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INCUBATION STRATEGY IN MARINE BIRDS

by

AKIKO SHOJI

Thesis submitted to the
Faculty of Graduate and Postdoctoral Studies
University of Ottawa
in partial fulfillment of the requirements for the
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ABSTRACT

The incubation shift length of the Ancient Murrelet (*Synthliboramphus antiquus*), an exceptionally long and varied for an auk. I studied colonies of this species at East Limestone Island (1993-1995, 2002-2003: data collected by Laskeek Bay Conservation Society) and Reef Island (2007-2008), Haida Gwaii, British Columbia. Incubation shift length was correlated between pair members and my results show that maintaining incubation schedule was an essential component of reproductive success. Incubation shift length varied in response to prevailing local weather and sea conditions (e.g. wind speed, wave height), perhaps as a consequence of reduced foraging efficiency. Incubation shift length was longer in years when sea surface temperature in April was high. In years with longer shift, birds had lower reproductive success and chicks departed the nest with a lower body mass. My results explained if we assume that multi-day incubation shifts in Ancient Murrelets are the adaptively preferred strategy, through reduction in predation risk, but that actual shift lengths are modified by immediate weather and foraging constraints.

RÉSUMÉ

La durée des tours d'incubation chez le Guillemot à cou blanc (Synthliboramphus antiquus), qui est exceptionnellement longue et variée pour un pingouin, a été étudiée sur une colonie à l'île East Limestone (1993-1995, 2002-2003: données recueillies par Laskeek Bay Conservation Society) et à l'île Reef (2007-2008), Haida Gwaii, en Colombie-Britannique. Je montre que la durée de la période consacrée à l'incubation est un puissant prédicteur du succès reproducteur. Cette durée est corrélée entre les membres du couple, et mes résultats montrent que le maintien du calendrier d'incubation est un élément essentiel du succès reproducteur. La durée des tours d'incubation varie aussi en fonction des conditions météorologiques et marines (par exemple la vitesse du vent, hauteur des vagues), peut-être comme conséquence d'une moindre efficacité de la quête de nourriture. Mes résultats s'expliquent si l'on suppose que les tours d'incubation de plusieurs jours chez le Guillemots à cou blanc sont la stratégie adaptative préférée, grâce à la réduction du risque de prédation, mais que les tours d'incubation réels sont modifiés par les contraintes météorologiques immédiates et par la recherche de nourriture.

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CO-AUTHORSHIP STATEMENT

My contributions to the research and results presented in this thesis were: (1) I provided input into the development of questions and areas of research addressed under the direction of my supervisor, Anthony J. Gaston; (2) I was primarily responsible for the design and implementation of field protocols used to address these questions; (3) I organised and analysed all of the data; (4) I wrote all of the chapters/manuscripts.

Appendix I of this thesis has already been published as:

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Elliott, K. H., A. Shoji, K. L. Campbell and A. J. Gaston. *In review*. Foraging behaviour of two sympatric, planktivorous auks. Aquatic Biology.

1. GENERAL INTRODUCTION

Unlike animals that bear live young, birds do not incubate their offspring internally. Instead they lay eggs which must therefore be kept within an appropriate temperature range and atmospheric requirements to allow for embryonic development (Drent 1975; Gill 1994; Tinbergen and Williams 2002; Reid et al. 2002a). Among birds, characteristics of life history traits of incubation such as nest sites/locations, egg colour/shape, mate systems and parental care vary from species to species and from region to region (Gill 1994; Bennett and Owens 2002; Reid et al. 2002a).

In seabirds, both sexes share incubation duties, except in the Emperor Penguin (*Aptenodytes forsteri*) where only the male undertakes incubation duties, allowing the female to replenish her body reserves (Hamer et al. 2002). Most seabirds divide incubation fairly equally between the sexes, and Auks divide the job very equitably (Gaston 2004). Pair members alternate incubation and feeding where shifts vary in length between 1-2 hours (Laridae) to 20 days (Diomedeidae; Fig 1.1) depending on life history strategies of the species.

While breeding, the area over which seabirds can forage is constrained by their need to return to the nest to relieve their mate or feed their nestlings (Gaston 2004). Black Guillemots (*Cepphus grylle*), which make up to ten trips per day to feed nestlings, forage within 10 km of the colony (Cairns 1987). In contrast, Wandering Albatrosses (*Diomedea exulans*) may move as far as 3,600 km from the nest during incubation (Weimerskirch et al. 1994) and the reported average incubation shift length was 8.1 days (Tickell 1968). In the case of the Thick-billed Murre (*Uria lomvia*), Gaston (2004) reported that incubation shift length varies widely among colonies and this relates to the distance that birds travel to the feeding area.

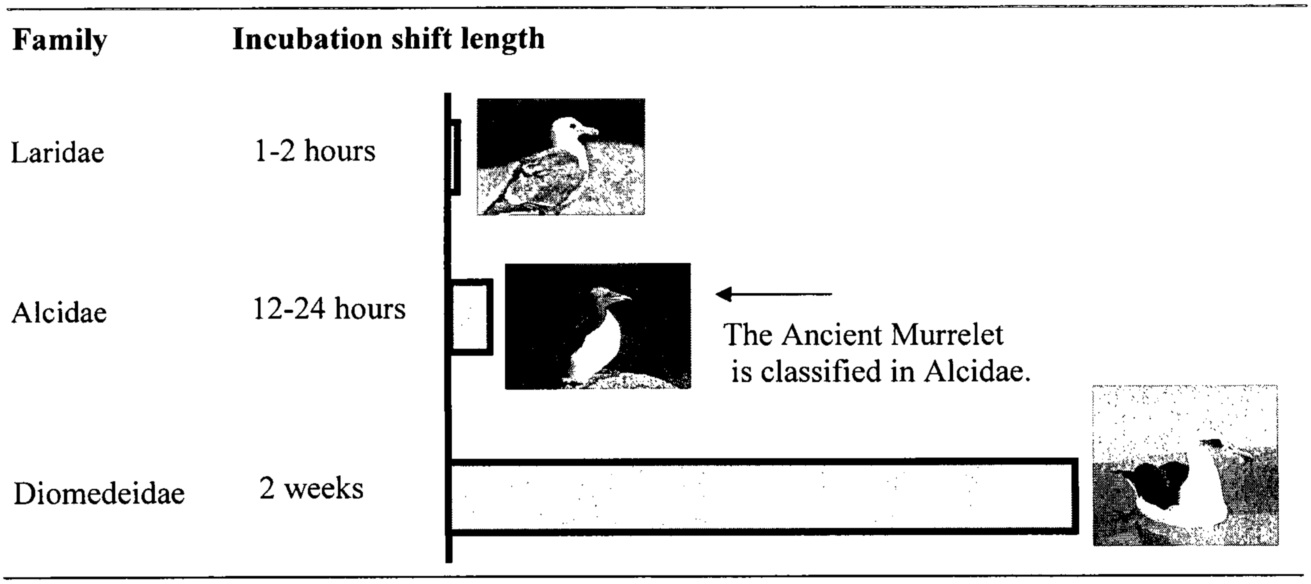

Figure 1.1: Variation of the incubation shift length among seabird families.
Photo copy right: Herring Gull *Larus argentatus* © Clint Anglin, Thick-billed Murre *Uria lomvia* © Grant Gilchrist, Laysan Albatross *Diomedea epomophora* © Susan Kaveggia.

On Coats Island, where most feeding takes place within 100 km of the colony, incubation shifts average 12 hours, whereas at the much larger Digges Island colony, birds travel well over 100 km to feed and incubation shifts exceed 24 hours (Gaston and Noble 1985). A general tendency for birds that forage farther from the breeding site to have longer incubation shifts has been noted (Lack 1968).

Many pelagic seabirds undergo large variations in their body mass during the incubating period when the male and the female alternate on the nest (Fisher 1967; Prince et al. 1981). The need to replenish body reserves may cause some incubators to leave the nest before their mate returns, resulting in the egg being temporarily unincubated – such interruption to incubation are referred to as "egg neglect", while "desertion" is used to describe a clutch where incubation has ceased altogether (Drent 1975; Gaston 2004). Temporary egg neglect may occur in successful as well as in unsuccessful breeding attempts, but it increases the risk of breeding failure (Wheelwright and Boersma 1979; Chaurand and Weimerskirch 1994a).

Interruptions to incubation occur routinely in many species of birds (Gaston and Powell 1989). Birds abandon their eggs during incubation when their reserves dwindle to critical levels (Gill 1994). This has been observed in a variety of seabird species (Davies 1982; Monaghan et al. 1992; Weimerskirch 1995; Erikstad et al. 1997). There appears to be a threshold value of body condition below which a bird will abandon the nest even if the partner has not returned to relieve its mate (Boersma and Wheelwright 1979; Chaurand and Weimerskirch 1994b). Maintaining the incubation schedule between the male and the female is critical in ensuring that the on-duty bird does not reach the threshold mass during fasting due to the partner's absence. Thus, incubation shift lengths are probably associated with distances to foraging areas (Lack 1968; Ashmole 1971), the ability to fast and the physical condition of the adult who needs to build up energy stores for its next incubation shift (Chaurand and Weimerskirch 1994a; Weimerskirch 1995). In species where mates contribute similar effort to incubation, the strategy of one parent necessarily is partially dependent on the behaviour of its mate. As a result, central-place foragers must decide how to trade-off travel time with foraging efficiency to allow for the physical conditions of the mates attending eggs.

Lack (1968) suggested that seabirds nest on inaccessible oceanic islands to avoid mammalian and avian predators. Most seabirds nest either on the open-ground where predators are absent, or a few nest on cliffs or in burrows that they dig themselves (Gaston 2004). Moreover, presumably colonial nesting and being nocturnal are anti-predator functions and predation pressure is a major factor in selecting breeding sites (Cody 1973; Martin and Roper 1988; Martin 1988). As seabirds are long-lived, it is particularly important to minimise the risk of adult mortality, thus parents should continuously evaluate the value of current reproductive efforts in offspring and the potential costs for future reproduction (Williams 1966; Partridge and Green 1985). Predation on seabirds at breeding colonies has been well studied and it appears that predation has a strong influence on the ecology of seabirds to adopt strategies to reduce predation risks (Watanuki 1986; Bretagnolle 1990; Mougeot and Bretagnolle 2000; Gaston 2004; Keitt et al. 2004; Riou and Hamer 2008; Ronconi and Hipfner 2009).

Generally seabirds are diurnal, but the majority of the *Procellariiformes* and burrow nesting *Alcidae* that are very vulnerable on land, are nocturnal on their breeding ground. Mougeot and Bretagnolle (2000) reported that the predation risk on Blue Petrels (*Halobaena caerulea*) and Thin-billed Prions (*Pachyptila belcheri*) was high and birds reduced their night time activities in the colony on moonlit nights. Jones et al. (1990) tested the factors affecting colony attendance on Ancient Murrelets (*Synthliboramphus antiquus*) and reported birds decreased night time activities (e.g. vocalization, colony visitation) when the moon light intensity was strong. Moreover, several studies have reported that adult birds reduced activity and altered arrival times at colonies on moonlit nights when the benefits of nocturnal activity are decreased (Leach's Storm-petrels *Oceanodroma leucorhoa*: Watanuki 1986; Manx Shearwaters *Puffinus puffinus:* Riou and Hamar 2008; Black-vented shearwaters *Puffinus opisthomelas*: Keitt et al. 2004). Several studies have clearly shown that being nocturnal is an adaptive response designed to reduce the predation risk from diurnal avian predators (Watanuki 1986; Brooker et al. 1990; Mougeot and Bretagnolle 2000; Riou and Hamer 2008).

Life History Theory plays a part in explaining the variation of life cycles observed in nature (Reid et al. 2002a). Key components of life history are body size, growth, reproduction and longevity (Stearns 1992). A principle of life history theory is that the individuals of a species are able to make limited shifts on the schedule of reproduction and survival in response to the prevailing environments (Stearns 1992). It provides a theoretical framework for describing how organisms allocate resources to maximize the individual's lifetime fitness and this is particularly important for long-lived species such as seabirds (Sibly and Mccleery 1985). Life History Theory predicts that reproductive decisions of an individual should be adapted to environmental conditions (e.g. food availability, predation risk, and weather conditions) and intrinsic properties (e.g., body size and foraging efficiency, Bety et al. 2003). Trade-off decision making is affected by the cost of reproduction (i.e. current reproductive effort and residual reproductive value; (Williams 1966; Pianka 1976). Research into the cost of reproduction and resource allocation trade-offs amongst life-history traits has been carried out intensely on avian species. Birds are ideal candidate organisms for studying resource trade-offs, because observing avian breeding behaviour is relatively easy, most species display iteroparity and breeding events can be divided into four discrete phases: courtship, egg production, incubation and chick-rearing (Deeming 2002). Several studies (e.g. Tveraa et al. 1997: Kato et al. 2008) have pointed out that studying incubation rhythm from the perspective of Life History Theory in central-place foragers may be particularly rewarding, as the breeding failure is high during this period and fasting birds undergo large variations of body mass (hence presumably energy reserves) when attending eggs (Chaurand and Weimerskirch 1994a; Tveraa et al. 1997). However most studies have focussed on trade-offs during the chick-rearing stage, and earlier reproductive stages, including the incubation phase, have been ignored (Deeming 2002).

The objective of this thesis is to examine the incubation strategy of marine birds using Ancient Murrelets as a model species: first, by identifying factors affecting incubation shift length in Ancient Murrelets (Chapter 2), and second determining the effect of various environmental conditions on reproductive success (Chapter 3). The Ancient Murrelet is a small, colonial, burrow nesting marine bird of the family *Alcidae* which, like most seabirds, employs a high survival and low-fecundity life-history strategy. In contrast, unlike most seabirds, murrelets are unusual for their extended incubation shifts and having a rearing strategy for their chicks that does not involve feeding them in the nest: they are truly precocial and leave for the sea within two days of hatching (Sealy 1976; Gaston 1992b; Gaston 1994; Gaston 2004). Elimination of the period of chick-rearing at the colony is thought to reflect the extreme demands of raising young on prey captured far from the colony (Lack 1968; Sealy 1975), and reducing predation risks when murrelets are most vulnerable to attack on close approaches to and landings in the colony (Lima 1993). Gaston (1992 b, 1994)showed changeovers occurred at intervals of 1-6 days (median 3). Three days is a long period of time in comparison with other members of the family

(Sealy 1976; Gaston 1992b). However, no explanation of why Ancient Murrelets have such long incubation shifts is available.

One possible reason why this strategy adapted is that birds may adjust their incubation schedule to reduce a number of nest visitations that accompany a high chance to be predated by diurnal avian predators in the colony; therefore extended shift length reflects an adaptation through natural selection. Alternatively, birds may be forced to take lengthy incubation shifts because of the demands of their peculiar feeding strategy. In that case, birds may be forced to undertake extended shifts due to longer foraging trips by their mates. This would increase the probability of a longer fast for the returned bird during its next incubation shift (Kato et al. 2008).

In Chapter 2, I examine factors affecting the extended shift length and its effects on reproductive success in Ancient Murrelets. I test the following two hypotheses that extended incubation shift length is the result of:

1. foraging constraint to search for food
2. reducing predation risks by diurnal avian predators

Although the two hypotheses may not be incompatible in their effect on the behaviour in Ancient Murrelets (Jones et al. 1990), I investigate the relative influences of different variables as a proximate factor to evaluate these predictions. To test the hypotheses, I compared incubations shift lengths with weather (wind speeds and moon light intensity), timing of colony visitation and the influence of mate's behaviour during incubation. In addition, I utilized an experimental approach to examine the incubation schedule corrected for the foraging trip duration of mates (foraging trip duration = shift length). By experimentally handicapping one member of the pair as to extend the shift length, I was able to investigate the reaction of handicapped birds and their mates to increased trip duration.

In Chapter 3, I examine the effect of inter-year variation in environmental conditions on various reproductive parameters. Annual incubation shift length of murrelets is compared to determine whether inter-annual variation of shift length exists, and consequently what effects this might have on reproductive success. In chapter 4, I review and discuss the incubation strategy and adaptation consequences of marine birds and how my findings relate to the hypotheses that environmental conditions are important for reproductive success.

2. FACTORS AFFECTING INCUBATION PATTERNS IN ANCIENT MURRELETS (*Synthliboramphus antiquus*)

2.1 ABSTRACT

As with all iteroparous organisms, long-lived seabirds face a conflict between current reproductive success and lifetime reproductive success. During the incubation shifts, nest desertion is sometimes necessary to avoid starvation, but may compromise the current reproductive attempt. However, the factors underlying this decision process are poorly understood. Here, I focus on the Ancient Murrelet (*Synthliboramphus antiquus*), a seabird of the family Alcidae with an exceptionally long incubation shift length, and test the impact of several environmental factors on incubation shift length in relation to reproductive success. The study was conducted at Reef Island, British Columbia, Canada during 2007 and 2008. Using an information theoretic approach, I show that incubation shift length was a strong predictor of reproductive success, and that the most important factor explaining an individual's incubation shift length was the length of it's mate previous shift. Environmental conditions such as wind speed also influenced shift length. This study demonstrates that species-specific reproductive strategies interact with environmental conditions to form multiple incubation patterns across the Alcidae, and provide the evidence that maintaining regular incubation shifts is an essential component of reproductive success. I conclude that extended incubation shift length favours higher foraging efficiency and longer trip duration.

2.2. INTRODUCTION

Life-history theory predicts that fitness is optimised by balancing the investment in current reproduction with the costs of reducing an individual's ability to invest in future reproduction (Stearns 1992). This reproductive trade-off is expected to evolve in order to increase the genetic contribution of an individual to future generations (Krebs 2001). One set of life-history decisions that seabirds face during the breeding season is the timing, frequency, and duration of their colony visits (Mallory et al. 2008). These decisions should be manifested in the activities of individual birds in such a way as to maximize their fitness (Jones et al. 1990).

Most seabirds have biparental incubation and therefore alternate fasting bouts while incubating with foraging trips to replenish their body reserves for the next incubation duty while away from the nest. Incubation shift duration in seabirds is of interest as incubation is energetically expensive (Chastel et al. 1995; Reid et al. 2002b; Cresswell et al. 2004). As a result, seabirds undergo large variations in body mass during fasting (Weimerskirch 1995; Tveraa et al. 1998; Criscuolo et al. 2002), and the rate of breeding failure at this stage may be high (Prince et al. 1994). Nevertheless, most studies have focused on nest attendance patterns while the parents rear their young and incubation shifts have received less attention (Hamer and Hill 1994; Weimerskirch 1995; Hamer and Thompson 1997; Gray et al. 2005; Kato et al. 2008).

Interruptions to incubation occur routinely in many species of birds (Gaston and Powell 1989). Such interruptions, when followed by the resumption of normal incubation behaviour, are known as "egg neglect". Temporary egg neglect may be observed during successful as well as in unsuccessful breeding attempts (e.g. Northern Fulmar *Fulmarus glacialis,* Blue Petrels, *Halobaena caerulea*), but egg neglect may increase the probability of breeding failure (Chaurand and Weimerskirch 1994a).

The probability of permanent egg neglect or "nest desertion" by the incubating partner is increased by long foraging trips (Kato et al. 2008), as there may be a physiological limit below which a bird will abandon the nest if the partner has not returned to relieve its mate (e.g. (Boersma and Wheelwright 1979; Chaurand and Weimerskirch 1994b; Gaston and Hipfner 2006a; Gaston and Hipfner 2006b). Therefore, it is important for a particular bird to decide how long to remain at sea to replenish its energy reserves so that its partner does not leave the nest. This reasoning suggests that incubation shift length should be synchronized between pair members with respect to their partners' ability to fast (Warham 1990; Bety et al. 2003).

It has been suggested that periods of neglect may originate from unusually poor foraging conditions, or from failure to coordinate incubation patterns between pair members. In seabirds, foraging trip durations may be prolonged due to the unpredictable weather conditions and patchy prey distribution (Lack 1968: Ashmole 1971, but see Weimerskirch 1995). When conditions for feeding are good, birds are expected to spend a shorter time away from their nest. However, the fasting duration of the incubating partner is also extended, resulting in the depletion of its body reserves (Chaurand and Weimerskirch 1994a; Tveraa et al. 1997). Prolonged fasting can lead to egg neglect. I will refer to the idea that incubation shift duration is determined primarily by foraging constraints as the "foraging hypothesis" (Table 2.1).

However, incubation behaviour may also be influenced by the risk of predation (Martin and Ghalambor 1999; Smith et al. 2007). Where behavioural flexibility allows, birds are likely to adopt strategies to reduce their predation risk (Caraco et al. 1980; Ydenberg and Dill 1986; Endler 1991; Martin and Li 1992). Previous studies suggested that nocturnal colony attendance among seabirds is an adaptation to minimize predation risk from diurnal avian predators (Cody 1973; Harris 1974; Watanuki 1986). Many seabirds are diurnal, but the majority of the petrels

Table 2.1: Predictions of two hypotheses relating extended incubation shift lengths of Ancient Murrelets to foraging and predation avoidance behaviour at Reef Island during 2007- 2008.

Hypothesis	Related parameters	Prediction	No.
Foraging	Wind speeds	Shift length will increase with higher wind speeds	P1
	Effects of mates	Correlation of the duration of shifts will be shown between pair members	P2
	Inter-annual variation	Inter-annual variation should exist as shift length should change with food availability	P3
Predation avoidance	Moon phase and cloud opacity	Shift length will be affected by light intensity in the colony	P4
	No effects of mates	Shift length will be independent of mate's behaviour	P5
	No inter-annual variation	No inter-annual variation of shift length will be shown, because a major predator in this colony is one pair of Ravens (Gaston personal communication)	P6

(Procellariiformes*)* and some auks (Alcidae*)*, which are vulnerable to predation on land, are nocturnal on their breeding grounds. Some nocturnal seabirds reduce night time activity and alter timing of colony visitation on moonlit nights, supporting the idea that nocturnal visitations is an adaptation to reduce predation risk (Jones et al. 1990; Riou and Hamer 2008).

Despite nocturnal colony attendance, many Ancient Murrelets are killed by predators on their breeding colonies (Gaston 1992b). Reducing the frequency of colony visits by extending incubation shift lengths in nocturnal, burrow nesting marine birds could therefore be an adaptive strategy to reduce their mortality from predators. This explanation proposes that parents may adjust the number of visits during the nesting season in order to maximize their life-time fitness (Gaston 1992b). I will refer to this explanation for incubation shift duration as the "predation hypothesis" (Table 2.1).

In this chapter, I evaluate support for these two hypotheses (foraging, predation) as determinants of incubation behaviour, especially the duration of shifts, in the Ancient Murrelet (*Synthliboramphus antiquus*). During incubation the parent murrelets, which nest in underground burrows, visit the breeding colony only at night. Members of this genus frequently neglect their eggs for a few days, and their mean incubation shifts are long in comparison with other members of the same family, but the reason for this is unclear (Sealy 1976; Gaston 1992b; Gaston and Jones 1998; Gaston 2004). Here, I assess the extent to which environmental factors explain variation in shift lengths observed in murrelets, whether longer foraging bouts increase the probability of egg neglect by their partner and whether this result affects reproductive success. Based on available information from previous studies, I hypothesized that incubation shift length should increase with: (1) increasing wind speed (Ojowski et al. 2001), and (2) decreasing ambient light intensity (Addison et al. 2007). I also predict that shift length should be affected by synchronization of activities between partners (DeForest and Gaston 1996) and may be related to reproductive success. Finally, I compare incubation strategies between murrelets and a sympatric auk, Cassin's Auklet *Ptychoramphus aleuticus* to consider how variation in strategies may have emerged. This work provides us with a novel understanding of the proximate factors influencing the incubation shift length in a seabird and of the importance of environmental conditions on reproductive success.

2.3. MATERIALS AND METHODS

2.3.1. Study area

The study was conducted on Reef Island (52°52'N, 131°31'W), BC, Canada. The experimental part of the study was conducted 5 April-29 June 2007 and 4 April-12 June 2008. Ten days of additional field work were carried out in May 2009 to obtain additional information on diving behaviour. Reef Island is situated in the temperate climate zone with superabundant rainfall (Gaston 1992b), and covered by a mature forest of Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) with smaller patches of red cedar. The Reef Island colony supports approximately 5,000 pairs of Ancient Murrelets (Gaston 1990). Most of the field work was conducted in an area of relatively steep slopes (the average slope was about 45 degrees), cut by ravines filled with unstable scree within 300 m of the coast.

2.3.2. Field methods

General monitoring procedures of nest attendance patterns in Ancient Murrelets followed (Gaston and Powell 1989). The majority of burrows are in soft soil susceptible to damage by investigators. Consequently, artificial nest boxes were used to monitor incubation behaviour (*n* = 72; for details, see (Gaston 1996). These boxes were installed ten years prior to the study, in

1997, so that disturbance is expected to be minimal. The total numbers of occupied boxes (at least one egg laid) were 58 in 2007 and 61 in 2008. Eggs were marked to identify laying order. Their length and width was measured to calculate the egg volume index (Length × Width^2) as a surrogate for egg volume.

I set up knock-down tags at all nest box entrances, and nest boxes were inspected only when these were displaced (Gaston and Powell 1989). Knock-down tags have been widely used in studies of burrow nesting seabirds (Gaston 1992b). This technique does not allow us to distinguish individuals and is likely to overestimate the frequency of visitations compared with direct methods (e.g. marking birds or radio telemetry). However, it does give a measure of the overall trend of attendance patterns (Gaston 1992b). In addition to the knock-down method, radio transmitters (LOTEK Engineering Inc, Canada) were used to measure exact shift lengths and to test the validity of the knock down method in 2008 (n = 17, see the evaluation by Shoji and Gaston in Appendix II). Furthermore, radio telemetry allowed comparison of the duration of shifts with previous studies (Sealy 1976) who also used a direct method to monitor incubation shift length. Once the first egg was laid, two types of temperature readings were collected with temperature probes (Onset TMC1-HD or Yellow Springs Instruments 400 series) connected to a data recorder (Onset: H08-006-04). Readings were taken every 60 seconds, and data were downloaded daily. The tips of the probes were secured in the nest cup with thumbtacks fixed into the floor of the box. In 2007, vocalization activities were recorded by inserting a microphone attached to an mp3 recorder into occupied nest boxes (n = 10). Nest boxes were recorded from 22:00 to 05:00, the period when changeovers may occur. An immediate burst of chatter-calling by both members of the pair signalled the arrival of the off-duty bird; this signal was used here to determine when a bird returned to the colony. After 30 days of incubation, most birds were weighed and 1 cc of blood was sampled and stored on protein-saver paper for sexing using Polymerase Chain Reaction (Egloff et al. 2009). Handling time was < 3 mins. Five non-breeding Ancient Murrelets were collected at the colony during the 2008 breeding season following procedures described elsewhere (Elliott and Shoji 2009). Stomach contents were removed immediately and preserved in alcohol and later examined in the laboratory under a low-powered microscope. Stomach contents were unsuitable for quantitative analysis; however, zooplankton and fish fragments could be recognized and were recorded in these broad categories (Sealy 1975). All field procedures were approved by the Animal Care Committee of the National Wildlife Research Centre and the Ontario Region of Environment Canada operating under the guidelines of the Canadian Committee for Animal Care (Permit Number 0700AG02, 0800AG02).

2.3.3. Weather conditions and ambient light

Wind data were obtained from a nearby weather station within the foraging range of the murrelets (Sandspit, 40 km to the north, www.weatheroffice.gc.ca). A previous study showed that wind speed affects the ability of Ancient Murrelets at Reef Island to forage at sea at various time scales (Jones et al. 1990). Thus, I used mean wind speeds over three different time scales (6 h, 24 h, and 48 h prior to a particular night) to see if foraging conditions were associated with incubation shift lengths and the timing of return to nest. The six-hour period preceding bird return corresponds to the bird's ability to navigate to the nest; the 24 and 48-hour durations correspond to the length of typical foraging trips (modal incubation shift length = 2-3 days, Fig 2.1). Hourly wave height data were obtained from a North Hecate Strait buoy station (http://www.dfo-mpo.gc.ca/index-eng.htm). Tide height was obtained from the Queen Charlotte City (http://www.waterlevels.gc.ca/) station.

I obtained lunar phase (= moon age, www.timeanddate.com), daily cloud opacity in tenths (Sandspit, 40 km to the north, www.weatheroffice.gc.ca), and rain conditions (Sandspit, 40 km to the north, four categories: rain; rain showers; drizzle; no rain; www.weatheroffice.gc.ca) online. To estimate visibility near the colony each night, I used a light intensity index based on lunar phase, the level of cloud opacity and rain conditions as follow: [light intensity index = lunar phase (age) * the level of cloud opacity (tenths) * rain conditions (rain, rain showers, and drizzle), Table 2.2]. To examine the effect of light conditions, I added these interaction as variables in my model.

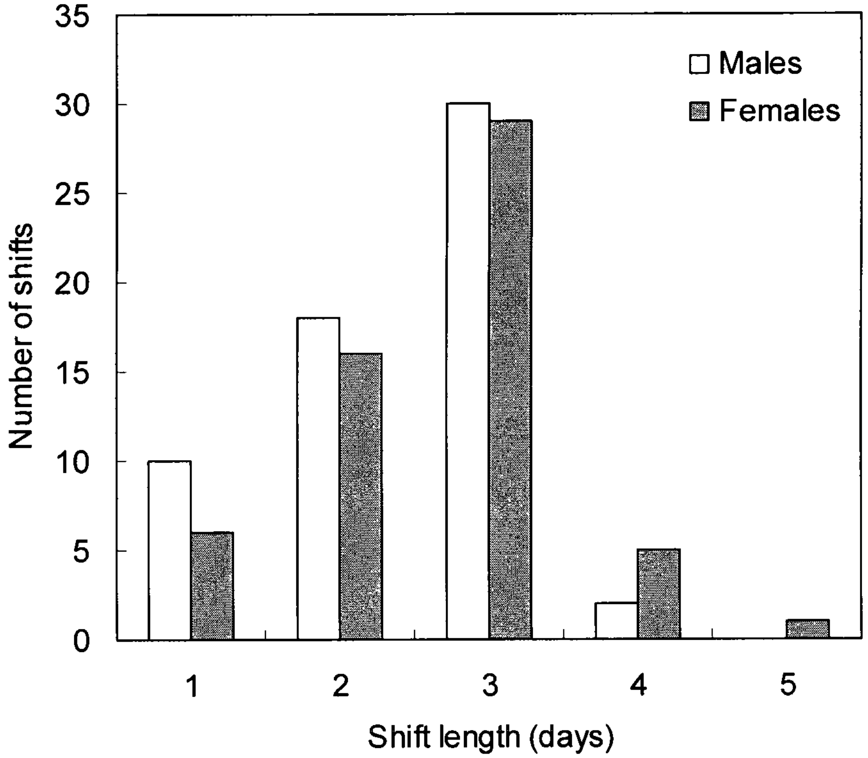

Figure 2.1: Distribution of incubation shift lengths of Ancient Murrelets at Reef Island measured by radio-telemetry at the artificial nest boxes in the study plot in 2008 (male: n = 61, female: n = 58).

Table 2.2: Variables used in models to statistically explain incubation shift length and reproductive success of Ancient Murrelet at Reef Island, Haida Gwaii, British Columbia in 2007 and 2008.

Variable abbreviation	Definition	Unit
pr_isl	Duration of the previous incubation shift length (= partner's trip duration)	day
year	Year of observation	year
beg	The date of clutch completion	date
egg	Egg volume index (Length * breadth^2) for 1st egg (Birkhead and Gaston 1988)	index
birdID	Bird identity, sexes are unknown	identity
shiftcal	Calendar date thatchangeover occurred between pair members	date
shiftstag	Days since incubation onset when changeover occurred	day
X6H	Windspeed of previous 6 hours to colony arrivals at 23:00	km/h
X24H	Windspeed of previous 24 hours to colony arrivals at 23:00	km/h
X48H	Windspeed of previous 48 hours to colony arrivals at 23:00	km/h
lunar_phase	Proportion of moon (full moon: 14-day, new moon: 1-day)	age
cloud_opacity	Cloud opacity	tenth
isl	Mean incubation shift length at each nest	day

2.3.4. Effects of partner's behaviour

I used a knock-down method to monitor the incubation shift length of partners: I considered a changeover to have occurred when tags were knocked down (Appendix II). Note that knock-down tags did not allow me to distinguish individual pair members. Comparisons of incubation shift lengths within pair members within a given year were made using Spearman correlation coefficients as incubation shift length was not normally distributed.

2.3.5. Reproductive success

After 30 days of incubation, the reproductive success of each pair was checked (Gaston et al. 1988). Forty-one of 58 and 35 of 61 pairs successfully departed at least one chick in 2007 and 2008, respectively. Because Ancient Murrelets are precocial (young are relatively mature and mobile from the moment of hatching, and leave the nest shortly after birth), I assumed all chicks that disappeared after 30 days departed successfully. Predated and hatched eggs were easily distinguished by tooth marks and shell remains (Gaston 1992a; Blight et al. 1999).

2.3.6. Foraging behaviour

To measure the frequency of dive times and dive depth (m), birds were instrumented during the daytime in the nests. During 27 April-20 May 2008, ten cylindrical Lotek 1100LTD Temperature Depth Recorder or TDRs (sampling interval = 3 s; memory = 128 Kb (55 hours); weight = 5g; diameter = 1 cm; length = 3.3 cm; accuracy = ±2m; (Elliott and Gaston 2009) were attached to incubating birds. The devices were attached with duct tape to a metal band, which was then attached to the foot with the pressure sensor facing towards the foot. I was able to retrieve three TDRs from ancient murrelets. During 28 April-12 May 2009, five birds were equipped with

Lotek 1100 LTD TDRs and eight were strapped with 1500LAT TDRs (sampling interval = 4 s with 1 s sampling when below 2 m for murrelets; memory = 512Kb; weight = 3.2g; diameter = 0.5 cm; length = 3.3 cm; precision = ±0.25m). For both TDR types, only duct tape was used without any additional metal band. Due to device measurement uncertainty, only depths >2 m were considered as actual dives. A custom-built Visual Basic macro, available from the TDR manufacturer, was used to correct for passive electronic drift (the last ten consecutive, identical pressure values before the dive), convert the pressure linearly into depth (assumed 1.00 m = 1.00 dbar = 1.41 psi) and calculate ascent and descent rates, maximum depth, dive duration and surface pause duration. The program assumed a constant descent rate of 0.98 $m \cdot s^{-1}$ to the first TDR observation and ascent rate of 0.90 $m \cdot s^{-1}$ from the last observation. Dives were broken into bouts using the sequential differences methods (70 s surface interval differences for murrelets (Mori et al. 2002). The temperature log was used to distinguish flying (temperature variable and medium) from resting on the surface (temperature constant and low or constant and high when the bird tucked its foot into its plumage) or at the colony (high temperature; low pressure). To minimize any bias associated with the diel light cycle, all dives between 22:00 to 04:00 hours were excluded as Ancient Murrelets are diurnal feeders (Sealy 1975).

2.3.7. Data Analysis

I performed all analyses with R 2.6.1 (www.cran.r-project.org). Normality of variables was checked with Komolgorov-Smirnov tests, and non-parametric tests were used where assumptions of normality were not met. I modelled the proportion of parents returning to their nests, and the proportion eggs neglected (i.e. left unincubated for a period of at least 24h) as a function of weather conditions (wind speed of previous 6 h: X6H, wind speed of previous 24 h: X24H, wind speed of previous 48 h: X48H, lunar phase (age): lunar_phase, Table 2.2) and ambient light intensity (cloud opacity: cloud_opacity, Table 2.2). The proportion of parents returning to the nest and the incidence of egg neglect were treated as proportion data, and I used a logit link function with a binomial error distribution. Because data were not normally distributed, I used a generalized linear model (GLZ).

I modelled individual shift length (days) and reproductive success (number of chicks successfully departed per nest) of pairs which had incubated their eggs >10 days, in relation to 6 environmental and 7 bird-specific predictor variables (Table 2.2). Because the data were not normally distributed with equal variances (homoscedasticity), and data were collected repeatedly at each nest box, I used a GLZ including a nest identity as a random effect (Bolker et al. 2009). Incubation shift lengths, reproductive success as the number of chicks departed were treated as count data, and I used a log link function with Poisson error distribution. For all model building exercises, I used Akaike's Information Criterion (AIC) to assess support for candidate models (Burnham and Anderson 2002). All candidate models were ranked according to their AIC score, computed as:

$$\text{AIC} = -2 \ln L + 2k$$

where k is the number of parameters in the model and L is the maximum likelihood for the candidate model (Akaike 1974). Modelswith $\Delta\text{AIC} \leq 2$ were included in the confidence set (Burnham and Anderson 2002). I computed Akaike weights to compare relative support for models .

I used a stepwise procedure to determine what factors affected each response variable. The selected explanatory variables in the best models were those that had received meaningful support (ΔAIC scores ≤ 2). Then, I used the variables selected in the first step and considered their interaction to examine the effects of individual and interacting factors on response variables. Because I had no a priori expectations for which factors would have the greatest influence on our response variables, I used an automated forward-stepwise approach. Variables were added sequentially until none reduced the AIC value. To this best additive model, I then added interaction effects to test for relationships among the retained variables.

To determine whether number of dives and dive depth are related to weather conditions, I used a GLZ with nest ID as a random effect. Dive times and depth were log-transformed to make their distribution approximately normal and therefore I used a GLZ with Gaussian distribution and log link function. Unless otherwise indicated, the results are expressed as means ± SD and all reported *P*-values are two-tailed.

2.4. RESULTS

2.4.1. Timing of nest arrivals

Exact timing of returns to the colony was available for 2007 only (from recordings of vocalisations). In this year, the average time of nest arrivals was later in the day during the incubation period (23:29, $n = 136$) than during the pre-incubation period (00:17, $n = 47$; $t = 6.89$, $P < 0.0001$). During the incubation period, the first nest arrivals on each night occurred about two hours after nautical twilight, and as the time of sunset changed throughout the season, the timing of first arrivals was predicted by calendar date ($r^2 = 0.15$, $P < 0.0001$, Fig 2.2). In contrast, timing of arrival was not significantly correlated with the calendar date during pre-incubation period ($r^2 = 0.07$, $P = 0.08$, Fig 2.2). This result suggests that adult nest arrival time during the incubation period is regulated by light conditions, but that this is less so during the pre-incubation period.

2.4.2. Adult nest arrival

The best model predicting the proportion of adults returning to their nests on a given night included effects of wind speed and ambient light (Table 2.3). Arrival rate decreased with wind speed during the preceding 48 h ($z = -16.54$, $P < 0.0001$), lunar phase ($z = -7.96$, $P < 0.0001$) and cloud opacity ($z = -3.36$, $P = 0.001$), while wind speed during the preceding 24 h increased the arrival rate ($z = 9.92$, $P < 0.0001$). In contrast, wind speed during the preceding 6 h had no effect on rate of nest arrivals. This result suggests that foraging conditions at sea have a stronger effect on the timing of return to the nest than weather conditions that may interfere with navigation while returning to the colony. Arrival rates decreased with moon phase and increased with cloud cover, suggeting that more birds arrived at their nests when the ambient light intensity was low.

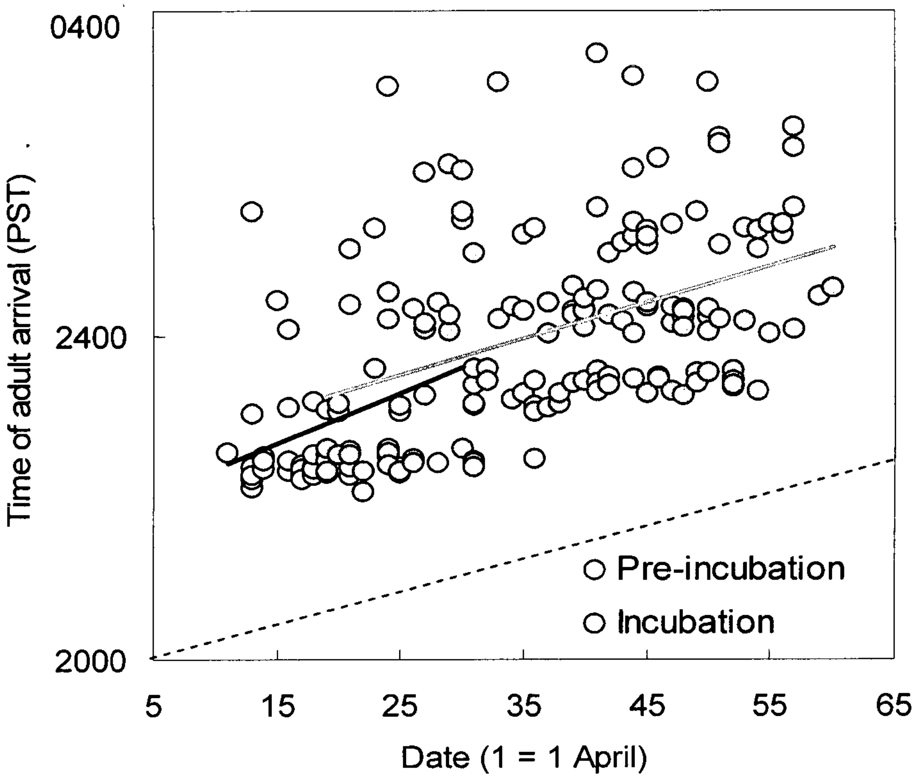

Figure 2.2: Arrival time of breeding Ancient Murrelets to entering their nest in relation to calendar date. Data points from Pre-incubation period are open circle (n = 47, black trend line), those from incubation period are filled circles (n = 136, gray trend line). Dashed line shows time of nautical dusk.

Table 2.3: Probability of adult nest arrivals (mean ± SD) and egg neglect of Ancient Murrelets in response to mean wind speeds (km/h) of various time scales in 2007 (n = 49) and 2008 (n = 51).

Model	Explanatory variables	βcoefficient	SE	Wald's statistic	df	*P*
Arrival	X24	0.033	0.003	9.922	1	< 0.0001
	X48	-0.074	0.004	-16.543	1	< 0.0001
	lunar_phase	-0.042	0.005	-7.965	1	< 0.0001
	cloud_opacity	-0.019	0.006	-3.366	1	0.001
Neglect	X6	0.011	0.004	2.624	1	0.009
	X48	0.014	0.007	2.196	1	0.028
	lunar_phase	0.049	0.009	5.203	1	< 0.0001
	cloud_opacity	-0.054	0.010	-5.528	1	< 0.0001

There was no significant difference in nest arrival time among individual nests (Kruskal-Wallis test: $KW = 13.4$, $P = 0.20$).

2.4.3. Egg neglect

The model receiving greatest support suggested that the proportion of eggs neglected on a given night was related to strong wind speed and ambient light conditions (Table 2.3). Egg neglect increased with wind speed during the preceding 6 h ($z = 0.01$, $P < 0.01$), and 48 h ($z = 0.01$, $P = 0.02$), and increased lunar phase ($z = 5.20$, $P < 0.0001$), while cloud opacity decreased the proportion of egg neglect ($z = -5.52$, $P < 0.0001$). In contrast, there was no effect of wind speed during the preceding 24 h on the proportion of egg neglect. From these results, it appears that egg neglect is likely to be affected by both foraging conditions and risk of adult predation.

2.4.4. Incubation shift length

Known sex pairs. Of 13 pairs where one of the partners was equipped with a radio transmitter in 2008, incubation shift lengths did not differ between males and females (female: 2.60 ± 0.88 days, $n = 58$; male: 2.38 ± 0.82 days, $n = 61$; $t = -1.45$, $P = 0.15$, Fig 2.1). The mean duration of 119 shifts measured by radio telemetry was 2.49 days, and 56% lasted three days or more.

Mate effects on shift length. As predicted, the duration of each incubation shift length was positively correlated with the duration of the previous shift by the partner ($r = 0.29$, $P < 0.05$, $n = 1385$), based on knock-down tags. In addition, the mean incubation shift length throughout incubation was positively correlated with that of the partner ($r = 0.64$, $P < 0.0001$, $n = 75$, Fig 2.4). The same was true of incubation shift lengths measured by telemetry, with shift length positively correlated with the duration of the previous incubation shift length by the partner for both males ($r = 0.33$, $P = 0.01$, $n = 13$) and females ($r = 0.26$, $P < 0.05$, $n = 13$). Mean incubation shift length differed among pairs ($KW = 259$, $P < 0.0001$).

2.4.5 Test of the models

Factors affecting incubation shift lengths. A stepwise procedure suggested that incubation shift length was influenced by duration of the partner's previous shift, year, egg volume index, and average wind speeds over previous 24 hours. This model had a fairly good predictive power ($R^2 = 0.37$). Other models in the confidence set included effects of breeding phase, average wind speeds over the previous 6 hours, and timing of incubation (Table 2.4). We found no support for interactions among variables in these best main-effects models(Table 2.4).

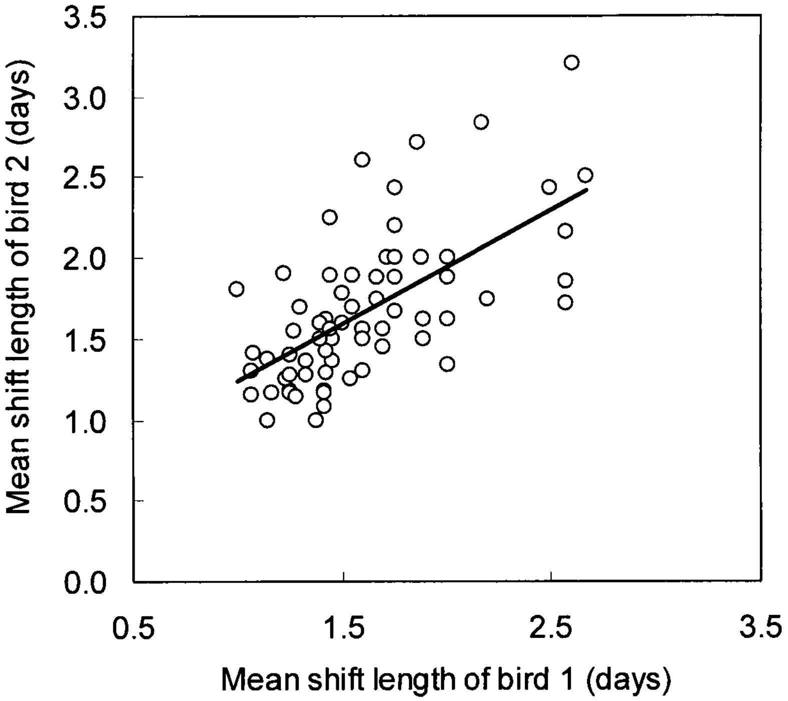

Figure 2.3: Scatter plot showing the relationship of incubation shift length (days) between pair members in Ancient Murrelets (n = 75).

Effects of incubation shift lengths on reproductive success. The number of chicks departed per pair (*n* = 41 in 2007, *n* = 35 in 2008) pairs), was best predicted by shift length, year, and egg volume index; this model had good predictive power ($R^2 = 0.78$), and included nest ID as a random effect to account for individual heterogeneity in reproductive success. A model including timing of breeding also appeared in the confidence set (ΔAIC < 2.0), and had similar predictive power ($R^2 = 0.77$). No other model received meaningful support (Table 2.4). Reproductive success tended to increase with shift length, and egg size and decrease with laying date and differed between years (Tables 2.4, 2.5). Egg size of non-deserting pairs was larger than that of deserting pairs (n = 133, 27 respectively, t = 2.18, $P = 0.03$), as found by Gaston and Jones (1998).

Table 2.4: Results of AIC model comparison to explain incubation shift length and reproductive success of Ancient Murrelets at Reef Island in 2007 and 2008. All main effects were tested (see methods and Table 2), and interactions were tested for main-effects retained in early stages of model building. Only models with ΔAIC <2 are shown. Explanatory variables in incubation shift length models included pr_isl, year, beg, egg, birdID, shiftcal, shiftstag, X6H, X24H, X48H, lunar_phase and cloud_opacity. Explanatory variables in reproductive success models included year, beg, end, egg and isl. Abbreviations were explained in Table 2.2.

Model	Explanatory variables	-2LL	LR^2	ΔAIC	w_i	K
Incubation shift length	pr_isl + year + egg + X24H	606.1	0.37	0.0	0.32	5
	pr_isl + year + shiftstag + egg + X24H	604.3	0.37	0.2	0.29	6
	pr_isl + year + shiftstag + egg + X24H + X6H	602.9	0.36	0.8	0.21	7
	pr_isl + year + beg + shiftstag + egg + X24H + X6H	601.5	0.36	1.3	0.19	8
	Null	731.7	–	117.6	0.00	1
Reproductive success	year + isl + egg	115.4	0.78	0.0	0.57	4
	year + beg + isl + egg	114.0	0.77	0.6	0.43	5
	Null	153.0	–	31.6	0.00	1

Table 2.5. Support and relative importance of explanatory variables used to model incubation shift length and reproductive success (number of chicks per nest) of Ancient Murrelets at Reef Island in 2007 and 2008. Parameter estimates, standard errors, and z value were calculated based on generalized linear models with binomial error distributions including a nest identity as a random effect, with the test statistic (P value) following a chi-square distribution. Variables with P>0.05 are not shown. Parameter definitions are described in Table 2.2.

Response variable	Parameter	βcoefficient	SE	Wald's statistic	df	*P*
Incubation shift length	pr_isl	0.22	0.04	5.75	1	<0.0001
	X24H	0.01	0.00	4.10	1	<0.0001
	year	0.12	0.06	2.10	1	0.0358
Reproductive success	isl	1.88	0.67	2.81	1	0.0005
	year	-1.62	0.47	-3.49	1	0.0049
	egg	0.07	0.02	2.82	1	0.0048

2.4.6. Diet of non-breeding Ancient Murrelets

As predicted by Sealy (1975), the stomach of breeding birds contained no whole prey. However, fragments of zooplankton (exoskeletons) and of unidentified soft tissues (species unknown) were recognizable (*n* = 5). A nematode was found in one sample. No stomach contained any evidence of fish tissues. As otoliths would be likely to persist longer than fragments of crustacean carapace, this result suggests that zooplankton was the major constituent of the diet of non-breeding murrelets at Reef Island.

2.4.7. Foraging behaviour

As found by Sealy (1975), Ancient Murrelets dove only during daylight (05:00 to 21:00). Mean hourly number of dives and dive depth varied greatly (Number of dives: range 1-141 times; SE = 1.29; n = 327, Dive depth (m): range 3-25 m; SE = 0.27; n = 327). Number of dives per hour significantly increased with wave height ($z = 8.64$, $P < 0.0001$) and varied with moon phase ($z = -8.8$, $P < 0.0001$), and wind direction ($z = 5.89$, $P < 0.0001$). There was no effect of tide height ($z = 0.76$, $P = 0.45$) or wind speed ($z = 0.55$, $P = 0.59$) on number of dives per hour (Table 2.6)

Table 2.6: Support for relative importance of explanatory variables used to model number of dives of Ancient Murrelets at Reef Island in 2008 and 2009. Parameter estimates, standard errors, and z value were calculated based on generalized linear models with Gaussian distributions including a nest identity as a random effect, with Parameter definitions are described in Table 2. Note that values are valid only within data sets.

Response variable	Parameter	βcoefficient	SE	Wald's statistic	*P*
Number of dives	Wave height	0.3882	0.0449	8.642	< 0.0001
	Moon phase	-0.0280	0.0032	-8.789	< 0.0001
	Wind direction	0.0009	0.0002	5.887	< 0.0001
	Tide height	0.0055	0.0072	0.763	0.4450
	Windspeed	< 0.001	0.0014	0.547	0.5850
Dive depth (m)	Tide height	0.0501	0.012	4.176	< 0.0001
	Moon phase	-0.0061	0.0020	-3.048	0.0023
	Wave height	-0.105	0.0007	-1.45	0.1469
	Wind direction	< 0.0001	0.0002	0.402	0.6879
	Windspeed	0.0004	0.0023	0.165	0.8691

2.5. DISCUSSION

To better understand the exceptionally long incubation shift length observed in Ancient Murrelet compared to other auks (Gaston 1992b; Gaston 1994), I conducted the first intensive study of incubation shift length with large sample sizes taken over a period of two consecutive years. Incubation shift lengths differed among individual Ancient Murrelet pairs, and the shift durations were highly correlated between pair members. The synchronization of a variety of reproductive behaviours during breeding, including shift lengths, is important for many seabirds (Weimerskirch 1995; DeForest and Gaston 1996; Nisbet and Dann 2009).

There was variation in shift lengths among pairs in this study, which is consistent with previous studies (Sealy 1976; Gaston 1992b). In chick-rearing Thick-billed Murres, individuals specialized in foraging behaviour, including trip time and shift length, and this was linked to specialization in diet, suggesting birds tended to visit the same site during the consecutive foraging trips (Watanuki 2004; Woo et al. 2008; Elliott et al. 2009a). Ochi and Watanuki (2008) observed that shift lengths of Japanese Cormorants (*Phalacrocorax capillatus*) during the chick-rearing periods varied among individuals and they suggested that this variation was linked to variation in distance to foraging sites and to high foraging site fidelity. Although I do not know where the Ancient Murrelets in my study fed, there is some weak evidence for a lack of individual variation in diet and foraging behaviour in Ancient Murrelets as there was little variation in stomach contents or dive profiles among individuals (Elliott and Shoji 2009). Consequently, factors other than specialization in foraging behaviour, such as food supply and parental quality/experience, may explain the large amount of individual variations in shift length.

2.5.1. Factors affecting shift length

My results suggested that foraging conditions and individual variations (i.e. parental quality), rather than predator avoidance, were the most important determinants of incubation shift length in Ancient Murrelets (Table 1, Table 4). Variation in shift lengths among individual pairs could result from a variety of individual traits including physiological body condition and age. Body condition in particular is known to be a critical factor affecting incubation shift lengths in seabirds (Chaurand and Weimerskirch 1994a; Weimerskirch 1995; Kato et al. 2008). In this respect, long foraging trips usually increase energy intake for central-place foragers (Elliott et al. 2009a; Elliott et al. 2009c) and that could also apply to Ancient Murrelets (Sealy 1975). However, for a species to have long foraging trips, the species must also have the physiological capacity to fast for an extended period of time, as the duration of foraging for one partner will equate the duration of fasting for the other partner. In a pair that begins incubation with large reserves, partners should be capable of longer shifts than those with small reserves (Gaston and Jones 1989). Variation in body condition presumably results from variation in the abundance or accessibility of prey and from variation in an individual's foraging efficiency, which usually increases with a bird's age (DeForest and Gaston 1996; Nisbet and Dann 2009). Monitoring body condition of Ancient Murrelets was not possible in this study, but the recent development of auto-weigh systems to measure mass of birds without handling (Granadeiro et al. 1998; Ochi et al. 2006) may allow the direct testing of these ideas in future.

Poor coordination of incubation shift length can increase breeding failure in seabirds (Davis 1988). Two theories have been proposed to explain the synchronization of shift lengths between pair members, as observed in this study. First, birds may tend to mate assortatively; high quality birds may choose high quality mates to avoid poor coordination in incubation shifts and reduce the need to compensate for a partner requiring more time at sea (Davis 1988). For example, successful pairs of Thick-billed Murres had synchronized shift lengths whereas unsuccessful pairs showed no correlation between pair members (DeForest and Gaston 1996). Second, birds may be constrained by the duration of their foraging trip and synchronize with their mates so as to minimize the probability of nest desertion by their partner (Kato et al. 2008). In essence, partners may "agree" upon a certain shift length that provides relatively equal foraging time to each bird, so that each partner will know when to "expect" its partner to return, minimizing the possibility that one bird will desert due to uncertainty about the other partner's status (Weimerskirch 1995; Kato et al. 2008). My results could be explained by either hypothesis.

In addition to synchronization, high wind speeds were found to increase incubation shift length of Ancient Murrelets. This result is consistent with previous studies, which suggested that high wind speeds lead to poorer foraging conditions at sea, and hence to longer shift lengths (Birkhead 1976; Finney et al. 1999; Ronconi and Hipfner 2009). Number of dives increased with wave height suggesting that birds need more foraging effort during the strong wave actions resulting from high wind speeds. Thus, Ancient Murrelets likely have lower foraging success and higher energy demands under unfavourable weather conditions, resulting in birds remaining at sea longer to replenish reserves. Furthermore, nest arrival rates decreased (and therefore egg neglect increased) after 48 hours of high winds, while shorter periods of high wind speed had no impact (see also Jones et al. 1990), providing further evidence that consecutive days of severe weather conditions at sea strongly affects foraging success in murrelets. Food scarcity is expected to amplify the negative effect of severe weather conditions on rates of egg neglect. Cassin's Auklets (*Ptychoramphus aleuticus*), for instance, neglected their eggs more frequently to increase foraging time when food supply was poor (Blight et al. 1999).

On the other hand, ambient light only affected nest arrival rates (and therefore egg neglect), but not incubation shift lengths. In particular, the rate of adult returns to their nests is lower with older (brighter) moons, which suggests that birds reduce nest visits under the threat of predation (Dale et al. 1996; Michl et al. 2000). Previous studies have found that many birds adjusted their behaviour in relation to ambient light, and this is especially true for nocturnal burrow nesting seabirds, which are vulnerable on the land (Imber 1975; Watanuki 1986; Montgomerie and Weatherhead 1988; Keitt et al. 2004; Riou and Hamer 2008). Despite the effects of ambient light intensity on adult nest arrival rates and egg neglect, ambient light did not affect incubation shift lengths. As the period of the full moon is just a few days every 28 days, the period of high predation risk may be short. The ability of predation risk to influence the mean of incubation shift length depends on the length of this interval; the threshold of light conditions that leads to increased predation risk is unknown and may merit further attention.

Overall, my results suggest that the foraging hypothesis and the predation avoidance hypothesis are not mutually exclusive. Birds take a flexible approach to meet the requirements of their life-history strategy. If adults decide not to return on a particular night due to predation risk, on-duty birds may decide to leave their nest even before the return of their partner, if body reserves are critically depleted. However, these decisions are influenced by both foraging conditions at sea and by ambient light conditions.

Incubation shift lengths, year, and egg size are all significantly related to reproductive success in Ancient Murrelets, with incubation shift length being the strongest predictor of reproductive outcome examined in this study. Presumably, better quality birds (DeForest and Gaston 1996) start their incubation shifts with higher reserves and consequently, are able to have longer at colony shifts, allowing their partners to spend more time feeding and therefore start their own shifts with higher reserves (Gaston and Jones 1998). Thus, I suggest that better quality birds have high reproductive success and longer shifts allowing for lower risk of neglect or desertion due to higher initial reserves. The idea that older birds have higher success is also supported by the relationship between egg size and desertion in this study (desertion probability decreases with egg size), as older auks are known to lay larger eggs (Hipfner and Gaston 1999a; Hipfner and Gaston 1999b; Hipfner 2000; Hipfner et al. 2001; Hipfner and Gaston 2003).

2.5.2. Comparison with a sympatric alcid with short incubation length

My results suggest that there is fitness advantages associated with extended incubation shift lengths in Ancient Murrelets. This result is expected because the probability of encountering prey that is sparsely distributed in discrete patches increases with foraging distance travelled (Weimerskirch and Robertson 1994; Weimerskirch 1995; Elliott et al. 2009a; Elliott et al. 2009c). If this is the case, then why don't all auks extend incubation shift lengths? To what degree can seabirds extend their shift length? For example, Cassin's Auklets are sympatric with Ancient Murrelets at many locations (e.g. Reef Island, Frederick Island, Langara Island) and share several life history traits (e.g. adult body size, nocturnality, burrow nesting, longevity, coloniality), yet they usually have 24 hour incubation shifts. A comparison of the two species may help explain the unusually long incubation strategy of Ancient Murrelets (Table 2.7).

Table 2.7: Comparison of life history traits between Ancinet Murrelets and Cassin's Auklet.

Species	Clutch size	Egg size (g)	Chick	Incubation shift length (day)	Egg neglect	Mass (breeder) (g)	Relay	Prey	Foraging range (km)
Ancient Murrelet	2	45.9	Reared at sea	1-6	common	213	never	larval fishes*, zoo plankton	< 70
Cassin's Auklet	1	27.4	Reared in burrow	1	fairly common, but risky	174	common	Euphausiids and larval fish	30
Reference	2,4	1,3,6	1,2	2,3,4	4,6,8	6	4,9,10	1,2,4,11,12	11

[1]Sealy 1972; [2]Manuwal 1974; [3]Sealy 1976; [4]Gaston 1992a; [5]Gaston 1992b; [6]Gaston and Jones 1998; [7]Birkhead and Gaston 1988; [8]Gaston and Powell 1989; [9]Manuwal and Thoresen 1993; [10]Ronconi and Hipfner 2009; [11]Elliott and Shoji; [12]This study

* Estimated prey items by characteristics of diving behaviour (see also Elliott et al. 2008).

Cassin's Auklets return to their nest even under unfavourable conditions, such as moonlit nights, although auklets occasionally neglect their eggs when wind speeds are high (Manuwal 1974; Ronconi and Hipfner 2009). Auklet eggs are vulnerable to mice, and when both parents are absent, many eggs are eaten by mice (Manuwal 1974; Gaston and Powell 1989; Ronconi and Hipfner 2009). Cassin's Auklets are able to lay a new egg within the same season, but replacement clutches are unknown for Ancient Murrelets. However, the survival rate of replacement eggs laid by Cassin's Auklets is lower than that of first eggs (Ronconi and Hipfner 2009). In species where incubation duties are shared equally between pair members, long foraging trips increase failure to maintain the incubation schedule (Gaston and Powell 1989), and thereby increase rates of egg neglect. As neglect is risky in Cassin's Auklets, there might be strong selection for auklets to retain short shifts so that birds are able to reduce predation risk on their eggs. In contrast, Ancient Murrelets have exceptionally large eggs, the largest in relation to female body size among seabirds (Gaston and Jones 1998). This large egg size increases the embryos' resistance to chilling conditions and the eggs appear practically invulnerable mice (Gaston and Powell 1989; Gaston 1992b). Taken altogether, these observations on predation risk and resistance to egg neglect suggest that the prolonged incubation shift length and high investment in embryos in Ancient Murrelets represent an alternative compromise between adult survival, female investment in eggs and parental investment in incubation.

Long shifts also facilitate long foraging trips and large foraging ranges; sometimes necessary to avoid inter-or intra-specific competition for food around the colony during the breeding season (Ashmole 1963; Furness and Birkhead 1984; Gaston et al. 2007; Ballance et al. 2009; Elliott et al. 2009c). For instance, Northern Gannets (*Morus bassanus*) at large colonies tend to travel farther for food (Lewis et al. 2001). Ancient Murrelets generally share their colony with several other seabird species (Gaston 1992b), and extended incubation shift lengths may reduce competition inter- and intra- species by allowing parents to travel longer distances to feed than other sympatric auks. It has been reported that it is more efficient to be a specialist in prey for marine predators (Roughgar 1974; Partridge and Green 1985), because there is a great variation of potential prey types and foraging habitats (Watanuki 2004). Given that specialization may be carried over from chick-provisioning to self-feeding (Woo et al. 2008; Elliott et al. 2009b), species that rear their chicks at the colony may be limited by prey abundance during the chick-rearing period (Elliott et al. 2009c), so population size may be limited by prey availability in the chick-rearing period and there may be little pressure to increase shift length to augment prey capture rates. Furthermore, the annual survival of breeding Ancient Murrelets is 77% (Gaston 1990), whereas survival for other auks, including those of the same body mass, are higher (e.g. Cassin's Auklets 88%;Gaston 1992a, Thick-billed Murres 88-89%; Gaston et al. 1994). It is therefore possible that there is trade-off between high investment in the offspring and low-survival for Ancient Murrelets. Thus, the penalty for the adoption of the *Synthliboramphus* breeding strategy may be lower adult survival. Consequently, I conclude that long and variable incubation shift lengths may increase at-sea energy intake rates and allow for egg neglect, but there might be a trade-off between such advantages and survival.

2.5.3. Conclusions

To summarize, incubation shift lengths of Ancient Murrelets varied among individual pairs and the duration was highly correlated within pairs. Shift lengths were influenced by the mate's behaviour and foraging conditions at sea (a presumed indicator of access to prey). Birds with higher reproductive success tended to have longer shifts and larger eggs, presumably because they were of higher quality. Therefore individual strategies interact with environmental conditions to determine incubation tactics and variation in individual incubation shift length can be explained in two ways; due to the experience (i.e. age) of birds and by environmental conditions that determine foraging success. Based on the correlation between shift length and egg size, experienced birds (i.e. older birds) and inexperienced birds (i.e. younger birds) have different incubation shift length. This may be due to variation in the certainty associated with the reliability of their partners. For example, when foraging conditions are favourable, younger birds may change-over more frequently than older birds to ensure that their partner is still present. This is presumably because younger birds have a weaker pair bond than older birds resulting in lower reliability for their partner. On the other hand, when foraging conditions were worse (e.g. high waves due to high wind speeds), incubation shifts were longer and egg neglect was higher, suggesting that younger birds needed more time to search for food. Ancient Murrelets often neglect their eggs at the beginning of incubation (Gaston 1992), possibly because birds need to adjust their body condition after the energetically expensive egg-laying phase of reproduction.

Light conditions had little effect on the pattern of incubation shift change-overs, but arrival at the colony was strongly affected by the time of sunset, with birds only arriving in complete darkness. This suggests that avoidance of predation has been a major factor in affecting the breeding strategy of Ancient Murrelets (Jones et al. 1998 , Gaston 1992) Compared with other auks, Ancient Murrelets have low adult survival, perhaps partly because of heavy predation at the colony. My results are best explained if we assume that multi-day incubation shifts in Ancient Murrelets are the adaptively preferred strategy, through reduction in predation risk, but that actual shift lengths are modified by immediate weather and foraging constraints.

Although this study provided novel information on incubation strategy in marine birds, future research should examine the timing of decision-making in relation to both the age and the body condition, as these two factors appear to play an important role in the breeding behaviour of other seabirds (Hipfner and Gaston 1999a; Hipfner and Gaston 1999b).

3. INTER-ANNUAL VARIATION OF INCUBATION SHIFT LENGTH BY ANCIENT MURRELETS (*Synthliboramphus antiquus*) IN RESPONSE TO OCEAN CLIMATE VARIABILITY

3.1. ABSTRACT

Large scale interannual and decadal variation in ocean conditions, including sea surface temperature (SST) has been shown to affect the breeding behaviour of marine birds in the North Pacific Ocean. However, as individual species respond differently to changing food supplies, our understanding of the role of climatic variation in seabirds is limited. Here, I examined incubation shift length of Ancient Murrelets (*Synthliboramphus antiquus*), a small marine bird with exceptionally long incubation shift length, from seven years between 1993 - 2008 on Queen Charlotte Islands in relation to Sea Surface Temperature (SST) variation. Incubation shifts were longer and the timing of breeding was later in years when April SST was high. My results suggest that food supply influences incubation shift length and therefore reproductive success in Ancient Murrelets because longer incubation shifts were associated with rapid changes in trophic level, later breeding and higher sea surface temperature.

3.2. INTRODUCTION

Colonial seabirds are useful indicators for monitoring the health of marine ecosystems and investigating the effects of climate change (Davoren and Montevecchi 2005; Gaston et al. 2009; Einoder 2009). Seabirds travel long distances between their breeding colonies and their foraging areas during the nesting period and often cover wide geographical areas to find the most accessible sources of prey. Seabirds are central-place foragers as they must return to their nest periodically during the breeding season. This allows researchers to collect data efficiently at breeding colonies and permits the study of foraging behaviour over multiple areas and trophic levels. Therefore, seabirds can be useful indicators of marine resources at various spatial scales. However, different seabird species respond differently to changing food supplies, and how a given species' sensitivity to changing marine environmental conditions differs will depend on its ecology, physiology, and life-history (Cairns 1987; Gill et al. 2002; Einoder 2009). Therefore, to interpret what foraging behaviour tells us about marine environmental conditions it is essential to understand the interaction between foraging behaviour, climate variability and reproductive success.

Animals should adjust their behaviour to match prey phenology so that energy demands are highest when prey is most accessible. Breeding is energetically demanding for seabirds (Ellis and Gabrielsen 2002) as parents must spend time incubating eggs or brooding chicks, limiting time available for energy intake, and must provision offspring, requiring additional energy expenditure. Thus, the timing of breeding in seabirds should be synchronized with the peak of prey abundance so that food supplies meet energetic demands. Short-term ocean climate variation affects both the phenology and the breeding success of seabirds in the northern Pacific Ocean (McGowan 1998; Gaston and Smith 2001; Gjerdrum et al. 2003; Quilifeldt et al. 2007; Hipfner 2008; Gaston et al. 2009), but the ability of birds to adjust their incubation patterns in response to environmental change is poorly understood (Mallory et al. 2008). Variation in physical marine conditions can affect the timing and abundance of prey items in surface waters, which can result in changes in populations of top predators such as seabirds (Bertram et al. 2001). In particular, sea surface temperature (SST) is known to affect the breeding performance of seabirds (Guinet et al. 1998; Piatt et al. 1999; Bertram et al. 2001; Ramos et al. 2002; Gjerdrum et al. 2003; Abraham and Sydeman 2004; Frederiksen et al. 2004). Warmer SST in a given year reduced the offspring survival rate of Rhinoceros Auklets (*Cerorhinca monocerata*; Thayer and Sydeman 2007) and Blue Petrels (*Halobaena caerulea*; Connan et al. 2008), Cassin's Auklets (*Ptychoramphus aleuticus*; Hipfner 2008) and Common Murre (*Uria aalge*; Irons et al. 2008) where as Thick-billed Murres (*Uria lomvia*) populations increased with warmer SST (Irons et al. 2008) . As seabird populations decline when SST shifts are large (Irons et al. 2008), the relationship is probably due to birds being unable to respond as fast as their prey base to changes in oceanography (Hipfner 2008).

Although many authors have reported correlations between SST and reproductive performance, the proximate mechanisms and behaviours that lead to these correlations have garnered less attention. The incubation pattern is one index of breeding performance that is sensitive to the abundance of prey species (Warham 1990a; Mallory et al. 2008). Throughout the incubation period, seabirds that alternate foraging bouts between pair members undergo large variations in body mass (Fisher 1967; Prince et al. 1981) because the bird that remains on the nest to incubate a pair's eggs is forced to fast for extended periods of time. The length of time one individual incubates the eggs until replaced by the other member of the breeding pair is the incubation shift length, and is affected by food supply and foraging conditions. This is one mechanism through which SST could affect reproductive performance.

There is evidence that similar climate fluctuations also affect the biology of several species of birds on Queen Charlotte Islands, British Columbia, Canada. The overall reproductive success of several species of songbirds was lower in cooler and wetter years and there was clear inter-annual variation in the timing of breeding (Gaston et al. 2006). Gaston and Smith (2001) compared the inter-year variation in breeding parameters for Ancient Murrelets (*Synthliboramphus antiquus*) with physical oceanographic data and found that departing chick mass in the Queen Charlotte Islands was lower in years of warmer SSTs, although they did not examine the proximate causes (e.g. incubation period) for these trends. The Ancient Murrelet is a long-lived species (Shoji and Gaston 2008) that feeds primarily on zooplankton and immature fish (e.g. *Euphausia pacifica* and *Thysanoessa spinifera*: Sealy 1975, Gaston and Smith 2001). These birds are small colonial burrow nesters with extended incubation shifts between 1-6 days, much longer than most other members of the Alcidae (Sealy 1976; Gaston 1992b; Gaston 1994). Because breeding adults forage up to 70 km from the study colony (Elliott and Shoji 2009), it is expected that the overlap between the energetically-demanding incubating period and the prey biomass peak is a key factor for successful breeding. The annual peak of prey biomass varies in response to ocean climate (Mackas et al. 1998). When prey biomass is low, birds will presumably require longer at-sea periods to accumulate body reserves or reduce incubation shift durations because they start incubation shifts with lower body reserves. Either option would be expected to lead to more frequent egg neglect and nest desertion and consequently reduced reproductive success (Gaston 1992b).

The overall goal is to better understand the role of short-term variation of ocean climate on incubation patterns, the timing of breeding and reproductive success of the Ancient Murrelets. Specifically, test for evidence of inter-annual variation of incubation shift lengths in relation to sea-surface temperatures, and assess to what extent inter-annual variation of incubation shift length is associated with reproductive success. Also investigate the trophic level of adult murrelets to examine their diet during the breeding season in 2007 and 2008.

3.3. MATERIALS AND METHODS

3.3.1. SSTs and SOI

Information on sea-surface temperatures (SSTs) and Southern Oscillation indices (SOI) were obtained from the Institute of Ocean Sciences Lightstation Data Web site (www.ios.bc.ca). For comparison with seabird breeding data, the means of SST anomalies reported for the four stations nearest to Haida Gwaii: Langara Island, Bonilla Island, McInnes Point, and Kains Island were used (Gaston and Smith 2001). Incubation stage SST anomalies (March to June) in a given year were used to see the impacts of annual climate conditions on the breeding parameters of Ancient Murrelets. Annual SOI used were the means of monthly values for pre-incubation stage (December-February).

3.3.2. Reproductive data

Biological parameters for Ancient Murrelets were measured at two breeding colonies in Laskeek Bay in the central part of Hecate Strait: East Limestone Island (52°55' N 131°36' W;1993-1995, 2002-2003) and Reef Island (52°52'N, 131°31'W ; 2007-2008). Long term research on Ancient Murrelets at both islands by Canadian Wildlife Service has been conducted since 1984. During the breeding season, incubation shift length, reproductive success, egg size, adult and chick mass at departure and median date of clutch completion were measured. Timing of breeding was similar at the two colonies in overlapping years (Gaston and Harfenist 1998), and no significant difference was found between colonies for any of the parameters measured by Gaston and Smith (2001). Therefore, data for the two colonies were combined and considered as representative of conditions in the area in a given year.

General monitoring procedures for nest attendance patterns and biological parameters in Ancient Murrelets were followed (Gaston and Powell 1989). All nests were checked during the daytime either in natural burrows (East Limestone Island) or nest boxes (Reef Island). On both islands, from April to early June, knock-down tags were placed in burrow entrances and burrows were inspected daily only when these were displaced. Once the first egg was laid, the egg was measured (length and breadth; accuracy = ± 0.1 mm), and either a temperature sensor (Onset TMC1-HD) or a YSI temperature probe (Yellow springs Instruments 400 series) was installed into the nest chamber so that the presence of incubating birds could be monitored without disturbing the breeders (Gaston 1990). Incubation period is the time between the laying of the last egg and the hatching of that egg (Drent 1975). Because I did not know the laying dates of second eggs, I derived the incubation period from the first date of incubation start to hatching date. After 30 days, the contents of the burrows were examined and the two chicks and one or both of the parents were banded and weighed. Adults were weighed with a 300- or 500-g Pesola spring balance (± 0.5 g). Egg size was estimated using an index of egg volume (length x breadth^2; (Gaston and Smith 2001). Incubation shift length (days) and reproductive success (number of chicks departed per nesting pair) were recorded on East Limestone Island in 1993-1995, and 2002-2003 and on Reef in 2007-2008 (seven colony-years). Pre-2007 data was collected by the Canadian Wildlife Service.

3.3.3. Stable isotope analysis

To determine the trophic level of adult Ancient Murrelets within breeding season and between years, muscle samples were collected (half life of isotopes from ingestion = about 4-6 month) from adult murrelet carcasses within the breeding colony at Reef Island in 2007 and 2008, and blood and plasma samples were obtained from live adults in 2008. All tissues were kept frozen (2008) or stored in 70% ethanol (2007) until preparation in the laboratory (Hobson et al. 1997). As preservation in alcohol can alter δC in at least some species and tissues, but not δN values, I ignored δC values in 2007, which were more depleted than 2008 (Hobson et al. 1997; Kaehler and Pakhomov 2001). All muscle and prey samples were freeze-dried and homogenized with electrical ball mills. To estimate the prey type base, potential prey items (krill *Euphausia* spp.) were collected at sea within 10km from Reef Island during the incubation stage in 2008. Prey items were frozen until preparation in the laboratory, where they were freeze-dried. All dried and homogenized samples were analyzed for carbon and nitrogen isotope ratios at the G.G. Hatch Stable Isotope Laboratory (University of Ottawa) using a continuous flow stable isotope-ratio mass spectrometer. Results were reported of carbon and nitrogen isotope analyses in delta (δ) notation relative to international standards (Vienna PeeDee Belemnite for C, atmospheric nitrogen for N) according to the following equation: $\delta X = ([R\text{sample}/R\text{standard}]-1) \times 1000$, with X denoting either 13C or 15N, and R representing the ratio of 13C /12C or 15N/14N, respectively. The analytical error was estimated to be less than ±0.2‰.

3.3.4. Data analysis

All statistical analyses were completed in R 2.6.1. I examined factors that affected incubation shift length (days), incubation initiation date (julian date) and reproductive success (number of chicks per pair; 0, 1 or 2) in relation to ocean climate. As explanatory variables, I used SST anomalies and SO indices. I created a generalized linear model with a Poisson distribution and log-link function for each shift as the independent variable with SST anomalies and SO index as independent variables. To avoid pseudoreplication I included the nest identity as a random effect in the analysis. Model simplification was carried out in each case by sequential removal of the least significant terms, using likelihood ratio tests to determine the minimum adequate model (Crawley 2007), with the test statistic following a chi-square distribution.

To provide a rough index of prey composition, I used IsoSource 1.3.1 (Phillips and Gregg 2003), which allows us to estimate the proportion of preys in diet. As the only measurements of Ancient Murrelet prey were obtained 30 years ago at Langara Island, near the continental shelf and in a different oceanographic regime (Sealy 1975), it was not possible to input isotopic values for prey items and determine prey composition, as the prey themselves are unknown. Rather, I used three fish and three invertebrates (my prey samples and those reported by Davies et al. 2009) to represent the range of possible prey items and used the model to provide a rough index of the proportion of invertebrates and fish in the diet. Because robust fractionation values for small auk blood are available (1.1‰; Davies et al. 2009), I used blood as my isotopic tissue for these analyses.

3.4. RESULTS

3.4.1. Weather

During the typical Ancient Murrelet incubation period (March-June) from 1993 to 2008, there was substantial inter-annual variation in SST anomalies (Fig 3.1) from the four stations. Colder temperatures occurred especially in 1995, 1999, 2002 and 2008 (Fig 3.1).

Longer mean incubation shift lengths of individual pairs were associated with lower SST anomalies in April ($n = 166$, $t = 4.64$, $P < 0.0001$) and May ($n = 166$, $t = -2.8$, $P = 0.004$). Also, later mean hatching dates were significantly associated with lower SST anomalies in April ($n = 7$, $z = 0.069$, $P < 0.0001$), May ($n = 7$, $z = 3.79$, $P = 0.000153$) and pre-incubation stage SOI ($n = 7$, $z = 2.57$, $P = 0.01$). However, there was no significant relationship between ocean climate and both egg size and reproductive success (number of chicks per pair).

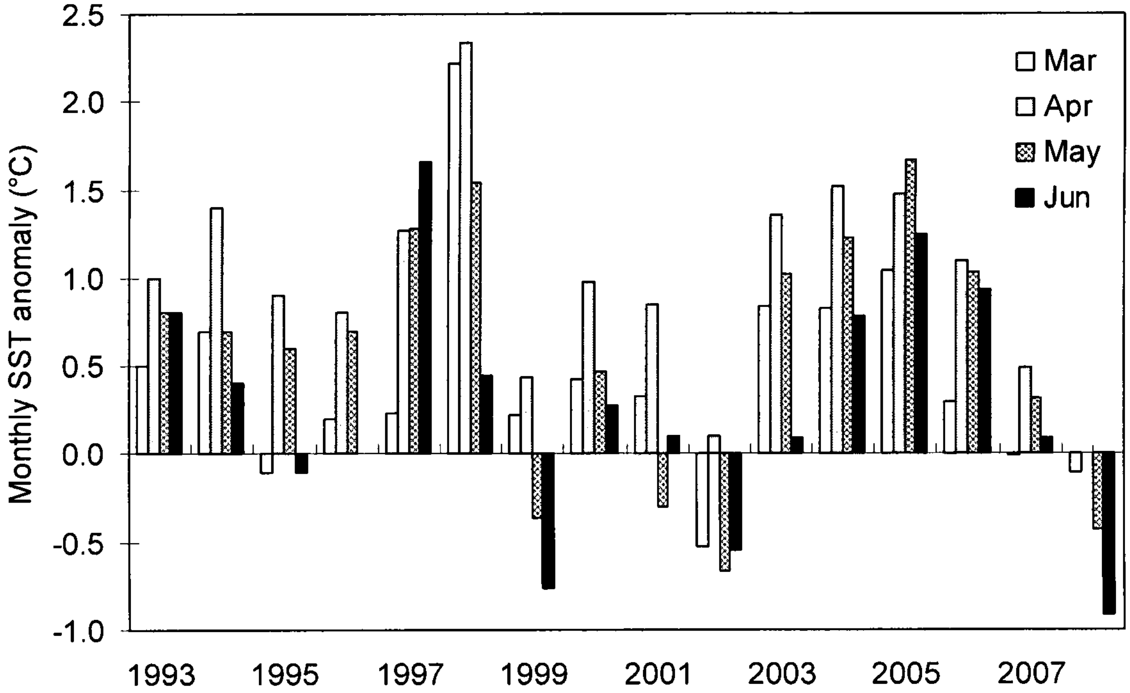

Figure 3.1: Breeding season SST anomalies during the study period from 1993 to 2008.

3.4.2. Time trend

Incubation initiation dates were correlated with SST in April (n = 7; z = -2.12; $P = 0.03$; Table 3.1). The earliest date of incubation start (= incubation initiation date) was 21 April in 1993-1994 and 2008, and the latest on 28 April in 2002 (Table 3.2). The timing of incubation start was particularly late in 2002 and 2003 (28 and 27 April, respectively); following the major ENSO event in 1997-1998 and La Niña events in 1999-2001 (Fig 3.1). Reproductive success was negatively associated with the mean incubation initiation dates (n = 7; $r^2 = 0.85$; t = -5.31; $P = 0.03$; Fig 3.2).

3.4.3. Correlation with ISL and reproduction

Combining data for all years, Incubation shift length varied between 1 and 6 days and differed significantly among years (n = 166; KW = 1.41, $P < 0.0001$; Fig. 3.3), while reproductive success also varied greatly among years (n = 166; KW = 7.21, $P = 0.02$; Fig 3.4). Mean incubation shift length increased with higher SST anomalies in April and lower in May (n = 2535; z = 5.73, $P < 0.0001$; n = 166; z = -4.14, $P < 0.01$; respectively, Table 3.1), while reproductive success was not associated with SST anomalies (Table 3.1). Mean annual chick mass at departure was negatively associated with annual mean incubation shift length (n = 7; t = -4.56; $P < 0.01$; Fig 3.5). However, the relationship between annual reproductive success and incubation shift length lacked statistical significance (n = 7, t = -1.49; $P = 0.20$). Hatch date and annual mean incubation shift length was correlated when I excluded data from 2003 ($P = 0.05$;

Fig 3.6). Reproductive success declined with number of cumulative days of egg neglect, although up to three days there was no effect on reproductive success (Fig 3.7).

3.4.4. Stable isotope analysis

There was no difference in trophic level between 2007 and 2008 (δ^{15}N: $P = 0.31$ in April, $P = 0.45$ in May), but trophic level increased over the course of the season in 2008 ($P = 0.03$; Fig 3.8). Differences in preservation method between years prevented a comparison between years, but there was no change in carbon input within years (δ^{13}C: $P = 0.90$ in 2007, $P = 0.49$ in 2008). Carbon plasma values were depleted by (-20.01 ± 0.15 SE) compared to blood (-18.75 ± 0.05 SE) and muscle (-18.52 ± 0.11 SE), which showed no difference ($P = 0.07$); nitrogen values were similar between plasma and blood, but muscle values were more enriched. The mixing model suggested that murrelets fed on 31 % invertebrates and 69 % fish in May (Fig 3.9). Assuming that the muscle value in May represented a similar relationship, this translated into 33 % invertebrates and 67 % fish in April and 18 % invertebrates and 82% fish in June. At East Limestone in June 2008, trophic level was lower than at Reef in May 2008 ($P = 0.01$) or June 2007 ($P = 0.04$).

Table 3.1: Results of GLZ based on likelihood ratio test examining the relationship between sea -surface temperature anomalies during the incubation period, incubation initiation date, incubation shift length and reproductive success of Ancient Murrelets.

Predicted	Explanatory Variables	Estimate	SE	*Z*	*P*
Incubation initiation date	SST March	0.07	0.15	0.45	0.65
	SST April	-0.24	0.12	-2.12	0.03
	SST May	0.09	0.11	0.78	0.44
	SST June	-0.08	0.10	-0.82	0.42
	SOI Pre-incubation	-0.07	0.05	-1.41	0.16
Incubation shift length	SST March	-0.12	0.16	0.39	0.70
	SST April	0.72	0.13	5.73	< 0.0001
	SST May	-0.40	0.13	-3.14	< 0.01
	SST June	0.07	0.11	-0.70	0.49
	SOI Pre-incubation	0.01	0.06	0.19	0.85
Reproductive success	SST March	-0.26	0.58	-0.45	0.65
	SST April	-0.01	0.43	-0.02	0.99
	SST May	0.16	0.44	0.37	0.71
	SST June	0.38	0.37	1.03	0.31
	SOI Pre-incubation	0.09	0.19	0.44	0.66

Table 3.2: Biological parameters for Ancient Murrelets during the study period.

Year	Lay dates (days from 1 April)	Incubation initiation dates (days from 1 April)	% success	no. of chicks per nest	Chick mass (g)	Hatch date (days from 1 April)	Mean incubation shift duration (days)
1993	12	21	92.0	1.72 ± 0.61	27.3	51	1.78
1994	13	21	93.8	1.50 ± 0.63	27.0	40	2.21
1995	13	23	72.4	1.45 ± 0.83	26.9	49	1.99
2002	17	28	63.6	1.18 ± 0.87	26.5	50	2.14
2003	21	27	76.9	1.31 ± 0.85	26.5	56	2.18
2007	16	23	94.7	1.47 ± 0.81	30.9	55	1.51
2008	10	21	90.0	1.64 ± 0.81	30.5	51	1.68

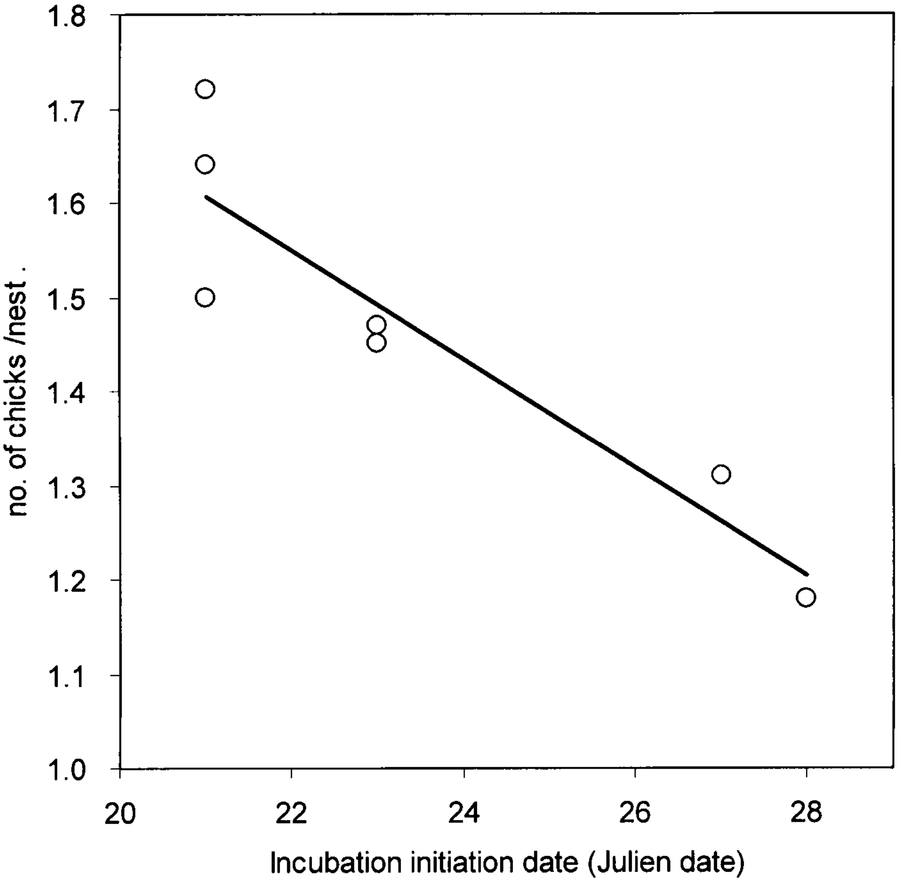

Figure 3. 2: Scatter plot showing relationship between annual mean number of chicks per pair departing from breeding sites and incubation initiation date for Ancient Murrelets at East LI (1993-Reef Island). Date indicates days from 1 April.

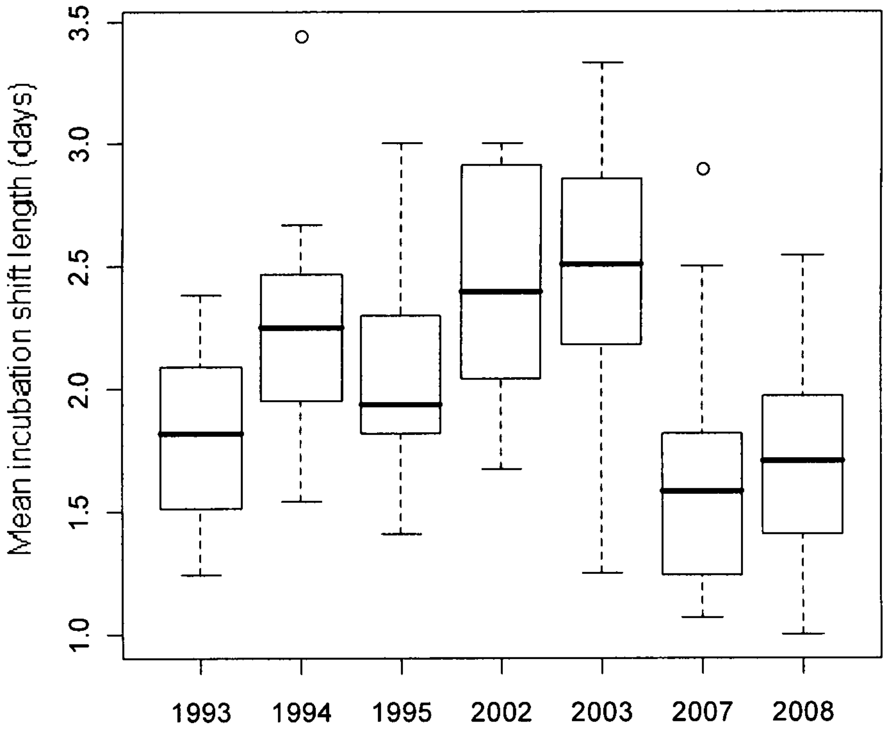

Figure 3.3: Inter-annual variation in incubation shift length of Ancient Murrelets at East Limestone (1993-2003) and Reef (2007-2008) islands.

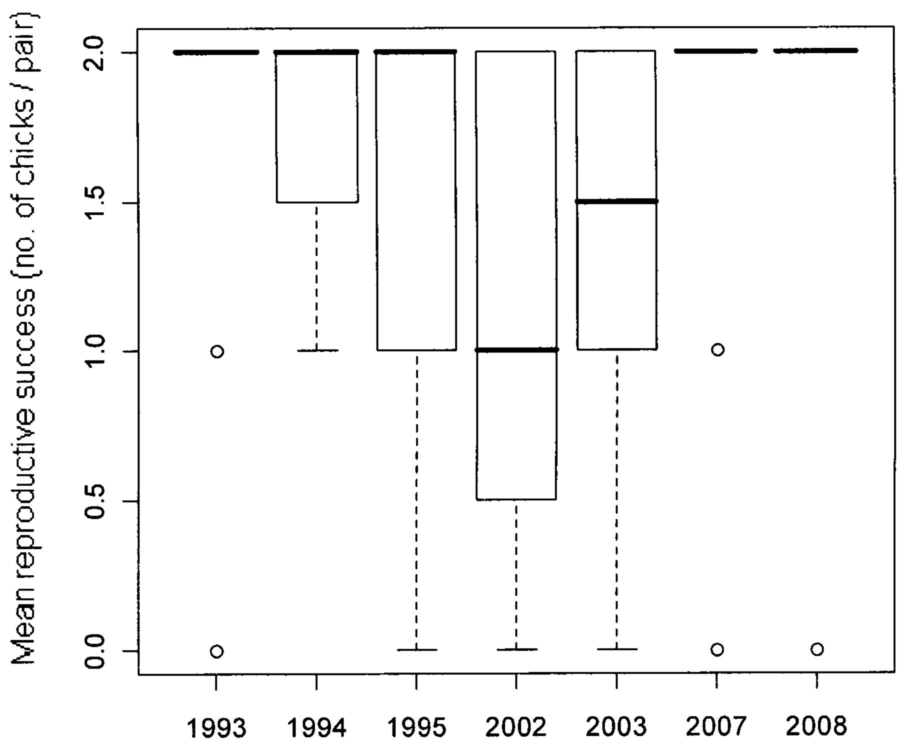

Figure 3.4: Mean number of chicks departing from breeding sites at East Limestone (1993-2003) and Reef (2007-2008) islands.

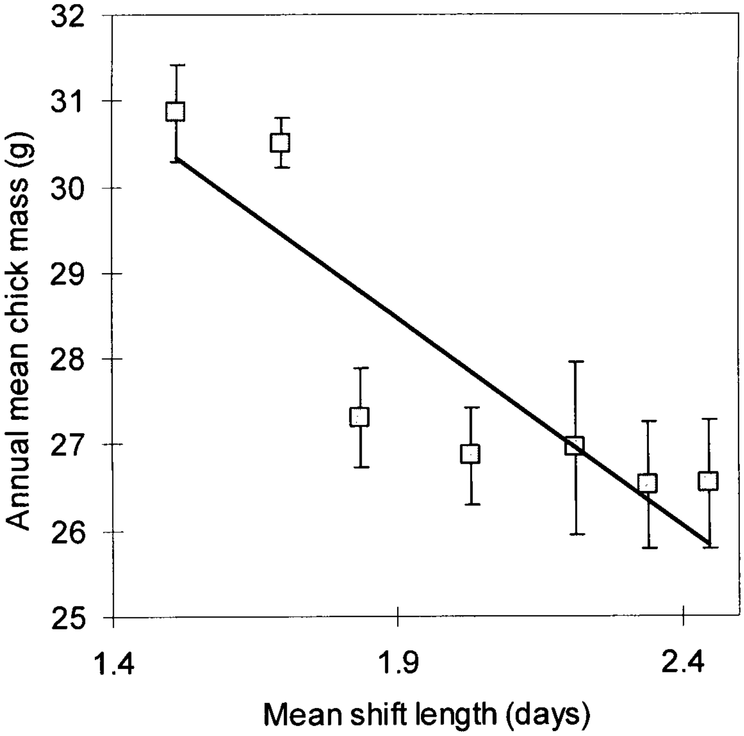

Figure 3.5: Annual chick mass (mean ± SE) in burrow in relation to incubation shift length for Ancient Murrelets at Reef Island.

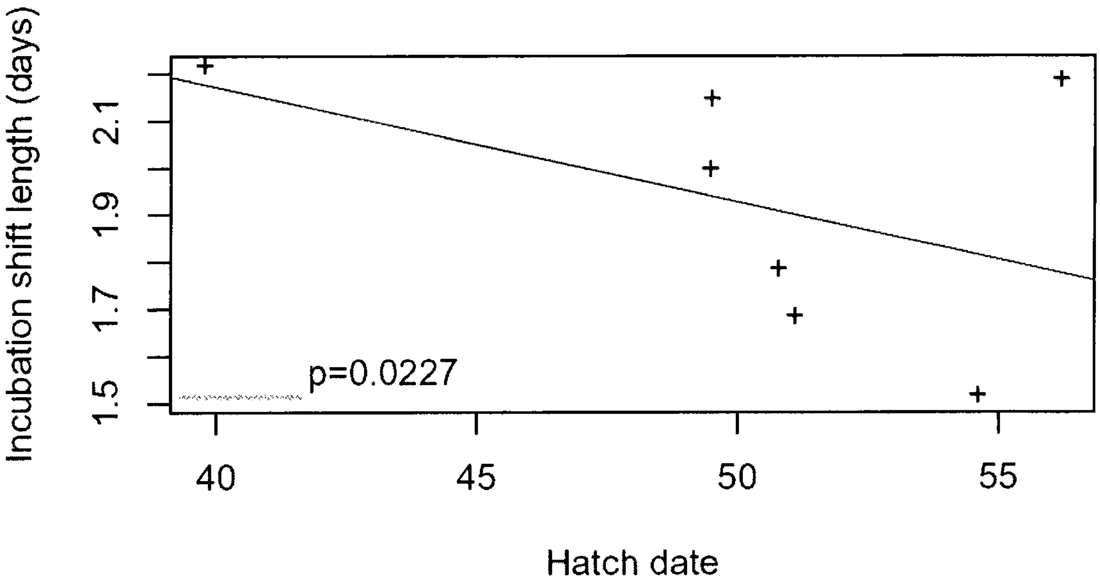

Figure 3.6: Mean incubation shift length in relation to hatch date of Ancient Murrelets at East Limestone (1993-2003) and Reef (2007-2008) islands. Hatch date indicated days from 1 April.

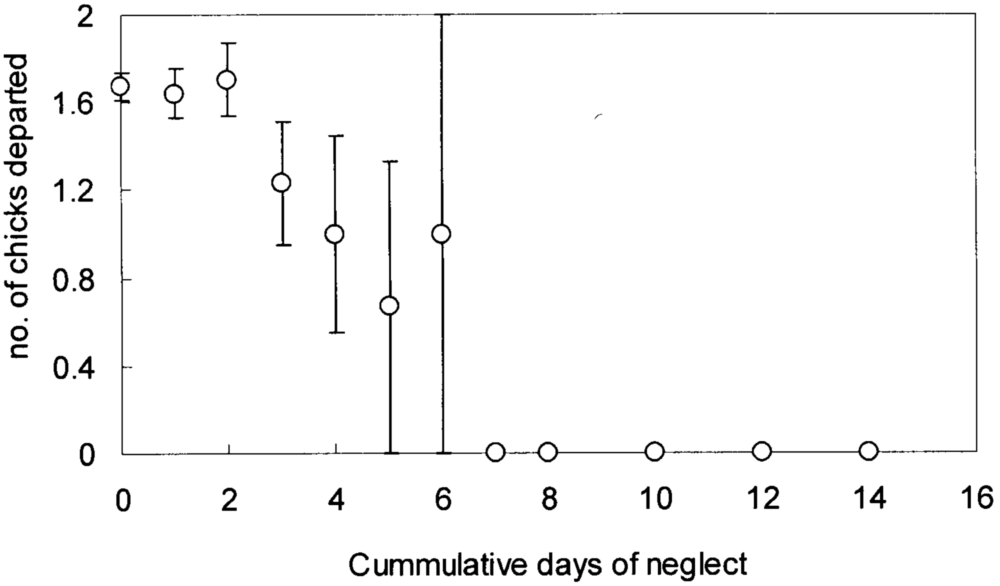

Figure 3.7: Mean number of chicks departed per pair (± SE) in relation to cumulative days of neglect for Ancient Murrelets at Reef Island in 2007 and 2008 (combined).

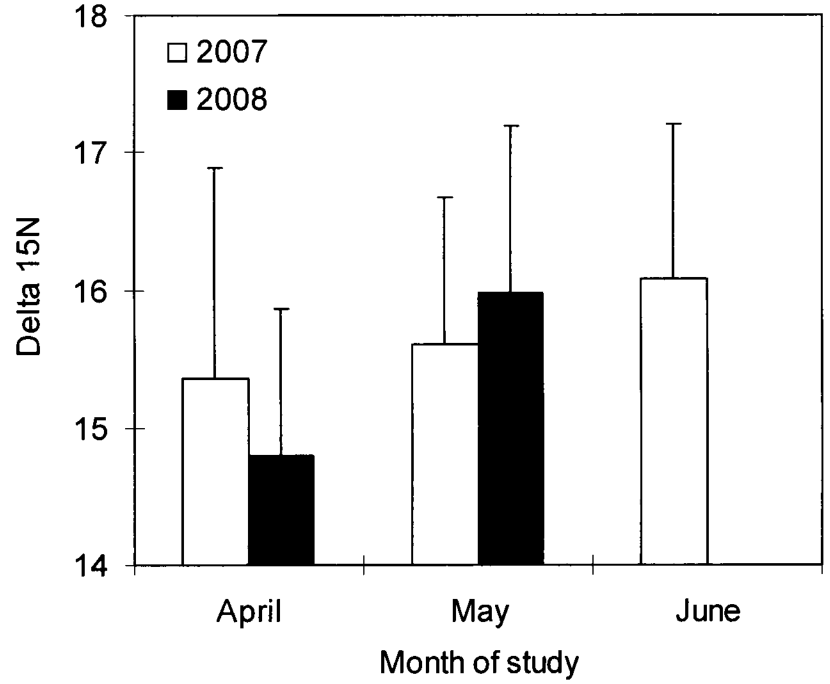

Figure 3.8: Stable isotope values from adult muscle for Ancient Murrelet carcasses. Vertical bars represent nitrogen isotope ratio (δ ^{15}N in ‰).

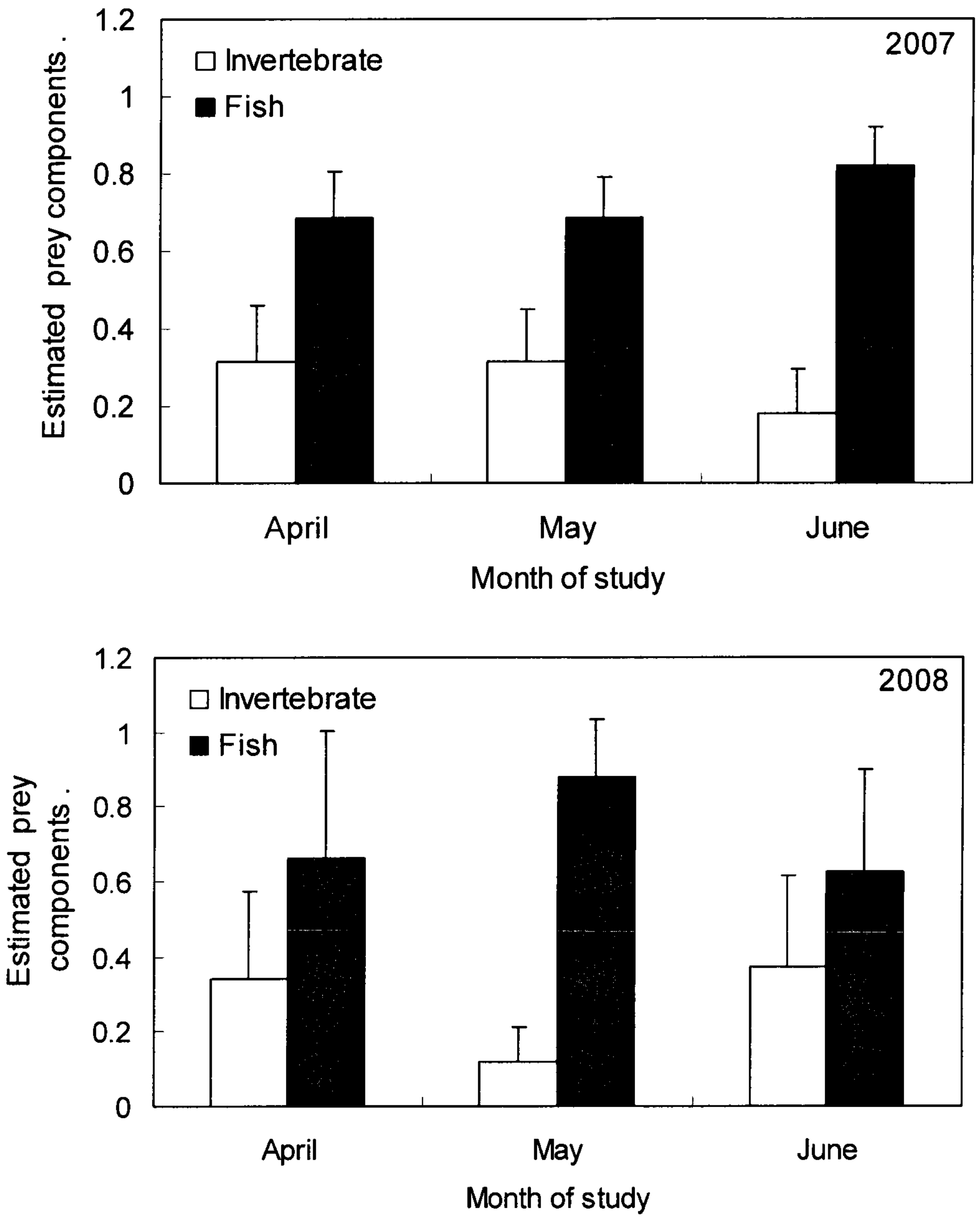

Figure 3.9: Results of mixing model of stable isotope values from adult Ancient Murrelet carcasses. Estimated proportion of invertebrates is shown by open bars, fish by filled bars.

3.5. DISCUSSION

Here I showed that variation in the timing of breeding, but not reproductive success, was significantly associated with sea surface temperature during the incubation stage. Because reproductive success was not affected by sea surface temperature, my results suggest that murrelets were capable of adjusting their incubation behaviour to accommodate fluctuations of climate, and thereby ensure that their chicks hatched successfully. I would then expect incubation behaviour to be a better indicator of oceanographic conditions than reproductive success. Indeed, interannual variation in shift length strongly correlated with ocean climate, as previously documented for sea surface temperature (Gjerdrum et al. 2003: reproductive success), chlorophyll concentrations (Wolf et al. 2009: reproductive success), upwelling (Roth et al. 2005: timing of breeding), and ice conditions (Mallory et al. 2008: incubation shift length).

Reproductive success tended to decrease with increasing incubation shift length. For example, reproductive success was lowest in 2002-2003, when mean incubation shift length was longest. This result appears to contradict the result obtained in Chapter 2, where I showed that, within a given year, reproductive success (number of chicks departed) increased with incubation shift length. A possible explanation for this apparent contradiction is that in years of high marine productivity, when birds are less likely to be food stressed, the proportion of young, inexperienced, or generally lower quality birds that succeed in completing incubation may be higher than in years of lower productivity. Because young birds tend to produce smaller clutches and a higher proportion of unhatchable eggs (Hipfner et al. 1997; Hipfner 1997), nest success in terms of mean brood size at hatching may actually be higher in years of lower marine productivity because in such years many lower quality birds fail before they complete incubation or may not even lay eggs. Consequently, variation in annual incubation shift length may be a better predictor of reproductive success than any actual sampling of marine productivity (Table 3.2). In addition, chick weight at departure from the nest was affected by longer incubation shift lengths. However, I could not find any significant relationship between reproductive success and SSTs or SOI, presumably, because incubation behaviour acted as a "buffer". Specifically, as most other species of auks have shift lengths of one-day or less (Gaston and Jones 1998), it can be posited that the longer shift lengths in Ancient Murrelets are an adaptive response to maintain reproductive success in the face of unexpected changes in prey abundance and distribution. For example, the related Rhinoceros Auklet (Blight et al. 1999) and Xantus's Murrelet (Murray et al. 1983) increase egg neglect in years with poor food supply.

Many pelagic seabirds undergo a large decrease in their body mass during the incubation stage (Fisher 1967; Prince et al. 1981). For instance, in Cassin's Auklet, a closely related species, adults lose about 8% of their body mass after the first 24-hour incubation shift (Ronconi and Hipfner 2009). It is possible that there exists a threshold in terms of adult body mass of incubating birds below which parents decide to desert the nest (Weimerskirch 1995; Gaston and Hipfner 2006a; Gaston and Hipfner 2006b). I therefore suggest that nest desertion occurs in response to a breeding pair's failure to maintain the incubation schedule (Wheelwright and Boersma 1979). Although Ancient Murrelets are known to occasionally neglect their eggs for a few days regardless of successful or unsuccessful nest outcomes (Gaston 1992b), I found here that the cumulative number of days of egg neglect has a dramatic effect on reproductive success. While up to three cumulative days of egg neglect had no effect on reproductive success, I found that cumulative egg neglect of four or more days was associated with reproductive failure (Fig 3.7). Consequently, if annual SST continues to increase, the "buffer" provided by incubation behaviour may "run out" and reproductive success may eventually decline.

Trophic level tended to increase over the season, and a mixing model suggested that birds switched from invertebrates to small fish over the course of the season. This concurs with previous results elsewhere 30 years previous based on stomach contents (Sealy 1975). In the year with longer incubation shifts (2008), trophic level increased much more rapidly in April-May. I suggest that this rapid switch may have created a mismatch between murrelet behaviour and prey abundance. For example, if birds relied primarily on memory to find prey (e.g. Woo et al. 2008), and prey distribution was changing rapidly, birds may have had difficulty re-accessing prey after extended periods at the colony. The idea that rapidly changing prey abundance may result in longer incubation shifts is also supported by the negative relationship between hatch date and incubation shift length (Fig 6)—in earlier years, food abundance may change more rapidly resulting in longer incubation shifts.

Murrelet plasma was depleted in carbon-13 compared to blood but of a similar trophic level, as has been found previously for Charadriiform birds (Ogden et al. 2004; Woo et al. 2008), while muscle was at a 3-4‰ higher trophic level than blood but of similar carbon output, as has been shown previously (Hobson et al. 1994; Davies et al. 2009). My values for murrelet blood were similar to breeding Cassin's Auklets at nearby Triangle Island (Ancient Murrelet: δ^{15}N ($^{o/}$oo) = 13.4; δ^{13}C ($^{o/}$oo) = -18.76; this study, Cassin's Auklet: δ^{15}N ($^{o/}$oo) = 15; δ^{13}C ($^{o/}$oo) = -18.81; Davies et al. 2009), but my values for muscle were much higher and more variable than those for Ancient Murrelets collected in Alaska in July (Hobson et al. 1994), suggesting that the Alaska birds may specialize on plankton while my birds feed on plankton and fish, leading to a higher and more variable trophic level. Finally, trophic level was lower at East Limestone Island, although I do not have comparable values for the same time period at Reef, suggesting that food conditions may exacerbate raccoon predation there, providing a potential secondary reason for population declines there; it is well known that nearby colonies can feed at very different locations (Hipfner et al. 2007).

Here I found that mean incubation initiation date was related to April sea surface temperature, which corresponds to the time when the first Ancient Murrelet eggs are normally found in Reef colony (Gaston 1992). If SST is related to prey abundance, I can expect that food availability in April will affect the quality of eggs produced, and therefore reproductive success. Moreover, parents with shorter shifts produced heavier chicks measured at nest departure (Fig.3. 5). Unlike other seabirds, Ancient Murrelets are precocial and do not feed young in the nest; and therefore chick mass at departure in this species depends largely on the amount of energy mothers invest in their eggs and the parental effort during the incubation. Thus, not only does incubation shift length mediate the relationship between SST and reproductive success at the colony, but it also appears to play an important role in mediating the relationship between SST and post-fledging reproductive success, provided chick mass at departing is an important component of post-fledging survival. In short, SST plays an important role in several demographic parameters for Ancient Murrelets, and an important proximate mechanism for its effects seems to be incubation shift lengths.

3.5.1. Conclusions

Ancient murrelets on Queen Charlotte Island can adjust their incubation patterns by extending their shift length. In years with longer shift length, birds have lower reproductive success and chicks depart the nest at a lower body mass. Several studies have shown that strong temporal mismatching between prey species and predators due to marine climate fluctuations causes poor breeding success in seabirds (Hipfner 2008; Gaston et al. 2009). Although I did not measure prey abundance, I conclude that food supply determines incubation shift length and therefore reproductive success in Ancient Murrelets because longer incubation shifts were associated with rapid changes in trophic level, later breeding and lower SST .Future studies should test the relationship between incubation shift lengths and prey accessibility by measuring prey abundance directly or using electronic recorders to develop a proxy for at-sea prey accumulation rates. Long-term climate change will likely be a major factor influencing the population dynamics of murrelets and other marine species.

4. GENERAL DISCUSSION

According to life-history theory, iteroparous species have to allocate resources between reproductive effort to producing their offspring and self-feeding to ensure their own individual survival (Williams 1966; Stearns 1992). Incubation strategies represent an example of how different species approach the issue of how to allocate resources during a critical period of reproduction (Lack 1968). Therefore, elucidating incubation strategies in iteroparous birds allows us to gain a better understanding of the ecological cues affecting resource allocation as well as the constraints under which their lifetime fitness is maximized. The Ancient Murrelet, has an exceptionally long incubation shift length in comparison with other species of Alcidae (Sealy 1976; Gaston 1992b; Gaston and Jones 1998); however, the reason why such an unusual life-history strategy has evolved in Ancient Murrelets is still unknown. The aim of this thesis was therefore to elucidate the factors influencing incubation shift length in this seabird species, and to determine the importance of environmental conditions in altering their behaviour and reducing reproductive performance.

Incubation shift length of Ancient Murrelets is affected by local environmental conditions (e.g. wind speed, wave height, tide) and prey availability. In Chapter 2, I showed that incubation shift length was affected by long-term wind speed during the foraging trip (24 h), rather than short term during the return journey (6 h). This result suggests that local marine conditions affected foraging efficiency, rather than flight performances from the foraging area to the colony. Wind speed increases as a result of the elevated barometric gradient, while wave height is generally closely related to wind speed, but lags it by some hours. As Auks are diving seabirds, the strong wave actions resulting from high wind speeds may reduce diving performances. Therefore, foraging efficiency may decrease and energy expenditure increase during foraging bouts on stormy days (Finney et al. 1999). Under similar unfavourable feeding conditions, Common Guillemot (*Uria aalge*), another species of Auk, change their behaviour by diving more frequently and / or changing their foraging area. Here, although I do not know the exact foraging area of Ancient Murrelets, birds increased their foraging effort, as measured by the number of dives, per bout during bad weather (Chapter 2). Increasing foraging effort reduces energy efficiency of birds, and thereby increases the time to feed at sea and corresponding shift lengths.

When bad weather persists, birds are therefore expected to extend the foraging duration to replenish energy reserves for their next incubation shift. However, the fasting duration of the incubating partner is also extended, which in return may cause it to have a longer trip when its turn comes. Previous studies suggested that reproductive success depends on the synchronized alternation between pair members (Croxall and Ricketts 1983). As a result, birds would avoid doing "extra work" because of poor coordination between the male and the female. In my study, incubation shift length was highly correlated between pair members and was associated with duration of previous shift (= partner's shift length). Incubating, and therefore fasting, birds lose weight. The longer this fasting period, the longer they will spend on their next foraging trip so as to replenish their own energy reserves. In Chapter 2, I showed that incubation shift length is the most important factor for reproductive success of Ancient Murrelets, and that maintaining a regular incubation schedule is therefore essential for reproductive success in this species.

Inter-annual variability of marine physical conditions may affect the geographical range and demographic patterns of species, which could impact on marine ecosystems. Large warming episodes linked with El Niño-Southern Oscillation (ENSO) cause (i) a low nutricline, (ii) the development of a deep chlorophyll maximum layer and (iii) a decrease in secondary productivity of zooplankton (McGowan 1998). As a result, the foraging efficiency of marine predators, including seabirds, is often reduced. Thus, seabird foraging efforts are expected to increase which may result in poor reproductive success of seabirds. Alternatively, climatic changes are asymmetrically altering the phenology of species at different trophic levels, sometimes causing a mismatch between the peak of prey abundance and the peak of energy demand of their predators. Therefore, a predators species which fails to adjust the timing of breeding to the peak of preys may face erratic food supply, which in turn may result in poor reproductive performance. In both cases, decreased prey abundance and discordant phenology between prey and predators, may be caused by warming conditions and could adversely affect the reproductive performance of Ancient Murrelets at the population level. In Chapter 3, I showed that sea-surface temperature (SST) affects incubation shift length, but not reproductive success. Presumably, this difference is because incubation behaviour acts as a buffer reducing the impact of longer shift lengths on reproductive success. However, if SST continues to increase, eventually the buffer provided by incubation shift length may run out and reproductive success decline (Chapter 3).

Among seabirds, Diomedeidae (Albatrosses) and Procellariidae (Petrels) travel great distances during the incubation period, which results in these birds having long incubation shifts that can range from days to weeks on average (Pennycuick et al. 1984; Chaurand and Weimerskirch 1994a; Chaurand and Weimerskirch 1994b; Weimerskirch 1995). Besides, birds extend the trip duration at sea under unfavourable weather conditions. Auks are deep-divers that employ the energetically expensive flapping flight; as a result, they are more adapted to diving and feeding rather than to flying long distances. Common Guillemots *Uria aalge*, a species of Alcidae, frequently alternate their incubation shifts every 12 h. They feed near the colony, so that flight costs can be expected to be small (Elliott et al. 2008). Ancient Murrelets were considered to be long-distance travellers when it comes to foraging during the incubation period (Sealy 1975). Like other Auks, Ancient Murrelets use flapping flight, but their weight to wing area ratio is lower than other auks (Gaston and Jones 1998). Consequently, they probably expend less energy on travelling than other auks, which is expected since energy costs associated with flight increase with body mass (Rayner 1999). However, as flight performance and dive performance in birds may represent a life-history trade-off, Ancient Murrelets probably specialized their predation habit and diet as a means to improving their flight performance to travel long distances to feed on presumable better and more diverse food resources.

Furthermore, the majority of seabirds with short incubation shift length visit their breeding sites by day (Gaston 2004). Reef Island, where I studied, is located at a relatively high latitude (53"N) where nighttime is short from April to June during the incubation period. As a nocturnal species at the colony, Ancient Murrelets come to their nests for only about 3-4 h during nighttime (Chapter 2; Jones et al. 1990). Thus, the timing and duration of colony arrival is highly constrained for Ancient Murrelets, presumably to reduce adult predation risk (Riou and Hamer 2008). As a result, birds lose an opportunity to return to their colony until next night if favourable conditions, such as the absence of predators and weather, permit. Here, I showed that the long incubation shift length of Ancient Murrelets is most likely an adaptive strategy to account for unpredictable food supply, and also for being nocturnal at the colony to reduce adult predation risk. My results suggest that multi-day incubation shifts in Ancient Murrelets are the adaptively preferred strategy, through reduction in predation risk, while actual shift length are modified by immediate weather and foraging constraints.

Some questions were left unanswered and I suggest that the following should be examined in future research.

(1) The importance of body conditions at certain point in time is expected to affect birds' decision process. Previous studies showed that the adult body condition is a key factor to decide when to desert their nests (Chaurand and Weimerskirch 1994a; Weimerskirch 1995; Kato et al. 2008). Therefore, it is expected that the decision to leave the nest is taken when body weight decreases to a certain threshold. However, in my study, I could only measure adult weight at the end of the incubation stage rather than performing continuous monitoring, as Ancient Murrelets are highly sensitive to human disturbance.

(2) The relationship between incubation shift length and age of parent could be examined to test whether older, presumably more experienced, birds are first able to synchronize their incubation shift length and second mate preferentially with birds of a similar age, as predicted in Chapter 2.

(3) The causes of variation in diving behaviour, both in terms of depth and frequency, are still unknown in this species. It is possible that prey distribution in terms of species compositions is a major determinant of diving variability. Therefore, the combination of dive-data with accurate identification of species preyed upon should be obtained. However, two factors limit prey identification. First, long foraging trips imply that most food items are partly to completely digested when birds return to the colony, and therefore cannot be identified from visual examination of stomach contents. Second, the absence of a chick-rearing period at the nest precludes the possibility of determining prey compositions as can be done for Cassin's Auklets by capturing adults returning to the colony and examining zooplankton carried to their young in a sublingual pouch.

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6. APPENDICES

6.1. Appendix I. A new longevity record for the Ancient Murrelet (*Synthliboramphus antiouus*)

Note: this appendix has been published in the Marine Ornithology.

A NEW LONGEVITY RECORD FOR THE ANCIENT MURRELET

SYNTHLIBORAMPHUS ANTIQUUS

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The Ancient Murrelet *Synthliboramphus antiquus* is a small member of the Alcidae widely distributed in the North Pacific temperate and subarctic zones during the breeding season. The species is completely nocturnal when coming and going from the colony and mainly nests in burrows or in cavities under tree roots (Sealy 1976, Gaston 1992). Chicks are precocial and the young are reared entirely at sea (Gaston 1992).

Seabirds generally exhibit low reproductive rates and high adult survival (Gaston 2004). However, although the survival and longevity of Ancient Murrelets are not well documented, they are thought to have a higher annual mortality than most other auks (Gaston 1990, Gaston & Jones 1998, Gaston 2004). The life expectancy of breeding Ancient Murrelets was estimated as approximately 4.5 years, based on banding and retrapping of adults and chicks at Reef Island, Haida Gwaii, British Columbia (52°52'N, 131°31'W) during the breeding seasons of 1984-1989 (see Gaston 1990 for details). This estimate of annual survival (77%) is relatively low compared to other Alcidae (Gaston & Jones 1998). Conversely, the average nest success (laying to departure) of 1.54 chicks per breeding pair per year is high compared with other auks (Gaston 1990).

There was trapping of adult or nestling Ancient Murrelets at Reef Island in 1990-1994, but banding of nestling and adult murrelets continued at the adjacent East Limestone Island from 1990 until 2003 (Charest & Epners 2004). In 2007, we resumed trapping adult Ancient Murrelets during their incubation period at Reef Island (April to June), using a plastic knock-down net (68 individuals: 52%) or taking birds from artificial nest boxes (63 individuals: 48%). A total of 131 adult birds were trapped, of which 11 birds had been banded in earlier years. Most adults were examined for the presence of brood patches to distinguish whether they were breeders (>20 mm maximum diameter), non-breeders (< 10 mm) or unknown status (intermediate) (Table 1). Nine of the recaptured birds were banded at Reef Island, eight as adults and one as a departing chick. The other two were banded at East Limestone Island (the shortest distance between Islands is 5.6 km), both as chicks departing to sea (for capture methods see Gaston 1992).

Among the recaptures, one bird, caught on 2 June 2007, was originally banded as an adult on 26 May 1987 at Reef Island (Table 2). When this bird was originally banded it had no brood patch and the wing length was 139mm. Breeders average 141.4±0.7 mm (males), 142.0±1.0 mm (females), non-breeders average 139.0±1.0 mm (males), and 138.5±0.9 mm (females) (Sealy 1976). The absence of a brood patch and the short wing length mean that this bird was almost certainly a non-breeding prospector when originally banded. Ancient Murrelets usually start to visit breeding colonies as pre-breeders at least a year before they actually breed, mainly at two or three years old (Gaston 1990).

Assuming that this bird was a non-breeder when first trapped, it was most likely 22, possibly 23 years old when recaptured in 2007. This makes it the oldest Ancient Murrelet so far reported. Previously, the oldest record was of a bird banded as a breeder in 1990—hence at least three years old at banding—and recaptured as a breeder at East Limestone island in 2003 (Charest *et al.* 2004). That bird was a minimum of 16 years old. Assuming that birds originally banded as non-breeding adults were two years of age at banding and that those banded as breeders were a minimum of 3 years old, the ages of the other birds retrapped in 2007 ranged from 5-15 years (Table 2). Our observations on the age of recaptured Ancient Murrelets in 2007 (Table 2, mean = 12 ± 4 years [SD]) was older than we anticipated on the basis of the survival rate estimated previously (Gaston 1990), but this was probably because the banding effort was intermittent between 1990-2007. Because the nest boxes were only placed on the island in 1997, and because occupancy in the early years was low, the majority have been occupied for less than seven years. Many natural burrows in the same area have been occupied since the 1980s at least.

Consequently, there seems no reason to expect that birds captured in nest boxes would be older than average for the population.

Gaston (1990) estimated that 44% of departing chicks survive to return to the colony at two years. If we assume that annual survival thereafter is constant at 77%, the chances of a bird surviving to age 22 are 0.0024, or just over two in a thousand. Moreover, mortality increases as birds age, through an increase in senescence effects (Ricklefs 2000). Hence, the survival of this particular individual appears to be a rather rare event. It serves to illustrate, however, that maximum longevity in birds may extend well beyond that attained by the majority of the population.

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TABLE 1

Details of banded birds trapped during the incubation period at Reef Island in 2007, divided by brood patch development. Brood patches of incubators were not inspected to reduce disturbance

Newly banded

	Maximum diameter of brood patch (mm)				
Date	no-sign	1 - 20	>20	unknown	Total
Before 30 April	3	3	0	0	6
1 - 31 May	0	24	44	41	109
After 31 May	0	0	0	5	5
Total	3	27	44	46	120

Recaptured[a]

	Maximum diameter of brood patch (mm)				
Date	no-sign	1 - 20	>20	unknown	Total
Before 30 April	0	0	0	0	0
1 - 31 May	0	2	6	2	10
After 31 May	0	0	1	0	1
Total	0	2	7	2	11

[a] Excluded in same year at Reef Island

TABLE 2

Ancient Murrelets banded in earlier years and recaptured on Reef Island in 2007. Birds with brood patches >20 mm, or those removed from nest boxes, were considered breeders, while those with brood patches 16-20 mm were considered of unknown breeding status. None had brood patches <16 mm across. Two birds were not inspected

Band no.	Year	Banded date	Banded as	Location	Retrap date 2007	Status	Estimated age at retrap (years)
1103-56514	1987	26-May	Non-breeder	Reef I.	2-Jun	Breeder	22
1313-63130	1995	15-May	Breeder	Reef I.	21-May	Unknown	15
1313-63137	1995	15-May	Breeder	Reef I.	13-May	Unknown	15
1313-63498	1995	22-May	Non-breeder	Reef I.	6-May	Breeder	14
1313-64689	1996	30-May	Chick	Limestone I.	21-May	?	11
1313-66186	1997	8-Jun	Non-breeder	Reef I.	25-May	Breeder	12
1313-66290	1997	4-Jun	Non-breeder	Reef I.	25-May	Breeder	12
1313-66293	1997	5-Jun	Non-breeder	Reef I.	18-May	?	12
1313-84198	1999	15-May	Chick	Reef I.	18-May	Breeder	8
1313-84925	1999	13-May	Non-breeder	Reef I.	18-May	Breeder	10
1313-96483	2002	26-May	Chick	Limestone I.	19-May	Breeder	5

6.2. Appendix II. Comparing methods for monitoring nest attendance in Ancient Murrelets.

Note: this appendix has been formatted for publication by the Waterbirds and is under the process of minor revisions at the time of thesis submission.

Comparing methods for monitoring nest attendance in Ancient Murrelets

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Abstract.– Knock-down tagsI are often used to monitor population and nest attendance patterns of burrow-nesting seabirds. However, the accuracy of the knock-down method has not been considered in detail. In this note, measurements of nest attendance patterns for Ancient Murrelets (*Synthliboramphus antiquus*) obtained by the knock-down and the radio telemetry methods were compared on a colony at Reef Island, Haida Gwaii, British Columbia. Radio transmitters and knock-down tags both indicated activity 79% of the time (range: 61–96%, N = 307), and the correlation between the two methods was significant (Cohen's kappa test, $k = 0.55$, $Z = 19.9$, $p < 0.01$; Table 1). Hence, knock-down tags provide information that, although coarse, can provide an adequate indication of reproductive behavior in Ancient Murrelets without disturbance to the birds.

Key words. – Ancient Murrelet, monitoring, nest attendance, *Synthliboramphus antiquus.*

Running head. – MONITORING METHODS IN MURRELETS

Burrow nesting alcids are sensitive to disturbance during the nesting season, especially in the early incubation period when accumulated parental investment is relatively lower than the chick rearing period (Wehle 1976; Pierce and Simons 1986; Gaston and Jones 1988; Rodway *et al.* 1996). Three common methods have been used to monitor their nest attendance: marking birds and inspecting burrows daily to see if birds are present, knock-down tags across burrow entrances and radio telemetry. Marking and daily inspection may affect measurements (Whidden *et al.* 2007) or cause the desertion of eggs and nestlings (Gaston *et al.* 1988). To record shift changes less intrusively, knock-down tags have been used in several studies (e.g. Gaston *et al.* 1988; Gaston and Powell 1989; Gaston 1992). Although this method provides potential benefits for researchers and birds, nest attendance patterns may not be as accurately measured as with direct methods (i.e. transmitters or marking), because knock-down tags are occasionally moved by other birds, mice or the incubating birds themselves. It is therefore important to evaluate the accuracy of the knock-down method to determine the frequency of true changeovers, based on actual radio telemetry measurements. Accuracy was measured for Ancient Murrelets breeding in Haida Gwaii (Queen Charlotte Islands), British Columbia, Canada.

Murrelets nest in colonies on conifer-forested islands, digging burrows in soft soil and often placing the entrance among tree roots or boulders (Vermeer and Lemon 1986, Gaston 1992). Two eggs are laid with an interval of about 8 days and they initiate incubation soon after the clutch is complete. Both eggs normally hatch within 24 hours of one another (Sealy 1976). Chicks are truly precocial and never fed in the nest, but leave with their parents usually within two days and all subsequent development takes place at sea (Sealy 1976; Gaston *et al.* 1988; Gaston 1992; Gaston 1994; Gaston 2002).

METHODS

The study was carried out at Reef Island, Haida Gwaii (52°52'N, 131°31'W), British Columbia, (see Gaston 1992) during the 2008 Ancient Murrelet breeding season. Observations were made of birds nesting in artificial nest boxes which had been set up within the breeding colony (Gaston 1996). First, we set up knock-down tags at all nest box entrances. Nest boxes were inspected only when these tags were displaced, indicating that a bird had entered the box (see Appendix I). Once the first egg was laid, either a temperature sensor (Onset TMC1-HD) or a YSI temperature probe (Yellow Springs Instruments; 400 series) was inserted into the nest chamber so that progress of incubation could be monitored. The temperature sensors were connected to an electronic recorder (Onset: H08-006-04) and downloaded daily. The YSI temperature probe was connected to a telethermometer and read once daily, as Ancient Murrelets only enter or exit their burrows at night (Gaston 1992). We secured the tips of the temperature probes in the nest cup with thumbtacks fixed onto the floor of the box during the daytime, prior to the laying of the second egg, when birds were not present. In 2008, 56 nest boxes were used and 25 pairs in those boxes completed the full term of incubation. We attached 17 transmitters randomly to one partner of each of 17 pairs. Nest attendance patterns were checked once daily during the daytime. At each check, shift changes were scored as either "change or "no change". The knock-down method indicates "change" when tags at the entrance have been displaced. The radio telemetry method indicates "change" when radio signals have appeared or disappeared (because only one member of each pair was fitted with a transmitter). Otherwise the shift status was scored as "no change". All procedures were approved by the Animal Care Committee of the National Wildlife

Research Centre and the Ontario Region of Environment Canada operating under the guidelines of the Canadian Committee for Animal Care (Permit Number 0800AG02).

To assess the validity of the knock-down method, we compared results between radio transmitters and knock-down tags in detecting changeovers by males and females (N = 14; three nests were deserted), and results were evaluated by Cohen's kappa (κ) test (Cohen 1960). This test provides a simple, effective, standardized statistic for evaluating or comparing change-no change (1 or 0) models (Manel *et al.* 2001). For the kappa test, values of 0.0-0.4 are considered in medical applications to indicate slight to fair model performance, values of 0.4-0.6 moderate, 0.6-0.8 substantial and 0.8-1.0 almost perfect (Landis and Koch 1977). To account for an asymmetry in the confusion table, increased weight is given to cells of disagreement. Statistical analysis was completed in R.2.6.1. Two-tailed probabilities are computed at the 5% level for weighted kappa statistics. Unless otherwise indicated, means ± SD are presented.

RESULTS AND DISCUSSION

The proportion of agreement between all nests using either knock-down tags or radio transmitters was 79% (range: 61–96%, N = 307) where results of the knock-down tags were correlated with that of radio transmitters (Weighted kappa test, $k = 0.55$, $Z = 19.9$, $p < 0.01$; Table 1). Knock-down sticks detected 93% of changeovers determined by radio telemetry, but they recorded changeovers on 35% of nights when telemetry showed that no changeovers occurred. The duration of incubation shift length measured by knock-down tags (mean = 1.65 ± 0.88 day, N = 186) was significantly shorter than that measured by radio transmitter (mean = 2.27 ± 0.88 day, N = 135; $t = -6.2$, $p < 0.001$; Fig. 1). The degree of agreement between the two methods varied among nests (range 62% to 96%; $\chi^2 = 25.8$, df = 13, $p < 0.05$, Fig. 2). Based on

Manel *et al.* (2001), our results ($k = 0.55$) suggest that knock-downs do provide useful indications of shift changeovers.

Knock-downs were a fairly accurate indicator of changeovers, when these occurred (93% agreement) but gave a high incidence of false positives, i.e., when no changeover occurred (35%). For most purposes, the assumption that no changeover has occurred when the knock-down sticks remain in place appears valid. Large false positive rates are unsurprising because (1) off-duty breeders may visit the colony without exchanging incubation duty (Gaston 1992), (2) tags may be displaced by high winds – in that case the exposure of nest entrances might be responsible for variation among nests, and (3) prospective breeders may enter, perhaps only partially, when searching for a suitable nest site. The variation in the frequency of agreement among nests may be caused by individual differences (e.g. incubator activity) or nest site characteristics (e.g. presence of mice). In spite of its low accuracy, we argue that the knock-down method is useful for monitoring populations (e.g. consistent trends in knock-down frequencies over several years), detecting reproductive activities (e.g. burrows where knock-downs occur at below a prescribed threshold can be regarded as unoccupied) and obtaining information on nest attendance patterns (e.g. changes in knock-down frequencies among years, at different light and/or weather conditions or among different areas of the colony), as knock-down sticks detected 93% of changeovers determined by radio telemetry. Furthermore, this simple method has no cost (e.g. twigs or a pieces of wood or plastic can be used as tags), is easy to use in field and is less invasive than other direct method (e.g. marking, radio transmitters, Gaston *et al.* 1988), and therefore may be especially applicable for endangered species such as Japanese Murrelets (*Synthliboramphus wumizusume*). In cases where more than one burrow shares the same entrance (e.g. Gaston 1992; Ryan and Moloney 2000), changeover rates are expected to be overestimated.

An assessment of the frequency of multiple entrances and interlocking burrows is therefore necessary before results from knock-down tags experiments could be properly interpreted. We recommend caution when planning, using and interpreting the results of knock-down tags. However, the knock-down method is the least invasive method to collect coarse data on reproductive behaviour with limited bias.

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	Radio transmitter	
Knock-down	Change	No change
Change	125 (93%)	61 (35%)
No change	10 (7%)	111 (65%)

Table 1. The results of agreement between a knock-down method and radio telemetry (Weighted kappa test, $k_w = 0.55$, 95% CL: 0.46-0.64, $Z = 9.86$, $p < 0.001$) and column percentages.

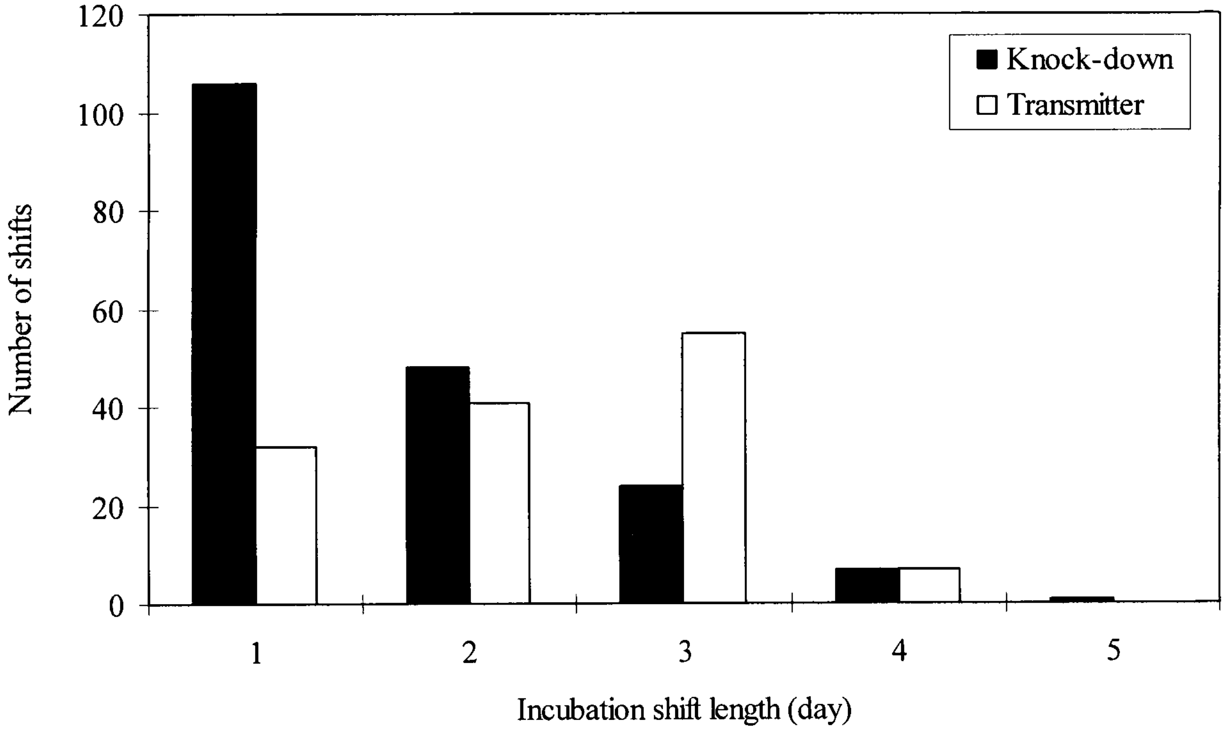

Figure 1. The distribution of incubation shift length of radio-marked Ancient Murrelets measured by knock-down tags (black, mean = 1.65 ± 0.88 days, N = 186) and by radio telemetry (white, mean = 2.27 ± 0.88 days, N = 135; observation = 278 days).

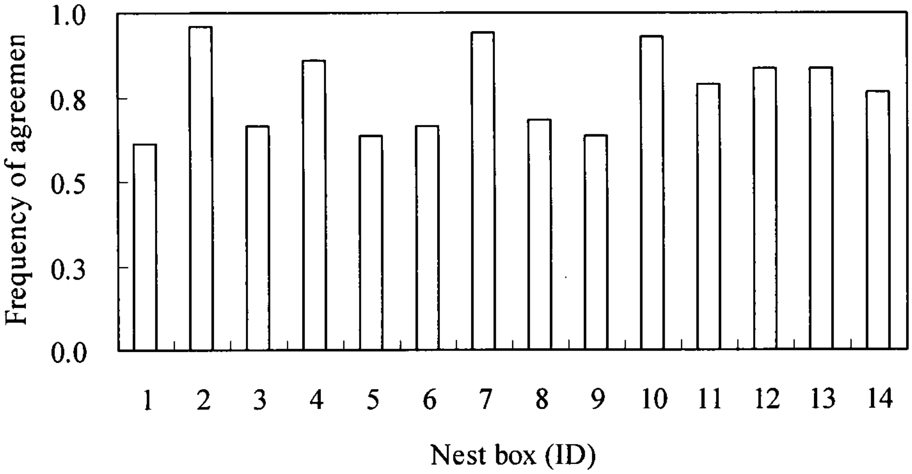

Figure 2. The degree of agreement between knock-down tags and radio telemetry ($\chi^2 = 25.8$, $df = 13$, $p < 0.05$).

Appendix I: The diagram of the knock-down method