AN EXPERIMENTAL STUDY OF THE AT-SEA MOVEMENT OF A SMALL DIVING SEABIRD AND THE BIOLOGICAL AND ETHICAL IMPLICATIONS OF WILDLIFE TRACKING RESEARCH

By Jill L. Robinson©

A thesis submitted to the
School of Graduate Studies
in partial fulfillment of the
requirements for the degree of
Master of Science

Department of Biology
Memorial University of Newfoundland
October 2015
St John's, Newfoundland and Labrador, Canada

ABSTRACT

Year-round ecology and behaviour of seabirds is poorly understood due to difficulties associated with measuring at-sea activity during the non-breeding season. Lightweight biologging devices permit the tracking of individual movement across seasons and periods of the breeding cycle. To examine at-sea distribution of small diving seabirds, I deployed tarsus-mounted geolocators (<1.1 % body mass) on 31 Crested Auklets (*Aethia cristatella*) in 2011, at a breeding site at Buldir Island, Alaska. I recovered ten of these geolocators in 2012 (three provided usable data), revealing for the first time, an unexpected long-distance migration with substantial habitat overlap among individuals. I also experimentally quantified effects of devices on individuals' behaviour to evaluate biological and ethical relevance of research. Deleterious effects were detected on chick condition, provisioning rates and social activity, with greatest impacts on return rates. To maintain the rigor required by basic scientific principles, wildlife tracking studies must quantify effects of attached devices and consider the biological relevance of the resulting measurement data concerning the behaviour of interest.

ACKNOWLEDGEMENTS

First and foremost, I would like to take the opportunity to thank my supervisor, Dr. Ian L. Jones. His unwavering academic support, boundless encouragement and enthusiasm for my project have helped make this experience overwhelmingly positive. Under the advisement of Ian, I have gained endless skills as a developing scientist and conservationist and throughout this learning process I've reaffirmed my passion for wildlife biology. I feel incredibly fortunate to have had the opportunity to spend three amazing summers in the Aleutian Islands; an experience I will forever cherish.

My study was made possible by the incredible support of the Alaska Maritime National Wildlife Refuge, who's Refuge Manager Steve Delehanty and Biologists Heather Renner and Jeff Williams grant us permission to conduct research on the refuge and always made us feel very welcome there. Research conducted in such a remote field site in the Aleutian Islands would not have been made possible without the efforts of a large team of hardworking, passionate individuals. The employees of the Alaska Maritime National Wildlife Refuge played an integral part in safely delivering field members and equipment to and from the field site, creating unforgettable memories aboard the research vessel, the Tiglax. Jeff Williams, Lisa Spitler, Billy Pepper and the entire boat crew were invaluable resources, providing necessary logistical support for my project, while instilling enthusiasm, good-natured humour, and professionalism into everything they do. A very special thanks goes out to a select group of people including

those previously mentioned, as well as Alex Bond and Gary Drew, who went above and beyond to help ensure the success of my project during my first year in the field when I was met with immense technical challenges.

Such an intensive project, located at one of the most remote islands in the world, requires support from generous grants and financial aid to make this important research possible. Financial support was provided by a Discovery Grant to ILJ from the Natural Sciences and Engineering Research Council of Canada, a Challenge Cost Share grant through the Alaska Maritime National Wildlife Refuge and student travel was subsidized by the Northern Scientific Training Program of the Department of Aboriginal Affairs and Northern Development of Canada.

My incredible field assistants, Michelle Valiant and Michelle Goh, both contributed endless time and energy into my project, and I cannot thank them enough for their field assistance and friendship. Additionally, members of the Buldir field crew in both years greatly enriched my summer research experience, making camp life on Buldir Island truly amazing. This includes John Warzybok, David Cockerill, Jamie Neil, Matt Henschen, Ronan Dugan, and Carley Schacter.

Throughout the learning process of my research involving geolocator deployment, recovery and analysis, and within the constantly changing and developing field of wildlife tracking research, continual technical support was provided by Mike VandenTillart, from Lotek Wireless Inc. Academic support and encouragement from my supervisory committee members, Ian Jones, Yolanda Wiersma and Evan Edinger, was critical in the completion of my project. As a member of the Seabird Ecology Research Group, I have received endless academic and most valuable moral support, without which I couldn’t have completed this project. Assistance from all staff and faculty in the biology department of Memorial University of Newfoundland has been incredibly helpful throughout my time at St. John’s campus, and their hard work never went unnoticed. A special thank you goes to my fantastic lab mates, Shanti Davis, Mark Maftei, and Carley Schacter who were there for me during all stages of this master’s experience, offering not only technical, and statistical help, but a strong network of moral support and above all else, friendship.

Lastly, I would like to thank the endless support of my family and close friends who were there for me throughout the many challenges I faced throughout my degree. My community of friends, in St. John’s, at home in Shanty Bay, and across the globe have provided continuous emotional support and encouragement that has been paramount to my success in this project. Most importantly, my parents and two sisters have motivated me to no end and I owe much of my success to their unconditional love and support. Thank you so much for helping me to pursue my passion and for encouraging me to never give up on my dreams.

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LIST OF ABBREVIATIONS

SST – Sea Surface Temperature

GIS – Geographic Information Systems

CMR – Capture Mark Recapture

PTT - Platform Transmitter Terminals (Satellite)

GPS – Global Positioning System

SD – Standard Deviation

Hr – Hours

Min – Minutes

km – Kilometers

Ha – Hectares

g – Grams

kg – Kilograms

m – Meters

i.d. - identification

df – degrees of freedom

CO-AUTHORSHIP STATEMENT

The following research chapters (Chapter Two and Three) are written in first person plural as stand-alone manuscripts and were developed in collaboration with my supervisor, Dr. Ian L. Jones (Department of Biology, Memorial University of Newfoundland, St. John's, NL A1B 3X9), who contributed to aspects of research design, logistics in the field, analysis of data, and manuscript preparation. The contents of Chapter Two were published in the journal *Behaviour* in August 2014, with Ian L. Jones as second author. The contents of Chapter Three are in preparation for submission to Marine Ornithology, with Ian L. Jones as second author.

Robinson, J. and I.L. Jones. 2014. An experimental study of the effects of a tarsus-mounted tracking device on the behaviour of a small pursuit-diving seabird. Behaviour DOI:10.1163/1568539X-00003217

CHAPTER ONE: INTRODUCTION

1.1 BACKGROUND AND OVERVIEW

The purpose of this thesis is to make a constructive contribution to the progress of migration research in wildlife biology and increase our understanding of the values and limitations associated with the use of rapidly advancing tracking technology. More specifically, my thesis will focus on empirically quantifying seasonal movement of a small pursuit-diving seabird originating at a breeding colony in the western Aleutian Islands, Alaska, by the use of attached positioning devices (light-based archival geolocators). Furthermore, it will outline my experimental approach to evaluating the effects of attached devices on the biology of equipped individuals (i.e., 'the observer effect') and assess the implications of its findings for further research.

1.1.1 Migration

Migration is the movement of animals, from one location to another and back, often in response to seasonal changes in local climate and resources (Webster et al., 2002). This phenomenon of large scale relocation occurs across many taxa including mammals, birds, fishes, insects and other mobile invertebrates and usually involves repeated seasonal movements to and from breeding areas (Webster et al., 2002; Marra et al., 2006; Wilcove & Wikelski, 2008). Migration is an essential component of the form and function of most organisms in occupying their ecological niche and enabling their fundamental drive to reproduce (Marra et al., 2006; Dingle & Drake, 2007; Robinson et al., 2010). The habitat occupied by the individuals must inherently sustain survival, and as most environments tend to be temporally variable, their movement across different landscapes is synchronized with changing habitat quality to optimize individual fitness (Dingle & Drake, 2007). While migration can take many forms, occurring across diverse media and varying in duration and distance, it most often refers to a specialized movement evolutionarily selected for at the individual level (Dingle & Drake, 2007).

Understanding all stages of an organisms' annual cycle, including their time spent migrating, time at stopover sites, and at breeding and non-breeding sites, lends itself to useful evolutionary, ecological, behavioural and conservation applications (Marra et al., 2006; Dingle & Drake, 2007). Increasing interest in behavioural and ecological migration biology has been focused on charismatic fliers and swimmers, shedding light on the life history of a growing number of birds, fish, turtles and insects (Dingle & Drake, 2007; Newton, 2008). Mechanisms that have shaped the evolution of migration in many animals have been heavily investigated, mostly in birds, however there still remain many major gaps in our fundamental understanding of animal migration (Taylor & Berthold, 1999).

1.1.2 Migration and birds

Birds in particular have received a great deal of attention in both past and recent migration research, ignited by the spectacular long distance migratory activity they exhibit (Dingle & Drake, 2007). Over 80% of birds in temperate regions of the world take part in migratory behaviour, capturing the attention of scientists and naturalists alike (Martin et al., 2007). A capacity for large scale mobility has shaped avian ecology, behaviour and demography, and is subsequently the source of intensive migration research over the last century (Newton, 2008). Bird migration is characterized by the movement of individuals between breeding (summer) and non-breeding (winter) sites, often travelling between two distinct locations (Webster et al., 2002). Migratory activity in birds varies significantly across families, species, and populations, as well as across age and sex, and is often driven by food and habitat availability, predation and competition (Newton, 2010).

The widespread occurrence of such large scale movement exists across most species of birds, and has led to highly specialized physiological, behavioural and ecological traits that optimize survival year-round (Newton, 2008). This movement often involves a biannual population shift from tropical latitudes in the non-breeding season to northern latitudes during the breeding season, while other populations undergo trans-equatorial migration from northern latitudes to southern temperate latitudes (Robinson et al., 2010). A highly developed ability to orient and navigate has allowed birds to move across diverse landscapes along specific routes, locating ideal foraging areas, remote breeding sites and wintering grounds (Newton, 2008; Garthe et al., 2012). Birds have developed a highly specialized ability to optimize timing of migratory events in response to endogenous cues and environmental stimuli in order to minimize risk of mortality and maximize foraging opportunities (Richardson, 1978; Alerstam, 2011) This timing is important in order to capitalize on seasonally variable habitat and essential to sustaining high energy costs associated with reproduction, molt and flight (Richardson, 1978; Marra et al., 2004). Physiological mechanisms have been developed in many highly mobile birds that reserve food stores in preparation for long distance migration that incur high energy costs (Gunnarsson et al., 2005; Newton, 2010). Many birds have also effectively adapted to a large range of climatic conditions to accommodate great variation in changing yearly distribution (Newton & Dale, 1996).

1.1.3 Migration and seabirds

Among avian species, seabirds live in a particularly harsh environment where food resources are the primary limiting factor on their survival (Wilson et al., 2002; Weimerskirch, 2007). Seabirds are capable of living independent of land for extended periods, spending only a brief period of time each year engaged in reproductive activity that links them to a terrestrial environment (Vilchis et al., 2006). Following their breeding cycle, true seabirds drastically shift their behaviour and ecology to a purely at-sea existence, often far from land. Most seabirds undertake this annual relocation in response to depleting resources in the area proximate to their breeding site, moving to areas with known, predictably rich resources (Marra et al., 2004). Fine-tuned selection of winter distribution and movement between winter and summer habitat in seabirds is particularly staggering as the landscape of their preferred winter habitat often lacks obvious geographic features across a seemingly homogenous ocean surface.

Many seabirds would be considered obligate migrants, as they routinely move to specified areas each year, travelling beyond other breeding sites or food resources along a trajectory (Dingle & Drake, 2007). Generally, seabirds distribute in resource-rich, highly productive areas where mixing of nutrients by upwelling, frontal zones and shelf edges support an abundance of accessible prey (Weimerskirch, 2007). Knowledge of specific seabird distribution is less known, but is expected to correlate with local features of the environment (sea surface temperatures, bathymetry, ocean currents, wind patterns) that concentrate patchy but predictable aggregations of prey (Gunnarsson et al., 2005; Newton, 2008)

Growing interest in seabird migration has led to an increasing number of studies that are investigating patterns in flight activity and relationships between annual bird distribution and variable characteristics of the environment. Studies aimed to determine seabird distribution face many challenges, primarily due to the remote habitat they often occupy and the highly mobile nature of seabirds (Martin et al., 2007; Burger & Shaffer, 2008). Seabirds tend to distribute across remote environments that are difficult to access, critically limiting our understanding of their ecology, behaviour, and demography throughout the year. Many studies have conducted exhaustive measures of their biology at the breeding colony, where large aggregated colonies can be monitored with greater ease (Burger & Shaffer, 2008). However, in most cases, very little is known about the dominant component of their life at sea.

1.1.4 Tracking technology applied to seabirds

The greatest challenge in studying seabirds at sea and increasing our understanding of their migratory biology is indeed, locating their whereabouts. In the last 130 years, increasing efforts have been made to quantify the impressive large scale movements exhibited by many birds (Newton, 2008). Until the 1820s, it was believed that the disappearance of some large bird populations for extended periods of time each year was a result of annual hibernation in hidden locations (Newton, 2008). While few birds do exhibit hibernation, it was later found that for the most part, this vanishing act could be explained by routine long distance migratory activity (Newton, 2008). This charismatic migratory behaviour observed in birds ignited a strong interest among naturalists to examine why birds were leaving, where they were going, and how they getting there. These and many other questions have led to the development of various tracking methods (e.g., bird leg rings or 'bands') derived many years ago to investigate bird movement and distribution (Newton, 2010). Many of these methods are still in use today making valuable contributions to our fundamental understanding of migratory biology. Thanks to recent advances in remote-sensing monitoring techniques, we are beginning to further uncover previously unknown aspects of seabird biology during the non-breeding season (Newton, 2008; Burger & Shaffer, 2008). Below I outline the progression of methods used to fill missing gaps in our knowledge of seabird migratory biology, beginning at its most rudimentary but fundamental form and ending with the utmost complex and sophisticated example of migration technology.

1.1.4.1 Ground-based surveys

The following examples of bird migration monitoring techniques are conducted from static observation platforms, used to measure moving flocks at a distance to detect large-scale patterns in movement and distribution of species at the population level.

***Observational counts*:** The earliest method used to quantify bird migration is conducted by counting numbers of birds and their direction of flight during migration at sites where high volumes of birds are expected to occur (Webster et al., 2002; Newton, 2006). This technique is valuable however it requires high degree of observational effort and also excludes large numbers of birds that fly at night or at high altitudes that exceed the limit of human observation. Despite limitations on human sight and variable local weather conditions on the reliability and quality of this surveying technique, it has contributed to general understanding of bird movement. Difficulties encountered in observing nocturnal migrants have been improved with the use of spotlights and detecting unique calls using a parabolic reflector and amplifier, which can identify species up to 3000 m away (Ralph et al., 1995). These counts have been conducted from on-land sites. In order to detect numbers of migrating seabirds at-sea, surveys from travelling ships have also contributed significantly to our knowledge of abundance and distribution of many species (Tasker et al., 1984; Clarke et al., 2003). While these data are valuable, they tend to be biased towards the transect routes taken, and have little value in detecting temporal variation in distribution at the individual level.

***Radar*:** In the 1950s, radar was developed to detect movement of aircraft primarily for military purposes and subsequently was applied to quantify numbers and behaviour of flocks of birds flying overhead (Newton, 2008; Bridge et al., 2011). Radar utilizes electromagnetic radiation frequencies in the microwave area (1 m to 1 mm wavelength) and records the echoes produced by nearby objects and has the practical benefit of being useful at very high altitudes and at great distances (Dokter et al., 2011).

This technology is very beneficial in determining bird flock density, timing, direction and relationships of flocking bird movement to environmental conditions (Newton, 2008). A crucial drawback to this technology however, is the general difficulty or inability to determine and distinguish between species (Bowlin et al., 2005; Bridge et al., 2011). Often size, flight speed and wing-beat patterns can be calculated to give rough estimates of species' identity, but with low accuracy (Dokter et al., 2011; Bridge et al., 2011). In addition, this method is costly and requires trained personnel to operate equipment at fixed locations. Radar is still used frequently, having the ability to detect a variety of flocks of birds, from small passerines at a range of 100 km to larger birds at 500 km, in order to quantify migration frequency both day and night, throughout the year (Newton, 2002).

Infrared sensors: The use of infrared sensors provide the ability to make general estimates of migration frequency and flock size by detecting heat emitted from birds flying overhead (Boonstra et al., 1995; Ropert-Coudert & Wilson, 2005). This can be valuable in detecting birds from distances of 300m – 3000m away in order to estimate flock sizes at approximated altitudes, but again, with little accuracy in determining species of detected flocks (Boonstra et al., 1995; Newton, 2010).

1.1.4.2 Individual-based tracking

While data collected from ground-based surveys are useful, they lack the ability to collect individual-based information that can be gained from the use of attached markers or remote-sensing equipment applied directly to individual animals. This approach aims to identify movement at the level of the individual, increasing the degree of detail to measure behaviour during migration including specific migration routes, habitat use and phenology of movement.

Capture-mark-recapture (CMR)**:** In the late 19th century, bird banding began to play an important role in migration studies, by monitoring uniquely marked individuals and this method continues to contribute to our knowledge on millions of migrating birds (Newton, 2008; Robinson et al., 2010). Particularly in the last few decades, an incredible effort has gone into banding large numbers of birds to gain valuable insight into population dynamics and habitat connectivity (Webster et al., 2002). This technique requires the attachment of a metal band (steel or aluminum) with a distinct alpha-numeric combination to the tarsus of the bird (Sutherland et al., 2004; Newton, 2010). The addition of distinct, tarsus-mounted colour bands or flags provides robust survival and colony attendance estimates through re-sightings within and between years (Calvo et al., 1992). Problems arise with this method in that it requires the recapture, or re-sighting of individuals under good viewing conditions, which is often a challenge. Recovery rates of marked individuals vary greatly across species, but if recovered can be a valuable and low-cost indication of demography and migratory biology (Calvo et al., 1992; Sutherland et al., 2004). Crucially for seabirds, CMR is problematic because this group by definition live far from land and from human observation for most of their annual migration cycles.

Radio telemetry (VHF)**:** In the past two decades advanced migration technology has made the study of seabird movement more attainable. The development of water-proof radio transmitters was the first of many individually attached devices that opened doors to our understanding of the movement of seabirds (Kenward, 2000; Sutherland et al., 2004). This technology, available since the 1980s is still valuable in monitoring movement over short distances, by communication between a transmitter and a receiver (Fiedler, 2009) . These light-weight radio transmitters are primarily used to interpret home range and foraging behaviour from colony sites, only transmitting at a distance of 12 – 20 km, with little precision (Bowlin et al., 2005). Such studies have produced valuable insight on seabird forage site fidelity, evidence for information transfer among populations, and relations of local tidal cycles and weather conditions on foraging activity (Irons, 1998). Radio tracking has also provided a tool for defining protected areas for seabirds, quantifying at-sea energy budgets, flight duration and relationships to commercially important prey distribution of pursuit diving seabirds (Wanless et al., 1989; Lewis et al., 2002; Adams et al., 2009). Despite limits on distance and precision, their low cost, small size and mass allow them to be attached to very small seabirds, where other devices cannot. Nevertheless, the short-range of most radio transmitter technology again is problematic for seabird studies because this group by definition live far from land and beyond the detectability range of VHF telemetry for most of their annual migration cycles.

Satellites: The use of platform transmitter terminals (PTTs) on seabirds has exploded since their introduction in 1990 (Newton, 2008). With the Argos satellite system in space, individuals can be tracked over long distances with very high location accuracy, to within a few kilometers (Shaffer et al., 2005; Burger & Shaffer, 2008). Satellite telemetry has been used on many species of seabirds, revealing valuable data on daily movements, with the capability to record multiple location fixes per day (Fiedler, 2009). These transmitters are superior in their ability to function for long periods of time, having both good battery life and solar recharging capabilities (Shaffer et al., 2005; Fiedler, 2009). They are also beneficial in that they transmit their data rather than storing it, and therefore attached transmitters do not need to be physically retrieved to obtain data. On the downside, due to the large batteries required and the antenna necessary to transmit signals over long distances, they have not been designed small or light enough to be successfully applied to many of the smaller seabirds. The most recent transmitters are 5 g and might be reasonably placed on birds as light as 300 g (Bridge et al., 2011). Additionally, the costs associated with purchasing the transmitters and recovering the satellite data are very high compared to other devices (Sutherland et al., 2004; Maxwell et al., 2011; Bridge et al., 2011). Nevertheless, satellite tags have and will continue to contribute greatly to our knowledge of highly cryptic and far ranging migrants among larger seabird species (generally > 1000 g, at the time of writing of this thesis).

Global Positioning Systems (GPS): Global Positioning Systems retrieve location from satellites, and either store or transmit the recorded data (Wilson et al., 2002; Wakefield et al., 2009). The accuracy of location fixes is unmatched by any other tracking device, with resolution of position fixes every second, within a few meters of accuracy (Wilson et al., 2002). In addition, battery life has recently been extended by the use of solar powered tags that can charge for up to 10 years with adequate light levels (Newton, 2008). These tags are also relatively inexpensive (compared to PTT devices) and small for use on some seabirds <1000 g body mass. The high degree of accuracy and resolution provides the opportunity to analyze details of ground speed, foraging behaviours, and inter-breeding movement. The limiting factors for GPS tag technology are again, primarily the size and mass of the equipment and the high costs associated with purchasing the equipment (Bridge et al., 2011). At present (2015), GPS tags are too large for deployment on small auks (<500g).

Light-based geolocation: These archival devices, 'geolocators', determine locations through the use of ambient light sensing technology by estimating length of day and timing of dusk and dawn (Phillips et al., 2004; Wakefield et al., 2009; Bridge et al., 2013). With internal calculations, latitude and longitude are recorded and stored on board the geolocator that is usually attached to a leg band. These estimates of location are quite coarse with an error of up 200 km (although in practice it may be much lower in ideal conditions), and limited memory space for only 1 or 2 position fixes per day (Phillips et al., 2004). For most compact geolocation devices, the recorded information cannot be transmitted to a remote receiving device, and thus, their use is limited by the feasibility of retrieving them (usually one year) after they have been deployed by recapture of the tagged individual (Fiedler, 2009). More recently, error estimates have been improved using on-board sea surface temperature records to increase location accuracy (Nielsen et al., 2006; Burger & Shaffer, 2008). Although geolocators do not provide the location accuracy or precision of satellite tags, they are low in mass (1 – 2 g, suitable for even small auks and storm-petrels with masses as low as 100 g or lower), compact and are capable of long battery life (sometimes > 1 year) because memory storage is not as energy consumptive as transmitting data (Phillips et al., 2004). Geolocators are also much less expensive than PTT and GPS units, while still providing reliable estimates of larger scale movements of seabirds. Growing use of geolocators has lent itself to many important discoveries in avian migration (Teo et al., 2004; Wakefield et al., 2009; Thiebot & Pinaud, 2010), making them a very effective method of tracking large numbers of small seabirds.

1.1.5 Effects of tracking devices on seabirds

Tracking the movement of seabirds has provided a new avenue for exploration into the behaviour, ecology and demography of highly-mobile, conspicuous species that was otherwise very challenging to ascertain (Calvo et al., 1992; Wilson et al., 2002; Quillfeldt et al., 2012). However, with the excitement of new ground breaking technology, concerns for scientific and ethical consequences of its application have often fallen to the wayside (Wilson et al., 2002). In the race to publish novel findings on wildlife migration, concern for animal welfare and research integrity has commonly been overlooked (Calvo et al., 1992). It has been generally accepted that tracking devices attached to seabirds should not exceed 3% of total body mass (Murray & Fuller, 2000; Sutherland et al., 2004; Vandenabeele et al., 2012), however growing evidence has shown that adverse effects of tracking devices has altered foraging behaviour, flight range and efficiency, body condition and breeding success, even within this 3% rule (Ackerman et al., 2004; Hamel et al., 2004; Navarro & González-Solís, 2007; Adams et al., 2009; Passos et al., 2010; Vandenabeele et al., 2011, 2012).

Tag effects have been found to affect the tagged individual, its mate and offspring, and effects tend to vary greatly across families of birds (Vandenabeele et al., 2012). For example, Adams et al. (2009) placed geolocators on adult Sooty Shearwaters (*Puffinus griseus*) that were only 1.4% body-mass and found a 35% reduction their chicks' body mass and skeletal size before fledging. In order to reduce overall impacts of tracking devices, attachment techniques and strategies of effective equipment attachment should be thoroughly considered to minimize detrimental effects. For example, in a study of satellite PTTs on albatross, it was found that taped wing attachment was much less encumbering than backpack attachment (Phillips et al., 2003). Additionally, to further reduce potential impacts, it is critical to limit bird handling times, particularly during the incubation period (Phillips et al., 2003). Again, although it is recommended that no attached device weigh more than 3% of individual body mass, it is evident that these guidelines are expected to vary, and should be specific to each family, and even species of bird (Casper, 2009), yet rigorous studies of many species response to tagging is lacking.

Aside from obvious ethical concerns, the use of tracking technology raises the question of the biological relevance of the data collected – a basic assumption of tracking studies (usually unstated in published papers) is that tagged individuals behave the same as untagged birds in a population. Without an understanding of how their biology is affected by an added load or added drag, data collected by individuals carrying tracking devices may not represent natural movement or behaviour of tag equipped individuals. Instead, researchers may be only observing non-representative movement or activity of handicapped individuals under the added stress of the device (Passos et al., 2010). A better understanding of the quality of data being recorded, and an emphasis on the importance of ethical practice in implementing geolocation technology is thereby critical in future migratory research. All use of devices should be therefore carefully examined and quantified on a case by case basis, before being applied more widely, and before conclusions about the biology of species' movement patterns are made.

1.1.6 Seabird distribution

Both summer and winter habitat selection, and the timing of movement between these locations have paramount implications for breeding success and survival in seabirds (Webster et al., 2002; Gunnarsson et al., 2005; Marra et al., 2006). Data collected from at-sea surveys, ground-based surveys and remote-sensing devices have made significant steps towards understanding the biology of seabirds, particularly during the non-breeding season (Burger & Shaffer, 2008; Fiedler, 2009). Year-round distribution of seabirds tends to be highly variable, corresponding to biotic and abiotic features of the marine environment that favour each species' unique ecology (Gunnarsson et al., 2005; Wakefield et al., 2009). Seabird breeding habitat has been heavily researched in most cases, since seabirds are tied to relatively accessible breeding locations on land (Springer et al., 1999). During the breeding season, selection of on-land breeding habitat favours locations with ideal nest sites, proximity to local prey resources and locations that minimize predator threat (Byrd et al., 2005; Renner et al., 2008). The key factors driving non-breeding distribution of seabirds correlates with locations that maximize access to high prey concentrations, while minimizing risk of mortality to severe weather or predation (Elphick & Hunt, 1993).

Identifying areas that are resource-rich, above all else, is essential to at-sea survival of seabirds (Hunt et al., 1993). Bathymetry, wind and ocean currents are dominant enduring physical features of the environment that play a critical role in supporting highly productive regions of the ocean (Wakefield et al., 2009). Physical processes acting on a number of dynamic biological processes, including predation, competition, nutrient mixing and primary and secondary production, contribute to the complexity of habitat selection (Elphick & Hunt, 1993; Wakefield et al., 2009).

Most seabirds can be classified into two main foraging groups: piscivores and planktivores (Vilchis et al., 2006; Wakefield et al., 2009). Piscivores are adapted to forage dominantly on larger prey items, including fish and squid, while planktivores are adapted to feed on aggregations of plankton, dominantly zooplankton (Byrd et al., 2005; Vilchis et al., 2006; Wakefield et al., 2009). These preferences have great implications for year-round distribution strategies to maximize survival and breeding success in the following reproductive cycle.

1.1.7 Focal Species: Crested Auklet (*Aethia cristatella*)

Crested Auklets, belonging to the family Alcidae, are small (mean mass of males 267 g ± 19 mass, females 253 g ± 1.0; Fraser et al. 1999) diving seabirds that are endemic to the North Pacific, Bering and Okhotsk Seas (Fraser et al., 1999; Jones & Hunter, 1999). They are one of five small planktivorous alcids, within the tribe Aethiinii, also including Cassin's Auklet (*Ptychoramphus aleuticus*), Parakeet Auklet (*Aethia psittacula*), Least Auklet (*Aethia pusilla*) and Whiskered Auklet (*Aethia pygmaea*), that range in size from 85 g (Least Auklet) to 289 g (Parakeet Auklet; Fraser et al., 1999). In order to satisfy the high energy demands associated with their inherent low flight efficiency, all species of auklet breed (and are presumed to overwinter) in oceanic regions proximate to high zooplankton concentrations, feeding primarily on macroplankton and occasionally on micronekton prey (Hunt et al., 1993).

1.1.8 Breeding biology

During the breeding season, adult Crested Auklets are distributed on remote islands or coastlines with ideal nesting habitat proximate to adequate prey resources, and minimal risk of predation (Byrd et al., 2005). Breeding colonies are dispersed at isolated islands in the western and central Aleutians, and Bering and Okhotsk Sea islands as well as the central Kurile islands and Chukotskiy peninsula (Gaston & Jones, 1998). Geographically tied to the land by their need to provision their offspring, Crested Auklets take on a central place foraging strategy, travelling as far as 110 km from the breeding site to collect food for their young (Hunt et al., 1993; Bond et al., 2011b). They breed in large mixed-species colonies, often with Least Auklets (Sowls et al., 1978), nesting within talus slopes, in subterranean crevices among piled boulders, sometimes reaching tens of metres beneath the surface (Zubakin, 1990; Jones & Hunter, 1993; Gibson & Byrd, 2007; Zubakin et al., 2010). Like other highly enigmatic, underground-dwelling seabird species, estimating population sizes of Crested Auklets is a great challenge (Byrd et al., 1983). Based on haphazard observation however, it is thought that both Crested and

Least auklets are the most abundant planktivorous seabirds in the North Pacific (Sowls et al., 1978). Rudimentary counts suggest at the very least, that there are 6 million breeding individuals of Crested Auklets worldwide (Zubakin et al., 2010).

Both male and female Crested Auklets display highly charismatic ornaments that include a significant black, forward curving crest on their forehead, white bilaterally symmetrical auricular plumes and a bright orange bill with accessory plates; all of which are most conspicuous during the breeding season (Fig. 1.1; Jones & Hunter, 1999; Jones et al., 2000). Crest size in particular, plays an important role in mutual sexual selection (both in males and females), where larger crests are favoured by mutual sexual selection (Jones & Hunter, 1993; Jones et al., 2000). This spectacularly ornamented forehead crests is thought to be a signal of mate quality, likely suggesting good health, and lack of parasites or disease (Engström et al., 2000). Crested Auklets are unique in that they emit a strong tangerine odour from their nape; an important social signal that plays an essential role in conspecific communication and perhaps mate selection (Jones & Hunter, 1999; Hagelin et al., 2003). Distinct sexual differences in behaviour and morphology, rare among other alcids, are present in Crested Auklets, although not always immediately obvious (Jones, 1993; Fraser et al., 2004). Males tend to be larger and more aggressive, having greater culmen length and bill depth, as well as a distinctly hooked bill, compared to the slightly smaller, less aggressive females that have relatively straight, triangular bills (Jones, 1993; Jones & Hunter, 1999).

Timing of Crested Auklet breeding activity varies latitudinally, but generally begins in early May, lasting until early August (Piatt et al., 1990a; Fraser et al., 1999).

Courtship behaviour takes place both at sea and on land, while copulation takes place only at sea (Hunter & Jones, 1999). Crested Auklets lay a single egg, rearing a single offspring with their monogamous partner (Hunter & Jones, 1999). Both males and females engage in parental activity, sharing roles of incubation, brooding, provisioning and defending their precocial chicks (Fig. 1.2; Fraser et al., 1999). Males, however play a larger role in defending offspring, particularly during the early brooding period (3-4 days), due to their larger and strongly hooked bill (Fraser et al., 2002). Time spent incubating the single egg until it hatches and subsequently, the time spent caring for the chick from hatch to fledge, each take approximately 35 days (Piatt et al., 1990a; Fraser et al., 1999). Chicks are brooded for 3-4 days after hatch where at least one parent is present in the crevice attending to their chick and keeping it warm until it becomes endothermic (Byrd et al., 1983; Fraser et al., 2002). Following the early brooding period, adults only occupy crevices at night or during brief, provisioning events (Fraser et al., 1999, 2002).

Crested Auklets are diurnally active and during the breeding season the majority of their time is spent at sea foraging and secondarily engaging in social activity in dense aggregations on the surface of boulders at their colony sites (Jones & Hunter, 1999). This social activity, characteristic of Crested Auklet behaviour, particularly during pre-laying and incubation periods, involves highly complex interactions with conspecifics (Zubakin et al., 2010) as well as with Least Auklets. Two distinct periods of peak social activity occur at morning and at night (Byrd et al., 1983), where large numbers of individuals aggregate simultaneously and interact through visual, vocal and olfactory displays and tactile communication (Jones & Hunter, 1993; Hagelin et al., 2003; Zubakin et al., 2010).

As highly social animals, a high degree of energy and time are invested into this charismatic behavioural activity at the colony throughout the breeding season. This activity is an important component of Crested Auklet mate selection, maintaining long term bonds between pairs, and providing learning opportunities for 'clubs' of non-breeding immature birds (one and two year-olds) as well (Zubakin, 1990; Zubakin et al., 2010). In a seabird where about one third of mates switch between years (Fraser et al., 2004), this energy-consumptive social activity is maintained throughout the breeding season, likely to establish mates for extra-pair copulations or to select preferred mates in upcoming years (Zubakin et al., 2010).

In such a long lived seabird that invests heavily into efforts to raise a single offspring, breeding success and annual survival is relatively high, although varies significantly between years, likely in response to weather conditions (Fraser et al., 1999, 2004; Kitaysky & Golubova, 2000; Bond et al., 2011a) . Crested Auklets exhibit a high degree of site fidelity to their colonies between years, and also to their densely concentrated nest sites. However, in the case of divorce, males are much more likely to retain the shared crevice due to their more dominant, aggressive nature (Zubakin, 1990; Jones et al., 2004). Following breeding activity, adults and fledglings leave their nesting crevices to begin their annual shift to a lifestyle at-sea. At this time, feather ornaments become significantly reduced and bill plates are shed (Jones et al., 2000). Studies investigating Crested Auklet moult confirm that body moult overlaps heavily with breeding activity, beginning with the shedding of primaries during early incubation, and completing the definitive moult long after the breeding cycle in mid-late November

(Bedard & Sealy, 1984). This elongated four to five month process allows energetic costs to be spread out over time, yet among auklets, Crested Auklets appeared to experience the highest degree of stress associated with their annual moult (Bedard & Sealy, 1984).

Compared to many other seabirds, Crested Auklets have a relatively high wing loading (body mass per unit wing area; Spear and Ainley 1997), resulting in limited flight efficiency, but well-adapted wing-propelled locomotion underwater; able to reach depths up to 45 m (Burger, 1991; Renner, 2006; Bond et al., 2013). Specializing primarily on zooplankton prey, Crested Auklets are low-trophic feeders, foraging mostly on euphausiids (especially of the genus *Thysanoessa)*, although copepods (particularly genus *Neocalanus*) also tend to contribute to a significant portion of their diet (Springer & Roseneau, 1985; Hunt et al., 1993; Bond et al., 2011b). It is predicted that the at-sea distribution of Crested Auklets reflects dense concentrations of their prey, where interactions between physical processes and the behaviour of their prey result in predictable aggregations of their favoured macro zooplankton where they can be foraged upon (Harrison et al., 1999).

Understanding the distribution and behaviour of prey species and their interactions with hydrological features of the environment is critical to understanding where auklets are most likely to aggregate and forage during the breeding and non-breeding seasons (Hunt et al., 1993). While larger prey items are able to swim against weak currents, most prey are not able to move against even the weakest currents, suggesting the physical oceanography of the marine environment have a strong influence of predicting zooplankton aggregations (Harrison et al., 1999). Copepods, unlike euphausiids, enter winter diapause, descending deep into the water column to conserve energy (lipid and waxy ester) reserves, beyond the expected maximum dive depth of most pursuit divers (Hagen, 1999). In turn, many seabirds rely on upwelling events to bring these prey items to the surface where they can be accessed.

1.1.9 Non-breeding biology

Considering that Crested Auklets make up such a high proportion of the abundance of seabirds in the North Pacific, it is surprising that so little is known about their non-breeding, at-sea biology (Hunt et al., 1993; Bond et al., 2011a). Similar to the even more abundant Least Auklet, knowledge of Crested Auklet winter distribution, behaviour, physiology, and ecology is severely lacking (Hunt et al., 1993). Most data concerning their at-sea distribution come from ship surveys, capture-mark-recapture studies and collection of dead specimens. General patterns of Crested Auklet at-sea aggregations in winter have been mapped and documented anecdotally, highlighting high abundance in the eastern Aleutians in large passes, as well as dense numbers further west, proximate to breeding colonies in the Sea of Okhotsk, and South of the Kuriles (Kuroda, 1955; Springer et al., 1999; Renner et al., 2008). Based on haphazard at-sea observations, it was believed that those Crested Auklets breeding in the western Aleutians likely move to productive upwelling areas in mid-sized oceanic passes in the eastern Aleutians (Renner et al., 2008; Sydeman et al., 2010; Bond et al., 2011a). While ship-based survey data provides valuable supplementary information on seabird biology, it lacks coverage and the fundamental ability to detect individual movement over spatial and temporal scales.

1.2 THESIS FRAMEWORK

1.2.1 Purpose

Tracking seabird movement is directing our understanding of seabird distribution and will provide an invaluable tool to reveal previously unknown aspects of seabird biology. Patterns of seabird movement will also assist in quantifying changes in ocean climate and productivity over time. However as the use of technology that determines year round distribution of seabirds increases, a stronger awareness of ethical and scientific integrity in migration research is necessary. The principal purpose of this thesis is to increase understanding of the distribution of a particular seabird, while evaluating practical and ethical implications of a rapidly developing technology, ultimately contributing to the improvement of conservation management practices for these highly mobile and often cryptic species.

1.2.2 Objectives

The first objective of this study, (Chapter Two) was to examine the scientific and ethical relevance of attaching light-sensing geolocators to a small, diving alcid, the Crested Auklet. In order to do this, I measured and analyzed as many biologically important components of Crested Auklet ecology and behaviour that could be affected by the attachment of tracking devices, to ensure that my geolocation data is representative of actual Crested Auklet activity in nature. The use of tracking devices in the last few decades have enabled researchers to measure the movement of many long distance migrants, however until recently, these devices were not compact enough to be deployed on small seabirds such as Crested Auklets.

Tracking devices have been applied to many related species of large and mid-sized alcids, including Common (*Uria aalge*) and Thick-billed (*Uria lomvia*) Murres, Razorbills (*Alca torda*), Cassin's Auklets (*Ptychoramphus aleuticus*), and Atlantic Puffins (*Fratercula arctica*) (Wanless et al., 1989; Hatch et al., 2000; Ackerman et al., 2004; Harris et al., 2009; Gaston et al., 2011). These studies proved valuable in revealing previously unknown aspects of at-sea movement and behaviour, however, negative effects of these devices have been detected in many cases and results must be interpreted with caution (Wanless et al., 1989; Meyers et al., 1998; Hamel et al., 2004; Paredes et al., 2005; Elliott et al., 2007; Whidden et al., 2007). Recent studies measuring movement of Dovekies *(Alle alle),* was the first to apply geolocator devices on such a small alcid, revealing exciting information on their movement and at sea ecology (Mosbech et al., 2011; Fort et al., 2013). Effects of these tracking devices on recapture rates were measured in one of these studies (Fort et al., 2013), however they were statistically insignificant, and concluded no substantial effects on body condition. As mentioned, the effects of tracking devices can be species specific and therefore an investigation into potential effects of geolocators to Crested Auklets is necessary.

The second objective (Chapter Three) was to measure and map the movement of the individuals equipped with geolocators to shed light on preliminary questions relating to their at-sea distribution and behaviour. Using advanced mapping methods, I aimed to quantify distances travelled and areas occupied during the non-breeding period and make connections between their temporal distribution and qualities of their oceanic environment. My results will build upon previous knowledge of Crested Auklet biology and test hypotheses of movement of populations originating from a particular breeding location. The final chapter (Chapter Four) summarizes my findings and places the research into a broader biological context.

1.3 STUDY AREA

Our research was conducted at Buldir, a relatively small island (2000-ha) situated in the western part of the Aleutian Archipelago (52°2 N, 175°5 E) (Byrd & Day, 1986), (Fig. 1.3). This chain of approximately 150 volcanic islands, latitudinally divides the Bering Sea to the north from the Pacific Ocean to the south (Croll et al., 2005; Gibson & Byrd, 2007). These islands extend approximately 1800 km, westward from the Alaskan Peninsula towards Russia and support 26 species of breeding seabirds (Gibson & Byrd, 2007). Comprising at least 10 million individual birds, this important marine bird habitat is managed by the Aleutian Unit of the Alaska Maritime National Wildlife Refuge (Byrd et al., 2005; Croll et al., 2005).

Buldir is the most isolated island in the Aleutians, located centrally in a 230 km oceanic pass between Kiska Island to the east and Semya Island to the west (Byrd & Day, 1986). Buldir is close to the southernmost limit of Crested Auklets’ breeding range and the most westerly breeding site of this species in the Aleutians (Sowls et al., 1978; Byrd & Day, 1986). As one of the very few Aleutian Islands that have evaded the introduction of foxes and/or rats, Buldir is a good example of a pristine Aleutian ecosystem (Byrd &

Day, 1986). In the absence of mammalian predators, and with rich food resources, it also has one of the largest and most diverse concentrations of seabirds in the Northern hemisphere, with 21 breeding species (Sowls et al., 1978; Byrd & Day, 1986). Having 12 species of breeding alcids, including all five members of the auklet tribe, Buldir arguably has the greatest diversity of breeding alcids of any seabird colony in the world (Byrd & Day, 1986).

The breeding biology of a number of birds, including an estimated 280 000 Crested Auklets at Buldir (Byrd et al., 1983, 2005; Byrd & Day, 1986), have been monitored for many years by personnel of the Alaska Maritime National Wildlife Refuge of the U.S. Fish and Wildlife. The specific study area is located at Main Talus (Fig. 1.4), a breeding site supporting more than 100,000 crested and least auklets (*Aethia pusilla*, Byrd *et al.,* 1983). Research on auklets at Main Talus, including a long term Capture-Mark-Recapture, has been conducted by Dr. Ian Jones and his colleagues in the Seabird Ecology Research Group (SERG), since 1990 and continues today.

Figure 1.1: Adult Crested Auklet banded with unique colour band identifier, standing on rocky talus at Buldir Island, Alaska.

Figure 1.2: Crested Auklet chick (5-7 days old) removed from nesting crevice for biometric measurements at Buldir Island, Alaska.

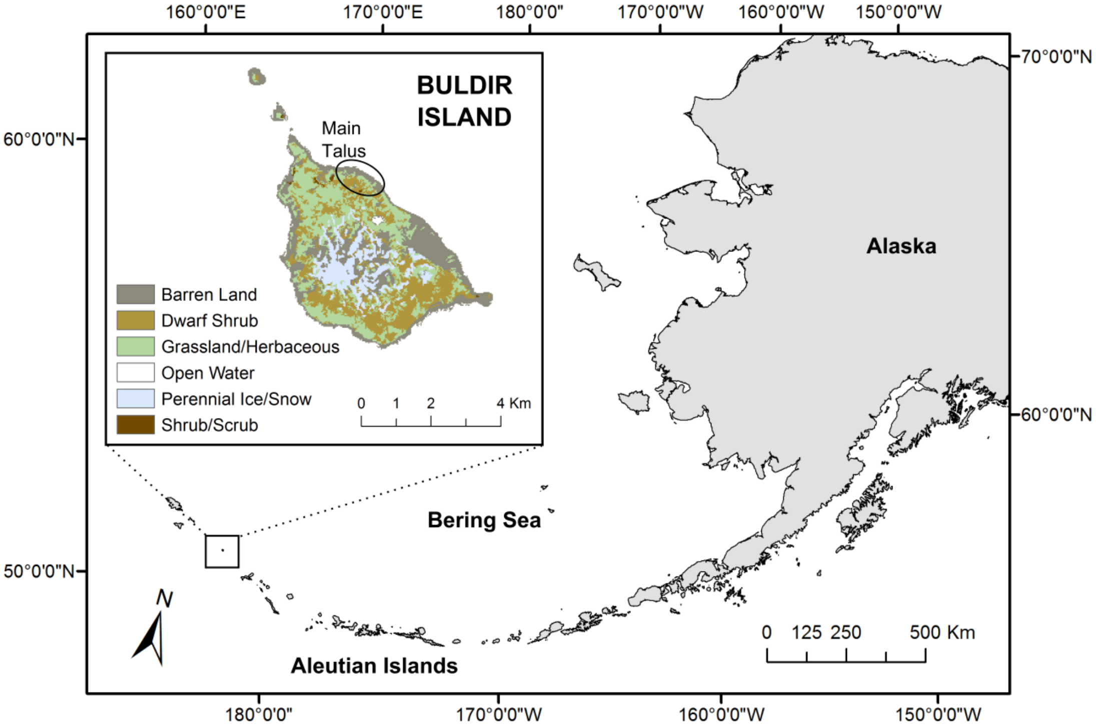

Figure 1.3: Map of Buldir Island land cover (National Land Cover Database Zone Land Cover Layer, USGS) situated in the western edge of the Aleutian Islands, Alaska. The study area is highlighted at Main Talus. Map projection: Alaska Albers Equal Area.

Figure 1.4: Breeding habitat for Crested Auklets and many other crevice nesting seabirds at the study site (Main Talus, Buldir Island, Alaska)

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CHAPTER TWO:

AN EXPERIMENTAL STUDY MEASURING THE EFFECTS OF A TARSUS-MOUNTED TRACKING DEVICE ON THE BEHAVIOUR OF A SMALL, PURSUIT-DIVING SEABIRD

Published: Robinson, J. and I.L. Jones. 2014. An experimental study of the effects of a tarsus-mounted tracking device on the behaviour of a small pursuit-diving seabird. Behaviour DOI:10.1163/1568539X-00003217

ABSTRACT

Miniaturized tracking devices are taking a rapidly increasing role in studies measuring animal movement and other aspects of behaviour, especially for wide-ranging species such as seabirds that are difficult to observe otherwise. A crucial, but questionable criterion of such migration research is assuming that effects of tracking devices on animal behaviour are negligible, to ensure results of tracking studies are biologically relevant. To address this concern, we experimentally quantified effects of a 2 g (c 1.1 % of body mass) geolocation device on crested auklet (*Aethia cristatella*) behaviour, including return rate, activity on the colony surface, and measures of reproductive performance in a two-year, two-part field study. In experiment one, we fitted tracking devices (or identical dummy devices) to one mate of a breeding pair in nesting crevices, to quantify effects on reproductive performance and nest fidelity. In experiment two, we assigned dummy devices to birds captured at the colony site surface, to quantify effects on social activity, return rate and provisioning behaviour. For birds tagged in crevices, we detected no effect on fledging success, or chick growth rate (mass and wing length). However mass at fledging age of chicks provisioned with one tagged parent was significantly lower than control, and nest site fidelity was lower in tagged birds than control birds. Individuals tagged on the colony surface showed significantly reduced colony surface activity, return rates and provisioning behaviour. This study shows strong ‘Observer Effects’ of an attached device well below the recommended maximum size limit for wildlife tagging. Future studies should both quantify effects of attached devices and consider the biological relevance of measures of the behaviour of interest.

2.1 INTRODUCTION

Tracking studies have greatly advanced our knowledge and understanding of the fundamental biology of many animals, lending itself to useful applications in wildlife management and conservation biology (Burger & Shaffer, 2008; Casper, 2009; Robinson et al., 2010; Maxwell et al., 2011). Insight into animal behaviour, ecology, and physiology have taken leaps forward with the use of geographical positioning devices, furthering our understanding of foraging and social behaviour, habitat range, and resource selection of many wide-ranging animals (Murray & Fuller, 2000; Wilson & McMahon, 2006; Recio et al., 2011; Le Corre et al., 2012). Tracking studies investigating animal movement across diverse taxa often ignore potential risk of ‘Observer Effect’, failing to acknowledge implications of device-attachment on species welfare and merit of research (Mellas & Haynes, 1985; Wilson & McMahon, 2006). An Observer Effect is the change in behaviour of the subject as a consequence of the observer’s presence (Sykes, 1978). The ‘Biological Uncertainty Principle’ refers to the disturbance caused by the investigator attempting to measure or observe normal behaviour of wildlife because, there is no way of knowing the behaviour without observing it (Mayfield, 1975; Mayer-Gross et al., 1997). However, tracking studies rely on the assumption that tracking devices used to measure movement do not significantly alter natural behaviour of tagged individuals in order to effectively extrapolate data to the larger, unmarked population (Murray & Fuller, 2000; Casper, 2009; Constantini & Moller, 2013).

With the development of increasingly light-weight, cost-effective tracking devices, birds have received growing attention in recent migration research (Casper, 2009). This has opened exciting avenues to understanding previously unknown avian foraging, social and breeding behaviour, migration routes, and year-round temporal and spatial distribution (Lisovski et al., 2012; Bouten et al., 2013). While many (c.80%) of avian migration studies acknowledge potential for device effect (Barron et al., 2010), few provide comprehensive experimental studies to detect it. Many experiments are poorly designed, with weak sample size, logistical constraints on duration of study, lack of appropriate control and haphazard qualitative observation (Calvo et al., 1992). This critically limits the statistical strength with which to make confident conclusions and recommendations for future device application (White & Garrott, 1990; Murray & Fuller, 2000).

Externally-mounted devices fitted to birds directly increases overall mass, aerodynamic drag, hydrodynamic drag, and in many cases, alters the balance of marked individuals (Adams et al., 2009; Vandenabeele et al., 2011). These direct changes to impacted birds translates to effects on behaviour and ecology of individuals to varying degrees, primarily influencing energy expenditures and likelihood of nesting the year following device deployment (Barron et al., 2010; Vandenabeele et al., 2012). To mitigate tag effect on birds, researchers have adhered to a rule that no tag deployed should exceed 5%, and more recently 3% of individual body mass (Phillips et al., 2003), however reasoning behind this rule is unclear and significant effects have been documented even within this set of constraints (Phillips et al., 2003; Adams et al., 2009; Vandenabeele et al., 2012; Bridge et al., 2013). Additionally, this rule does not account for potential impacts of drag induced by cross-sectional area of the tags, found to significantly reduce flight range in a number of tagged individuals (Barron et al., 2010; Bridge et al., 2013). Forming generalized guidelines for tag deployment is clearly problematic as adverse device effects are specific to attachment methods, species, age, sex, and environment. Moreover, authors may only focus on particular behavioural activities with varying degrees of biological importance and many less obvious device effects may go unnoticed (Murray & Fuller, 2000; Casper, 2009; Vandenabeele et al., 2012; Bridge et al., 2013). Taken together, studies of varying tag effect cast doubt on the biological relevance of many studies, as tagged individuals were likely not behaving normally.

Seabirds are a popular subject for tag-enabled migration tracking, as they are highly mobile and tend to inhabit remote areas, far from direct land observation for the majority of the year (Vandenabeele, Wilson, & Grogan 2011). Few tracking devices have been applied to the family of long-lived, highly monogamous seabirds, the auks (*Alcidae*). Auks, while generally small in size, have a high body mass to wing area ratio , i.e., high wing loading, limiting their load bearing capacity (Ackerman et al., 2004). This morphology allows them to be efficient underwater pursuit-divers, however they consequently have an energetically expensive mode of continuous flapping flight (Ackerman et al., 2004; Whidden et al., 2007). Most auklets (Aethiini), a tribe within the auks, nest in crevices below the surface of talus slopes, producing a single offspring annually and exhibit bi-parental care during a lengthy breeding season (c. 35 days incubation, 35 days chick rearing) (Fraser et al., 1999). Both parents invest heavily in rearing their young, sharing roles of incubation, brooding and provisioning; although brooding and defense of the nest site are often dominated by males (Fraser et al., 1999, 2002). Daily aggregations at the surface of the colony and large swarming behaviours play a critical role in breeding and social behaviour of the smaller auks, particularly in crested auklets (*Aethia cristatella*) (Zubakin et al., 2010). This investment of time and energy in conspecific interaction at the surface of the colony site, including complex visual, acoustic and olfactory displays among breeders and non-breeders is associated with courtship activity, establishment of social hierarchies, and habitat familiarization (Klenova et al., 2011). The unique ecology, physiology and social behaviour of auks suggests that they may be particularly vulnerable to adverse effects of additional mass and drag imposed by a tracking device (Ackerman et al., 2004; Paredes et al., 2005; Whidden et al., 2007, Elliot et al., 2013).

The objective of my study was to rigorously quantify the behavioural effects of tarsus-mounted devices (well within the 3% body mass recommendation) on a small, pursuit diving auk, the crested auklet, through two distinct experiments. The aim of experiment one was to quantify reproductive performance, nest site fidelity and body condition of individuals fitted with a device from nesting crevices (the null hypothesis being no tag effect on these aspects of biology). The aim of experiment two was to measure return rates, frequency of activity on the colony site surface and provisioning behaviour of tagged individuals captured at the surface of the colony (again, the null hypothesis being no tag effect). From these experiments, I inferred mitigation measures for deploying tracking devices in order to maintain ethical practice and biological relevance of research.

2.2 METHODS

2.2.1 Study area

My research was conducted at Buldir Island (52º11 N, 175º56 E), situated in the western range of the Aleutian chain of Alaska (Sowls *et al.* 1978, Byrd & Day, 1986). The study area is located at Main Talus, a breeding site supporting more than 100,000 crested and least auklets (*Aethia pusilla*, Byrd *et al.,* 1983). Over 200 crested auklet crevices are accessible to investigators at Main Talus, most of which have been previously monitored for breeding biology studies. An observation blind, constructed on Main Talus, overlooks the research plot where individual banding and re-sighting has been conducted from 1990 until present.

2.2.2 Experiment One: device effects on birds captured in nesting crevices

2.2.2.1 Device attachment

To assess the behavioural effects of archival light-sensing geolocation devices (herein referred to as tags or devices) on crested auklets, I quantified the breeding performance of tagged (fitted with a geolocator) and untagged (no geolocator) individuals captured from nesting crevices located throughout the study area at Main Talus. During the early brooding period (0-4 days after hatch; Knudtson et al., 1982), one pair member only was removed from crevices for tag deployment. This deployment timing was critical to ensure the presence of either mate and reduce the risk of early nest abandonment due to crevice disturbance (Piatt et al., 1990a; Whidden et al., 2007). In summer 2011, I deployed 31 LAT 2900 geolocator tags (Fig. 2.1; 8 x 15 x 7 mm, 1.9 g, LOTEK, St. John’s, Newfoundland) to breeding individuals (21 males, 10 females). I also deployed LAT 2900 dummy tags, manufactured by LOTEK, identical in size and mass to LAT 2900 geolocator tags but without internal electronics to 14 individuals (9 males, 5 females). In summer 2012, we deployed LAT 2900 dummy tags to 19 previously unmarked individuals (8 males, 11 females). Dummy tags were deployed to increase sample size of the tagged bird population, in order to compare to birds in a control group.

Banding effort was covered by Animal Care protocols 11-01-IJ and 12-01-IJ from the Institutional Animal Care Committee of Memorial University.

Using light green Darvic colour bands with a single cable-tie, I secured the tags onto the right tarsus above a single numbered aluminum USFWS band. The combined mass of the tag, aluminum band, and cable tie was 2.93 + 0.12 g, *N* = 31; 1.1 % of the mean body mass of all tagged individuals. At capture I determined sex by bill depth and shape (Jones 1993) and recorded biometric measurements of relative body size (mass, wing, tarsus, culmen length, and bill depth) and feather ornament size (crest, auricular plume and rectal plate length; Jones 2004). Mass was measured to the nearest 1 g using a 300g Pesola® spring scale, and linear measurements were recorded to the nearest 0.1 mm using Vernier calipers. Average individual handling time for tag attachment was limited to 7:11 + 0:14 min, *N* = 45, before returning the adult to its chick in the nesting crevice. Untagged pair members were left undisturbed.

2.2.2.2 Fledging success and chick growth

In order to assess the effect of fitting one pair member with a device on reproductive performance of a breeding pair, I measured productivity at the study crevices comparing three levels of disturbance: i) highly disturbed (one member per pair tagged and chick handled, ii) partially disturbed (adults untagged and chick handled), and iii) undisturbed (adults untagged and chick unhandled). In 2011, I monitored 45 disturbed crevices (31 geolocator tags + 14 dummy tags), 26 partially disturbed and 73 undisturbed crevices (Table 2.1). In 2012, I monitored 18 disturbed crevices (all dummy tags), 17 partially disturbed, and 79 undisturbed crevices. After tag deployment, crevices were examined every 4-5 days using a small light to determine fledging success. Chick age was determined using the mean date between an observed egg and a chick occurrence in consecutive crevice checks (± 2 days) and was known more precisely (±1 day) in cases when the chick was observed hatching or piping. Chicks were excluded from analysis if hatch date uncertainty was greater than ±3 days. Fledging success was calculated as the percentage of known crevices where the chick reached fledging age (≥ 26 days after hatch). Differences in fledging success were compared across disturbance levels, testing for sex-specific effects in all groups using Chi-Square and Fisher's Exact tests.

To detect device effect on chick quality, I measured both mass and wing length of chicks removed from crevices in control group (untagged parent) and a disturbed group (single parent tagged) every 3-4 days. In 2011, I recorded a single measurement of mass and wing length for each chick, dispersed across varying ages. Comparisons among age cohorts were conducted using ANOVAs assessing mass and wing chord in control and tagged groups. In 2012, I measured chicks every 3-4 days, during the linear growth phase (6 - 24 days after hatch; Fraser et al. 1999), taking 5 measurements of mass and wing chord for each chick in control and tagged groups. An ANCOVA was conducted to compare rate of growth (mass and wing length) across disturbance levels. Fledgling mass and fledgling wing length were determined to be the last measurement recorded prior to chick fledging, including only measurements of chicks that reached fledging age (26 days) and were compared between disturbance groups.

2.2.2.3 Nest site fidelity and body condition

In order to test for a tag effect on nest site fidelity, I re-checked all 31 crevices in 2012 from which an individual had been tagged in 2011. When an attached tag was observed during a re-check, the individual was recaptured, the tag detached and biometric measurements again taken. Tag recovery rate, representing the degree of nest site fidelity for 2011-2012 was compared to a control group from a long-term data set (1993-2000) of breeding Crested Auklets captured from crevices, banded and re-captured in the following year. I tested for sex-specific effects, and tag year effect within the control data and tested for significant differences in nest site fidelity between the control group (1993-2000) and the tagged group (2011-2012), using Chi-square and Fisher's exact tests. I also compared parameters of body condition between returning birds against that of non-returning birds in 2011-2012, using the biometric measurements taken at time of tag deployment. To detect any device effect on body condition of individuals that did return the year following tag deployment, I compared biometric measurements of body and ornament size between 2011 (prior to tag attachment) and 2012 (taken at recovery), using paired student t-tests. Recaptured individuals were also examined for direct physical injuries attributable to the tag on their right tarsus.

2.2.3 Experiment Two: Device effects on birds captured on the colony surface

2.2.3.1 Device attachment

In order to evaluate device effects on social behaviour of Crested Auklets on the colony site surface and further quantify return rates of tagged individuals, I simultaneously conducted a second tag effect experiment in both years. This experiment was conducted at a single study plot, occupied by an estimated 1000 Crested Auklet breeding pairs (Jones et al. 2004), where c. 1200 Crested Auklets have been colour banded for capture-mark-resight studies since 1990. From June 6 – July 30, 2011, 167 Crested Auklets were trapped on the surface of the 100 m^2 marked plot using noose carpets. Breeding individuals ($N = 94$) identified by the presence of a full brood patch (Jones et al. 2000), were selected for the experiment and alternately assigned to a control or dummy tagged group. The 48 experimental group birds had the same LAT 2900 dummy tags cable-tied to a Darvic plastic colour band and the USFWS aluminum band as described in experiment one (except dummy tag was attached on left tarsus and a unique 2-colour Darvic band combination attached on the right tarsus; contributing an additional 0.2 g), for individual identification. The control group (46 individuals) received a stainless steel band, as well as a unique 3-colour Darvic band identifier as previously used at the study plot (Jones et al. 2004). All banded birds were sexed and measured (Jones et al. 2000), and released back to the colony site.

2.2.3.2 Surface activity

Daily re-sighting of banded birds was conducted throughout the 2011 breeding season (May 31 – August 2), and repeated in 2012, (May 26 – August 3) from the observation blind for 4-6 hours every day during the morning surface activity period (1000-1400 h) and a brief period of activity at night (2230-0030 h). To assess behavioural effects of tags on daily surface activity at the colony, I calculated individual resight frequency across control and tagged groups, from tallied observations of experimental individuals each day. Daily resight frequency was calculated for each group (control and tagged) as: number of individuals observed in a day / total number of individuals in the group. In 2011, this total increased throughout the season as I added to the banded population. To graphically illustrate this data, I calculated daily resight ratios as: resight frequency of control group / resight frequency of tagged group. To account for temporal differences in surface activity caused by breeding activity, I compared observation frequency in tagged and control groups before and after the mean hatch date, using Wilcoxon Signed Rank test for paired observations.

2.2.3.3 Return rate and provisioning behaviour

We examined the return rates of tagged (disturbed) and control (undisturbed) birds in 2011 and 2012, accounting for sex specific differences using Chi-square and Fisher's Exact test. For historical context, I compiled a control dataset for return rate from banded resights in 1992-2011. Including only adult, breeding Crested Auklets (with full brood patches), I measured the proportion of birds captured at the plot and seen the following year, testing for tag effect, year effect and sex-specific effects using Chi-square and Fisher's exact tests. Provisioning behaviour was compared across tagged and untagged individuals in 2012, recorded as the number of individuals observed carrying food to their young, identified by an enlarged throat (proventriculus) pouch. I also tested for the effect of individual mass on colony behaviour, as quantified by resight frequency of individuals that returned in 2012, to detect any variability in tag effect with increasing relative tag to body mass. In both 2011 and 2012, daily observations were made at the study plot to assess any direct physical effects of the dummy tags and potential indirect impacts on behaviour of birds interacting at the surface of the colony. I looked for abnormalities in social behaviour, or evidence of impeded walking or flight in dummy-tagged Crested Auklets. All analyses were computed using R software (R Development Core Team 2012), and all values are presented as means + SE.

2.3 RESULTS

2.3.1 Experiment One: Device effects on birds captured in nesting crevices

2.3.1.1 Fledging success and chick growth

Fledging success in both years was not significantly different across levels of disturbance. In 2011, fledging success was 79% from tagged crevices ($N = 42$; 3 crevices were excluded due to poor hatch date accuracy), 81% from partially disturbed crevices ($N = 26$) and 81% in undisturbed crevices ($N = 73$; Chi-square test: $X^2_2 = 0.093$, $P = 0.95$). In 2012, fledging success was 94% in tagged crevices ($N = 18$, 1 crevice excluded due to hatch date accuracy), 88% from partially disturbed crevices ($N = 17$) and 90% in undisturbed crevices ($N = 79$) (Fisher's Exact, $P = 0.89$). Fledging success did not differ significantly according to the sex of the tagged pair member (2011: $X^2_2 = 2.24$, $P = 0.130$; 2012: $X^2_2 = 0.05$, $P = 0.810$). Fledging success in crevices where tagged individuals were recaptured and geolocator tags were successfully removed one year after deployment, was also not significantly different from other groups ($X^2_2 = 0.04$, $P = 0.98$). Sex-related differences in fledging success at 'tag-recovered' crevices could not be detected as only one tagged female was recovered.

In evaluating chick quality, I found that in 2011, there was no significant difference between mean mass (ANOVA: $F_{2,71} = 1.39$, $P = 0.243$), or wing length (ANOVA: $F_{2,71} = 1.19$, $P = 327$) of each age cohort of chicks, comparing control and tagged groups. In 2012 rates of growth for mass and wing chord were also not significantly different between control and tagged groups (ANCOVA (mass): $F_{2,158} = 0.50$, $P = 0.480$, (wing): $F_{2,161} = 0.208$, $P = 0.650$). However, I did determine that slope intercepts were significantly different for mass and wing length between tagged and control groups (mass: $F_{1,159} = 23.04$, $P < 0.0001$, wing: $F_{1,162} = 16.84$, $P < 0.0001$, Fig 2.2). Additionally, significant difference in fledgling mass (Welches t-test: $t = -2.27$, $df = 28.9$, $P = 0.031$), but not wing length, (Welches t-test: $t = -0.62$, $df = 30$, $P = 0.538$) was detected. Mass of chicks in the tagged group (213.8 + 7.6g, $N = 17$), was considerably (12%) lower than chicks in the control group (242.2 +7.8 g, $N = 16$; Fig 2.3).

2.3.1.2 Nest site fidelity and body condition

Of the 31 geolocator tags deployed in crevices in 2011, 10 were recovered in 2012 (32% recovery). All tags were recovered from their original crevice, with the exception of one individual recaptured near a neighbouring crevice, and all tags detected visually were recovered. Control data of nest fidelity in untagged birds, compiled from 1993-2000, revealed no effect of year ($X^2_5 = 5.31$, $P = 0.379$), allowing us to make between-year comparisons. I did detect a significant effect of sex on probability of untagged individuals returning between years ($X^2_5 = 4.57$, $P = 0.033$) with males showing 16% greater nest site fidelity compared to females. Treating sexes independently, return rate in tagged males (43%, $N = 21$) was significantly lower than in untagged males (92%, $N = 51$; Fisher's Exact, $P < 0.0001$). Return rate in females was significantly reduced from 76% ($N = 47$) in the untagged group, to 10% ($N = 10$) in the tagged group (Fisher's Exact, $P < 0.0001$; Fig 2.4). The difference in nest fidelity between tagged male and females was not statistically significant (Fisher's Exact, $P = 0.106$).

Upon recapture of tagged individuals, no physical evidence of tag damage was observed and no significant difference in body condition of tagged individual biometric measurements between 2011 and 2012 was detected ($P > 0.05$). In testing for differences in body condition between returning and non-returning tagged individuals from 2011-2012, I found returning individuals had slightly greater body size (mass, tarsus, wing, bill depth, culmen, rectal plate) and ornament size (crest length, average auricular plume length), however for all biometric parameters, this difference was not significant ($P > 0.05$).

2.3.2 Experiment Two: Device effects on birds captured on the colony surface

2.3.2.1 Surface activity

Surface activity throughout the breeding season, based on daily resight frequency of individuals banded and resighted in 2011, was significantly reduced in tagged individuals (0.107 + 0.090 daily resights/individual) compared to control individuals (0.188 + 0.149 daily resights/individual; Wilcoxon signed-rank test: $V = 81$, $N = 35$, $P =$

0.0001), particularly after mean hatch (June 28 + 7.7 days; Wilcoxon signed-rank test: V = 51, N = 35, P = 0.003). Similarly throughout the breeding season in 2012, surface activity of individuals banded in 2011 was also significantly reduced in the tagged group (0.078 + 0.052 daily resights/individual) compared to control (0.173 + 0.133 daily resights/individual; Wilcoxon signed-rank test: V = 319, N = 77, P < 0.0001). However, prior to mean hatch date (June 29 + 5.5 days), there was no difference in surface activity of returning birds (Wilcoxon signed-rank test: V = 232, N = 33, P = 0.391). Only after mean hatch was a distinct divergence of surface activity detected, with far more daily re-sightings of individuals from the control group (0.248 + 0.147 daily resights/ individual) compared to tagged individuals (0.081 + 0.060 daily resights/individual; Wilcoxon signed-rank test: V = 9, N = 67, P = 0.0004, Fig.2.5(a)).

2.3.2.2 Likelihood of return and provisioning behaviour

In 2011, there was a significant difference between tagged and control birds returning to the surface of the colony within the same year of tag deployment: 85% of control individuals (N = 46) were seen again, while only 56% of tagged individuals (N = 46) were seen again (Fisher's Exact, P = 0.010), with no difference between sexes (G squared: $G^2_1 = 3.0$, P= 0.080). In 2012, the proportion of returning individuals the year after tag deployment was again significantly greater in the control group (87%, N = 46), compared to the tagged group (46%, N = 46, Fisher's Exact = 0.0001). Additionally, the proportion of individuals observed to exhibit chick provisioning behaviour in 2012 was much greater in the control group (82%, N = 39) than in the tagged group (36%, N = 22; $X^2_2 = 11.1$, P = 0.001). I also found that there was no linear relationship between return rate in 2012 and relative tag mass (mean 0.99% - 1.4% body mass) for each individuals ($F_{1,19} = 0.366$, $P = 0.55$).

Incorporating archival data of breeding individuals banded and colour-marked (1993-2011), 81% (N=365) of individuals were seen the year following banding, with no effect of year on return likelihood (Chi-Square: $X^2_5 = 5.3$, $P = 0.379$). Sex-specific effects were detected however, with males 9% more likely to return between years than females ($X^2_1 = 4.16$, $P = 0.041$). Treating sex separately and pooling archival control data with the 2012 control data, the proportion of males tagged with geolocators in 2011 and seen again in 2012 (30%, $N = 23$) was significantly lower than the 85% ($N = 201$) of returning males in the pooled control dataset (1993-2012; Fisher's Exact, $P < 0.0001$). The proportion of tagged females returning between years (39%, $N = 23$) was also significantly lower than the 79% ($N = 208$) of returning females from the long term dataset (1993-2012; Fisher's Exact, $P = 0.0002$).

2.3.2.3 Anecdotal observation

No birds were observed with any leg injuries attributable to LAT 2900 archival geolocator tag or dummy tag attachment. Birds carrying tarsus-mounted geolocator or dummy tags appeared to move normally.

2.4 DISCUSSION

The fundamental limitation on behavioural biology is that while attempting to describe or measure any natural behavioural activity, an observer effect is always present

(Wilson et al., 1986; Wilson & McMahon, 2006). Animal tracking studies impose added stress on tagged individuals outside of natural conditions, inflicted by not only the device itself, but also by associated handling and attachment procedures (Murray & Fuller, 2000; Casper, 2009). Carefully designed experiments that monitor and control for tag effect are critical in maintaining animal welfare and in improving validity of migration research (Wilson & McMahon, 2006). However, with the rapidly increasing number of animal tracking studies conducted in recent years, the number of corresponding device effect studies has not increased similarly (Vandenabeele et al., 2011). Strict standards upheld in all other scientific fields to insure biological merit through structured experimental design seem to have been dissolved in the thrill of this booming, new technology, at least as applied to marine birds (Ropert-Coudert & Wilson, 2005).

Previous to recent miniaturization of tracking devices, most alcids have been too small to track, and were considered particularly vulnerable to adverse effects due to high metabolic rate necessary to sustain energetically expensive flapping flight and diving behaviour (Ackerman et al., 2004; Burger & Shaffer, 2008). One prior study that attached radio transmitters to adult Crested Auklets concluded that there were no adverse effects on tagged individuals' behaviour or provisioning rates (Fraser et al., 2002). This in-depth study, however indicated that while some aspects of Crested Auklet reproductive performance appeared to be unaffected by geolocator tags, fundamental aspects of their behavioural activity at the surface of the colony and their at-sea survival have been critically changed. This intensive, two year study thoroughly examined these effects using sufficient sample size and appropriate controls to make effective inferences from the results.

2.4.1 Reproductive performance

The degree in which chicks are provisioned by their parents has important implications for chick growth, fledgling mass and fledging success, providing valuable predictors of the chick's subsequent survival to recruitment (Williams & Croxall, 1990; Golet et al., 2000; Whidden et al., 2007; Adams et al., 2009). In a monogamous seabird that exhibits shared provisioning of a single offspring (Fraser et al. 2002), the quality of the chick reflects the combined ability of both adults to sufficiently provide for their offspring (Golet et al. 2000). Provisioning is very energetically costly for heavy wing-loaded Crested Auklet, requiring parents to travel from the breeding site (50 – 110 km; (Hunt et al., 1993)), locate at-sea prey aggregations, engage in underwater pursuit foraging, and return back to the nest site carrying a large food load. We would then expect that in a long-lived seabird, with a life-history strategy favouring long-term preservation of the individual over that of a single reproductive season (Navarro & González-Solís, 2007), increased stress induced by carrying a tracking device, would be reflected in reduced fledging success or poor chick quality. However, in experiment one, fledging success and rate of chick growth (mass and wing) were not significantly affected. I did however detect a slight, but significant reduction of chick mass at fledging age in the tagged group. While the body condition of fledging chicks was marginally reduced in the tagged group, sufficient provisioning allowed for equally successful fledging rates of chicks in both control and tagged birds.

2.4.2 Mate compensatory behaviour

We believe that the most likely explanation for the observed behavioural effects of tracking devices on Crested Auklets was mate compensation. This behaviour, observed in other mid-sized alcids, occurs when the untagged individual in the pair compensates for reduced parental quality of their mate (Hamel et al., 2004; Paredes et al., 2005). In a long-lived seabird, maintaining a long-term monogamous relationship is beneficial in synchronizing parental activities, and minimizing energy allocated for courtship and mating activity (Paredes et al., 2005). It is therefore advantageous to engage in compensatory behaviour in order to benefit from increased lifetime reproductive success. As seen in Thick-Billed Murres, the untagged mate likely increased parental investment above its normal limits to cover for the mate's deficiency, and successfully reared the single young to fledging age (Paredes et al., 2005). Similarly, in a study of Common Murres equipped with subcutaneous radio transmitters (<1%), reduced provisioning rates were detected in tagged individuals, making fewer and lengthier foraging trips, but breeding success was unaffected (Hamel et al., 2004) This indicates a level of flexibility in time-budgeting and foraging roles, allowing individuals to survive in an unpredictable, variable environment (Hamel et al., 2004; Paredes et al., 2005). In a good food year, when prey is more readily available, this behavioural flexibility may accommodate tag effect (Hamel et al., 2004), without having detrimental reproductive consequences. However, negative effects on breeding success may emerge in poor food years, when increased effort by the untagged mate to ensure adequate nestling provisioning can no longer be sustained (Abraham & Sydeman, 2004).

These findings are somewhat inconsistent with other tag effect studies on ecologically similar auks that appear to be unable to engage in compensatory behaviour at the cost of their young. In a study of Cassin's Auklets (*Ptychoramphus aleuticus*) effects of subcutaneous radio transmitters (<2% body mass) were detected in reduced chick growth, also impacting fledging success, and clutch size of offspring in tagged individuals (Ackerman et al., 2004). Detrimental effects on breeding success were observed in Tufted Puffins (*Fratercula cirrhata*), equipped with radio transmitters (<1.2% body mass) (Whidden et al., 2007), Common (*Uria aalge*) and Thick-billed Murres (*U. lomvia*) fitted with satellite transmitters (Meyers et al., 1998) and Common Murres and Razorbills (*Alca torda*) fitted with radio transmitters (Wanless et al., 1989).

2.4.3 Nest site fidelity

Nest site fidelity, measured one year after device deployment was greatly reduced in tagged individuals. This failure of tagged individuals to return to previously occupied nest sites between years is likely a result of mate death or divorce, conspecific nest site competition, predation during the breeding season, or over-winter mortality. Divorce in a monogamous seabird engaged in bi-parental care is much more likely to occur if there is a reproductive failure or if one pair member shows poor quality as a parent (Paredes et al., 2005). Increased stress on tagged individuals may also reduce their ability to defend good quality nest sites, or may increase susceptibility to predation (Wilson & McMahon, 2006; Whidden et al., 2007; Rodri-guez et al., 2009). In Crested Auklets, predation at sea is thought to be marginal, however, during the breeding season Glaucous-winged Gulls (*Larus glaucescens),* Bald Eagles (*Haliaeetus leucocephalus*) and Peregrine Falcons

(*Falco peregrinus*) can present significant threat to their survival (Knudtson & Byrd, 1982) and may take advantage of reduced flight maneuverability or speed of load-carrying individuals (Aldridge & Brigham, 1988). An increased prevalence of divorce, crevice loss or predation during the breeding season in tagged individuals would partially explain the observed decrease in nest site fidelity, caused by reduced parental quality, and decreased ability to avoid predation. However, the results show that not only do fewer tagged individuals return to the same crevice, but the number of individuals returning to the colony surface is also greatly reduced, suggesting that the effects of carrying a tag for a long period of time likely impacts over-winter survival the most.

2.4.4 Return rates

The mechanism responsible for low return rates to the colony in tagged individuals between years was not entirely clear, but likely resulted from lower over-winter survival rate of tagged individuals. In Auks, adapted to underwater pursuit-diving and poorly adapted to long distance flight, one would presume that additional mass, aerodynamic and hydrodynamic drag would have compounding effects on migration and foraging ability (Wanless et al., 1989; Hamel et al., 2004). Reduced swimming and foraging efficiency caused by increased drag of tags has been recorded in a variety of marine wildlife, including Chinstrap (*Pygoscelis Antarctica;* Croll et al. 1991), Adelie (*P. adeliae*; Ballard et al. 2001) and African Penguins (*Spheniscus demersus;* Wilson et al. 1986), Atlantic Salmon (*Salmo salar*) smolts (Moore et al., 1990), Rainbow Trout (*S. gairdneri*) and White Perch (*Morone Americana*; Mellas & Haynes 1985), juvenile Green Turtles (*Chelonia mydas;* Watson & Granger 1998) and Leatherback Turtles

(*Dermochelys coriacea;* Fossette et al. 2008) and Antarctic Fur Seals (*Arctocephalus gazella*; Walker & Boveng 1995). In a study assessing the effect of increased drag and buoyancy on the diving behaviour of Thick-billed Murres, significant reduction in dive depth and duration was detected (Elliott et al., 2007). Increased aerodynamic drag caused by tags has led to reduced flight ranges in a number of long distance migrating birds (Phillips et al., 2003; Bowlin et al., 2010; Vandenabeele et al., 2012), which may also translate to devastating over-winter effects in highly mobile species.

Locating and accessing available prey items, and avoiding severe weather conditions is paramount to overwinter survival in seabirds (Byrd et al., 2005; Renner et al., 2008). In a species already limited by poor flight efficiency, highly productive wintering areas that tend to be patchily distributed may be too dispersed for individuals carrying additional mass to travel (Jessopp et al., 2013). Impacts of severe winter storms may be much more devastating in individuals already stressed by carrying additional mass and drag as well. This has particular implications in a changing oceanic climate with increasing environmental variability causing yearly fluctuations in prey availability and distribution, and increased prevalence of storm events (Schumacher & Kruse, 2005). Reduced swimming and flight efficiency associated with carrying a tag engenders high energetic costs over time, likely responsible for the steep drop in return rates detected in tagged Crested Auklets (Fig 2.5(b)). With such severe device impacts on overwinter survival, it was surprising that chick quality and fledgling success during the breeding season were little affected; however this phenomenon is likely explained by mate compensatory behaviour.

2.4.5 Activity at the colony site surface

In a highly social and ornamented bird, daily aggregation at the colony is a fundamental component of crested auklet behaviour, important in courtship activity, establishment of social hierarchies, and habitat familiarization (Hagelin *et al.*, 2003; Jones & Hunter, 1999). Significant reduction of daily activity in tagged individuals at the colony therefore suggests a biologically significant impact on social and breeding behaviour. Tagged individuals had the greatest reduction of surface activity after mean hatch date during the chick provisioning period (Fig. 2.6). This decrease is likely due to reduced frequency of chick provisioning, extended duration of foraging trips and increased foraging range of tagged individuals, as seen in penguins and shearwaters (Wilson et al., 1986; Ballard et al., 2001; Navarro & González-Solís, 2007; Passos et al., 2010). These effects were not only observed in the same year of device attachment, but also in the following year. This suggests that tagged individuals are not quickly adapting to the presence of the tag as documented with Cory's Shearwaters (Igual et al., 2004), and even after carrying the device for a year, individuals were clearly experiencing long-term effects, as seen in King Penguins (Le Maho et al., 2011). This is likely explained by differences in foraging guilds, as both penguins and alcids rely on underwater pursuit diving strategies, compared to surface feeding shearwaters that have high flight efficiency.

2.4.6 Implications for future tracking research

Based on inferences from return rates and behavioural observations at the breeding colony, I can speculate on how tracking devices affect individuals at sea, but I have not measured it directly. To accurately determine the biological relevance of migration data collected from tagged individuals, I need to know the effects of tracking devices on the behavioural measures I are trying to obtain (i.e., movement patterns, seasonal distribution) rather than just the effects as far as I can measure it at breeding sites. Additionally, designing experiments to quantify at-sea device effects by controlling for mass and drag could provide useful insights on the flexibility of migration strategies in seabirds. Under a changing climate, evidence has shown that migratory behaviour may be significantly affected, altering routes, destinations and movement phenology (Jenni & Kéry, 2003; Frederiksen et al., 2004; Marra et al., 2004; Dias et al., 2011). Migratory plasticity, illustrating the degree at which species can adapt sufficiently in a changing environment, has only been studied in a few marine vertebrates (sharks, turtles, whales and seabirds), but would have important applications for wildlife management and conservation efforts for seabirds living in a variable environment (Burger & Shaffer, 2008).

Currently, many studies measuring animal movement continue to push limitations of the ethical and meaningful use of tracking devices. Hard and fast rules, maintaining 3-5% tag mass threshold, and 1% tag cross-sectional area threshold for device attachment (Vandenabeele et al., 2012) are problematic because they do not recognize species-specific responses to tagging associated with differences in behaviour, ecology, physiology, and sensitivity to disturbance and environmental variability (Adams et al., 2009; Casper, 2009; Bridge et al., 2013). The 3-5% body mass rule, acknowledged and adopted by most seabird studies, focuses exclusively on the effect of additional mass, ignoring potential consequences of decreased camouflage and more notably, increased drag that affects flight speed and maneuverability, underwater mobility, and foraging efficiency (Caccamise & Hedin, 1985; McMahon et al., 2008; Bowlin et al., 2010; Vandenabeele et al., 2012) Although efforts are being made to quantify tag effects impacting seabirds, this necessary component to tracking research is critically lacking in tracking fish (Mellas & Haynes, 1985; Thorstad et al., 2000), sea turtles (Watson & Granger, 1998) and marine mammals (Walker & Boveng, 1995).

Lastly, an additional limitation on our understanding of device effect on animal behaviour is a reflection of the competitive nature of scientific publication, with lowered likelihood of studies publishing results that detect no effect (Barron et al., 2010). This perspective needs to be shifted in order to better understand which methods are least invasive in wildlife tracking studies. Monitoring and controlling for device effects is therefore a necessary component of any wildlife tracking study that imposes a potential handicap to the natural movement and behaviour of individuals to insure biological relevance and ethical practice in research.

Table 2.1: Summary of Crested Auklet (*Aethia cristatella)* crevice sample sizes to detect tag effect on fledging success and chick condition with varying levels of disturbance at Buldir Island, Alaska

Disturbance Level	Fledging success		Chick condition	
	2011	2012	2011	2012
Highly disturbed crevices [a]	45	18	30	19
Partially disturbed crevices [b]	26	17	30	16
Undisturbed crevices [c]	73	79	-	-
Total crevices	144	114	90	35

[a] chick handled and measured; adult equipped with tag
[b] chick handled and measured; adult undisturbed
[c] chick undisturbed; adult undisturbed

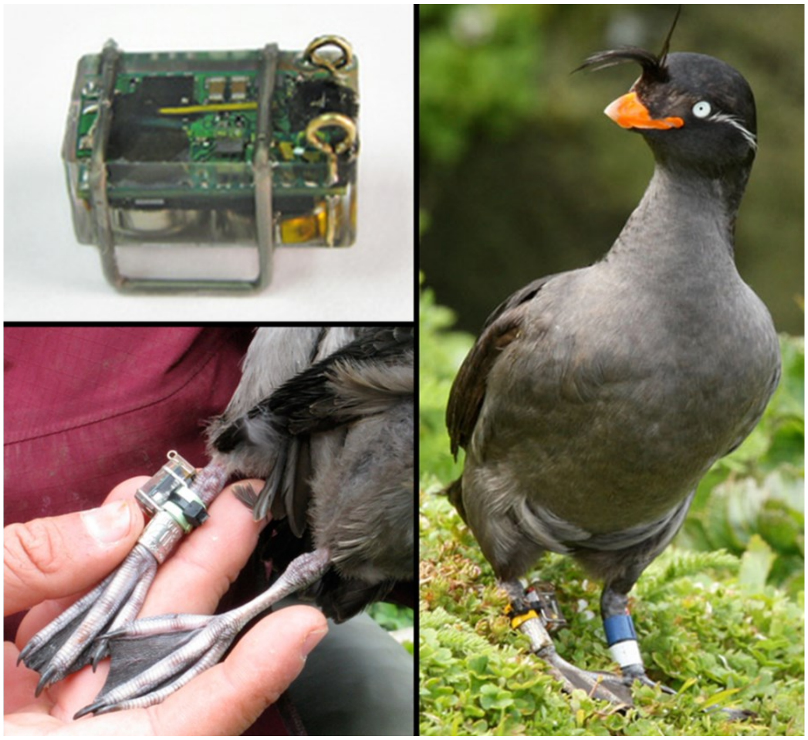

Figure 2.1: Photograph of Lotek Wireless, Lat-2900 Series Avian Geolocator and placement of device attached to an adult Crested Auklet at Buldir Island Alaska.

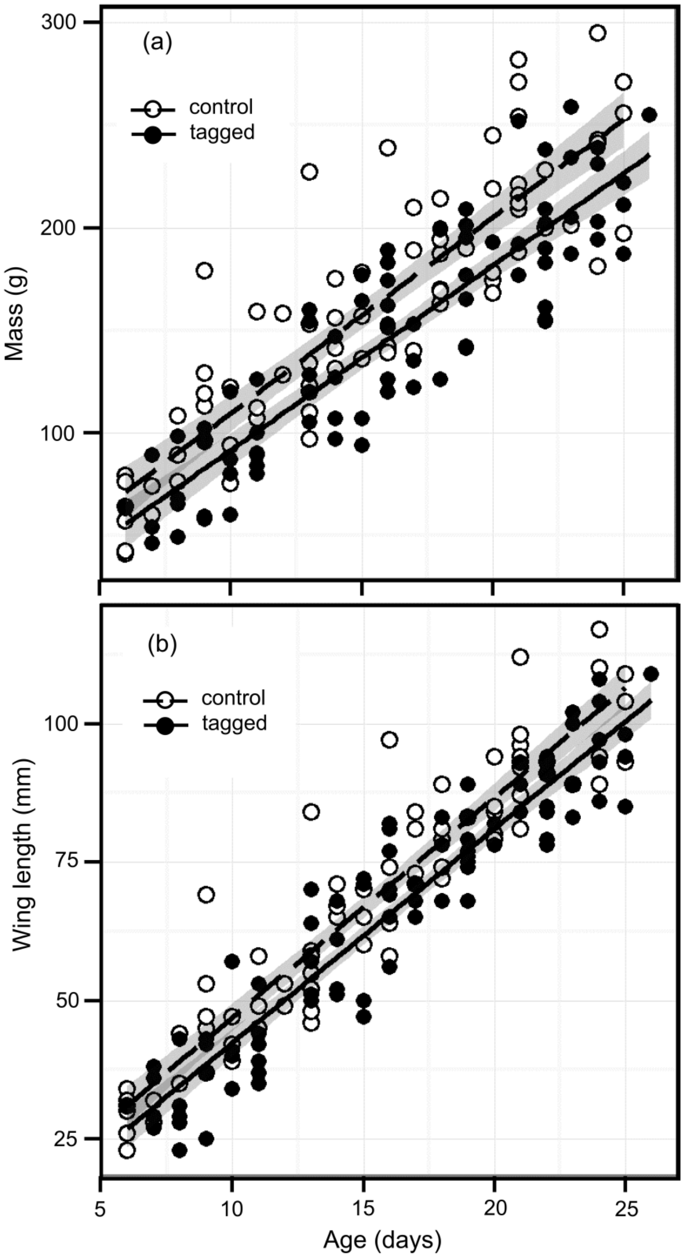

Figure 2.1: Reduced mass (a) and wing length (b) in Crested Auklet chicks measured from tagged group (provisioned by one parent carrying geolocator tag) compared to control group (provisioned by parents, neither carrying geolocator tag) at Buldir Island Alaska. While, the rate of growth between tagged and control groups are not significantly different, the intercept is significantly different. The grey area delimits the 95% confidence intervals.

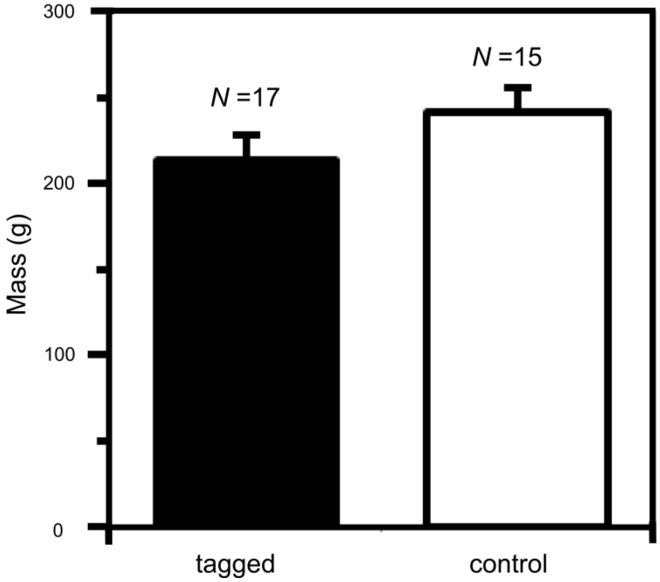

Figure 2.2: Reduced mass of fledging Crested Auklet chicks (after 26 days old) in tagged group (provisioned by one parent carrying geolocator tag) and control group (neither parent carrying geolocator tag) at Buldir Island Alaska in 2012.

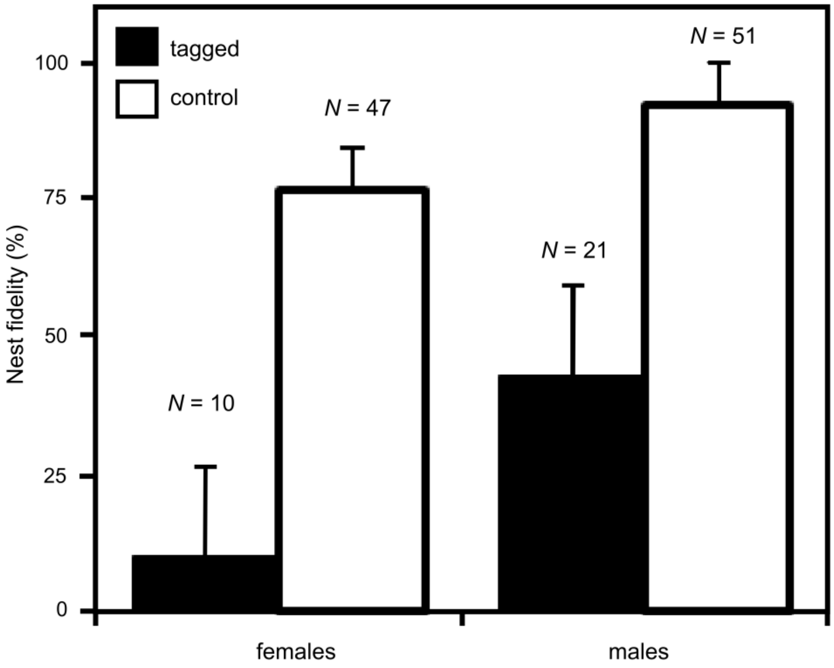

Figure 2.3: Reduced nest fidelity in tagged group of Crested Auklets (2011-2012), observed both in males and females, as compared to control group (long-term dataset, 1993-2000) at Buldir Island Alaska.

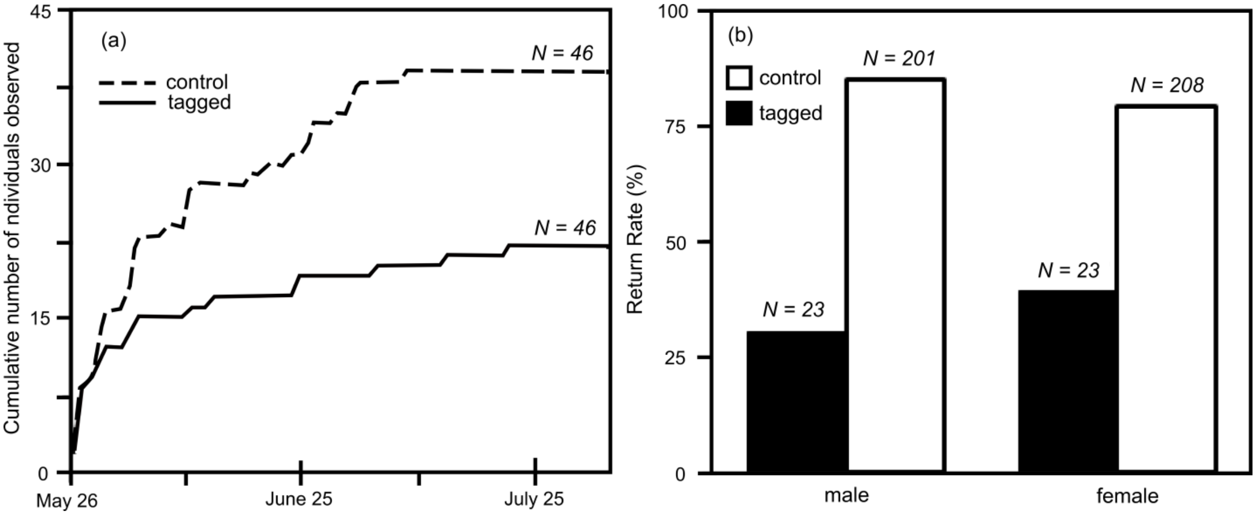

Figure 2.4: (a) Decreased cumulative number of geolocator- tagged Crested Auklet individuals compared to untagged, control group, identified from daily plot observation throughout the breeding season, one year following tag deployment at Buldir Island, Alaska. (b) Reduced return rate of tagged individuals one year following deployment in both males and females compared to pooled control group from archival return data (1993-2012).

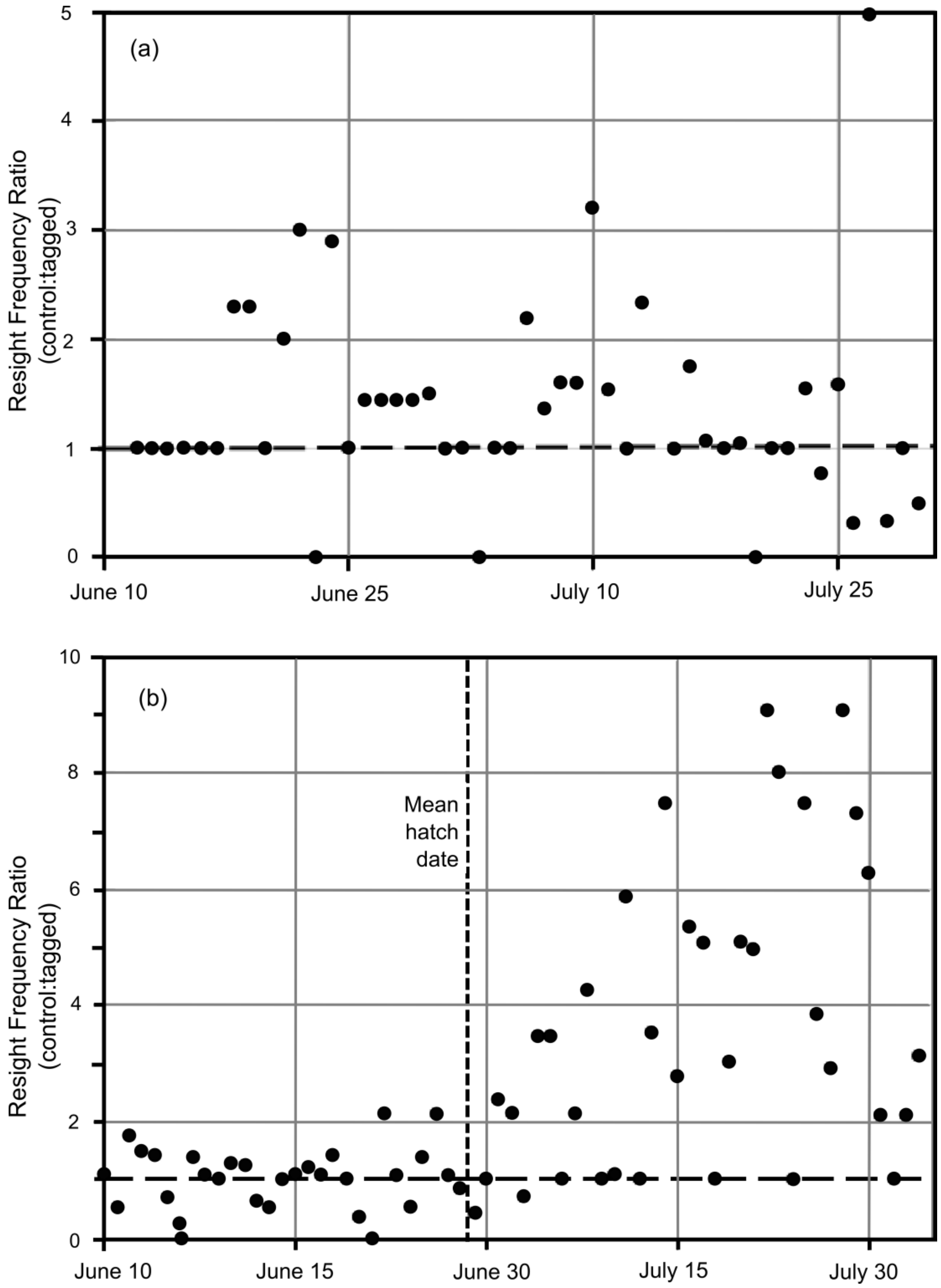

Figure 2.5: **Daily resight frequency ratio of a control group of Crested Auklets (birds not carrying geolocators) to a tagged group (birds carrying geolocator tags) from observation plot on the surface of the colony at Buldir Island, Alaska (a) within banding year (2011), showing most resights occurring in control group (ratio>1); and (b) year following banding (2012), showing most resights occurring in control group (ratio>1) after mean hatch date.**

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CHAPTER THREE:

YEAR ROUND AT-SEA MOVEMENT OF CRESTED AUKLETS *AETHIA CRISTATELLA* FROM AN ALEUTIAN ISLAND BREEDING COLONY, A PRELIMINARY STUDY

ABSTRACT

Year-round ecology and behaviour of most seabirds is poorly understood due to difficulties associated with measuring their at-sea activity during the non-breeding season, in often harsh and remote environments. However, the development of compact and lightweight biologging devices has permitted tracking of individuals' movement across large oceanic distances over time periods of a year or more. To examine the movement of a small, pursuit-diving seabird, I deployed tarsus-mounted geolocators (Lotek LAT2900, 2 g, <1.1 % body mass) on 31 Crested Auklets (*Aethia cristatella*) in 2011, at a breeding colony at Buldir Island, Aleutian Islands, Alaska. I recovered ten geolocators (32% recovery) in 2012, three of which provided usable data, revealing, for the first time, migration routes and important wintering areas for individual Crested Auklets. Immediately following breeding, the three tagged individuals migrated c.1400 km north to the Gulf of Anadyr and Bering Strait regions. In December, they travelled c.3400 km directly south-west to productive waters off the Kurile Islands and Hokkaido,

Japan, finally moving directly c.2300 km east to Buldir Island in April. Prior to this study, knowledge of Crested Auklet winter distribution was limited to haphazard at-sea boat surveys. Despite the small sample size, results reveal an unexpected triangular, long-distance migration pattern, providing preliminary results for the feasibility of tracking auklets using archival-light geolocators. These results also identify potentially important winter foraging areas for planktivorous seabirds, important to future strategic actions that aim to conserve species through the protection of their necessary habitat.

3.1 INTRODUCTION

Patterns in seabird movement, distribution and abundance are expected to vary on spatial and temporal scales as an adaptive and learned strategy to changing food availability and seasonal weather conditions (Elphick & Hunt, 1993; Garthe et al., 2012). Seabirds, being long-lived animals that spend the majority of their time at sea may travel great distances across highly variable marine environments. For a brief period of time each year, seabirds such as auklets (Alcidae, Aethiini) are necessarily constrained to the land by their need to lay eggs and raise young in rocky crevices, where they heavily focus their energy on behaviours associated with breeding (Ashmole, 1971; Birt et al., 1987; Furness & Monaghan, 1987). Outside the breeding season, seabirds shift their distribution to a primarily oceanic existence, often far from their terrestrial breeding grounds to avoid inclement weather and seasonal declines in food availability (Frederiksen et al., 2012). Due to the highly mobile, inaccessible nature of most seabirds during the non-breeding season, important aspects of their behaviour, ecology and distribution at sea remain largely unknown (Dettmers & Bart, 1999; Byrd et al., 2005; Renner et al., 2008).

Until recently, most seabird at-sea distribution data was derived from the retrieval of banded specimens found dead or from land- and sea-based observational counts of birds flying or sitting on the surface of the water (Tasker et al., 1984; Robinson et al., 2010). While these techniques are valuable and have revealed important insight into poorly known facets of seabird biology, they lack the ability to effectively account for spatiotemporal movement and cannot discern activity at the individual level (Tasker et al., 1984; Thompson, 2002; Garthe et al., 2012; Frederiksen et al., 2012). Additionally, directly surveying seabird populations from land, sea or air is often costly, labor intensive and at times, logistically impossible due to the remoteness and the harsh characteristics of the environments they tend to inhabit (Ferrier et al., 2006).

Development of tracking technology has allowed researchers to bridge critical gaps in our understanding of the cryptic migratory behaviour of seabirds, lending itself to useful applications in wildlife conservation (Robinson et al., 2010; Bowlin et al., 2010; Dias et al., 2013). At the cost of reduced location accuracy (185 – 200 km; Phillips et al. 2004), miniaturized light-sensing tracking devices have become an increasingly popular alternative to more expensive tracking methods (satellite PTT, GPS tags), permitting researchers to quantify migration routes, staging and wintering areas of not just a few individuals, but of multi-colony populations of seabirds (Harris et al., 2009; Frederiksen et al., 2012). These compact archival geolocating devices (also referred to as 'geolocators' or 'tags'), use ambient light levels to estimate the timing of sunrise and sunset at the tagged individual's location, from which daily estimates of latitude and longitude are inferred (Wilson et al., 2002). These geolocators often have additional capacity to sample and measure environmental variables including ambient temperature, sea surface temperature, salinity and depth-sensing water pressure (Wilson et al., 2002; Adams et al., 2009; Robinson et al., 2010). Growing interest and demand for cost-effective, light-weight geolocators has driven rapid improvements in this technology, creating exceptional opportunities to track more species of birds that were previously too small to carry such devices.

In this study, for the first time, I applied geolocators to Crested Auklets (*Aethia cristatella*) originating from a breeding site at Buldir Island in the western Aleutian Islands. During the breeding season, these pursuit-diving seabirds forage offshore on euphausiids (e.g., *Thysanoessa* spp.) and large copepods (*Neocalanus cristatus* and *Eucalanus bungii*) (Springer & Roseneau, 1985; Fraser et al., 1999; Kitaysky & Golubova, 2000; Gall et al., 2012). During the breeding season (May - August), while their distribution is limited to areas within proximate flying distance to their land breeding sites, Crested Auklets are present in large numbers at mixed-species colonies with Least Auklets (*A. pusilla*) (Byrd et al., 2005). These colonies are located at remote islands in the western and central Aleutians, various Bering Sea and Okhotsk Sea islands as well as the central Kurile islands and on the Chukotka peninsula (Gaston & Jones, 1998)

Information concerning at-sea distribution of Crested Auklets during the non-breeding season has previously been limited to observational data collected from ship surveys that tend to be strongly biased by transect routes, weather conditions and the viewing ability and competence of the observers that conduct them (Tasker et al., 1984). I would expect, however that following the breeding season (September-April), Crested Auklet distribution would reflect patchily distributed prey concentrations, targeting specific hydrographic features of the marine landscape that meet their specific foraging preferences (Renner et al., 2008; Bond et al., 2011a; Gall et al., 2012).

In a dynamic pelagic system, the seasonal variability of zooplankton abundance has a great influence on distributional patterns of planktivores, including many seabirds (Elphick & Hunt, 1993; Hunt et al., 1998). Ecologically important foraging areas, characterized by complex biological and physical interactions are influenced by large scale enduring features and fine scale localized conditions that produce spatially and temporally predictable concentrations of seabirds' prey (Hunt et al., 1998; Byrd et al., 2005). Predicted to reach maximum dive depths of 45 m, Crested Auklets feed on concentrated patches of energy-rich copepods and euphausiids in productive shelf waters and cold, nutrient-rich oceanic waters that are advected to the surface and sub-surface (Springer & Roseneau, 1985; Burger, 1991; Hunt et al., 1998). Upwelling events that produce favourable foraging conditions force prey upward in the water column, often occurring at the border of frontal areas (where water masses meet), tidal currents through island passes and coastal interaction of currents and changing bathymetry (Hunt et al., 1998; Piatt & Springer, 2003).

Previous observational studies conducted at-sea have shown that the high abundance of Crested Auklets present in the western Aleutians (surrounding Buldir Island) during the summer months drastically decreases in winter, suggesting a local decline in prey availability and a shift in distribution to productive habitat elsewhere

(Renner et al., 2008). Increased numbers of Crested Auklets have been observed in the eastern Aleutians (Unalaska Island/ Krenitzen Islands/Unimak Pass area) during the winter (Renner et al., 2008), suggesting a possible eastward shift in the western population, however this has not been confirmed.

Mechanisms that influence the seasonal variation in seabird distribution throughout their annual cycle have important implications for designing conservation measures that protect them year-round. Following the breeding cycle, the onset of fall migration is predicted to heavily correspond with changing local weather conditions and depleting prey availability that persists at the colony site (Richardson, 1978). Sea ice movement in the arctic has historically played a significant role in the timing of seabird migration and over-winter distribution in a number of species (Kondratyev et al., 2000). The annual movement of floating ice, progressing into the Bering Strait in late autumn is an important factor driving southerly migration off the continental shelf in a number of alcids (Kondratyev et al., 2000; Bond et al., 2013) and was observed for northern breeding Crested Auklets dating back to 1919 (Sealy, 1968). Crested Auklets have also been previously observed to use predictable areas of open water within the pack ice, i.e., polynyas, in the Sea of Okhotsk, suggesting a close association with ice habitat (Kondratyev et al., 2000).

In this pilot study, the objectives were to: 1) map year-round movement of individuals equipped with geolocators from their breeding colony at Buldir Island, Alaska, 2) quantify distances travelled and timing of migratory events, and 3) identify wintering habitat, while examining oceanographic characteristics of these ecologically important areas for descriptive and conservation purposes.

3.2 METHODS

3.2.1 Study area

Fieldwork was conducted at Buldir Island (52º11 N, 175º56 E) in the western Aleutian Islands, close to the southernmost limit of Crested Auklets' breeding range and the most westerly colony site in the Aleutians (Fig. 3.1; Byrd & Day, 1986; Sowls et al., 1978). Geolocators were deployed at Main Talus, a colony site on the north slope of the island, supporting more than 100,000 breeding Crested and Least Auklets (Byrd et al., 1983).

3.2.2 Device deployment and recovery

In summer 2011, I deployed 31 LAT2900 geolocators (8 x 15 x 7 mm, 1.9 g, Lotek, St. John's, Newfoundland) to individual adults (21 males, 10 females) captured from their marked breeding crevices (one mate per pair) while they were brooding chicks, less than 4 days after hatch. Geolocators were attached with a single cable-tie to a double-wrapped grooved light green Darvic colour band on the right tarsus above a numbered aluminum USFWS band. The combined mass of the tag, colour band, aluminum band, and cable tie was 2.93 ± 0.12 g (n=31); 1.1% of the mean body mass of all tagged individuals, well below recommended tag mass threshold of 3%).

At the time of capture, I determined sex by bill depth and shape (Jones 1993) and recorded measurements of body size (mass, wing, tarsus, and culmen length, and bill depth) and ornament size (crest, auricular plume and rictal plate length; Jones 2004). Mass was measured to the nearest 1 g using a 300g Pesola® spring scale, ornament length to the nearest 0.1mm using Vernier calipers, and wing length to the nearest 1 mm using a wing rule. Individuals were handled very briefly for geolocator attachment (< 9 min) and returned immediately to their crevice. In summer 2012, I returned to their respective crevices during the incubation and chick-rearing period and recaptured tagged individuals to remove geolocators, repeating all measurements taken in 2011. Geolocation data was later downloaded from functional recovered tags, using LAT Tag Talk Application (v. 1.9.30, Copyright 2006-2010, Lotek Wireless Inc.).

3.2.3 Data analysis

Geolocation data from Lotek LAT2900 devices produces a single daily position fix using a template-fit algorithm with associated position error, expected to range from 185-200 km (Phillips et al., 2004). Template fit is an objective algorithm that quantifies light data as it is collected onboard the device (Ekstrom, 2004; Bridge et al., 2013). After data downloading I used LAT Viewer Studio (Lotek Wireless Inc.), to remove unreliable position fixes that surround bi-annual equinox periods, resulting from ambiguous latitudinal trends in day length (Phillips et al., 2004; Frederiksen et al., 2012). A number of position fixes were interpolated during equinoctial periods using sea surface temperatures (SSTs) recorded and logged daily by the tags, using the SST module in LAT Viewer Studio (Lotek Wireless Inc). This module matches daily SST values sampled by the geolocators with remotely sensed Modis Aqua SST data, using a search radius of 200 km (Shaffer et al., 2009). Additionally, I ran a speed filter (McConnell et al., 1992), to exclude successive points that exceeded a threshold of 13.1 m/sec, representing predicted flights speeds of Crested Auklets (Spear & Ainley, 1997). Spatial analyses and mapping was conducted in Geospatial Modelling Environment (Beyer, 2012), concurrently with R Studio (R Development Core Team 2012) and ArcMap 10.1 (ESRI, Redlands CA).

3.2.4 Non-breeding habitat

Ecologically important wintering areas were identified for Crested Auklets by producing occupancy contours from individual position fixes using the kernel density tool in Geospatial Modelling Environment (Beyer, 2012). These contours represented locations of frequent occurrence for each individual, mapped in ArcMap 10.1 under Alaska Albers Equal Area projection with cell size of 200 km. I divided their at-sea distribution into four seasonal categories based on general trends in their movement during the non-breeding season, including: Post-breeding (15 August – 15 Nov), Primary winter (16 Nov – 31 Dec), Secondary winter (1 Jan -31 Mar) and Pre-breeding (c. 1 April – April 20).

I defined core habitat within each seasonal category as the area confined within 50% occupancy contours. In order to illustrate the degree of habitat use overlap across individuals, I calculated the pairwise and total intersecting area confined within 50% occupancy contours. Pairwise proportions of overlap were calculated as: $(2*A)/(a_1+a_2)$, and similarly, total overlap among all three individuals was calculated as:

$(3*A)/(a_1+a_2+a_3)$; where A is area of overlap, a_1, a_2, *and* a_3 are respective areas of 50% contours for each individual, (adapted from Frederiksen et al. 2012.*)*

3.2.5 At-sea movement and phenology

The timing of departure from Buldir following the breeding season (shift to a pelagic distribution) was defined as the last day individuals were present within 250 km of this island. This strategy attempted to accommodate for the precision of geolocators (185 – 200 km, Phillips et al., 2004) and the average central-place foraging range during chick provisioning (55 – 100 km Hunt et al., 1993; Jessopp et al., 2013). Precise arrival and departure times to and from wintering areas were defined as the first and last day individuals were present within the 50% occupancy contour. Distances travelled between the breeding site and successive wintering areas were approximated using great circle distances between mean centers of each wintering area, assuming a spherical earth and strictly over-water travel, using Equal Area Azimuthal projection. Rates of travel between wintering areas are calculated conservatively, determined by the quotient of great circle distances and number of days travelled before reaching wintering areas, not accounting for variable, non-direct movement en route.

In order to better understand the potential role that sea ice played in Crested Auklet distribution and migratory behaviour, I compared the marginal sea ice extent (<10% concentration) with 50% occupancy contours estimated for individuals during each of four seasonal categories previously described (post-breeding, primary and secondary, and pre-breeding). In order to evaluate sea ice conditions just prior to each migration event, sea ice data was taken on the last day of each seasonal category (15 Nov, 31 Dec, 31 Mar, and April 20). Daily ice data was obtained from NOAA, US. National Ice Center (http://www.natice.noaa.gov/Products_On_Demand/pod.html).

Essential to biologically relevant migration studies that attach foreign objects to individuals, I simultaneously conducted an experimental study to quantify the effect of deployed geolocators on individuals' behaviour, body condition, breeding success, return rates and colony activity. Biologically significant parameters were compared between control and tagged individuals to account for potential impacts of a geolocator handicap on individual migratory behaviour (Robinson & Jones, 2014, and Chapter Two of this thesis). In this study, because significant tag effects were detected, inferences about movement were assumed to apply only to individuals carrying 2 g leg-mounted tags, and not necessarily representing the movement of untagged individuals.

3.3 RESULTS

3.3.1 Device recovery

In 2012, I recaptured 10 of 31 (32%) of individuals equipped with geolocators, and removed devices for data retrieval. Of the 10 recovered Lotek LAT 2900 devices, I successfully extracted data from three. The remaining seven geolocators had either malfunctioned due to water entry recording no data, or batteries failed early (Mike Vandentillaart (LOTEK), pers. comm.). This failure rate (70%) was disturbingly high, and was followed by a 100% failure rate of 11 LAT-2900s deployed on Parakeet Auklets at Buldir during 2012-2013 (Carley Schacter pers. comm.). A subsequent switch to

Migrate Tech Integeo C-65 tags resulted in a very low failure rate. All three working tags came from males. Complete geolocation data were collected from two devices (LAT-0302, LAT-0278), sampling daily position fixes for the entire non-breeding season (August 2011 – May 2012), and one device (LAT-0250) yielded geolocation data until the battery failed on Dec 12, 2011.

3.3.2 At-sea movement and phenology

Geolocation data indicated that all three birds followed a similar movement pattern during the non-breeding season, and occupied similar geographic areas (Fig.3.2). Immediately following their departure from their Buldir Island breeding site in the western Aleutian Islands (c.52 º N) on 4 August, all three tagged individuals travelled c. 1480 km north, to post-breeding area in the northern Bering Sea and Gulf of Anadyr (c.64 º N, Table 3.1, 3.2). Individuals spent three – six days on their initial northern migration, moving an average 370 km/day. All individuals occupied this post-breeding area from mid-August to late-October/ mid-November (c. 92 days), before departing to their primary wintering areas. One individual (LAT-0250) departed on 29 Oct, travelling for five days (660 km/day), followed shortly after by the other two individuals (LAT-0278, LAT-0302) along a similar route, travelling 550 km/day and 850 km/day respectively. During this second phase of migration, individuals travelled c.3340 km from the northern Bering Sea, south-west along the Kamchatka Peninsula, following the Kamchatka current, to a winter habitat south of the Kurile Islands. Due to battery failure, no geolocation data was obtained for LAT-0250 following December 12, however the final data shows that, like the other birds, LAT-0250 moved to the same primary winter habitat. Additionally, since geolocator LAT-0250 was recovered from the breeding site, I know at the very least, that this individual travelled an additional 2200 km back to the colony, migrating an absolute minimum total distance of 6900 km throughout the non-breeding season.

Data for LAT-0278 and LAT-0302 revealed two different migration patterns for the remainder of the season. Both individuals occupied a similar area south of the Kurile Islands (primary winter habitat), however on Dec 31, LAT-0278 travelled further west 850 km (213 km/day) to a location off the eastern coast of Japan (secondary winter habitat), reaching c. 40 º N in March. During this time, LAT-0302 remained in the region south of the Kuriles. Both individuals occupied these respective areas until late March, when both simultaneously travelled north 1600 km (800 km/day) to a location in the Sea of Okhotsk (pre-breeding). They spent c.20 days in this pre-breeding area before leaving in late April for the last leg of their migration. Travelling at 155 km/day, they moved 1400 km southwest, stopping briefly near the Kurile Islands, and returning 800 km northeastwards to Buldir Island to complete their migration. Both individuals LAT-0278 and LAT-0302, undertook an extensive migration, travelling a minimum distance of 9500 km and 11 800 km, respectively. The proportion of pairwise habitat use overlap was greatest between LAT-0250 and LAT-0302 (52%), followed by LAT-0302 and LAT-0278 (41%), with lowest overlap between LAT-0250 and LAT-0278. The proportion of habitat that was used by all three individuals was calculated as 22% overlap. (Table 3.3)

3.4 DISCUSSION

Prior to this study, an understanding of the biology of Crested Auklets during the non-breeding season had been limited due to logistical constraints on studying movement and behaviour at-sea. With energetically expensive flapping flight, it was previously thought that Crested Auklets might not travel far from their colonies following breeding activity in the summer (Whidden et al., 2007; Renner et al., 2008). From observed changes in Crested Auklet density during the winter (Renner et al., 2008), it appeared that habitat use shifted from depleted resources at breeding sites in the western Aleutians to active passes among the eastern Aleutian Islands. However, with the application of miniaturized biologging geolocators, this study reveals surprising long-distance migratory behaviour of three individuals, initially travelling from Buldir Island, to habitat in the northern Bering Sea (c. 64 º N), and further south and west to pelagic wintering grounds off the Kuriles and Hokkaido (c. 40 º N). While Crested Auklets have been observed in high numbers in the eastern Aleutian passes, the colony of origin of these individuals remains unknown. This study highlights important areas used by Crested Auklets originating from Buldir Island including: post-breeding habitat, primary/secondary winter habitat, and pre-breeding habitat (Fig 3.3). These observations pertain to only three individuals that were all equipped with 2 g tags and have been shown to effect Crested Auklet behaviour, (Robinson & Jones, 2014), and so results must be interpreted with caution.

3.4.1 Non-breeding habitat

3.4.1.1 Post-breeding habitat

Post-breeding habitat was centered in the north-western Bering Sea and Gulf of Anadyr (c. 63ºN 173ºW), and was occupied by all three tagged individuals for three months following the breeding season. This habitat is characterized by the convergence of cold oceanic Anadyr Waters (AW), with the Alaska Coastal Current (ACC) and Bering Sea Waters (BSW) that are known to concentrate zooplankton near the surface (Springer & Roseneau, 1985; Elphick & Hunt, 1993; Hunt et al., 1998; Russell et al., 1999). This area is also dominated by highly productive, shallow waters on the Bering Shelf, where currents move against the continental slope, forcing concentrations of zooplankton upwards in the water column, Fig 3.4 (Hunt et al., 1998; Gall et al., 2012).

According to other sources, a high abundance of Crested Auklets occurs in the western Bering Sea, straddling Anadyr Shelf waters and Bering Shelf waters and west of St. Lawrence Island (e.g., Piatt & Springer, 2003). This post-breeding habitat in the sub-arctic North Pacific, represents one of the world's most biologically productive regions (Sasaoka et al., 2002), supporting a large number of planktivorous marine animals (Abraham & Sydeman, 2004; Renner et al., 2008; Bond et al., 2011b, 2013) and likely an important refueling area for Crested Auklets travelling from Buldir, and other distant breeding sites. Locating these predictable aggregations of high-energy prey is essential in sustaining both the physiological demands of post-breeding molt and migration, particularly in high energetic cost flyers like Crested Auklets (Bridge, 2006, 2011; Guilford et al., 2009, 2012). The three tagged birds left this area when daylight shortened and advancing sea ice covered open water in November.

3.4.1.2 Winter habitat

Following a second rapid migration of more than 3000 km from the *post-breeding habitat* along the Kamchatka Peninsula, individuals arrived at productive offshore waters south of the Kurile Islands (c. 48ºN 155ºE), known as the Oyashio Shelf region (*primary winter habitat*). Frontal areas formed by the converging Kamchatka Current and Oyashio Current, bring cold, productive waters south of the Kurile Islands and promote highly aggregated zooplankton near the surface (Sasaoka et al., 2002). Very powerful upwelling are produced in this region due to rapid changes in ocean bottom relief where the narrow continental shelf meets the steep slope at its south-east margin, effectively advecting zooplankton to the surface (Sakurai, 2007). Studies on foraging behaviour of Crested Auklets have shown that they have a strong affinity for moderately sized passes in the Aleutian chain, where powerful tidal currents force water over sills and bring nutrient rich waters to the surface (Hunt, 1997; Sasaoka et al., 2002; Byrd et al., 2005). Passes between closely linked islands are also characteristic of the Kurile islands, similarly producing favourable conditions for surface and subsurface zooplankton foragers, (Hunt et al., 1998), and have historically supported large concentrations of seabirds in early winter (Springer et al., 1999).

Waters east of Hokkaido and Honshu, Japan (c. 41ºN 143ºE) represent another wintering area occupied by one tagged individual from January to early April (*secondary winter habitat*). Anticyclonic eddies formed by the Oyashio Current moving through the Kurile Straights, drift south interacting with the shelf of the Southern Kurile islands to offshore areas east of Japan promoting highly biologically productive waters (Kusakabe et al., 2002). Characterized by coastal and frontal upwelling at the convergence of the cold Oyashio Current flowing south and warm Kuroshio Current flowing north, this region supports a diverse abundance of marine mammals and seabirds (Sakurai, 2007). Records have shown high numbers of Crested Auklets and other planktivorous seabirds in this area south of the Kuriles, the Sea of Japan and along the eastern shores of Sakhalin and Hokkaido (Sealy, 1968; Kondratyev et al., 2000). My data indicate that at least some proportion of these Crested Auklets is of Aleutian Island origin.

3.4.1.3 Pre-breeding habitat

Prior to their return migration to Buldir, with high energy demands necessitated by the subsequent breeding season, the two birds temporarily moved north to exploit highly productive waters at the spring ice edge in the Sea of Okhotsk (c. 56ºN 147ºE). An estimated 2.5 million Crested Auklets have been documented in the central basin of the Sea of Okhotsk, along with other small alcids that flock to high plankton concentrations, particularly as ice begins to recede in the region (Kondratyev et al., 2000; Shiga & Koizumi, 2000). Again, although many Crested Auklets have previously been observed in this area, we now know that these birds include birds that originated from a western Aleutian Island breeding site.

3.4.2 Migration phenology

Arrival time at the *post-breeding habitat* was highly synchronized across individuals (7 – 9 August, $N = 3$), and followed a remarkably rapid evacuation of the location of the breeding sites for productive waters 1500 km farther north. Subsequent departure from this habitat, towards the *primary winter habitat* was somewhat less synchronized (2 – 16 November, $N = 3$). While localized wind direction, wind speed, and air temperature likely influence the timing of this second migration, the movement of sea ice into the Bering Sea, timed with the completion of their autumn molt, was likely also responsible for the onset of their southern migration. Individual movement during spring migration to the *pre-breeding habitat* (28, 31 March, $N = 2$) followed by the final arrival at the breeding site (1, 6 May, $N = 2$) was also highly synchronized. The onset of spring migration is believed to be primarily cued endogenously, influenced by large scale shifts in photoperiod and localized environmental changes at the *primary* and *secondary winter habitat* (Marra et al., 2004). Timing movement to and from ecologically important habitat is a critical component of at-sea survival in seabirds; correlating distribution with physiologically demanding activity (reproduction, migration and molt) and environmental conditions that maximize access to available prey and minimizes risk of mortality (Guilford et al., 2009).

3.4.2.1 Molt

The completion of Crested Auklet autumn molt in November was likely an important migratory cue that initiates the southern movement of individuals from their *post-breeding habitat*. Little information is available on molt of alcids outside the breeding season (Mosbech et al., 2011; Bond et al., 2013), however collections of specimen recovered at sea, suggest that the definitive molt for Crested Auklets reaches completion in mid-November to mid-December (Bedard & Sealy, 1984). Crested Auklets begin their molting process in early July, and continue until completion 5-6 months later, utilizing a strategy favouring the spreading out of an energetically costly activity (Sealy, 1968). Members of the auklet tribe (Aethiini) all show this unique quality in that molt overlaps significantly with breeding, occurring sequentially to avoid periods of flightlessness, that is exhibited by most other Alcids (Sealy, 1968; Bedard & Sealy, 1984; Bond et al., 2013). Bridge (2006) suggested that seabirds with a degree of molt and breeding overlap live in seasonally non-variable habitats and exhibit low degrees of post-breeding migration or dispersal. Molt results however, confirm a long-distance post-breeding migration, where individuals travel great distances to take advantage of high productivity in the north Bering Sea, where they complete their molt. Their flight feathers are then fully developed for the southward leg or their migration to their primary wintering areas.

3.4.2.2 Sea ice

Migratory phenology of Crested Auklets correlated with the movement of sea ice and likely was an important influence on movement of individuals to *post-breeding* and the *pre-breeding habitat* (Fig 3.3). Departure of Crested Auklets from the northern Bering Sea in late November also coincided with shortening day length at this latitude (c. 63° N). At both the *primary* and *secondary winter habitat*, pack ice does not often form, providing favourable open-water habitat for many seabirds, including Crested Auklets (Kondratyev et al., 2000). During this time, the Sea of Okhotsk is characterized by extensive sea-ice cover, significantly restricting seabird activity (Kondratyev et al., 2000). As pack ice begins to break up and recede in early spring, the northern movement of this highly productive ice edge greatly influences timing of seabird migration (Kondratyev et al., 2000). This study showed that as ice retreated northward, the two tagged individuals moved well into the Sea of Okhotsk, proximate to the ice edge (Fig 3.3). While it is unclear if the coinciding movement of Crested Auklets with sea ice edge was a result of individuals specifically targeting ice edges, or whether sea ice strictly constrained their distribution by closing accessible habitat, ice edges still appear to have had an important relationship to timing of their movement.

Although Crested Auklets have been previously observed to use predictable areas of open water within pack ice (Kondratyev et al., 2000), it cannot be confirmed that individuals in the study were indeed using this particular type of habitat due to the low accuracy of geolocation fixes. A recent study measuring the movement of Little Auks (*Alle alle*), a small alcid endemic to the North Atlantic, found a similar affinity for ice edges among many individuals, however further research is necessary to better understand the mechanisms that are driving this relationship (Fort et al., 2013). Many other seabirds, including Black Guillemots (*Cepphus grylle*), Ivory Gulls (*Pagophila eburnea*), Ross' Gulls (*Rhodostethia rosea),* as well as large surface-feeding gulls, exhibit strong dependence on ice environments that form favourable conditions for prey aggregation (Kondratyev et al., 2000). This relationship to sea ice holds important ecological implications for Crested Auklets and other neritic marine animals in a changing climate where sea ice extent is decreasing on large scales, ultimately affecting prey availability and significantly altering winter habitat over time (Ṕron et al., 2010; Mosbech et al., 2011; Fort et al., 2013).

3.4.3 Flight behaviour

Crested Auklets are adapted to underwater, wing-propelled locomotion at the expense of poor flight efficiency in the air (Renner, 2006; Bond et al., 2013). This small, pursuit diving alcid has relatively high wing-loading (97 ±11 N◦m^{-2}; (Spear et al., 1992)), and comparatively low ground flight speeds, estimated to vary from 13.1 – 19.0 m/s, depending on wind speed and direction (Spear & Ainley, 1997) Based on flight speeds estimated from displacement calculations of the data that assumes constant, non-stop flight (Table 3.3) ranging from 1.80 m/sec to 9.40 m/sec, it can be deduced that my three Crested Auklets did not travel all day. Rather, to maintain actual observed speeds, it is likely that individuals most often exhibit bouts of higher sustained flight speeds, punctuated by regular foraging and resting stops along the way, as observed in other low flight efficiency migrants (Mosbech et al., 2011; Jessopp et al., 2013). In the most extreme case that an individual was travelling at its lowest observed speed of 13.1 m/sec, for the greatest recorded distance of 825 km, that individual would be required to be in flight for 17.6 hrs in a 24 hour period. However, based on average distances travelled, individuals likely travel for 8-12 hours of the day during migration periods, breaking to forage and rest.

Inferences made from this study are limited to the movement and behaviour of three Crested Auklet individuals carrying a tarsus-mounted tag, comprising ~1.1% of their body mass. Gaining knowledge on how species respond to additional mass or drag, such as the attachment of an external device, is critical in qualifying the validity of data collected in these tracking studies that are intended at measuring natural movement and habitat use of a species. Migratory studies such as this, that employ tracking devices raise the question whether individuals potentially handicapped by additional drag and mass significantly alter their behaviour at sea in response to the device. Further investigation into the degree to which Crested Auklets are behaviourally flexible, potentially adapting their behaviour to changing environmental or anthropogenic variables, could reveal important insights on resultant data from tracking research.

3.5 CONCLUSIONS

My study was the first of its kind to reveal previously unknown winter movement of Crested Auklets, identifying migration routes, distances travelled and ecologically important habitat used by individuals. This research is among very few studies that have applied tarsus-mounted tracking devices to small alcids (e.g., Mosbech et al. 2011; Fort et al. 2013), demonstrating the feasibility of measuring the movement of small, pursuit diving seabirds. As a low trophic feeder, Crested Auklets are regionally important marine birds, impacting the food web and the flow of energy throughout the marine environment (Gall et al., 2012). Mortality in adult seabirds is likely at its greatest during this poorly understood, but dominant portion of their annual cycle at sea (Harris et al., 2009). Understanding mechanisms that influence year-round distribution of such a highly enigmatic, pelagic animal is a challenging, but fundamental component to their conservation (Braunisch et al. 2008, Hirzel et al. 2002, Hirzel et al. 2001). Particularly as anthropogenic threats to seabird survival continue to increase, understanding their movement and how it relates to dynamic oceanic processes is paramount in implementing effective wildlife management strategies (Frederiksen et al., 2012; Gilg et al., 2013; Militão et al., 2013).

Recent studies have shown that seabirds, and other long distance migrants, display varying degrees of fidelity to migration routes and over wintering habitat, specific to species, sex and unique individuals (Phillips et al., 2005; Fossette et al., 2008; Ismar et al., 2011; Dias et al., 2011, 2013, Fifield et al., 2013). Investigating whether an individual hindered by carrying a tracking device will alter its migratory activity in order to accommodate the addition of a geolocator, or whether they maintain fidelity to winter habitat despite the potential handicapping engendered by the device and likely increase risk to survival would be very telling. As tracking technology improves (and devices get smaller), I hope to effectively measure movement of a larger number of Crested Auklets and investigate sex-specific, between-year and inter-species migratory patterns.

Table 3.1: Detailed summary of individual movement phenology of Crested Auklets equipped with geolocation devices at Buldir Island, Alaska.

Migratory Event	**0250 (male)**	**0302 (male)**	**0278 (male)**
Departure from breeding site	01 Aug 2011	07 Aug 2011	05 Aug 2011
Arrival at post-breeding habitat	07 Aug 2011	09 Aug 2011	08 Aug 2011
Departure from post-breeding habitat	29 Oct 2011	14 Nov 2011	11 Nov 2011
Arrival at primary winter habitat	02 Nov 2011	17 Nov 2011	16 Nov 2011
Departure from primary winter habitat	*NA	**NA	31 Dec 2011
Arrival at secondary winter habitat	*NA	**NA	03 Jan 2012
Departure from winter habitat	*NA	31 March 2012	28 March 2012
Arrival at pre-breeding habitat	*NA	01 April 2012	29 March 2012
Departure from pre-breeding habitat	*NA	20 April 2012	17 April 2012
Arrival at the breeding colony	*NA	01 May 2012	06 May 2012

**NA data are not available for 0250 following battery failure on Dec 2, 2011.*
***NA data are not available for 0302*

Table 3.2: Distances travelled and mean flight speeds of Crested Auklets between important wintering habitats, originating from Buldir Island, Alaska (assuming constant (24h/day) daily flight speed and using a conservative estimate of minimum distance travelled.

Movement between migratory locations	LAT-0250	LAT-0302	LAT-0278	Mean Speed ± SD
Breeding site – Post-breeding habitat	1 480 km (6 days)	1 450 km (3 days)	1 500 km (4days)	4.26 m/sec ± 1.12
Post-breeding habitat – primary winter habitat	3 300 km (5days)	3 400 km (4days)	3 320 km (6 days)	7.96 m/sec ± 1.42
Primary winter habitat – Secondary Winter habitat	*NA	**NA	850 km (4days)	2.46 m/sec
Winter habitat – Pre-breeding habitat	*NA	1 650 km (2 days)	1 600 km (2 days)	9.40 m/sec ± 0.15
Pre-breeding habitat – Breeding habitat	2 200 km (*NA)	2 100 km (19 days)	2 200 km (11 days)	1.80 m/sec ± 0.52
Total distance travelled*	6 900 km	11 800 km	9 500 km	-
Mean Overall Speed ± SD	5.25 m/sec ± 2.40	6.57 m/sec ± 3.48	4.96 m/sec ± 2.62	-

**data is not available for 0250 following battery failure on Dec 2, 2011.*
***data is not available for 0302*

Table 3.3: Summary of individual habitat use and overlap of Crested Auklets equipped with geolocation devices at Buldir Island, Alaska.

Geolocator LAT- i.d. #	**0250 (male)**	**0302 (male)**	**0278 (male)**
Total Area occupied within 50% Kernel Density contour	469 690 km^2	532 580 km^2	892 850 km^2
Geolocator LAT- i.d. #	**0250 and 0278**	**0302 and 0250**	**0278 and 0302**
Area overlap between individuals	224 130 km^2	250 750 km^2	298 200 km^2
Percent Area Overlap between individuals	35%	52%	41%
Total Area overlap among ALL individu		142 750 km^2	
Total Percentage overlap among ALL individuals		22%	

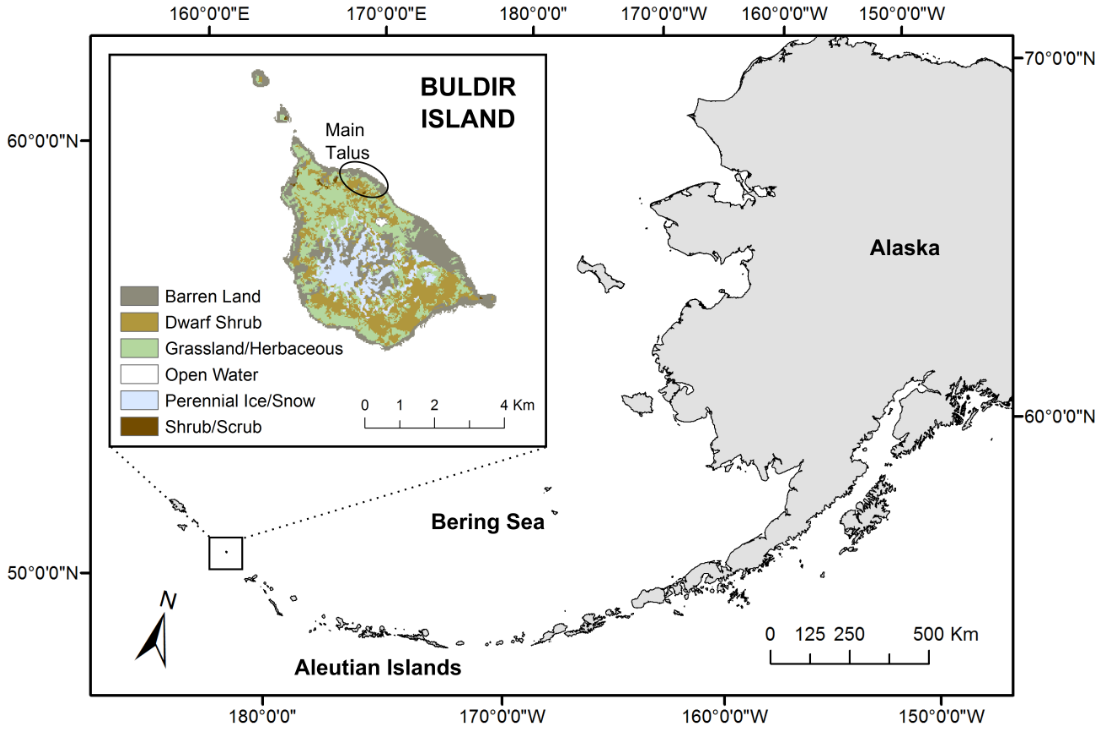

Figure 3.1: Map of Buldir Island land cover (National Land Cover Database Zone Land Cover Layer, USGS) situated in the western edge of the Aleutian Islands, Alaska. The study area is highlighted at Main Talus. Map projection: Alaska Albers Equal Area.

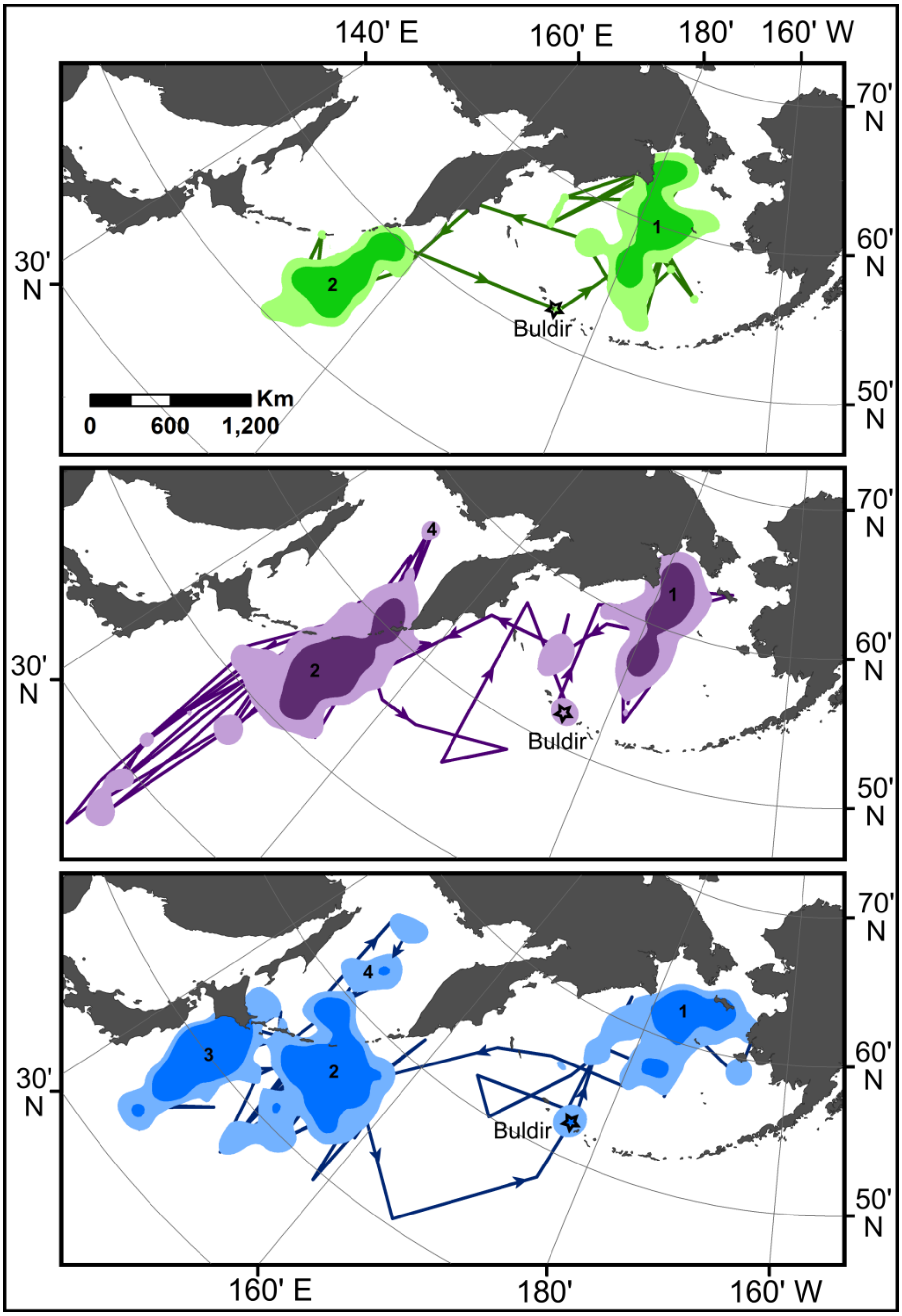

Figure 3.2: Crested Auklet (*Aethia cristatella*) distribution of bird 0250 (green; 1 Aug – 2 Dec), bird 0302 (purple; 7 Aug – 1 May), and bird 0278 (blue; 5 Aug – 6 May) during non-breeding season. Important habitat is identified by 50% (dark) and 80% (light) kernel density contours, with dark lines representing approximate flights paths between 1. Post-breeding habitat, 2. Primary winter habitat, 3. Secondary winter habitat, 4. Pre-breeding habitat. The star represents breeding origin at Buldir Island, Alaska. Map projection: Alaska Albers Equal Area.

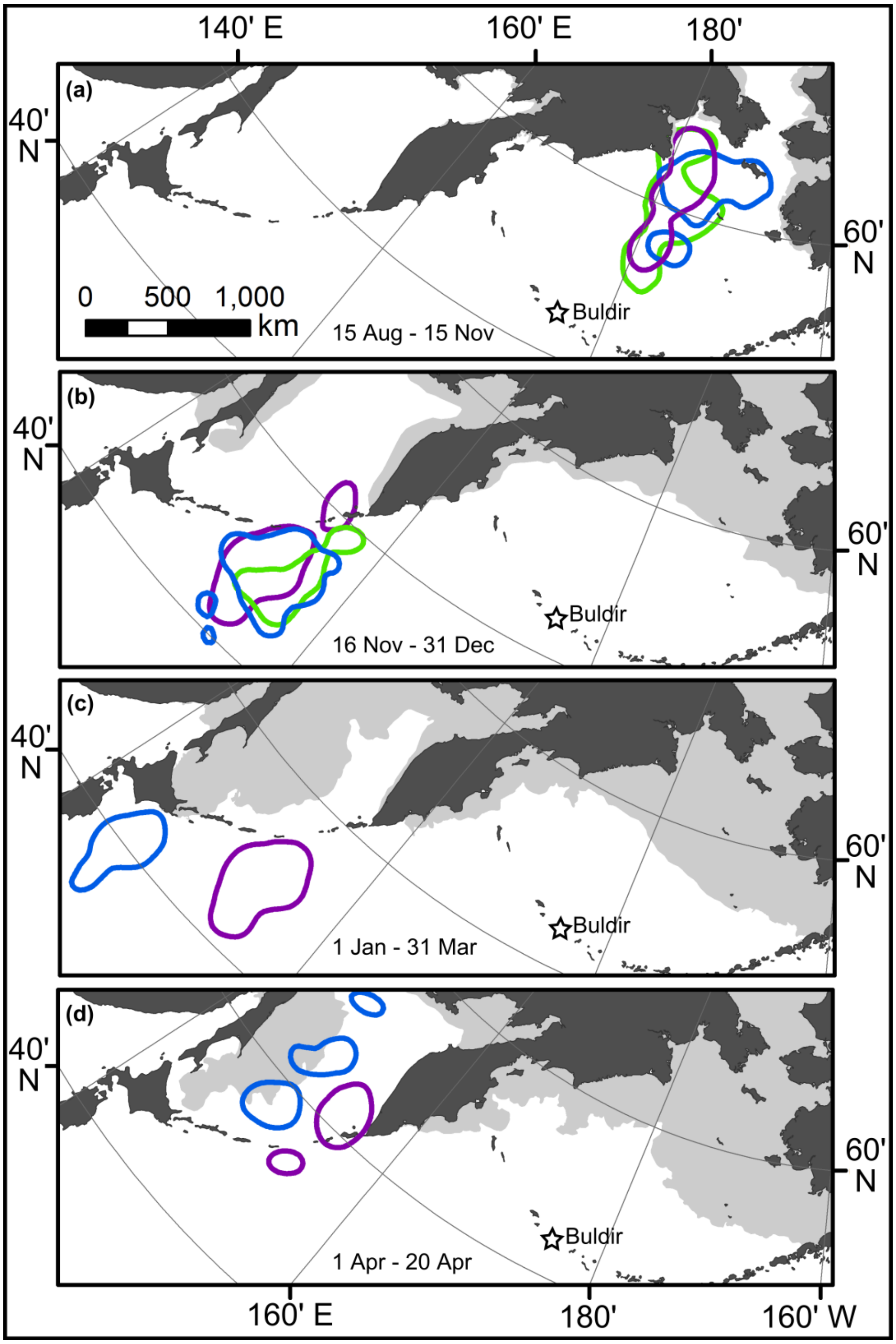

Figure 3.3: Seasonal distribution of bird 0250 (green), bird 0302 (purple) and bird 0278 (blue) Crested Auklets (*Aethia cristatella*) originating at Buldir Island, represented by 50% occupancy contours. Temporal sea ice extent (gray) on (a) 15-Nov (b) 31-Dec (c) 31-Mar and (d) 20-Apr. Map projection: Alaska Albers Equal Area.

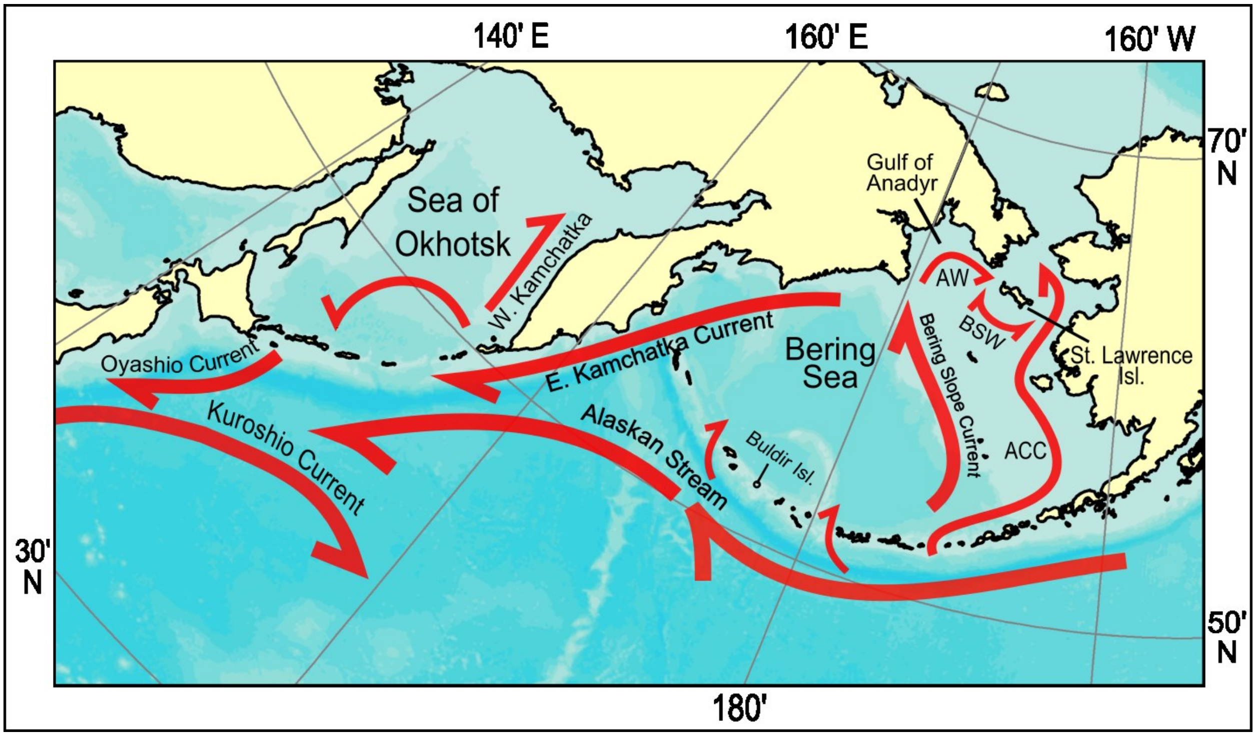

Figure 3.4: Ocean bathymetry and primary ocean currents of the North Pacific, demonstrating productive areas of upwelling important to planktivorous seabirds, where water currents meet at a front, move between islands or move up inclines in bathymetry. Map projection: Alaska Albers Equal Area. Adapted from (Harrison et al., 1999; Renner et al., 2008)

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CHAPTER FOUR:

SUMMARY AND CONCLUSIONS

4.1 SUMMARY OF RESULTS

The objectives of my thesis were to examine the feasibility of attaching tracking devices to adult Crested Auklets, (Chapter Two) and to quantify the movement of tagged individuals during the non-breeding season, (Chapter Three). The results of my thesis provide a valuable stepping stone for the increasing number and value of geolocation tracking studies, specifically those applied to small, diving seabirds. This work has revealed novel results of previously unknown migratory biology of Crested Auklets and at the same time, delivered further understanding into the critical repercussions associated with using tracking devices to infer migratory behaviour of wildlife in general. Despite the experimentally detected device effects, my study revealed new and startling information about the movement of Crested Auklets, including an unexpected post-breeding northward migration (c.1500 km) followed by previously undocumented wintering areas of Aleutian birds in productive waters off northern Japan. In a changing climate, with increasing anthropogenic threats, this field of research becomes ever more essential in developing strategic management plans for seabird conservation, and must be met with equally stringent research to investigate effects of devices in order to reach biologically relevant conclusions.

Prior to my study, very little was known about the distribution of Crested Auklets during the non-breeding season, particularly those breeding at ice-free Aleutian islands (Bond et al., 2011a). Most knowledge of their movement following the breeding season was speculative and derived from trends observed in their abundance from opportunistic at-sea ship surveys. My study rejects the previous hypothesis that Crested Auklets originating from Buldir Island (and other western Aleutian breeding sites) exclusively travel east during the winter to occupy productive waters in the eastern Aleutians (Renner et al., 2008; Bond et al., 2011a). With the use of geolocation tracking devices, these results have uncovered an unexpected, long distance migration of individuals travelling from Buldir Island to the north-western Bering Sea, and further east off the coast of Hokkaido and the Kurile Islands before returning back to Buldir. This new knowledge has important implications for future conservation plans for Crested Auklets and other ecologically similar marine life.

In light of these exciting results provided by the geolocators, questions relating to the relevance of these data are of particular interest in order to maintain biological and ethical integrity of migratory research. Behavioural artifacts of tracking devices used on individual Crested Auklets were detected, significantly altering nest site fidelity, colony return rates, provisioning behaviour and daily social activity on the surface of the colony. These detrimental effects on individual behaviour, in turn, further translated to reduced mass of chicks being provisioned by tagged adults. Tracking devices that alter a birds' natural behaviour hold important meaning for the quality of data collected by these tagged individuals. While this thesis presents previously unseen migratory biology of Crested Auklets, the results should be interpreted with caution due to surprising evidence for significant effects of tarsus-mounted geolocators on tracked individuals. Fortunately, smaller and lighter geolocation tags (50% of the mass of the LAT2900 tags used in my study) are now available, providing the opportunity to measure Crested Auklets' movements with a predicted decrease in encumbrance to the birds.

4.2 APPLICATIONS OF SEABIRD TRACKING RESEARCH

4.2.1 Seabirds as environmental samplers

Knowledge about current physical and biological characteristics of the marine ecosystem that fluctuate spatially and temporally is important in implementing wildlife management strategies (Wilson et al., 2002). Remote sensing devices currently have the capacity to sample and store data of multiple environmental variables, including SST (sea surface temperatures), salinity, and water pressure (Burger & Shaffer, 2008). With the use of these devices seabirds can provide a valuable indication of existing oceanographic conditions by sampling the specific variables of the immediate environment they inhabit (Piatt & Sydeman, 2007). By quantifying movement of a low-trophic species, such as Crested Auklets, my results revealed the distribution of prey and allow researchers to evaluate spatial and temporal variability of highly productive areas. Through the use of tracking devices, we can better understand the status of marine prey and can improve our ability to conserve those species higher up the food chain that ultimately depend on primary and secondary ocean productivity.

4.2.2 Seabird biology year-round

Due to the high degree of mobility observed in birds and across a broad diversity of taxa, understanding animal movement across resource-rich habitats is critical to implementing conservation strategies specific to each species (Webster et al., 2002). Most seabirds occupy vast areas, moving across variable habitats to exploit patchily distributed resources (Weimerskirch, 2007; Wakefield et al., 2009). This poses a serious challenge in designing and implementing conservation strategies that protect seabirds year-round, as their distribution spans great distances and often fluctuates considerably in space and time (Martin et al., 2007).

Seabird distribution is often studied independently during breeding and non-breeding seasons, and consequently management strategies developed and applied to their conservation tend to also be implemented independently (Martin et al., 2007). Much of what we know about Crested Auklet biology comes from studies conducted at their breeding sites. While they have been studied intensely during the breeding season (Zubakin, 1990; Fraser et al., 1999; Zubakin et al., 2010), even their most basic biology during the non-breeding season remains poorly known (Bond et al., 2011a). Often aspects of seabird behaviour, ecology and physiology during the breeding season are assumed to be unchanged during the non-breeding season. In order to better understand any species and the factors that limit their survival as a whole, we must directly measure and evaluate their biology holistically and implement strategies that manage their conservation during their entire annual cycle. Through the use of highly advanced tracking equipment and remote-sensing technology, researchers aim to obtain a complete and comprehensive approach to understanding year-round biology of seabirds.

4.2.3 Threats to seabird conservation

Our environment is rapidly changing as a result of human activity which has led to a number of devastating outcomes causing extreme climatic variation, pollution, and habitat fragmentation (Bouquegneau, 1997). Seabirds are among the most threatened organisms on the globe, facing many direct and indirect pressures that challenge their survival both at sea and at the breeding sites (Sydeman et al., 2012; Gilg et al., 2013). Growing industrial activity in marine environments (oil, pollution, fishing, shipping) and rapid climatic change can significantly affect large-scale oceanographic processes, and consequently impact critical seabird habitat (Gilg et al., 2013, Hedd et al., 2011). Due to the patchy distribution of prey, seabird distribution is also very patchy, aggregated in dense clusters to exploit predictably productive areas (Hunt et al., 1993), making them particularly vulnerable to localized anthropogenic or environmental catastrophe (Hunt et al., 1993). Furthermore, there is often a high degree of overlap among important seabird habitat, and sites for existing or proposed oil and gas development, intensive fishery activity or major shipping lanes, which poses a great concern for the future of seabirds through habitat loss and degradation (Le Corre et al., 2012; Fort et al., 2013).

Seabirds from the Alcid family that spend the majority of their time on the surface of the water, resting or diving for food (Gaston & Jones, 1998; Fort et al., 2013), are particularly vulnerable to surface marine pollution, primarily from accidental oil leakage from ships or large scale spills (Piatt et al., 1990b). In addition, plastic pollution aggregated mostly at the surface of the water by wind and ocean currents, creates marine debris that is often confused for prey by many animals, notably surface feeders, as well as planktivorous diving seabirds (Robards et al., 1995; Blight & Burger, 1997).The ingestion of plastics has been documented to occur in a number of auklets and is a growing problem for the world's population of seabirds (Robards et al., 1995; Avery-Gomm et al., 2013).

Lastly, because seabirds occupy habitat across both marine and terrestrial environments they may be particularly sensitive to variability in climate and provide a valuable indication of major changes in various ecosystems (Sydeman et al., 2012). According to Gaston et al. 2009, seabirds also have a limited range of responses to climatic change. Evidence for changing climatic regimes influencing reproductive performance has been documented for a number of planktivorous seabirds, including Crested Auklets (Kitaysky & Golubova, 2000; Bond et al., 2011a). There is temporal lag that exists between physical changes to the environment attributable to shifting climatic conditions and its subsequent impact on species at higher trophic levels (Wakefield et al., 2009). This is very concerning for conservation of these species that cannot respond fast enough to changing climate. For species like Crested Auklets that are known to distribute close to sea ice edge habitat and occupy a low trophic position, they may be directly impacted by changes to sea ice in the Arctic, as documented for a number of other Alcids

(Mosbech et al., 2011). Using tracking technology, we can monitor seabird movement over time to measure how they respond to changes in their environment and in turn, work towards improving conservation efforts.

4.3 FUTURE RESEARCH

With an increasing number of tracking devices being applied to wildlife across a wide range of taxa, it is not only important to scientifically control studies to maintain biological merit, but also in order to maintain a high standard of ethical practice in research. It is of particular importance to ensure that such devices are not having an impact on survival of endangered or threatened those species, which often tend to be the target of this type of research (Guilford et al., 2012). In order to fully substantiate the tracking results from my study, and to ensure that data is representative of the population of Crested Auklets, and reflects natural migratory behaviour without causing harm to tagged individuals, further research is required. Here I propose future studies that would help better understand the results I've presented and how they can be effectively interpreted.

4.3.1 Future Research to improve wildlife tracking practices

A new experimental approach that directly measures how these detected effects impact non-breeding movement must be implemented. In Chapter Two, I clearly outlined how these effects are disturbing aspects of Crested Auklet biology as far as I can measure them, during the breeding season. Using these findings, I predicted expected effects on aspects of their biology during the non-breeding season, including reduced foraging and flight efficiency. While this study is valuable, I was unable to directly measure how these effects impact their at-sea movement, the measure of which we are most interested in. These data suggest that the most striking evidence for a strong tag effect was experienced at-sea, as shown by the reduced proportion of tagged individuals that returned to the breeding site between years. This could be the result of increased aerodynamic and/or hydrodynamic drag, or reduced flight maneuverability and agility due to altered centre of mass, translating to increased vulnerability to predators, and most likely, increased vulnerability to severe weather conditions characteristic of North Pacific winters.

An experiment designed to measure how geolocators directly affect at-sea movement is necessary to filter out the many potential sources for the observed low return rates in tagged individuals. Being able to pinpoint the aspect of their biology most affected by the tags would also be important to effectively diminish these effects in order to maximize biological relevance and minimize undue harm to tagged individuals. A field study to determine best tracking practices could be developed by deploying a number of geolocators of different device mass and shape, and attachment technique. This research could further benefit from laboratory experiments designed to evaluate aerodynamic and hydrodynamic efficiency of tags in closed systems. These types of experiments would allow us to investigate thresholds of mass and size that significantly alter behaviour and movement of the study species. Additionally, a meta-analysis of existing tracking data is recommended as a valuable means of assessing tag disturbance to particular species prior to tag deployment.

4.3.2 Future Research to improve knowledge of seabird biology

In order to effectively evaluate the quality of collected migration data and understand its significance on a broader scope, research that expands into a broader-based, multi-year tracking study would be valuable. Building upon current knowledge to incorporate migration data that can evaluate spatial and temporal trends in movement over time specific to sex, mating pairs, and breeding origin will allow us to better understand how consistent or variable their movement is through time and how it differs in response to changing external variables. This area of research could provide useful information important to the conservation of Crested Auklets, and other highly mobile species. Knowing how Crested Auklets may respond to changes in their environment, including habitat loss and degradation, and shifts in climate and weather patterns would be very valuable. An investigation into the degree of migratory flexibility that Crested Auklets exhibit could also be very beneficial in interpreting results from tracking research. For example, it would be very helpful to know whether a stressed individual, under added mass and/or drag of a tracking device, would alter their migratory behaviour to accommodate this change, or have fixed migratory behaviour in response to various stimuli.

In Crested Auklets, summer distribution during breeding season is strongly conserved, with a high degree of fidelity to not only the same colony between years, but also to the same nest site in consecutive years (Zubakin, 1990). The degree of individual fidelity to specific locations during the non-breeding season is unknown in Crested Auklets. Although this field has recently gained increasing attention, it remains a poorly understood area of research for many species of seabirds (Dias et al., 2013). In some cases, variation in habitat selection occurs between years, and across different sexes, mates, and age cohorts (adult, vs. juveniles). A number of studies have begun to reveal interesting information relating to non-breeding site fidelity of many marine animals, illustrating diverse degrees of plasticity across species. One study showed that some long-distance migrants exhibit a high degree of fidelity to non-breeding locations (Dias et al., 2013), including Black-browed Albatross (*Thalassarche melanophrys;* Phillips et al. 2005). This fixed migratory behaviour could be problematic, leading to devastating consequences for the survival of these species in a rapidly changing climate (Dias et al., 2013).

In some cases, climate has been documented to significantly alter migratory phenology in species, which in turn could cause a temporal mismatch between consumer needs and prey availability (Jenni & Kéry, 2003; Marra et al., 2004; Gunnarsson et al., 2005; Gaston et al., 2009). Few studies have described this high degree of migratory flexibility in pelagic migrants, including Cory's Shearwaters, (*Calonectris diomedea;* Dias et al. 2013), and Australasian Gannets (*Morus serrator;* Ismar et al. 2011). Migratory plasticity could be a great evolutionary advantage in a changing and shifting environment where individuals are able to adapt migratory routes and winter areas in response to environmental conditions (Dias et al., 2011). With further long-term research on their migratory activity, we can better understand how this applies to Crested Auklets and subsequent conservation strategies.

4.4 IN SUMMARY

Migratory behaviour is prevalent in 80% of avian species, posing a unique challenge to developing conservation strategies (Martin et al., 2007). The key to effectively protecting highly mobile species is to build a strong foundation of knowledge on their habitat use, connectivity between habitats and understanding challenges to their conservation by identifying primary threats to their survival (Martin et al., 2007). Using tracking devices, we can better understand the distributional relationship between seabirds to their prey, and form an understanding of how they respond to large-scale disturbances to habitat and prey abundance, ultimately making us better equipped to protect them (Piatt & Sydeman, 2007). By continually monitoring the temporal distribution of seabirds, the aim is to protect them from year-round threats to their survival and adapt to changes in their habitat use, driven by climate changes that alter habitat selection through time. By identifying hot spots that are important to seabirds, and recognizing the most prevalent threats to their survival, marine protected areas can be effectively established.

In the last century, we have made astounding biological leaps by advancing our understanding of bird biology, and their incredible migratory behaviour. Through the use of advanced tracking technology, we have come a long way from initial theories that the disappearance of many species of birds during the winter was a result of mass population hibernation (Robinson et al., 2010; Bridge et al., 2011). Currently, we are able to capture profound information on migration routes and at-sea behaviours of many seabirds at finer scales than were previously unattainable. Although tracking studies certainly have their limitations, remote sensing devices are capable of collecting biologically important information, not only about the tagged individual, but also about the environment it inhabits (Burger & Shaffer, 2008). In the future, it is hoped that sensors attached to seabirds can be used to quantify additional variables of the environment, including measurements of pollutants and nutrient content (Burger & Shaffer, 2008).

New areas of study that have budded off from seabird tracking research continue to answer important questions relating to their ecology and conservation measures, linking their pelagic and terrestrial lifestyles. By interlacing various migration technologies, we move towards an interdisciplinary strategy that incorporates a combination of data from stable isotopes in feathers, at sea observation, tracking devices, and on-site behavioural observation (Robinson et al., 2010; Bridge et al., 2011). This rapidly advancing area of wildlife research is a place for genetic, evolutionary, ecological and behavioural studies to come together, pooling knowledge, and expertise holistically (Dingle & Drake, 2007). This thesis has provided an effective building block in developing our knowledge of the migratory behaviour of a poorly understood Alcid in the North Pacific, encouraging future investigation into this species biology, while maintaining the ethically and biologically sound use of advanced tracking technology.

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APPENDIX A: Lotek Wireless, Lat-2900 Series Avian Geolocator

Product specifications of the Lat-2900

LAT-2900	Production Specifications
Dimensions	8 x 15 x 7 mm
Weight in air	2.0 g
Logging memory	Up to 56 kilobytes
Standard depth range	200m
Sample rate settings	≥1 s in 1 sec. increments
Data downloads	Gold electrical contacts
Typical life	1 year
Data resolution	Up to 12 bits
Sensors	Temperature, light, sea water
Temperature measurement	-5 °to +45 °C
Temperature accuracy	Better than 0.2 °C (when within -5 °to +35 °C)
Temperature resolution	0.05 °C or better
Log Types	Basic Log

*Basic Log: allows the sampling of a number of variables at a prescribed interval, depending on the duration of time sampling. (Higher sampling rate has reduced sampling days)

APPENDIX B: Tag Talk: data download software

Example of data collected from Lat-2900 (bird-0250)

Date	01/09/2011	02/09/2011	03/09/2011	04/09/2011	05/09/2011
Sunrise	958	960	957	966	976
Sunset	1925	1918	1843	1897	1889
TF Lat North [degs]	65.153	66.297	47.74	61.479	61.699
TF Lat South [degs]	65.153	66.297	31.57	61.479	61.699
TF Noon North	1447	1425	1446	1434	1445
TF Noon South	1447	1425	1450	1434	1445
TF Lat Error North	2.08	8.194	16.757	5.826	3.247
TF Lat Error South	2.08	8.194	27.788	5.826	3.247
TF Lon Error North	3.164	10.223	5.039	7.271	3.523
TF Lon Error South	3.164	10.223	5.203	7.271	3.523
SST [C]	4.14	4.16	3.34	2.44	2.54
SST Time	25	1333	159	1240	206
+Latitude [degs]	70.49	70.49	64.16	70.14	69.43
Longitude [degs]	179.61	-179.85	-170.18	-178.13	-178.47
TF Lon North [degs]	178.23	-176.35	178.32	-178.76	178.41
TF Lon South [degs]	178.23	-176.35	177.32	-178.76	178.41

Definitions of data types:

TF : Template Fit: complex algorithm designed to estimate position fix for Lotek, Lat2900 (Ekstrom, 2004)

Lat: Latitude estimate; **Lon**: Longitude estimate for both **North** AND **South** hemispheres and associated **Error** estimates (in degrees).

SST: Sea surface temperature, and **Time** of measurement.
If the tag is wet for more than two samples (60 second intervals). If the new measurement of temperature is smaller than the previous, then current values will replace the previously saved.

APPENDIX C: ArcGIS MetaData

Sea Ice Data

Source: NOAA, U.S. National Ice Center, Naval Ice Center

Products on Demand; http://www.natice.noaa.gov/ps/javascriptproductviewer/index.html

Data Type: Shapefile Feature Class

Shapefile: C:\Users\iljones\Documents\R working Directory\ice\arctic_daily_11152011\Arctic_Daily_11152011.shp

Geometry Type: Polygon

Coordinates have Z values: No

Coordinates have measures: No

Projected Coordinate System: North_Pole_Lambert_Azimuthal_Equal_Area

Projection: Lambert_Azimuthal_Equal_Area

False Easting: 0.00000000

False Northing: 0.00000000

Central Meridian: 0.00000000

Latitude of Origin: 90.00000000

Linear Unit: Meter

Geographic Coordinate System: GCS_WGS_1984

Datum: D_WGS_1984

Prime Meridian: Greenwich

Angular Unit: Degree

Lat 2900 – Bird Geolocation Data

Data collected from all three geolocators, downloaded using TagTalk

Data Type: Shapefile Feature Class

Shapefile: C:\Users\iljones\Documents\R working Directory\ARC\Filtered\0250L_pr.shp

Geometry Type: Point

Coordinates have Z values: No

Coordinates have measures: No

Projected Coordinate System: NAD_1983_Alaska_Albers

Projection: Albers

False Easting: 0.00000000

False Northing: 0.00000000

Central Meridian: -154.00000000

Standard_Parallel_1: 55.00000000

Standard_Parallel_2: 65.00000000

Latitude Of Origin: 50.00000000

Linear Unit: Meter

Geographic Coordinate System: GCS_North_American_1983

Datum: D_North_American_1983

Prime Meridian: Greenwich

Angular Unit: Degree

Basemap – Continent

World Continents represents the boundaries for the continents of the world.

Data Type: Shapefile Feature Class

Shapefile: C:\Users\iljones\Documents\MUN 2011\CRAU_GISdata\Collected Maps\world_basemap\continent.shp

Geometry Type: Polygon

Coordinates have Z values: No

Coordinates have measures: No

Geographic Coordinate System: GCS_WGS_1984

Datum: D_WGS_1984

Prime Meridian: Greenwich

Angular Unit: Degree

Basemap – Shade relief/ Ocean bottom

This map is designed to be used as a base map by GIS professionals to overlay other thematic layers such as demographics or land cover. The base map features shaded relief imagery, bathymetry, and coastal water features designed to provide a neutral background for other data layers. The map was compiled from a variety of sources from several data providers, including the U.S. Geological Survey, Tele Atlas, AND, and ESRI. The base map currently provides coverage for the world down to a scale of ~1:1m and coverage for the continental United States and Hawaii to a scale of ~1:70k. For more information on this map, visit us online at http://goto.arcgisonline.com/maps/World_Terrain_Base.

Basemap – Land Cover (Buldir Island)

Source:

Originator: U.S. Geological Survey

Publication_Date: 2003/09/01

Title: National Land Cover Database Zone Land Cover Layer

Edition: 1.0

Geospatial_Data_Presentation_Form: remote-sensing image

Publication_Place: Sioux Falls, SD

Publisher: U.S. Geological Survey

References:

Homer, C., C. Huang, L. Yang, B. Wylie and M. Coan, 2004. Development of a 2001 national land cover database for the United States. Photogrammetric Engineering and Remote Sensing Vol.70,No.7,pp 829-840 or online at www.mrlc.gov/publications.

The USGS acknowledges the support of USGS Alaska Science Center in development of data in this zone.

Online_Linkage: http://www.mrlc.gov

Abstract:

The National Land Cover Database 2001 land cover layer for mapping zone ak01 was produced through a cooperative project conducted by the Multi-Resolution Land Characteristics (MRLC) Consortium. The MRLC Consortium is a partnership of federal agencies (www.mrlc.gov), consisting of the U.S. Geological Survey (USGS), the National Oceanic and Atmospheric Administration (NOAA), the U.S. Environmental Protection Agency (EPA), the U.S. Department of Agriculture (USDA), the U.S. Forest Service (USFS), the National Park Service (NPS), the U.S. Fish and Wildlife Service (FWS), the Bureau of Land Management (BLM) and the USDA Natural Resources Conservation Service (NRCS). One of the primary goals of the project is to generate a current, consistent, seamless, and accurate National Land cover Database (NLCD) circa 2001 for the United States at medium spatial resolution. This land cover map and all documents pertaining to it are considered "provisional" until a formal accuracy assessment can be conducted. For a detailed definition and discussion on MRLC and the NLCD 2001 products, refer to Homer et al. (2004) and http://www.mrlc.gov/mrlc2k.asp.

The NLCD 2001 is created by partitioning the U.S. into mapping zones. A total of 66 mapping zones within the conterminous U.S., with an additional 13 in Alaska, were delineated based on ecoregion and geographical characteristics, edge matching features and the size requirement of Landsat mosaics. Mapping zone ak01 encompasses a portion of Alaska. Questions about the NLCD mapping zone ak01 can be directed to the NLCD 2001 land cover mapping team at the USGS/EROS, Sioux Falls, SD (605) 594-6151 or mrlc@usgs.gov.

Purpose: The goal of this project is to provide the Nation with complete, current and consistent public domain information on its land use and land cover.