GEOGRAPHICAL VARIATION IN INCUBATION SHIFT LENGTH OF ANCIENT MURRELETS SYNTHLIBORAMPHUS ANTIQUUS DETERMINED FROM GEOLOCATOR DEVICES

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ABSTRACT

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Incubation shift lengths were estimated from geolocator devices attached to 48 Ancient Murrelets *Synthliboramphus antiquus* at four colonies in Haida Gwaii, British Columbia, during 2014 and retrieved during 2015. Light-level data were used to determine the timing of colony departures in 2014 and the start of incubation in 2015, and to measure the length of incubation shifts. Incubation started and ended 12 d later at colonies on the west coast of Haida Gwaii than at those on the east coast. First at-sea shifts after devices were attached (mean 3.6 d) were longer than later shifts (2.8 d), and longer than corresponding mate shifts (2.9 d), suggesting that attachment had some effect on behaviour. However, by the time of colony departure, shift lengths were unaffected by the devices. During 2014, excluding the last shift before departure, most shifts at colonies on the east coast were 1–3 d, whereas those at west coast colonies were 3–5 d. Shifts during 2015 were also longer at west coast than at east coast colonies, although sample sizes were smaller because time between start of incubation and recapture was mostly brief. This is the first demonstration of regional variation in incubation shifts among Ancient Murrelet populations. Although geolocators are generally used to study long-distance movements in seabirds, our results support to the idea that they can provide substantial additional information on the breeding biology of birds.

Key words: Ancient Murrelet, British Columbia, geolocator, incubation, shift length, phenology, geographical variation

INTRODUCTION

In British Columbia, Ancient Murrelets Synthliboramphus antiquus breed in burrows under mature rainforest canopy. Their young leave the natal burrow within 48 h of hatching and are fed entirely at sea (Sealy 1976, Gaston 1992). The genus Synthliboramphus exhibits the longest incubation shifts of any auks, sitting for up to six days at a time (craveri, Murray et al. 1983; antiquus, Gaston 1992, Shoji et al. 2012). Most other auks undertake incubation shifts of <24 h (Gaston and Jones 1998). Incubation shift length of Ancient Murrelets may vary among years (Gaston 1992), and this variation has been linked to inter-annual variation in oceanographic conditions (Shoji et al. 2012). Within years, shift length is influenced by local weather conditions, as well as by the duration of the last shift carried out by the mate (Shoji et al. 2011). Shift duration may be correlated with reproductive success, suggesting that maintaining a coordinated incubation schedule between pair members is an important component of individual fitness (Shoji et al. 2011, 2015).

Because disturbance at the burrow can cause Ancient Murrelets to desert their nests, methods of measuring incubation shift length have attempted to minimize burrow inspections. The most precise and benign technique previously deployed was to fit breeders with lightweight telemetry transmitters and monitor shift length with a receiver held close to the burrow entrance (Gaston & Shoji 2010). This method requires only a single intrusion into the burrow, but is time-consuming because it requires daily checking of a sample of burrows for at least a month. Moreover, because the breeders cannot be trapped until after incubation has begun, information on the start of incubation is lacking. Measures of incubation shift length that did not involve repeated disturbance to burrows were used previously at only one colony: Reef Island in the Haida Gwaii, an archipelago of British Columbia (Shoji *et al.* 2011).

The recent deployment of geolocator devices on samples of breeding Ancient Murrelets at several breeding colonies in Haida Gwaii for migration tracking (Gaston *et al.* 2017), allowed us to obtain additional information on incubation shift length. We addressed the following questions: (1) Does the deployment of geolocator devices disrupt incubation in any way? (2) How does shift length vary in relation to sex or stage of incubation? (3) Is there geographical variation in incubation shift length?

METHODS

Field work

Geolocators were deployed on breeding Ancient Murrelets during 2014 at four islands of Haida Gwaii: Hippa and Susk Gwaii (west coast) and George and Reef (east coast). Geolocators were attached to only one member of each pair. Details of deployment and retrieval dates of the 49 recovered units are given in Gaston *et al.* (2017, Table 1). The geolocator (Intigeo-C65, Migrate Technology, Cambridge,

UK) was attached to a metal band on the right leg. The geolocator and band together weighed 1.7 g (<1% of adult body mass), and device dimensions were 14 × 8 × 6 mm. Burrows at which geolocators were deployed during 2014 were revisited during 2015 to recapture tagged adults. On recapture, adults were weighed, and a small blood sample (1 mL) was collected from the brachial vein using a 27 gauge, 0.5 inch needle and 3 mL syringe for use in a related study of contaminant burdens, for which analysis is underway. Blood was stored in a vacutainer with sodium heparin and two small circles of whole blood were dotted on filter paper (~ 10 μ L blood/circle), air dried and stored at room temperature. Filter paper samples were used to determine sex from DNA using PCR via test method MET-DNA-SEX-01C at the National Wildlife Research Centre, Environment and Climate Change Canada, Ottawa.

Data processing

Geolocators sampled light levels every minute and recorded maximum light every 5 min. The light-level scale ranged from 1.1 lux (total darkness) to 74 418.6 lux (maximum light intensity). Data were downloaded and light levels plotted against time in MS Excel (Fig. 1). Ancient Murrelets do not remain in their breeding burrows during the day until they begin incubation, after which the members of breeding pairs alternate incubation shifts, which generally last 1–5 d (Gaston & Shoji 2010). Incubating birds never emerge from their burrow during daylight (Gaston 1992). Hence, incubation behaviour can be identified from geolocator data based on days when no light was recorded during daylight hours. The first such day each year represents the start of the first incubation shift for that individual, and the last such day, the last day of that individual's final incubation shift. Days when light was recorded represent days spent at sea, equivalent to the mate's incubation shift.

We used these light data to calculate shift length for geolocatorequipped birds and their partners and to compare these data among colonies and between the two coasts of Haida Gwaii. Because shift length may change over the course of the incubation period, we compared shift lengths in relation to apparent dates of family departure (first day during 2014 after which no days without light were recorded) and apparent dates of start of incubation (first day without light during 2015). These dates are not known with certainty; we cannot determine whether, in 2014, the bird with the geolocator returned after its final at-sea shift and then departed with its mate the same night. Likewise, in 2015, we do not know whether the first shift recorded for the geolocator-equipped bird was actually the first shift for the pair, or whether its mate had preceded it; hence, we refer to the "apparent dates." In making comparisons among colonies, we assumed that this uncertainty would be similar for all colonies. We also compared the length of shifts by geolocatorequipped birds with those of their partners, to determine whether device attachment had any effect on incubation behaviour (2014 data only).

All variables were tested for normality using the Lilliefors test, and, for data that were not normally distributed, non-parametric probability tests were used. For non-parametric comparisons among colonies, we used the Kruskal–Wallis *H*-test and, for two-way comparisons, the Mann–Whitney *U*-test. All statistics were calculated using Statistica 7.1 (Statsoft 2005). All shift-length data are given in Appendix 1 (available on the website). Means are expressed \pm standard errors.

Permits

The project was approved in 2014 by the Simon Fraser University Animal Care Committee (protocol #974B-94), and in 2015 by the Environment and Climate Change Canada Western & Northern Region Animal Care Committee (project #15LW01). The following permits were obtained: BC Ministry of Environment: Ecological Reserve Permit #107132 (for Hippa Island), and Park Use Permit Research Permit #106604 (for Frederick and Reef islands); Parks Canada: Parks Canada Research & Collection Permit #GWA-2013-



Fig. 1. Sample of light-level record to illustrate the information used to describe Ancient Murrelet incubation shifts: one bird at Susk Gwaii, Haida Gwaii, BC, in 2014.

13715 (for George); Environment and Climate Change Canada Scientific Permits for 2014: #BC14-0026, and for 2015: #BC-15-0008, Banding Permits (Canadian Wildlife Service): Laurie Wilson 10667J, Dan Shervill 10667K, Glen Keddie 10067L, and Jake Pattison 10425AB.

RESULTS

2014

In 2014, data were obtained for the last part of the incubation period. Forty-eight of 49 birds recaptured provided suitable information, with one bird omitted from the analyses because it apparently departed soon after the device was attached and never returned to the burrow. The duration of incubation between the day on which the geolocator was attached and the apparent day (actually night) of colony departure by the family party varied from 7 to 46 d (mean 20 ± 7.9 d, excluding one outlier of 46 d). Mean date of departure varied among colonies



Fig. 2. Mean dates of apparent colony departure for geolocatorequipped Ancient Murrelets at four colonies in Haida Gwaii, BC, during 2014.

(Fig. 2), with birds in the two west coast colonies departing later than those in the east coast colonies. In post-hoc comparisons, departures from Susk Gwaii (west coast) were significantly later than at those from Reef Island (east coast), and departures from Hippa Island (west coast) were significantly later than those from both George and Reef islands (east coast) (Duncan multiple range tests, all P < 0.01). No other pairings were significant.

Incubation shift lengths did not differ between sexes for any of the last five shifts before departure (all P > 0.1, Mann-Whitney *U*-test). Sample sizes before that may have been influenced by the progressive departure of the sample. Duration of shifts varied over the incubation period, with the last shifts being shorter than preceding ones (Table 1). The lengths of the last shift before departure were mostly 1 or 2 d for both east and west coast colonies, whereas the penultimate shift was mainly 2 d at east coast colonies and 3–4 d at west coast colonies. The difference between east and west coast colonies was also seen for earlier shifts (three to five shifts before departure; Table 1). Earlier than that, samples became very small for west coast colonies, where the longer shifts reduced the number represented within the geolocator-deployment period.

Comparing the first shift at sea by the geolocator-equipped bird with the next shift (partner at sea), the geolocator-equipped birds were absent for longer, on average (3.6 d), than their mates (2.9 d, t = 2.52, df = 88, P = 0.01; Fig. 3), mainly because a small number of geolocator-equipped birds were absent for exceptionally long periods of more than six days (four birds, all males). They were also absent for longer on their first shift than on their next at-sea trip (3.5 d vs. 2.8 d, t = 2.34, df = 87, P = 0.02). Two birds spent eight days at sea. However, comparing the final at-sea periods between pair members, there was no difference between geolocator-equipped birds and their mates (see penultimate and third shifts in Table 1).

2015

In 2015, data were obtained for the start of the incubation period. One device battery expired before incubation started, and six were recovered on the first day of incubation for that bird, leaving 42 birds for analysis. The duration between the apparent start of

TABLE 1									
Ancient Murrelet shift durations, counting backwards in relation to time (days) of the last shift									
before departure from the colony in 2014: comparison of west and east coast colonies									

Shift	Coast -	Shift length (d)							Total		7a	D
		1	2	3	4	5	6	>6	- Iotai	U	Ľ	r
Last	West	13	8	2	1	0	0	0	24	267	0.42	0.68
	East	15	8	1	0	0	0	0	24			
2nd	West	3	4	5	7	3	1	0	23	135	3.15	< 0.01
	East	8	12	2	1	0	1	0	24			
3rd	West	1	2	7	13	0	0	0	23	99	3.77	< 0.01
	East	7	10	5	1	0	0	0	23			
4th	West	2	0	7	5	3	2	1	20	94.5	3.26	<0.01
	East	3	10	7	3	0	0	0	23			
5th	West	3	1	8	7	1	0	0	20	145	2.03	0.02
	East	2	12	6	2	1	0	0	23			

^a Z-values are based on Mann–Whitney U-tests.

incubation and the date of retrieval of the geolocator ranged from 0 to 30 d (mean 11 ± 7.2 d). Apparent start of incubation varied significantly among colonies ($F_{3,44} = 11.7$, P < 0.001) in the same order as for date of departure in 2014 (Reef < George < Hippa < Susk Gwaii; Fig. 2), with mean dates for west coast colonies (4 May) differing significantly from those for east coast colonies (22 April), but with no significant difference within coasts (Duncan multiple range tests, all P > 0.1).

The first incubation shift at both east and west coast colonies was predominantly 1 d, but duration differed between males and females, with most females spending only 1 d on their first shift, whereas most males spent 2–3 d (Fig. 3). However, there was no difference in shift duration between males and females in subsequent shifts (shifts 2 to 4, all P > 0.1). With sexes combined, there was a difference between coasts, with the second shift being 2–3 d on the east coast and 3–4 d on the west coast. The duration of the third shift was more variable and did not differ between coasts (P > 0.1); after that, samples were too small to be meaningful.

DISCUSSION

Our results indicate that the process of capture and geolocator attachment may have affected the incubation regime of some geolocator-equipped birds, by causing them to spend longer at sea on the first shift post-attachment than they would have done otherwise, although it seems to have involved only a small proportion of birds. Other estimates of incubation shift length suggest that >6 d is beyond the normal range of incubation shifts (Gaston 1992, Shoji et al. 2012). In the case of the four birds that remained at sea for >6 d, it seems likely that their eggs were unattended for a period. However, we cannot determine this for sure. Such neglect has been observed previously and does not usually lead to breeding failure (Gaston & Powell 1989). The evidence from comparison of the final two shifts before departure indicates that the effect had worn off by then, as the duration of these did not differ between geolocator-equipped birds and their partners.

Dates of colony departure during 2014 and of the start of incubation during 2015 both varied among colonies, with east coast colonies being consistently earlier than west coast colonies. This finding supports earlier observations (Gaston & Harfenist 1998, Gaston *et al.* 2017) that colonies on the east coast of Haida Gwaii have an earlier breeding schedule than those on the west coast. Dates derived here differ slightly from those given in our earlier study (Gaston *et al.* 2017) because a re-appraisal of the data allowed inclusion of several birds that were omitted from the earlier analysis. No conclusions changed as a result, but the difference between coasts was greater in the current analysis (west coast 8 d later in Gaston *et al.* 2017; 12 d later in current analysis).

Our observations of incubation shifts at the two east coast colonies showed that shifts had similar length (mostly 1–3 d) as those recorded previously at Reef Island (Gaston 1992, Shoji *et al.* 2012), but those at west coast colonies were longer, especially during the latter part of the 2014 incubation period. Unfortunately, we cannot distinguish year effects from stage of incubation effects, so we have no way to know whether the difference between the two coasts becomes greater as incubation proceeds, or simply that shifts were longer on the west coast during 2014 than 2015 because of differences in environmental conditions.

The two west coast colonies are substantially larger than those on the east coast (Hippa Island 40000 pairs, Susk Gwaii 31300 pairs, vs. George Island 17400 pairs; Reef Island 6600 pairs: Environment Canada 2015). The size of the western colonies may require birds to forage farther away from the colony (Gaston 2007, Gaston et al. 2013). This could increase the length of commute times and hence the duration of incubation shifts. Our data refer to only two seasons, so it is plausible that the difference between east and west coast colonies during 2014 and 2015 was a function of year-specific, rather than colony-specific effects. However, previous data from Reef Island, although limited, where mean incubation shifts ranged from 1.6 to 2.5 d in seven years during 1993-2008 (Shoji et al. 2012) and from Langara Island, on the west coast, where they averaged 3 d during 1971 (Sealy 1976), tend to support the idea that shifts are longer at west coast colonies. Our results demonstrate that geolocators can provide substantial information on the breeding biology of birds on which they are deployed, in addition to the information they provide on movements.

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Fig. 3. Distribution of durations of first incubation shift by male and female Ancient Murrelets during 2015, data from the four Haida Gwaii study colonies combined.

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