay, Y., Shaffer, S.A., Fowler, S.L., Kuhn, C.E., McDonald, B.I., Weise, M.J., Bost, C.A., Weimerskirch, H., Crocker, D.E., Goebel, M.E., Costa, D.P., 2006. Interpolation of animal tracking data in a fluid environment. J. Exp. Biol. 209, 128–140. https://doi.org/10.1242/jeb.01970

Turley, C., Keizer, T., Williamson, P., Gattuso, J.-P., Ziveri, P., Monroe, R., Boot, K., Huelsenbeck, M., 2013. Hot, sour and breathless-Ocean under stress.

Vermeer, K., Fulton, J.D., Sealy, S.G., 1985. Differential use of zooplankton prey by Ancient Murrelets and Cassin's Auklets in the Queen Charlotte Islands. J. Plankton Res. 7, 443–459. https://doi.org/10.1093/plankt/7.4.443

Weimerskirch, H., 2007. Are seabirds foraging for unpredictable resources? Deep. Res. Part II 54, 211–223. https://doi.org/10.1016/j.dsr2.2006.11.013

Whitworth, D.L., Nelson, S.K., Newman, S.H., Van Vliet, G.B., Smith, W.P., 2000. Foraging distances of radio-marked Marbled Murrelets from inland areas in Southeast Alaska. Condor 102, 452–456. https://doi.org/10.1093/condor/102.2.452

Whoriskey, K., Auger-Méthé, M., Albertsen, C.M., Whoriskey, F.G., Binder, T.R., Krueger, C.C., Mills Flemming, J., 2017. A hidden Markov movement model for rapidly identifying behavioral states from animal tracks. Ecol. Evol. 7, 2112–2121. https://doi.org/10.1002/ece3.2795

Wilson, R., Grémillet, D., Syder, J., Kierspel, M., Garthe, S., Weimerskirch, H., Schäfer-Neth, C., Scolaro, J., Bost, C., Plötz, J., Nel, D., 2002. Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. Mar. Ecol. Prog. Ser. 228, 241–261. https://doi.org/10.3354/meps228241

Zhang, J., Rayner, M., Vickers, S., Landers, T., Sagar, R., Stewart, J., Dunphy, B., 2019. GPS telemetry for small seabirds: using hidden Markov models to infer foraging behaviour of Common Diving Petrels (*Pelecanoides urinatrix urinatrix*). Emu - Austral Ornithol. 119, 126–137. https://doi.org/10.1080/01584197.2018.1558997

Zucchini, W., Macdonald, I.L., Langrock, R., 2017. Hidden Markov models for time series: An introduction using R, 2nd ed. CRC Press, Boca Raton. https://doi.org/10.1201/b20790

Chapter 3. A preliminary investigation into breeding season foraging habitat of the Ancient Murrelet in coastal waters of British Columbia

3.1 Introduction

Understanding the relationship between seabirds and their at-sea habitat is an essential step to protecting these species, many of which have been experiencing population declines worldwide (Croxall et al., 2012; Dias et al., 2019). In an attempt to provide new knowledge for seabird conservation, a substantial research effort has been dedicated to determining locations where seabirds are foraging in order to inform management measures that can then be directed at these critical habitats (Hays et al., 2019; Maxwell et al., 2016; Thaxter et al., 2012). Along with identifying specific locations where seabirds forage, developing an understanding of characteristics of foraging habitat is often of interest; foraging habitat is critical for survival, especially when seabirds are constrained to a limited area when breeding. By understanding locations and characteristics of foraging habitat, these critical locations can be protected (Oppel et al., 2018) or habitat with similar features can be included in seabird management planning (Chivers et al., 2013).

The characteristics of seabird foraging habitat are typically assumed to be defined by controls on prey abundance and availability (Ballance et al., 2001; Fauchald, 2009). Seabirds, by necessity, must forage where their prey species are present (Hunt, 1991), although the relationships between seabird foraging locations and prey concentrations are not always evident, as observations must be made at the correct temporal and spatial scales (Benoit-Bird et al., 2013; Fauchald et al., 2000). These relationships can be studied using biophysical variables representing mechanisms that increase seabird prey presence and availability. In previous studies, important predictors of seabird distribution were determined to be the biophysical mechanisms that concentrate prey in the surface waters (Boyd et al., 2017), such as currents, tides, and upwelling (Hunt et al., 1998). Oceanographic processes such as upwelling increase prey abundance in surface waters by increasing nutrients and primary productivity (Mann and Lazier, 2006), while mechanisms such as tidal flow physically move and concentrate prey at the surface (Hunt, 1991; Ladd et al., 2005). Tidal mixing can increase nutrient levels in surface waters, in turn increasing primary and secondary productivity (Mann and Lazier, 2006).

In addition to spatial characteristics of prey abundance, seabird foraging locations depend on the life stage of the individual bird, as well as the physiology (Ballance et al., 2001; Gaston, 2004; Harding et al., 2007) and foraging strategy of the species (Hunt et al., 2014). During the breeding season, seabirds act as central-place foragers, transiting to and from nest-sites at terrestrial breeding colonies to foraging grounds at sea (Hamilton and Watt, 1970; Orians and Pearson, 1979). Available habitat is limited by how far a bird can travel within the constraints of returning to its nest site to exchange incubation shifts with its mate or feed its young. For example, seabirds are limited by the physical constraints of flight speeds and energy requirements for flight (Gaston et al., 2007). Preferred foraging habitat can depend on foraging strategy—whether the species is a pursuit-diver or a surface-feeder (Hunt et al., 2014)—and on prey type (Hunt, 1991).

The Ancient Murrelet (*Synthliboramphus antiquus*) is a seabird species for which we know relatively little in terms of foraging habitat characteristics. This member of the Alcid family nests on island along the Pacific coast of Canada and throughout the north Pacific. Ancient Murrelets are pursuit-divers, and propel themselves with their wings underwater to forage, mostly on large zooplankton and small fish (Gaston, 1992). Unlike most seabirds, Ancient Murrelets provision their young at sea (Sealy, 1973), and as a result, it is arguably more challenging to study their diet and foraging behaviour because prey samples cannot be collected at the nest when nestlings are being fed (Gaston, 1992). Diet studies carried out by collecting samples of foraging birds and analyzing their stomach contents found Ancient Murrelets were foraging almost entirely on euphasiids, and some larval and juvenile fish (Gaston et al., 1993; Sealy, 1975; Vermeer et al., 1985).

Until recently, Ancient Murrelet foraging locations and behaviour investigations have been based on at-sea surveys (e.g. Ladd et al., 2005), as well as observational studies and anecdotal descriptions (reviewed in Gaston, 1992). Vessel surveys of seabird density provide the majority of data on seabird habitat at sea (Tremblay et al., 2009), and although useful, they have some limitations when trying to understand habitats associated with specific behaviours. Often high seabird density observed during at-sea surveys is equated with preferred foraging locations, when in reality birds may not be foraging where they are observed in high densities (Camphuysen et al., 2012). Through at-sea survey observations it is not possible to know whether birds are breeders or non-breeders, and if they are breeders, breeding locations of birds observed at sea are unknown. Through developments in technology, tracking of individual birds and detailed modelling of movement behaviour at sea is giving us new information on movement patterns of individual birds from specific colonies, which improves our understanding of the relationship between behaviour and habitat use (Camphuysen et al., 2012; Grecian et al., 2018).

Previous studies have revealed some habitat characteristics of Ancient Murrelet foraging locations. For example, transect surveys off the northwest coast of Haida Gwaii suggested Ancient Murrelets forage in deep water along the continental shelf break and slope (Vermeer et al., 1985). Meanwhile, previous research in Alaska found that Ancient Murrelets foraged in deep channels between islands where there were strong tidal currents (Ladd et al., 2005). Another study, using time-depth loggers mounted on adult birds, revealed that wind and tide were influences on Ancient Murrelet foraging activity; strong winds were found to increase total foraging trip duration (Shoji et al., 2011). Through transect surveys and observational studies, strong tidal currents have also been shown to indicate preferred foraging habitat (Gaston et al., 1993; Holm and Burger, 2002).

Here, Ancient Murrelet foraging locations identified from Global Positioning System (GPS) tracking and movement modelling using hidden Markov models (Chapter 2) were related to several habitat descriptors to investigate whether movement data from tracking produced similar relationships between Ancient Murrelets and their foraging environment. Several static environmental variables were used to investigate whether unchanging features of the environment can explain foraging locations of this species. Habitat variables were chosen because the data were easily accessible and comparable to other studies in the region (e.g. Domalik et al., 2018), and do not change over time. They were also chosen based on previous research into indicators of Ancient Murrelet foraging habitat. We used seafloor depth and slope, and investigated whether birds in our study region foraged in relatively deeper water and in steeper sloping areas, as Vermeer et al. (1985) found. We included average tidal speed to investigate if birds in Hecate Strait foraged in areas with stronger tidal currents, following patterns found in Alaska (Ladd et al., 2005) and southern British Columbia (BC; Holm and Burger, 2002). We used regression models of environmental and spatial explanatory variables to investigate two lines of inquiry: (1) to what degree are environmental variables influencing where Ancient Murrelets decide to forage along a given movement path?; and, (2) in what ways do environmental variables explain how long Ancient Murrelets choose to forage in a location?

3.2 Methods

3.2.1 Study region

In Canada, all Ancient Murrelet breeding colonies are located on the islands of the archipelago of Haida Gwaii, BC (Figure 3-1; Gaston, 1992). Colonies are located along both the east and west coasts of Haida Gwaii. The western coastline is adjacent to the steep continental shelf break, and deep pelagic water that is less than 35 kilometers offshore (Perry and Waddell, 1997). The archipelago is separated from the mainland by Hecate Strait, a wide, shallow body of water with extensive mixing by strong tidal currents (Crawford, 1997). The more northern part of the strait is shallow and flat, while to the south it opens into Queen Charlotte Sound, where deep canyons cut into the continental slope. Haida Gwaii is located in the path of the Alaska Current that flows north along the coast (Weingartner et al., 2009). Eddies and upwelling off the coast of BC transport nutrients and phytoplankton from the continental slope onto the shelf, and tidal flow also contributes to vertical mixing of nutrients and increased primary productivity (Weingartner et al., 2009).

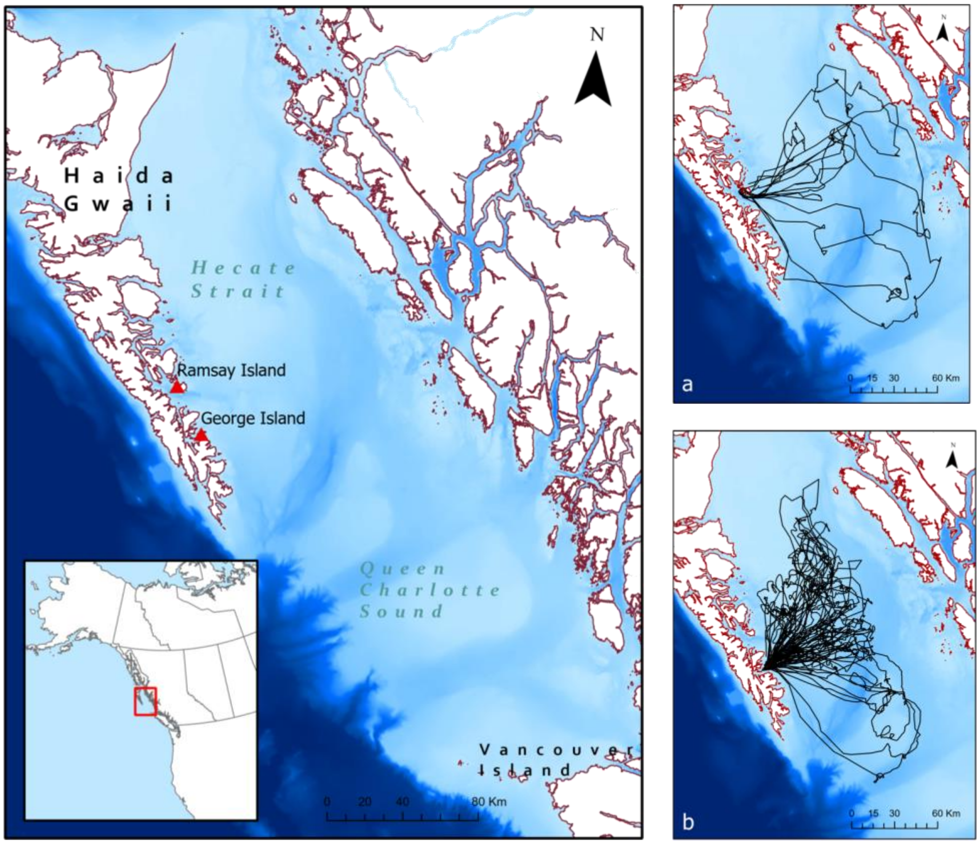


Figure 3-1. Map of the study region showing the location of the Haida Gwaii archipelago along the coast of North America (inset), and the surrounding water bodies and bathymetry. Colonies where Ancient Murrelet tracking took place are shown as red triangles. Tracks show foraging trips in 2018 (a) and 2019 (b).

3.2.2 Foraging data

The dataset used in this study consisted of Ancient Murrelet foraging locations identified from GPS tracks collected from two colonies over two years, detailed in Chapter 2. In brief, Ancient Murrelets were tagged with GPS tracking devices on Ramsay Island in 2018 and on George Island in 2019, both of which are located along the southeast coast of Haida Gwaii (Figure 3-1). GPS location observations were collected throughout one to two foraging trips from each individual, at a temporal resolution of 30 minutes in 2018 and 20 minutes in 2019. From these data, a hidden Markov model was used to classify locations along the movement paths into three states, based on characteristics of the paths, namely step length (distance between points) and turning angle (change in direction from one point to the next). Three behaviour states from the models were interpreted as transit, foraging, or resting behaviour, with 36 % (2018) and 41 % (2019) of GPS locations along these tracks classified as foraging behaviour (See Chapter 2 for further details).

In the present analysis, in which foraging locations are of the most interest, only the GPS locations identified as the foraging behaviour state were retained. These locations were further filtered to remove points that were less likely to represent true foraging behaviour; based on model validation using tag immersion data, it appeared that the movement model mis-identified some locations as foraging. These could have been other behaviours not accounted for in the model, as it only differentiated data into three behaviour states. Previous research on Ancient Murrelet foraging using time-depth recorders found that Ancient Murrelets did not undertake foraging dives (dives greater than 2 m in depth) between one hour after sunset and one hour before sunrise (Elliott et al., 2010). Therefore, we filtered out locations that were at night (between 05:00 to 22:30). Past studies also suggest that Ancient Murrelets do not forage in the staging area (Sealy, 1975), which is usually within 3 km of the colony (Vermeer et al., 1985), but for the George Island colony could extend up to 8 km into Hecate Strait (Rodway et al., 1988). We filtered out locations from both colonies that were within 8 km of shore. Additionally, locations near the colonies were removed due to a lack of suitable bathymetric data; information derived from bathymetric data such as depth and slope was not available within 2 km of shore. The data filtering process resulted in a total of 2588 GPS locations classified as foraging for this analysis: 305 points from 6 individual birds in 2018, and 2283 points from 33 individual birds in 2019.

3.2.3 Environmental data

In order to identify and describe important characteristics of habitats where Ancient Murrelets were foraging, the study region was divided into a grid, and environmental variables were associated with each grid cell (Figure 3-2). Consistent with previous seabird studies in the area (e.g. Fox et al., 2016), the region was divided into hexagonal grid cells, each 4 km across, amounting to an area of 13.86 km$_2$ per grid cell. This grid cell size also reflects the scale at which previous studies have found seabirds and their prey to be most closely associated (patch sizes of 2 to 8 km radii; Burger et al., 2004). Bathymetric data were taken from the ETOPO1 Global Relief Model (Amante and Eakins, 2009), with a resolution of one arc-minute. Seafloor depth was calculated as the mean depth within each grid cell. Seafloor gradient, i.e. the percent change in depth within a cell and the surrounding cells, was derived from bathymetric data.

Seafloor gradient was calculated as follows:

$$\frac{((Max\ Depth - Min\ Depth) \times 100)}{Max\ Depth} \qquad \text{(Eq. 1)}$$

which represents the rate of change in depth within a grid cell and its neighbours, as a percent, weighted by the maximum depth. This variable is similar to what Nur et al. (2011) refer to as the ‘contour index’, and provides an indication of relative seafloor steepness, with low values representing flat areas of seafloor and high values representing steep bathymetry.

Two other habitat descriptor variables were considered in the analysis: distance to colony and tidal current. Distance to colony was calculated separately for both year and colony, and was calculated as the distance between the colony and the centroid of each grid cell. For analysis in which the two years were pooled, distance to colony was averaged over the two years. The tidal current value in each grid cell was the root mean square (RMS) tidal speed in meters per second, averaged over many tidal cycles, from a 500 x 500 m resolution raster dataset. The raster was produced from a high resolution tidal model of the North Pacific (Foreman et al., 2000), available online through the British Columbia Marine Conservation Atlas (British Columbia Marine Conservation Analysis Project Team, 2011).

Spatial coordinates were included as explanatory variables in the models, as a simple method to account for spatial autocorrelation (e.g. Cleeland et al., 2019). The northing coordinate of the centroid of each grid cell provided a measure of position in the north-south direction. Easting was not included because it was highly correlated with colony distance (Pearson's correlation coefficient = 0.92). Colony distance was included and provided an approximate measure of east-west position for each grid cell. Possible collinearity between the other explanatory variables was also investigated by plotting all variables and calculating the Pearson's correlation coefficient for each combination of explanatory variables (Appendix B Figure B-2 and B-3). As no combination of variables other than easting and colony distance had a correlation coefficient greater than 0.7 (the cut-off recommended by Harrison et al. (2018)), all other variables were retained in the models. All other combinations of variables produced Pearson's correlation coefficient values that were below an absolute value of 0.4.

For all analyses, the explanatory variables were centred and standardized by subtracting the mean and dividing by the standard deviation (Table 3-1), in order to improve model convergence and interpretability of coefficients (Harrison et al., 2018; Schielzeth, 2010). Initial attempts at running the generalized linear mixed models (GLMMs) did not converge. In cases in which explanatory variables have vastly different scales, as in this data set (e.g. depth ranging from 0 to 400 m and tidal current ranging from 0.08 to 0.3 m/s), standardization can solve convergence issues (Harrison et al., 2018). Therefore, variables were centered around the mean and standardized by dividing by the standard deviation. All variables are then on a scale that is centered around 0, with units of standard deviation of the original scale of the variable. Schielzeth (2010) suggests that standardizing also improves interpretability of coefficients. To maintain consistency in our methods, and to improve the interpretability of the coefficient estimates and odds ratios estimated from the logistic regression (see below), explanatory variables used in the logistic regression were also standardized. Odds ratios from the models using standardized explanatory variables were more easily interpreted, as they did not depend on the units of the variable, and were comparable to each other (Schielzeth, 2010).

Table 3-1. Mean and standard deviation of explanatory variables used for standardizing each variable. Values differ between the two models due to differing samples of grid cells.

	Logistic regression		**Generalize linear mixed model**	
Variable (units)	**Mean**	**Standard deviation**	**Mean**	**Standard deviation**
Sample size (grid cells)	512		477	
Depth (m)	156	81	138	70
RMS Tidal speed (m/s)	0.188	0.049	0.196	0.041
Colony distance (km)	78.0	32.4	66.2	28.2
Seafloor gradient (%)	28.2	22.3	23.7	14.4

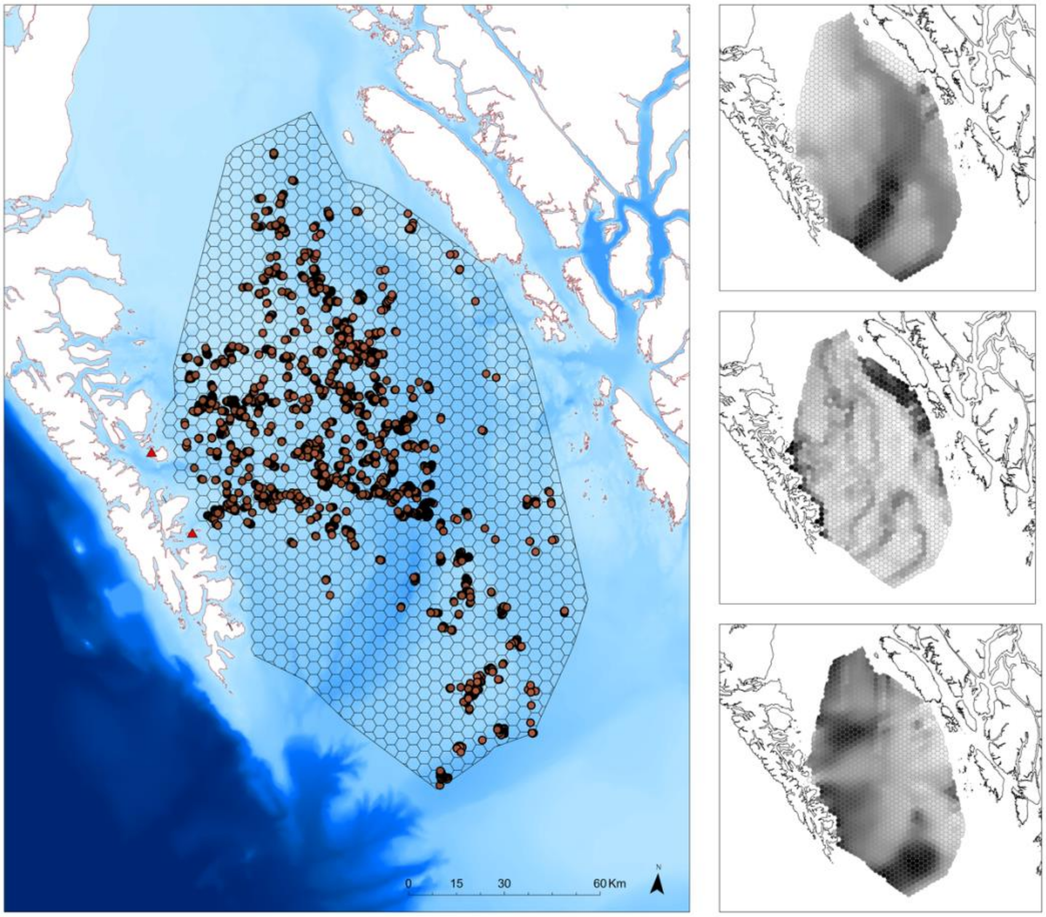


Figure 3-2. Study area (left) showing 4 km diameter hexagonal grid cells, colony locations (red triangles) and foraging locations from all birds (brown circles). Right: grid cells shaded by value of depth (top), ranging from 0 to 400 m, seafloor gradient (0 – 100 %; middle) and RMS tidal speed (0.1 to 0.3 m/s; bottom). Darker shades indicate higher values.

3.2.4 Foraging location analysis

Logistic regression models with a logit link function were used to investigate the probability of foraging in a given cell. Environmental explanatory variables used in these models were ocean depth, seafloor gradient, distance to colony, tidal current, and northing. Similar to Boyd et al. (2015), we used the grid cells that any Ancient Murrelet had visited on a foraging trip, whether foraging took place in that cell or not. All visited cells were selected (512 cells in total) and the cells were classified as a location of foraging (assigned a value of 1) or non-foraging (assigned a value of 0).

An initial model was fit using main effects of all variables, and model simplification was performed using stepwise deletion of non-significant explanatory variables (Crawley, 2015). We assumed this method is appropriate for model simplification as this study is an initial investigation of multiple possible explanatory habitat characteristics describing where seabirds forage (Aarts et al., 2008; Bolker, 2008). The significance of each explanatory variable in the model was tested by investigating the change in deviance with each iteration of the model with fewer covariates using a likelihood ratio test. The likelihood ratio test compares multiple nested models and takes into account the balance between increased goodness-of-fit with additional covariates, and added complexity due to additional parameters (Bolker, 2008). The change in AIC for each model was also used to suggest the model with the best fit. Because a logit link function was used to fit the model, coefficient estimates represented the log of the odds of foraging in each grid cell, based on the linear explanatory variables. Odds ratios were calculated from the final model, including 95% confidence intervals, by exponentiating the coefficient estimates. Odds ratios represented the predicted change in the odds of foraging, for each unit of change in the explanatory variable. Logistic regression models were run using the ‘glm’ function in base R (R Core Team, 2019). The approximate amount of variability in probability of foraging within a grid cell that was explained by the model was evaluated using McFadden’s R_2, a pseudo-R_2 applied to logistic regression models (Hemmert et al., 2018).

3.2.5 Foraging intensity analysis

We used generalized linear mixed models (GLMMs), as suggested by Whoriskey et al. (2019), to investigate the relationship between the environment in which Ancient Murrelets were foraging and the intensity of foraging, measured as minutes spent foraging in a grid cell. These models were run using the R package *lme4* (Bates et al., 2015). The gamma distribution with a log link was used, as the response was a positive continuous variable (minutes spent foraging; Bolker, 2008). Explanatory variables used in this analysis were the same as the logistic regression: ocean depth, seafloor gradient, distance to colony, tidal current, and northing. The sample for this analysis was all grid cells in which there was at least one GPS point classified as foraging ($n = 477$).

The maximal model was initially fit with all main effects of covariates, including individual (bird ID) as a random effect. Bird ID was included to account for non-independence of data from the same individual (Aarts et al., 2008). Models with various combinations of fewer covariates were also fit, and the final model was chosen based on removing non-statistically significant covariates, and likelihood ratio tests, and further guided by the use of AIC. To check the fit of the models we plotted standardized Pearson residuals versus fitted values (Wood, 2006), and also plotted quantile-quantile (Q-Q) plots of simulated residuals versus observed residuals using the R package *DHARMa* (Hartig, 2020). The amount of variation explained by the model was estimated as both marginal and conditional pseudo-R_2 values using the ‘r.squaredGLMM’ function in the R package *MuMIn* (Barton, 2019). As the estimated coefficients are given on the scale of the link function (Bolker, 2008), intercept and slopes were converted to predicted values of minutes spent foraging by exponentiating the coefficients.

3.3 Results

3.3.1 Foraging location analysis

Of the models included in the analysis, the logistic regression model with the most support included depth, gradient, tidal current, and distance from colony (Table 3-2). The coefficients estimated from this model (Table 3-3) indicated that all explanatory variables had a negative influence on the probability of whether an Ancient Murrelet would forage in a certain location or not (Figure 3-3). The McFadden's R_2 of 0.085 indicated that the model explains approximately 8.5 % of the variability in whether birds foraged in a grid cell. The range in probability of foraging determined by each explanatory variable was varied (Figure 3-3); At the shallowest depths there was a greater than 50 % probability of foraging, while in the deepest locations (400 m depth) there was a 0 – 20 % probability of foraging. The gradient variable exhibited a similar range, although the change in probability was not as dramatic; in the flattest locations (0 – 20 % gradient), there was approximately 40 – 50 % probability of foraging, and in the steepest locations an approximate 10 – 30 % probability of foraging. The change in probability of foraging at different distances to the colony was from approximately 45 – 65 % probability of foraging 20 km from the colony, down to approximately 20 – 35 % probability of foraging 120 km from the colony. The change in probability over the range in average tidal speeds had wider confidence intervals: at the lowest tidal speeds (0.1 m/s) there was approximately 35 – 60 % probability of foraging, while at the highest tidal speeds (0.3 m/s) there was approximately 10 – 40 % probability of foraging.

Table 3-2. Model selection of logistic regression models. The model with the most support is the one including four environmental explanatory variables: depth, seafloor gradient, tidal current, and colony distance.

Model covariates	Log likelihood	Number of parameters estimated	Residual deviance	AIC	Δ AIC	AIC weights
Depth + gradient + current + colony distance	-309.8	5	619.57	629.57	0.0	0.56
Depth + gradient + colony distance	-311.66	4	623.32	631.32	1.8	0.23
Depth + gradient + current + colony distance + northing	-309.75	6	619.50	631.5	1.9	0.21
Depth + gradient	-317.45	3	634.89	640.89	11.3	0.002

Table 3-3. Estimates from logistic regression model with four environmental explanatory variables. Coefficient estimates from the model, odds ratios calculated from the coefficients, and 95 % confidence intervals (CI) of the odds ratios. Explanatory variables were centred around the mean and standardized using the standard deviation.

Variable	Coefficient	Odds ratio (95 % CI)
Depth	-0.638	0.528 (0.401, 0.684)
Current	-0.224	0.799 (0.634, 1.00)
Gradient	-0.469	0.626 (0.495, 0.782)
Colony distance	-0.397	0.672 (0.544, 0.827)

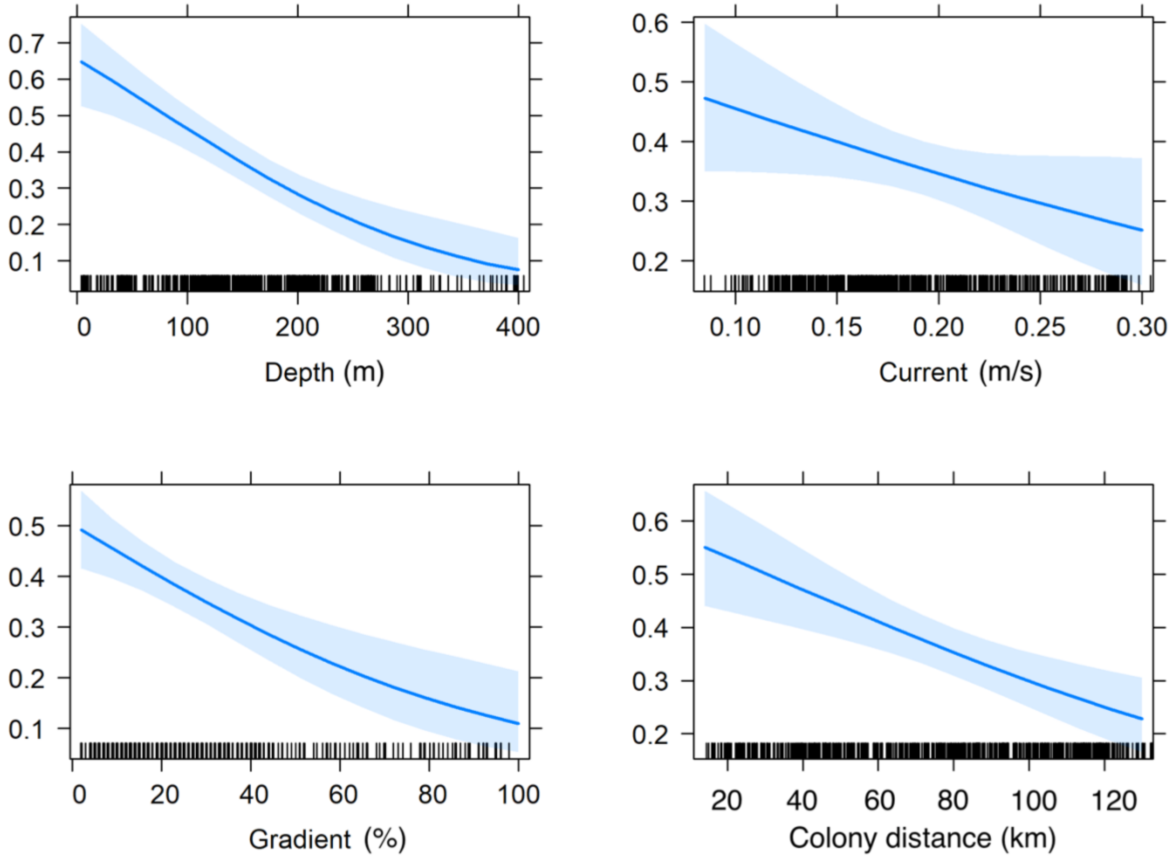


Figure 3-3. Predicted probabilities of Ancient Murrelet foraging, based on logistic regression of four explanatory variables, with 95% confidence intervals. Each plot is the predicted probability based on one variable, holding other variables at their mean value. The rug plot along the *x* axis shows observed data.

3.3.2 Foraging intensity analysis

Grid cells used for this analysis were all cells in which foraging took place (477 cells). Years were pooled, but individual birds were kept separate, and the response variable was the number of minutes spent foraging. The GLMM with the most support was the model with only depth as a fixed effect and bird ID as a random effect (Table 3-4). As shown by plots of simulated versus observed residuals (Appendix B Figure B-5 and B-6), the model under-predicted minutes spent foraging for the lower quartile of values. The estimated coefficients from this model were an intercept of 4.698 (SE = 0.06) and a slope of 0.124 (SE = 0.04). When exponentiated, the intercept indicated that at the mean value of depth (standardized depth = 0), the predicted number of minutes spent foraging was 110 minutes. The positive slope indicated that as depth increased, the number of minutes spent foraging also increased, by a factor of 1.13 for every one standard deviation change in depth (Figure 3-4). For example, in a location with an ocean depth of approximately 100 meters, birds were predicted to forage for approximately 1.6 hours, while in a location with a depth of 310 meters, they were predicted to forage for approximately 2.5 hours. The 95 % confidence intervals are wide, and at the greatest depths predictions of minutes spent foraging are not especially precise. The marginal pseudo-R_2 from this model was 0.013, and the conditional pseudo-R_2 was 0.089, indicating that the model with only the fixed effect (depth) explained approximately 1.3 % of the variability in foraging intensity, while the model including bird ID as a random effect explained approximately 8.9 % of the variability in foraging intensity.

Table 3-4. Model comparison of generalized linear mixed models (not all covariate combinations that were investigated are reported). All models include individual bird as a random effect.

Model covariates	**Log likelihood**	**Number of parameters estimated**	**Deviance**	**AIC**	**Δ AIC**	**AIC weights**
Depth	-2700.3	4	5400.5	5408.5	0.0	0.429
Depth + current	-2699.5	5	5399.1	5409.1	0.5	0.327
Depth + current + colony distance	-2699.0	6	5398.0	5410.0	1.5	0.204
Depth + current + colony distance + gradient + northing	-2698.7	8	5397.3	5413.3	4.8	0.039

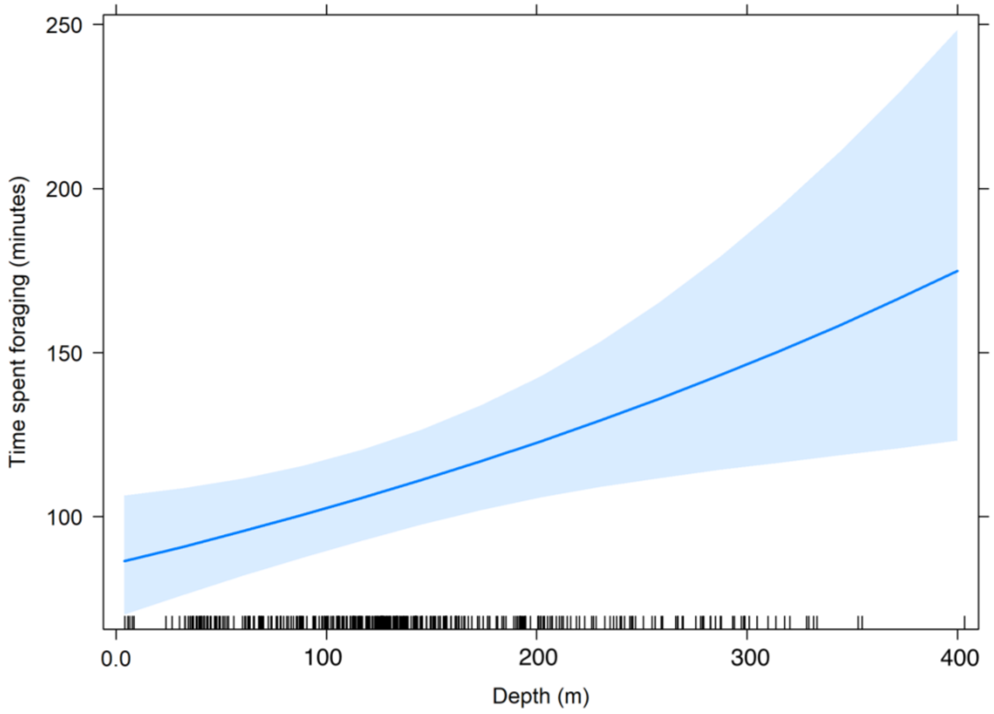


Figure 3-4. Model predictions from GLMM with bird ID as a random effect, with 95 % confidence intervals. Depth was the only significant explanatory variable in this set of models. The rug plot along the *x* axis shows the observed data points.

3.4 Discussion

In this study, we investigated the degree to which certain habitat characteristics explain where Ancient Murrelets chose to forage and whether these environmental variables were associated with how long birds spent foraging in a given location. The selection of environmental variables was based on those that could indicate locations of prey concentration, such as features that might induce upwelling (i.e. deep water areas and steeper seafloor slope) and high tidal current areas, or measures of habitat location or accessibility (such as distance from the colony). The main findings from the analyses performed in this study are that seafloor depth was present in the models for both foraging location and foraging intensity. Depth exhibited a negative relationship with foraging location, while it had a positive relationship with foraging intensity. Furthermore, tidal current, seafloor gradient, and distance to colony all exhibited a negative relationship with the locations where birds chose to forage along their movement paths. Some of these findings were inconsistent with seabird foraging theory and prior research specific to Ancient Murrelet foraging locations, while others support known seabird theory.

In general, seabirds tied to a breeding colony with limitations on accessible habitat are predicted to preferentially forage at features that will concentrate prey (Hunt, 1991), which are small fish and zooplankton in the case of Ancient Murrelets. On the west coast of Haida Gwaii, during the breeding season, Ancient Murrelets had been previously observed in high densities at the continental shelf break (Vermeer et al., 1985). There they were utilizing the deep water over an area of steep seafloor slope: an area predicted to have a high zooplankton biomass (Mackas and Coyle, 2005; Vermeer et al., 1985). Interestingly, we did not observe the same relationship at our colonies on the east coast of Haida Gwaii, where Ancient Murrelet foraging locations did not appear to be explained by deep-water features that we would expect to be highly biologically productive (e.g. the shelf break and canyons; Mackas and Coyle, 2005). The oceanography and bathymetry off the east coast of Haida Gwaii differs greatly from the west coast (Crawford, 1997; Perry and Waddell, 1997), therefore it is possible that birds tracked in Hecate Strait were foraging in association with other features, such as fronts or eddies, that we were unable to represent using the static environmental variables we used. Fronts, transitions between water masses with different characteristics, are often areas of high productivity and prey concentration that are important to foraging seabirds (Hunt et al., 1998; Scales et al., 2014), and would be identified by including variables such as sea surface height or temperature anomalies in habitat models (e.g. Scales et al., 2014). Investigating the association of fronts with Ancient Murrelet foraging locations in Hecate Strait would be a useful future study, as Perry and Waddell (1997) suggest there is a persistent tidal front in Hecate Strait that is an indicator of high-quality seabird habitat.

It was somewhat surprising that we found Ancient Murrelets did not preferentially forage in areas of higher average tidal speed, although this could be because the mechanisms that cause strong tidal currents to increase prey availability might not be acting in Hecate Strait in the same way as other locations where this relationship has been observed. High tidal currents can be a benefit to foraging seabirds by concentrating prey, through physical forcing (pushing prey to the surface) or through tidal mixing, which increases nutrients in the more productive surface waters, and in turn increases biomass of higher trophic levels (Hunt et al., 1998; Ladd et al., 2005). Ancient Murrelets have been found preferentially foraging in areas of stronger tidal current (Gaston et al., 1993; Holm and Burger, 2002). In our study, tidal current did not explain the intensity of foraging, possibly because tidal flow is usually assumed to physically concentrate prey, and in order to do so must be constricted (Hunt et al., 1998). In previous research, the increase in prey availability caused by strong tidal currents was due to constriction of water flow in narrow channels (Holm and Burger, 2002; Ladd et al., 2005), whereas in Hecate Strait there are no islands or narrow channels that would constrict tidal flow and cause prey concentrations by the same mechanism. Another possibility is that there was a mismatch in temporal resolution between the Ancient Murrelet movement data and the averaged tidal flow (Cox et al., 2013).

Holm and Burger (2002) found that intensity of foraging by Ancient Murrelets was dependent on the rate of tidal flow at the time the birds were present; Ancient Murrelets foraged for longer in areas of faster tidal speeds and did not forage at slack tide. Here, because we used tidal speed averaged over many cycles, and not the flow rate at the time the birds were actually foraging, we may have not captured the appropriate relationship between tidal speed and foraging. In future, the tidal flow at the time the Ancient Murrelets were present in a certain location could be used to investigate this further.

Depth and seafloor gradient had a negative influence on the probability of Ancient Murrelets foraging in a given location. This suggests that Ancient Murrelets were not seeking out areas of deep water or of steep sloping seafloors, even though given the distances they were travelling (several hundred kilometers in a single trip; Figure 3-1a and 3-1b), they could travel to the continental shelf break to the south of Haida Gwaii. The shelf break is a steeply sloping feature that in many regions is expected to increase seabird prey concentrations (Perry and Waddell, 1997), and the shelf break to the south of Haida Gwaii is where Cassin’s Auklets, another Alcid species, were found to travel when foraging from a colony to the south (Domalik et al., 2018). Depth and seafloor gradient were used here as proxies for locations of higher productivity, as the deeper outer continental shelf and slope waters are typically areas with high primary productivity (Hunt et al., 2014; Mackas and Coyle, 2005).

Although the Ancient Murrelets in this study were possibly not directing their trips to deep-water features, counterintuitively, they did spend longer foraging in deeper water, indicating a relationship between water depth and prey abundance or availability. This pattern could indicate that birds were searching for prey and sampling often throughout their foraging trips, and then foraging for a longer time period in areas with higher concentrations of prey, which corresponds with relatively deeper water. From our model, at the shallowest depths birds were predicted to forage for approximately 1 hour, while at the deepest (approximately 300 to 400 m depth) they foraged for 2.5 hours (Figure 3-4). This suggests that instead of directing their foraging trips to known, predictable features of high prey concentration, it may be that they have to search for prey throughout their foraging trip, a strategy described by Weimerskirch (2007). Gaston (2004) suggests that this strategy of locating prey, requiring sampling throughout the foraging trip versus transiting directly to a known foraging area, is likely quite common among seabirds.

The relationship between foraging location and depth found here supports previous work suggesting that seabirds associate with zones of differing water depths along the continental margin depending on their foraging strategy (reviewed in Schneider, 1997). Pursuit-divers such as Alcids are often found in the shallower waters on the continental shelf, while surface-foragers such as Procelleriiformes utilize deeper slope and offshore waters (Hunt et al., 2014; Stone et al., 1995). In a large-scale and long time-period study on seabird distribution in the Bering Sea, pursuit-diving seabirds, including Ancient Murrelets, were found in the highest densities over the shallower shelf areas, in waters with a mean depth of 57 m (Hunt et al., 2014). There are several hypotheses as to why pursuit-divers might prefer shallower water, one being that shallow waters might be more productive due to turbulent mixing (Schneider, 1997) or due to interactions of currents with bathymetry (Hunt et al., 2014). Another hypothesis is that pursuit-divers may simply be limited by their flying ability and the distances they are able to travel from a colony (Schneider, 1997; Stone et al., 1995). Using movement data, our results provide an interesting case-study to suggest that this is not the case for Ancient Murrelets, as they have access to both very shallow water in northern Hecate Strait and deep water at the continental shelf break in

Queen Charlotte Sound. Although the directions they chose to travel on leaving the colony varied greatly (Figure 3-1a and 3-1b), based on this analysis, Ancient Murrelets in this area are not choosing shallower water simply because it is more accessible.

Only static variables were included in this analysis, which do not change over time, because the relationship between static habitat descriptors and animal movements can be more apparent than the relationship with temporally-variable dynamic habitat descriptors (Aarts et al., 2008). Using variables that are unchanging year to year allowed us to combine two years of data and use the full set of available data on Ancient Murrelet foraging locations. The relationship between biophysical descriptors of the environment, primary productivity, and seabird prey is complex (e.g. Benoit-Bird et al., 2013), making the relationship between habitat characteristics and foraging behaviour a challenge to tease apart. In order to capture the relationship between the environment and foraging, the correct temporal and spatial scale must be used (Fauchald et al., 2000), and appropriate variables that are proxies for the mechanisms believed to be driving prey concentrations must be identified. Multiple biophysical habitat characteristics are often considered in seabird distribution and foraging studies (Tremblay et al., 2009), including dynamic predictors of prey such as sea-surface temperature and chlorophyll-*a* concentration. These are used as indicators of upwelling and primary productivity. The foraging locations of Cassin's Auklets, a similar species of pursuit-diving Alcid breeding to the south of our study region, were found to be associated with variations in sea surface temperature rather than static bathymetric features (Domalik et al., 2018), suggesting that other important drivers of foraging location need to be included in future work on Ancient Murrelets in this region.

In this study, tracking data provided information on the habitat associated with foraging behaviour, and was attributed to individual Ancient Murrelets from known breeding colonies.

These details of foraging locations could not be investigated without tracking data, but there are limitations in the broader application due to the limited number of individuals tracked. Here, we have found information on foraging habitat for Ancient Murrelets from two colonies on Haida Gwaii, but further investigations of Ancient Murrelets from other colonies, incorporating a more complex suite of biophysical factors to characterized marine habitats, and over longer time periods, are necessary. A comparison of foraging locations taken from tracking data and from at-sea survey data (e.g. Fox et al., 2017) could give a more extensive regional picture of Ancient Murrelet at-sea habitat, and provide necessary knowledge for marine management of threats to this species. This study has provided the essential first step to investigating the relationship between Ancient Murrelet movement behaviour identified from tracking, and at-sea habitat requirements of this species. We now have a greater understanding of the variability in locations and environment used by this species during foraging trips, when breeding on the southeast coast of Haida Gwaii.

3.5 References

Aarts, G., MacKenzie, M., McConnell, B., Fedak, M., Matthiopoulos, J., 2008. Estimating space-use and habitat preference from wildlife telemetry data. Ecography 31, 140–160. https://doi.org/10.1111/j.2007.0906-7590.05236.x

Amante, C., and Eakins, B.W., 2009. ETOPO1 Global Relief Model converted to PanMap layer format. NOAA-National Geophysical Data Center, PANGAEA, URL https://doi.org/10.1594/PANGAEA.769615

Ballance, L.., Ainley, D.G., Hunt, G.L., 2001. Seabird foraging ecology, in: Encyclopedia of Ocean Sciences, Volume 5. Elsevier Ltd., pp. 227–235.

Barton, K., 2019. MuMIn: Multi-Model Inference. R package version 1.43.15. URL https://CRAN.R-project.org/package=MuMIn

Bates, D., Bolker, B.M., Machler, M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67. https://doi.org/10.18637/jss.v067.i01

Benoit-Bird, K.J., Battaile, B.C., Heppell, S.A., Hoover, B., Irons, D., Jones, N., Kuletz, K.J., Nordstrom, C.A., Paredes, R., Suryan, R.M., Waluk, C.M., Trites, A.W., 2013. Prey patch patterns predict habitat use by top marine predators with diverse foraging strategies. PLoS One 8, e53348. https://doi.org/10.1371/journal.pone.0053348

Bolker, B., 2008. Ecological Models and Data in R. Princeton University Press. https://doi.org/10.1086/644667

Boyd, C., Castillo, R., Hunt, G.L., Punt, A.E., VanBlaricom, G.R., Weimerskirch, H., Bertrand, S., 2015. Predictive modelling of habitat selection by marine predators with respect to the abundance and depth distribution of pelagic prey. J. Anim. Ecol. 84, 1575–1588. https://doi.org/10.1111/1365-2656.12409

Boyd, C., Grünbaum, D., Hunt, G.L., Punt, A.E., Weimerskirch, H., Bertrand, S., 2017. Effects of variation in the abundance and distribution of prey on the foraging success of central place foragers. J. Appl. Ecol. 54, 1362–1372. https://doi.org/10.1111/1365-2664.12832

British Columbia Marine Conservation Analysis Project Team, 2011. Marine Atlas of Pacific Canada: A Product of the British Columbia Marine Conservation Analysis. URL www.bcmca.ca (accessed 2020-01-15)

Burger, A.E., Hitchcock, C.L., Davoren, G.K., 2004. Spatial aggregations of seabirds and their prey on the continental shelf off SW Vancouver Island. Mar. Ecol. Prog. Ser. 283, 279–292. https://doi.org/10.3354/meps283279

Camphuysen, K.C.J., Shamoun-Baranes, J., Bouten, W., Garthe, S., 2012. Identifying ecologically important marine areas for seabirds using behavioural information in combination with distribution patterns. Biol. Conserv. 156, 22–29. https://doi.org/10.1016/j.biocon.2011.12.024

Chivers, L.S., Lundy, M.G., Colhoun, K., Newton, S.F., Houghton, J.D.R., Reid, N., 2013. Identifying optimal feeding habitat and proposed Marine Protected Areas (pMPAs) for the black-legged kittiwake (*Rissa tridactyla*) suggests a need for complementary management approaches. Biol. Conserv. 164, 73–81. https://doi.org/10.1016/j.biocon.2013.04.022

Cleeland, J.B., Alderman, R., Bindoff, A., Lea, M-A., McMahon, C.R., Phillips, R.A, Raymond, B., Sumner, M.D., Terauds, A., Wotherspoon, S.J., Hindell, M.A., 2019. Factors influencing the habitat use of sympatric albatrosses from Macquarie Island, Australia. Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps12811

Cox, S., Scott, B., Camphuysen, C., 2013. Combined spatial and tidal processes identify links between pelagic prey species and seabirds. Mar. Ecol. Prog. Ser. 479, 203–221. https://doi.org/10.3354/meps10176

Crawford, W.R., 1997. Physical oceanography of the waters around the Queen Charlotte Islands, in: Vermeer, K., Morgan, K.H. (Eds.), The Status, Ecology, and Conservation of Marine Birds of the North Pacific. Canadian Wildlife Service Occasional Papers, Ottawa, pp. 8–17.

Crawley, M.J., 2015. Statistics: an Introduction using R, 2nd ed. Wiley, West Sussex.

Croxall, J.P., Butchart, S.H.M., Lascelles, B., Stattersfield, A.J., Sullivan, B., Symes, A., Taylor, P., 2012. Seabird conservation status, threats and priority actions: a global assessment. Bird Conserv. Int. 22, 1–34. https://doi.org/10.1017/S0959270912000020

Dias, M.P., Martin, R., Pearmain, E.J., Burfield, I.J., Small, C., Phillips, R.A., 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

Domalik, A.D., Hipfner, J.M., Studholme, K.R., Crossin, G.T., Green, D.J., 2018. At-sea distribution and fine-scale habitat use patterns of zooplanktivorous Cassin's auklets during the chick-rearing period. Mar. Biol. 165, 177. https://doi.org/10.1007/s00227-018-3434-8

Elliott, K.H., Shoji, A., Campbell, K.L., Gaston, A.J., 2010. Oxygen stores and foraging behavior of two sympatric, planktivorous alcids. Aquat. Biol. 8, 221–235. https://doi.org/10.3354/ab00236

Fauchald, P., 2009. Spatial interaction between seabirds and prey: review and synthesis. Mar. Ecol. Prog. Ser. 391, 139–151. https://doi.org/10.3354/meps07818

Fauchald, P., Erikstad, K., Skarsfjord, H., 2000. Scale-dependent predator-prey interactions: the hierarchical spatial distribution of seabirds and prey. Ecology 81, 773–783. https://doi.org/10.2307/177376

Foreman, M.G.G., Crawford, W.R., Cherniawsky, J.Y., Henry, R.F., Tarbotton, M.R., 2000. A high-resolution assimilation tidal model for the northeast Pacific Ocean. J. Geophys. Res. 105, 28,629-28,651. https://doi.org/http://dx.doi.org/10.1029/1999JC000122

Fox, C.H., Hara, P.D.O., Bertazzon, S., Morgan, K., Underwood, F.E., Paquet, P.C., 2016. A preliminary spatial assessment of risk: Marine birds and chronic oil pollution on Canada's Pacific coast. Sci. Total Environ. 573, 799–809. https://doi.org/10.1016/j.scitotenv.2016.08.145

Fox, C.H., Huettmann, F.H., Harvey, G.K.A., Morgan, K.H., Robinson, J., Williams, R., Paquet, P.C., 2017. Predictions from machine learning ensembles: marine bird distribution and density on Canada's Pacific coast. Mar. Ecol. Prog. Ser. 566, 199–216. https://doi.org/10.3354/meps12030

Gaston, A.J., 2004. Seabirds: a Natural History. Yale Univeristy Press, New Haven.

Gaston, A.J., 1992. The Ancient Murrelet: a Natural History in the Queen Charlotte Islands. T & AD Poyser, London.

Gaston, A.J., Carter, H.R., Sealy, S.G., 1993. Winter ecology and diet of Ancient Murrelets off Victoria, British Columbia. Can. J. Zool. 71, 64–70. https://doi.org/10.1139/z93-010

Gaston, A.J., Ydenberg, R.C., Smith, G.E.J., 2007. Ashmole's halo and population regulation in seabirds. Mar. Ornithol. 35, 119–126.

Grecian, W.J., Lane, J. V, Michelot, T., Wade, H.M., Hamer, K.C., 2018. Understanding the ontogeny of foraging behaviour: insights from combining marine predator bio-logging with satellite-derived oceanography in hidden Markov models. J. R. Soc. Interface 15. https://doi.org/10.1098/rsif.2018.0084

Hamilton, W.J., Watt, K.E.., 1970. Refuging. Annu. Rev. Ecol. Syst. 1, 263–286.

Harding, A., Piatt, J., Schmutz, J., 2007. Seabird behavior as an indicator of food supplies: sensitivity across the breeding season. Mar. Ecol. Prog. Ser. 352, 269–274. https://doi.org/10.3354/meps07072

Harrison, X.A., Donaldson, L., Correa-Cano, M.E., Evans, J., Fisher, D.N., Goodwin, C.E.D., Robinson, B.S., Hodgson, D.J., Inger, R., 2018. A brief introduction to mixed effects modelling and multi-model inference in ecology. https://doi.org/10.7717/peerj.4794

Hartig, F., 2020. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.2.7. URL https://CRAN.R-project.org/package=DHARMa

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., Bruyn, P.J.N. de, Dias, M.P., Duarte, C.M., Dunn, D.C., Dutton, P.H., Esteban, N., Friedlaender, A., Goetz, K.T., Godley, B.J., Halpin, P.N.,… Sequeira, A.M.M., 2019. Translating marine animal tracking data into conservation policy and management. Trends Ecol. Evol. 34, 459–473. https://doi.org/10.1016/J.TREE.2019.01.009

Hemmert, G.A.J., Schons, L.M., Wieseke, J., Schimmelpfennig, H., 2018. Log-likelihood-based pseudo-R_2 in logistic regression: deriving sample-sensitive benchmarks. Sociol. Methods Res. 47, 507–531. https://doi.org/10.1177/0049124116638107

Holm, K.J., Burger, A.E., 2002. Foraging behavior and resource partitioning by diving birds during winter in areas of strong tidal currents. Waterbirds 25, 312–325.

Hunt Jr, G., Russell, R., Coyle, K., Weingartner, T., 1998. Comparative foraging ecology of planktivorous auklets in relation to ocean physics and prey availability. Mar. Ecol. Prog. Ser. 167, 241–259. https://doi.org/10.3354/meps167241

Hunt Jr, G.L., Renner, M., Kuletz, K., 2014. Seasonal variation in the cross-shelf distribution of seabirds in the southeastern Bering Sea. Deep Sea Res. Part II 109, 266–281. https://doi.org/10.1016/j.dsr2.2013.08.011

Hunt Jr, G.L., 1991. Occurrence of polar seabirds in relation to prey concentrations and oceanographic factors. Polar Res. 10, 12–16. https://doi.org/10.3402/polar.v10i2.6766

Ladd, C., Jahncke, J., Hunt Jr, G.L., Coyle, K.O., Stabeno, P.J., 2005. Hydrographic features and seabird foraging in Aleutian Passes. Fish. Oceanogr. 14, 178–195. https://doi.org/10.1111/j.1365-2419.2005.00374.x

Mackas, D.L., Coyle, K.O., 2005. Shelf–offshore exchange processes, and their effects on mesozooplankton biomass and community composition patterns in the northeast Pacific. Deep. Res. II 52, 707–725. https://doi.org/10.1016/j.dsr2.2004.12.020

Mann, K.H., Lazier, J.R.N., 2006. Dynamics of Marine Ecosystems: Biological-Physical Interactions in the Oceans, 3rd ed. Blackwell Publishing Ltd, Malden. https://doi.org/10.1002/9781118687901

Maxwell, S.M., Conners, M.G., Sisson, N.B., Dawson, T.M., 2016. Potential benefits and shortcomings of marine protected areas for small seabirds revealed using miniature tags. Front. Mar. Sci. 3. https://doi.org/10.3389/fmars.2016.00264

Nur, N., Jahncke, J., Herzog, M.P., Howar, J., Hyrenbach, K.D., Zamon, J.E., Ainley, D.G., Wiens, J.A., Morgan, K., Balance, L.T., Stralberg, D., 2011. Where the wild things are: Predicting hotspots of seabird aggregations in the California Current System. Ecol. Appl. 21, 2241–2257. https://doi.org/10.1890/10-1460.1

Oppel, S., Bolton, M., Carneiro, A.P.B., Dias, M.P., Green, J.A., Masello, J.F., Phillips, R.A., Owen, E., Quillfeldt, P., Beard, A., Bertrand, S., Blackburn, J., Boersma, P.D., Borges, A., Broderick, A.C., Catry, P., Cleasby, I., Clingham, E., Creuwels, J., Crofts, S., …Croxall, J., 2018. Spatial scales of marine conservation management for breeding seabirds. https://doi.org/10.1016/j.marpol.2018.08.024

Perry, I.R., Waddell, B.J., 1997. Zooplankton in Queen Charlotte Island waters: distribution and availability to marine birds, in: Vermeer, K., Morgan, K.H. (Eds.), The Status, Ecology, and Conservation of Marine Birds of the North Pacific. Canadian Wildlife Service Occasional Papers, Ottawa, pp. 18–28.

R Core Team, 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Rodway, M.S., Lemon, M.J.F., Kaiser, G.W., 1988. British Columbia seabird colony inventory: report # 1 - east coast Moresby Island, Technical Report Series No. 50. Canadian Wildlife Service, Delta.

Scales, K.L., Votier, S.C., Miller, P.I., Embling, C.B., Ingram, S.N., Pirotta, E., 2014. Mesoscale fronts as foraging habitats: composite front mapping reveals oceanographic drivers of habitat use for a pelagic seabird. https://doi.org/10.1098/rsif.2014.0679

Schielzeth, H., 2010. Simple means to improve the interpretability of regression coefficients. Methods Ecol. Evol. 1, 103–113. https://doi.org/10.1111/j.2041-210x.2010.00012.x

Schneider, D.C., 1997. Habitat selection by marine birds in relation to water depth. Ibis 139, 175–178. https://doi.org/10.1111/j.1474-919x.1997.tb04520.x

Sealy, S.G., 1975. Feeding ecology and the Ancient and Marbled murrelets near Langara Island, British Columbia. Can. J. Zool. 53, 418–433.

Sealy, S.G., 1973. Adaptive significance of post-hatching developmental patterns and growth rates in the Alcidae. Scand. J. Ornithol. 4, 113–121.

Shoji, A., Elliott, K.H., Aris-Brosou, S., Crump, D., Gaston, A.J., 2011. Incubation patterns in a central-place forager affect lifetime reproductive success: Scaling of patterns from a foraging bout to a lifetime. PLoS One 6, 1–10. https://doi.org/10.1371/journal.pone.0017760

Stone, C.J., Webb, A., Tasker, M.L., 1995. The distribution of auks and procellariiformes in north-west european waters in relation to depth of sea. Bird Study 42, 50–56. https://doi.org/10.1080/00063659509477148

Thaxter, C.B., Lascelles, B., Sugar, K., Cook, A.S.C.P., Roos, S., Bolton, M., Langston, R.H.W., Burton, N.H.K., 2012. Seabird foraging ranges as a preliminary tool for identifying candidate Marine Protected Areas. Biol. Conserv. 156, 53–61. https://doi.org/10.1016/j.biocon.2011.12.009

Tremblay, Y., Bertrand, S., Henry, R.W., Kappes, M.A., Costa, D.P., Shaffer, S.A., 2009. Analytical approaches to investigating seabird-environment interactions: A review. Mar. Ecol. Prog. Ser. 391, 153–163. https://doi.org/10.3354/meps08146

Vermeer, K., Fulton, J.D., Sealy, S.G., 1985. Differential use of zooplankton prey by Ancient Murrelets and Cassin’s Auklets in the Queen Charlotte Islands. J. Plankton Res. 7, 443–459. https://doi.org/10.1093/plankt/7.4.443

Weimerskirch, H., 2007. Are seabirds foraging for unpredictable resources? Deep. Res. Part II 54, 211–223. https://doi.org/10.1016/j.dsr2.2006.11.013

Weingartner, T., Eisner, L., Eckert, G.L., Danielson, S., 2009. Southeast Alaska: Oceanographic habitats and linkages. J. Biogeogr. 36, 387–400. https://doi.org/10.1111/j.1365-2699.2008.01994.x

Whoriskey, K., Martins, E.G., Auger-Méthé, M., Gutowsky, L.F.G., Lennox, R.J., Cooke, S.J., Power, M., Mills Flemming, J., 2019. Current and emerging statistical techniques for aquatic telemetry data: A guide to analysing spatially discrete animal detections. Methods Ecol. Evol. 10, 935–948. https://doi.org/10.1111/2041-210X.13188

Wood, S.N., 2006. Generalized Additive Models: an Introduction with R. Chapman & Hall, Boca Raton.

Chapter 4. Conclusion

The goal of this research was to provide a greater understanding of Ancient Murrelet movements during foraging trips, and to characterize foraging habitat near breeding colonies. We used a combination of individual movement analysis and regression models to infer behaviours and to quantify the relationship between these behaviours and physical environmental variables in order to describe foraging habitats.

The GPS tracking data collected through two field seasons showed that Ancient Murrelets were foraging throughout Hecate Strait, and undertaking trips of several hundred kilometers over several days. Trips were varied in style, and some birds travelled more directly while others undertook large loops. Trips over the two years of tracking covered similar areas. By using the GPS tracking data in the individual movement analysis with hidden Markov modelling (HMMs), three behaviour states were identified from movement paths based on the path characteristics of step-length and turning angle. The inclusion of immersion data from the GPS tags, that indicated when tags were underwater and when birds were most likely diving, allowed the two slow-moving states to be differentiated into resting and foraging. The foraging state had the shortest mean step length, and varied turning angles, suggesting area-restricted search behaviour.

Habitat analysis using static physical and spatial explanatory variables indicated that tidal current, seafloor slope, depth, and distance from the colony all had a negative relationship with explaining where Ancient Murrelets chose to forage along their movement path. This is inconsistent with previous research suggesting Ancient Murrelets will forage in higher tidal current areas (Holm and Burger, 2002), although this could be due to differing mechanisms of prey concentration at work in the different study regions investigated, or due to a temporal mismatch of tidal data and foraging data in this study. The results here also indicate that birds from these colonies did not choose to forage in deeper water areas, unlike Ancient Murrelets surveyed on the west coast adjacent to the continental shelf break, where they were found at higher densities in deeper waters (Vermeer et al., 1985). Interestingly, depth was positively correlated with the number of minutes that birds spent foraging in a certain area. This combination of results suggests that Ancient Murrelets were searching for food throughout their foraging trips as environments vary spatially and temporally (i.e., they have incomplete knowledge of their environment and must sample often to find higher quality foraging locations). In deeper water areas, which are typically considered more biologically productive (Hunt et al., 2014), prey may be more concentrated or more available to Ancient Murrelets, as we found that they foraged in deeper locations for longer time periods.

This study was a preliminary analysis of this new dataset of GPS tracks from breeding Ancient Murrelets. There are many avenues for future research in both the realm of movement analysis, and of habitat modelling. Here, I investigated how the physical environment related to foraging behaviour by first classifying foraging locations. Another option using HMMs is to incorporate environmental variables that might be expected to influence behaviour directly into the movement models, allowing for an investigation of how the environment influences movement behaviour. Furthermore, for a greater understanding of foraging habitat characteristics, more non-static biophysical explanatory variables could be incorporated into future models; variables such as sea surface temperatures, chlorophyll-*a* and sea surface height have all proved useful for understanding dynamic aspects of seabird foraging habitat (Tremblay et al., 2009). Several limitations of this dataset are the sample size of individuals that were tracked, and the short time-period of tracking (Sequeira et al., 2019). These limitations can only be addressed by undertaking more data collection, which will be possible through increased accessibility and improvements in technology, and collaborations with researchers studying Ancient Murrelets in other regions. Another limitation in this study is the relatively simple structure of the movement models used for defining foraging locations. There are many variations and additions to HMMs that can make these models more reflective of biologically meaningful behaviours. For example, hidden semi-Markov models incorporate higher-order Markov chains to model persistence of behaviour states over multiple time lags (Joo et al., 2013), and hierarchical HMMs can be used to allow behaviour patterns to differ between individuals (Jonsen et al., 2013; Langrock et al., 2012). Addressing the challenges of added model complexity can be done in the future through making this dataset available to other researchers and through collaborations with others working on problems of animal movement modelling.

The findings from this thesis are important as they improve our understanding of Ancient Murrelet movement patterns, behaviour, and habitat use at sea. This is a seabird species for which relatively little is known about at-sea movements and habitat use, and this study provides the first known research using GPS tracking to gain insight into specific movement patterns of breeding individuals of this species. By determining movement characteristics of breeding Ancient Murrelets on foraging trips, where they are foraging, and the characteristics of the habitat use by foraging birds, this research can help inform protection of Ancient Murrelets by identifying important at-sea foraging habitat. Furthermore, it is anticipated that future research can use the findings from this thesis to continue to explore characteristics of Ancient Murrelet foraging habitat, that will further help to delineate and predict locations of high-quality at-sea habitat for this species. Finally, as high precision GPS tracking becomes more readily accessible for smaller seabirds, the use of advanced movement modelling techniques can be employed across a wider range of seabird species. It is anticipated that this thesis will contribute insights on data collection and model design for future studies to use for producing new knowledge on protecting seabirds from threats to their at-sea habitat.

4.1 References

Holm, K.J., Burger, A.E., 2002. Foraging behavior and resource partitioning by diving birds during winter in areas of strong tidal currents. Waterbirds 25, 312–325.

Hunt Jr, G.L., Renner, M., Kuletz, K., 2014. Seasonal variation in the cross-shelf distribution of seabirds in the southeastern Bering Sea. Deep Sea Res. Part II 109, 266–281. https://doi.org/10.1016/j.dsr2.2013.08.011

Jonsen, I.D., Basson, M., Bestley, S., Bravington, M. V, Patterson, T.A., Pedersen, M.W., Thomson, R., Thygesen, U.H., Wotherspoon, S.J., 2013. State-space models for bio-loggers: A methodological road map. Deep. Res. II 88–89, 34–46. https://doi.org/10.1016/j.dsr2.2012.07.008

Joo, R., Bertrand, S., Tam, J., Fablet, R., 2013. Hidden Markov models: the best models for forager movements? PLoS One 8, e71246. https://doi.org/10.1371/journal.pone.0071246

Langrock, R., King, R., Matthiopoulos, J., Thomas, L., Fortin, D., Morales, J.M., 2012. Flexible and practical modeling of animal telemetry data: hidden Markov models and extensions. Ecology 93, 2336–2342. https://doi.org/10.1890/11-2241.1

Sequeira, A.M.M., Heupel, M.R., Lea, M.A., Eguíluz, V.M., Duarte, C.M., Meekan, M.G., Thums, M., Calich, H.J., Carmichael, R.H., Costa, D.P., Ferreira, L.C., Fernandéz-Gracia, J., Harcourt, R., Harrison, A.L., Jonsen, I., McMahon, C.R., Sims, D.W., Wilson, R.P., Hays, G.C., 2019. The importance of sample size in marine megafauna tagging studies. Ecol. Appl. 29, 1344–1360. https://doi.org/10.1002/eap.1947

Tremblay, Y., Bertrand, S., Henry, R.W., Kappes, M.A., Costa, D.P., Shaffer, S.A., 2009. Analytical approaches to investigating seabird-environment interactions: A review. Mar. Ecol. Prog. Ser. 391, 153–163. https://doi.org/10.3354/meps08146

Vermeer, K., Fulton, J.D., Sealy, S.G., 1985. Differential use of zooplankton prey by Ancient Murrelets and Cassin’s Auklets in the Queen Charlotte Islands. J. Plankton Res. 7, 443–459. https://doi.org/10.1093/plankt/7.4.443

Appendix A

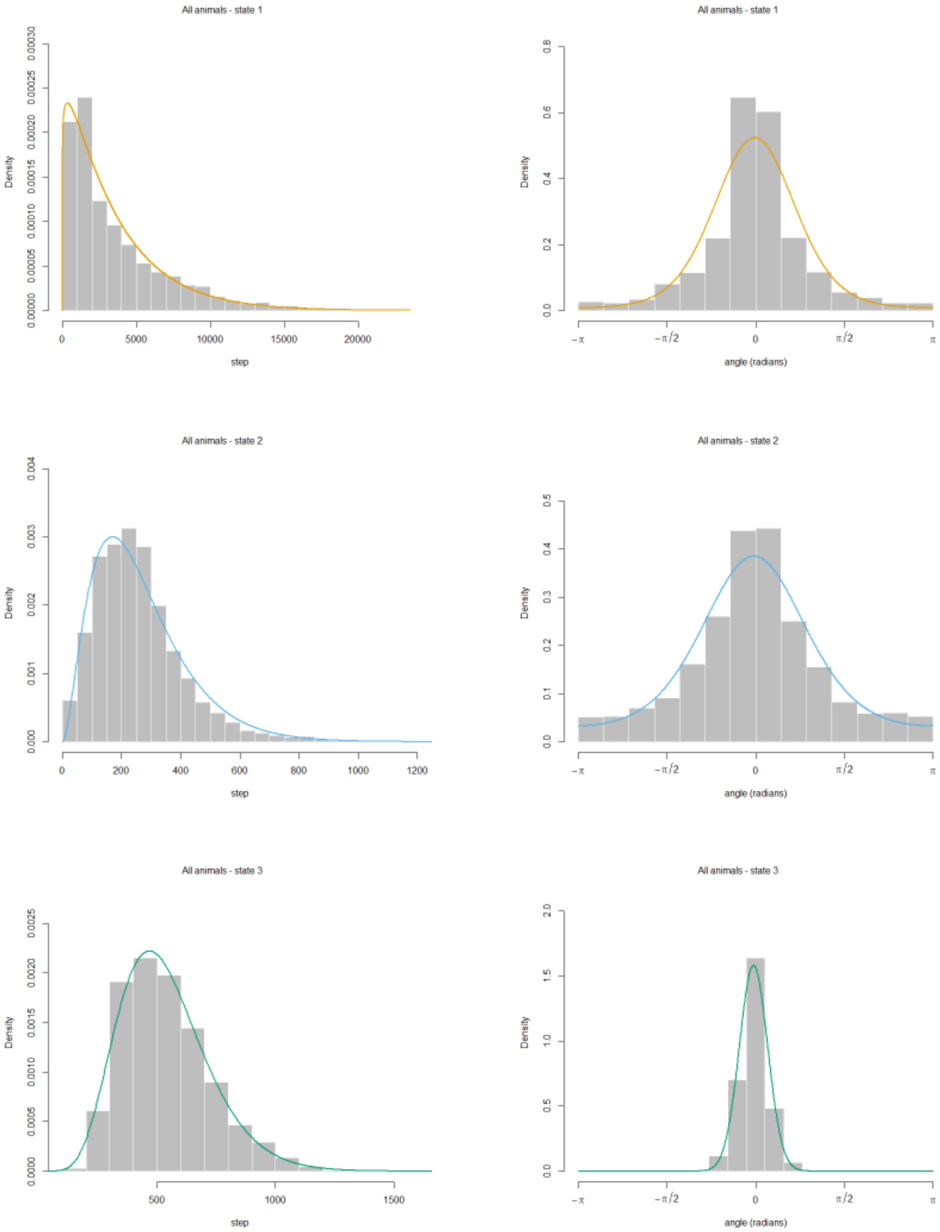


Figure A- 1. Probability density plots for step length and turning angle, separated by state, from the three-state HMM.

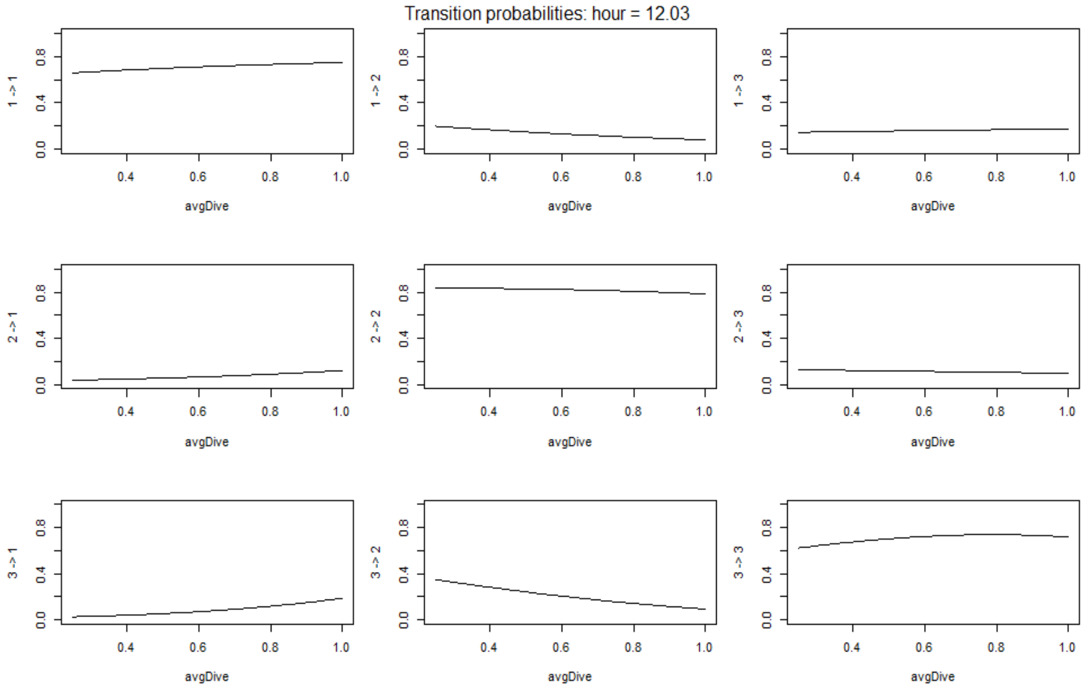


Figure A- 2. Transition probabilities over different proportions of tag immersion (avgDive = immersion index; 1 = dry tag, 0 = wet tag). Each figure shows transitions between two states; state 1 is transit, state 2 is foraging, and state 3 is resting.

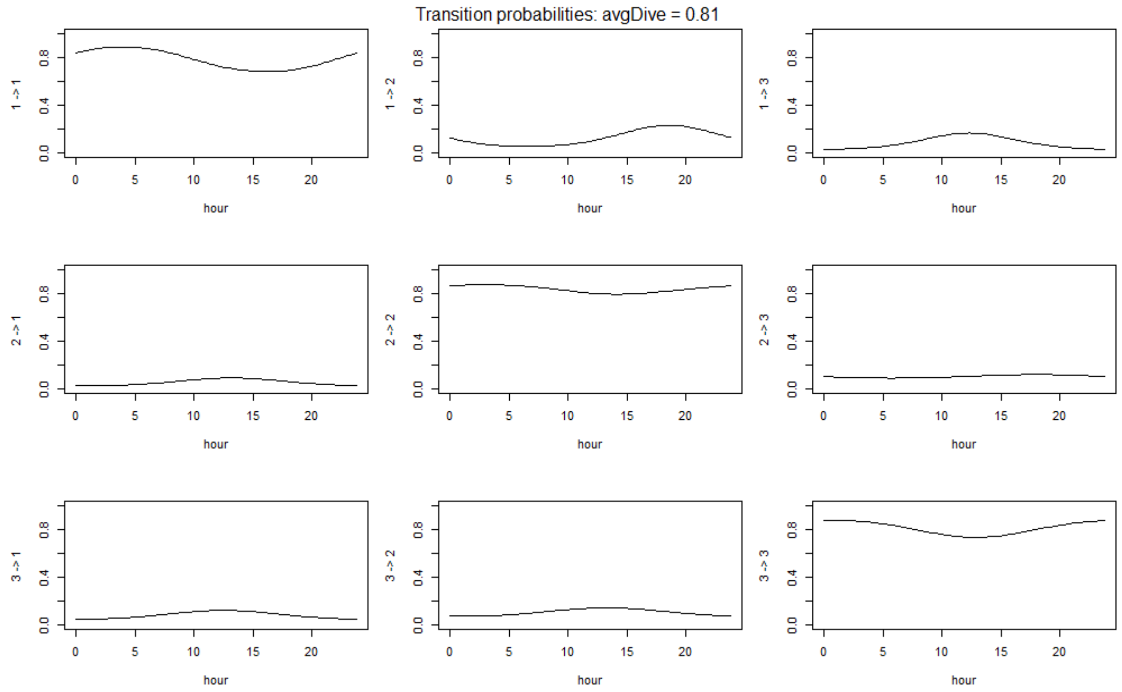


Figure A- 3. Transition probabilities throughout the day (0 hours = midnight). Each figure shows transitions between two states; state 1 is transit, state 2 is foraging, and state 3 is resting.

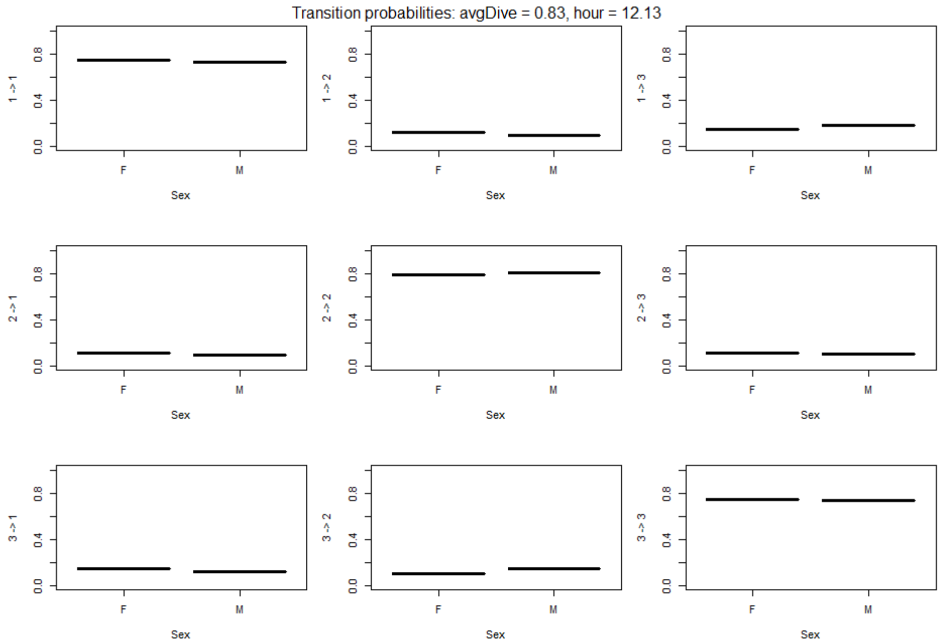


Figure A- 4. Transition probabilities throughout the day (0 hours = midnight). Each figure shows transitions between two states; state 1 is transit, state 2 is foraging, and state 3 is resting.

Appendix B

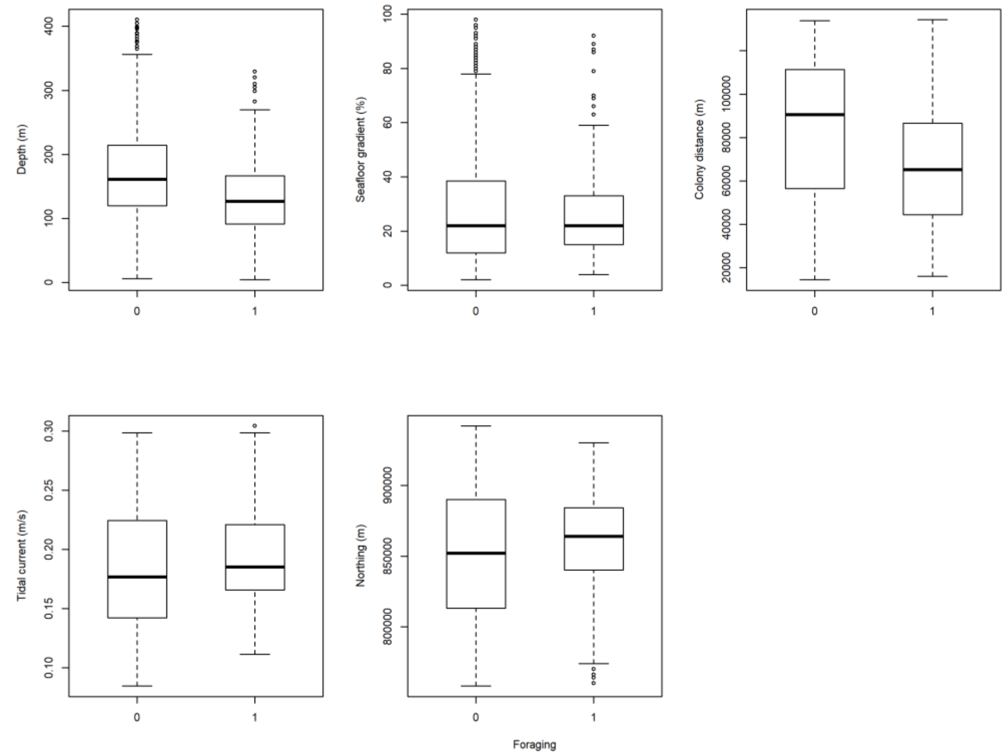


Figure B- 1. Boxplots to visualize distribution of environmental data used in the logistic regression. 0 = no foraging in grid cell, 1 = foraging in grid cell. The two years and all individual birds were pooled (sample size = 512). Middle line is the median, the box represents the 25th (lower) and 75th (upper) percentiles, and the points above or below the whiskers are outlier.

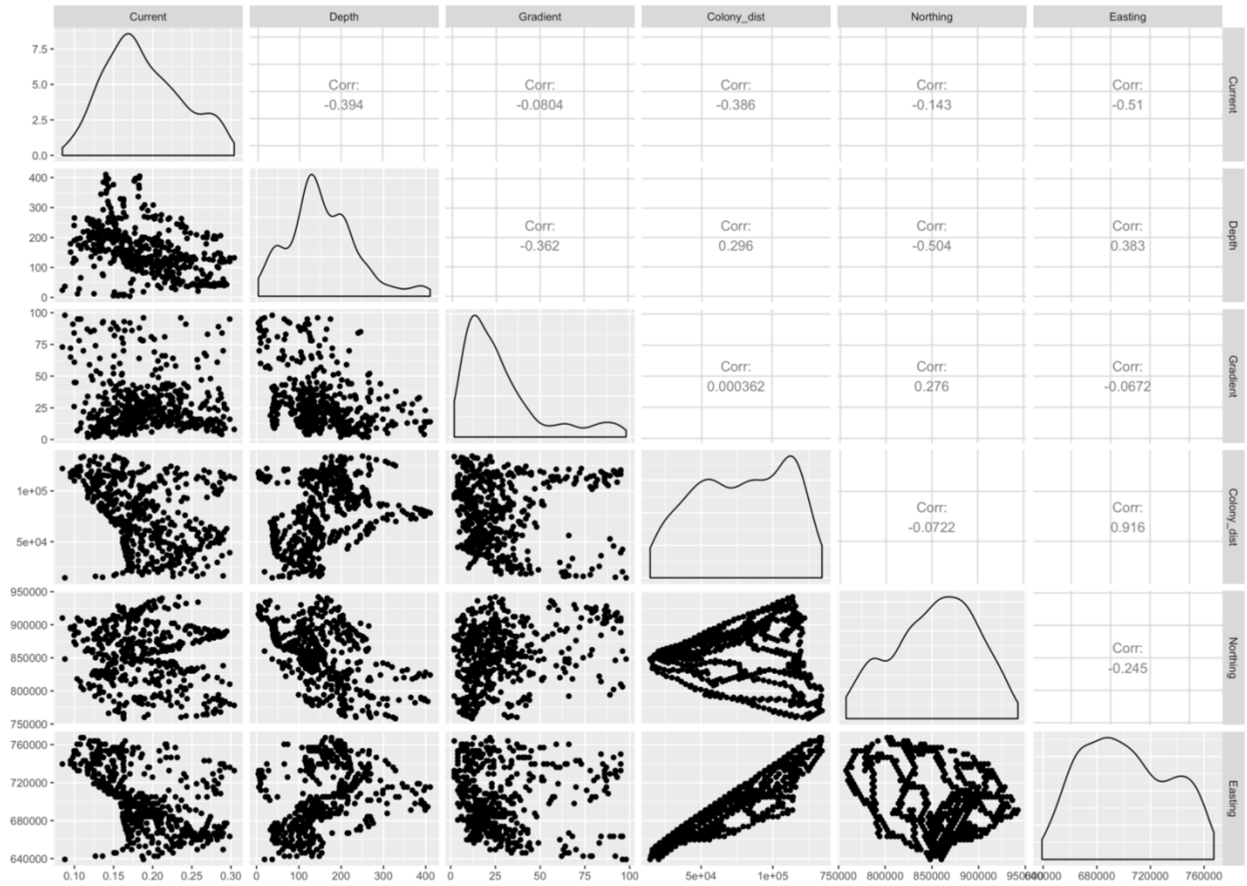


Figure B- 2. Investigation of collinearity between explanatory variables used in logistic regression, and Pearson’s correlation coefficient. Density plots showing the distribution of data for each variable are shown along the middle diagonal. Here, variables are displayed before being centered and standardized.

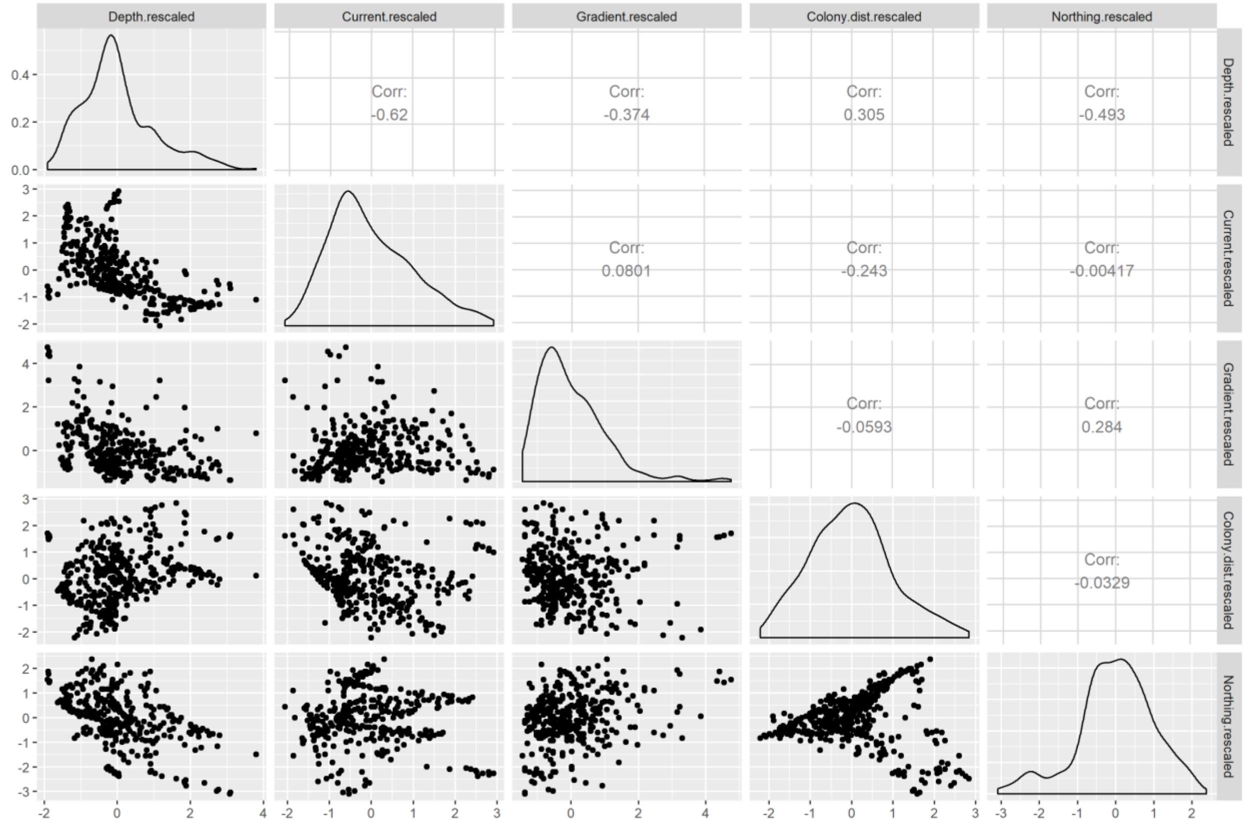


Figure B- 3. Exploration of collinearity of explanatory variables used in GLMM. All variables are displayed as the values centered around the mean and standardized using the standard deviation. The sample for this analysis was all grid cells that contained foraging by any individual in 2018 and 2019 (n = 477). Pearson's correlation coefficients are shown in upper right, and density plots showing the distribution of data for each variable are shown along the middle diagonal.

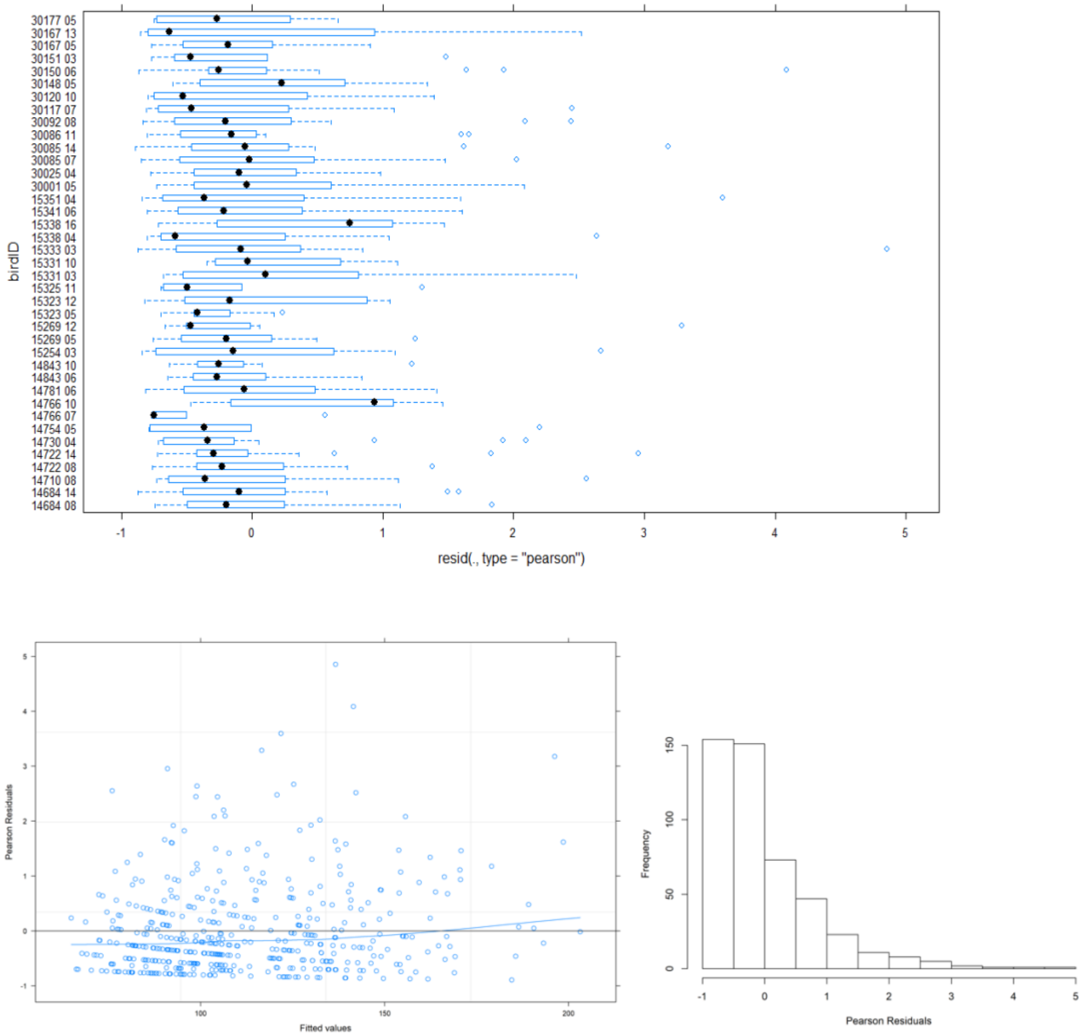


Figure B- 4. Pearson standardized residuals from final GLMM that included depth as a fixed effect and bird ID as a random effect. Response variable was minutes spent foraging per grid cell. Top: residuals for each individual showing variation between individuals. Left: all residuals versus fitted values. Right: frequency plot of residuals.

Plots of simulated scaled residuals from GLMM (explanatory variables are depth as a fixed effect and bird ID as a random effect, the response variable is minutes of foraging in grid cell). Using the *DHARMa* package (Hartig, 2020), simulated residuals are calculated from new, simulated data that uses parameter estimates from the fitted model. The simulated residuals can then be compared to the observed residuals from the true data.

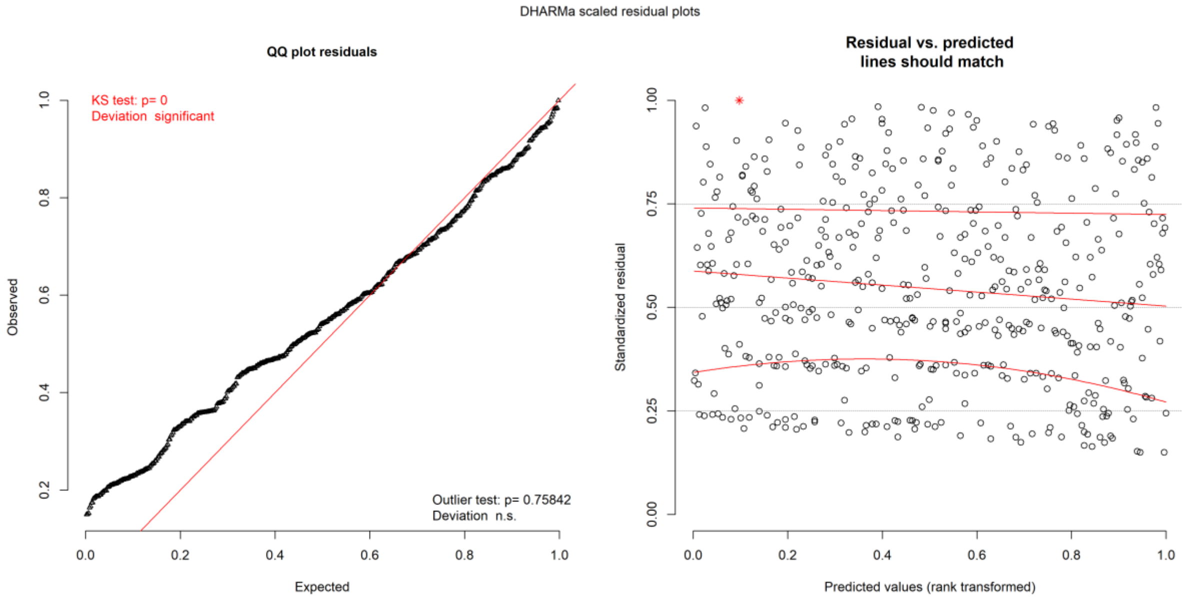


Figure B- 5. Simulated residuals from model. Left: observed residuals from the model fit against the expected residuals from the simulation (there is no assumption that they are normally distributed). Right: observed residuals from model against predicted residuals from simulations, with quantile regression lines (red lines). The regression lines should be horizontal. Both plots suggest that the model does not explain the observed data well for lower values of the explanatory variables.

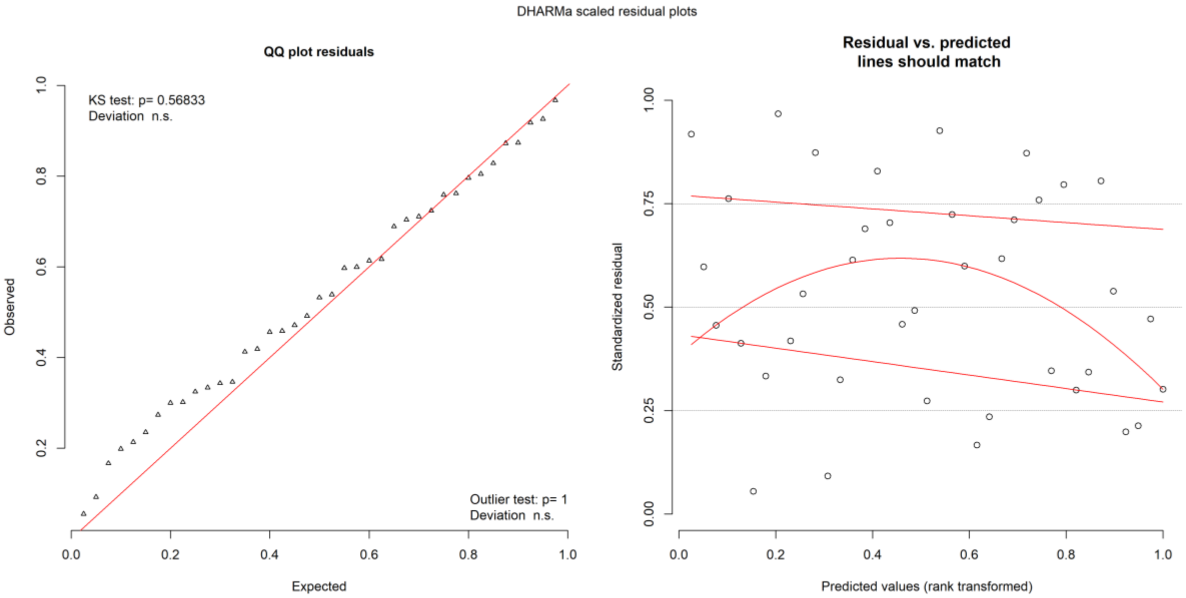


Figure B- 6. The same two plots of model residuals versus simulated residuals from above but grouped by bird ID. The non-horizontal lines on the right could be due to the low sample size (because it is now grouped by bird, sample size is now 39).