ANCIENT MURRELET *SYNTHLIBORAMPHUS ANTIQUUS* COLONY ATTENDANCE AT LANGARA ISLAND ASSESSED USING OBSERVER COUNTS AND RADAR IN RELATION TO TIME AND ENVIRONMENTAL CONDITIONS

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SUMMARY

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The decision to attend a colony on any given day or night is arguably the result of a trade-off between survival and reproductive success. It is often difficult to study this trade-off, as monitoring patterns of colony attendance for nocturnal burrow-nesting seabirds is challenging. Here, I 1) examined the effectiveness of monitoring Ancient Murrelet colony arrivals using marine radar, and 2) evaluated differences in colony attendance behavior in relation to time, light, and weather. I found a strong correlation between the number of Ancient Murrelets counted by observers in the colony and the number of radar targets counted, with estimated radar target counts being ~95 times higher than observer counts. My hypothesis that patterns of colony attendance are related to environmental conditions (i.e. light and weather) and that this relationship changes with time after sunset was supported. The top supported model included interactions between time after sunset and light and weather variables, suggesting that they were important predictors of colony arrivals. Contrary to my prediction, results suggest that light conditions (moon absence and cloud cover) and wave height were most important for individuals arriving three hours after sunset (when >75% of arrivals would be breeders). Assuming the majority of birds arriving early in the night are breeders and those arriving late in the night are non-breeders, these results suggest differences in patterns of colony attendance that may be attributed to age and/or breeding status.

Key words: Ancient Murrelet, *Synthliboramphus antiquus*, Langara Island, marine radar, colony attendance, weather, light

INTRODUCTION

Trade-offs between reproductive investment and survival are central to theories of animal behavior (Drent & Daan 1980, Stearns 1989). Most studies focus on when animals breed, how many offspring they produce, and how long they care for young (e.g. Blomquist 2009). The decision concerning whether to breed in a given year is argued to be a strategy to increase overall lifetime reproductive success (Schaffer 1974, Reichert *et al.* 2012). Similarly, the daily decision to attend a colony may be fixed for breeders, which need to attend the colony to ensure their current reproductive effort is successful (Rice & Kenyon 1962, Weimerskirch 1998, Calvert & Robertson 2002). In contrast, non-breeders can be more flexible in their colony attendance, and they exhibit behaviors aimed at minimizing risk and ensuring survival (Watanuki 1986, Mougeot & Bretagnolle 2000).

Many colonial burrow-nesting seabirds attend their colonies nocturnally, which is widely accepted as a strategy to avoid avian predators that require at least moderate ambient light levels for successful hunting (Watanuki 1986, Mougeot & Bretagnolle 2000). However, nocturnal activity does not eliminate the risk of predation completely (Stenhouse & Montevecchi 1999, Mougeot & Bretagnolle 2000, Votier *et al.* 2006), and many nocturnal seabirds decrease colony attendance during bright and anticipated bright-light conditions (i.e. moon phase), when they are most vulnerable (Watanuki 1986, Bretagnolle 1990, Mougeot & Bretagnolle 2000, Bourgeois *et al.* 2008). Furthermore, adverse weather conditions (high winds and waves, and heavy precipitation) may decrease foraging efficiency, increasing energetic stress on individuals and making them less likely to attend colony sites (Gaston & Nettleship 1982, Finney *et al.* 1999, Shoji *et al.* 2011). Such conditions may also decrease the ambient light at the colony site, which can increase the risk of colliding with trees in forested landscapes, and thus decrease colony attendance during very dark conditions (Jones *et al.* 1990).

Ancient Murrelets *Synthliboramphus antiquus* are a small, nocturnal, burrow-nesting seabird whose North American range stretches from Haida Gwaii, British Columbia, through the Aleutian Islands, Alaska. Throughout their range, populations have declined owing to introduced species (Gaston & Shoji 2010). In British Columbia, Ancient Murrelets attend their colonies from March until the end of June; egg laying occurs in April, and the peak of chick departures and prospecting (i.e. colony attendance by non-breeders searching for a nest site) occurs during late May and early June (Sealy 1976, Gaston 1992, Gaston & Shoji 2010). Ancient Murrelet chicks are precocial and depart the colony two days after hatching, when adults lead chicks from breeding burrows to the ocean with a series of distinctive calls (Sealy 1976, Jones *et al.* 1987). Family groups depart the colony one to four hours after sunset, with almost

90% departing within two hours of complete darkness (Jones *et al.* 1987, Jones *et al.* 1990, Gaston 1992). Non-breeding prospectors begin their annual period of colony attendance mid-way through the incubation period, peaking during the peak of family group departures (Jones *et al.* 1987, Jones *et al.* 1990). Furthermore, their attendance tends to occur later in the evening than the attendance of breeding adults (Gaston 1992). Thus, patterns of Ancient Murrelet breeder and non-breeder colony attendance can be measured using timed counts of arrivals at the colony.

The objectives of this study were to evaluate patterns of colony attendance by Ancient Murrelets to assess 1) the effectiveness of using marine radar to monitor Ancient Murrelet colony activity, and 2) daily patterns of colony attendance in relation to time since sunset and environmental conditions. I predicted that counts of radar targets approaching the island would match counts of arriving individuals completed by observers in the colony and hypothesized that patterns of colony attendance are related to weather and light conditions, as found for colony activity (the sum of vocal activity and arrivals) by Jones et al. (1990). Further, I hypothesized that this relationship changes with time after sunset, as the majority of individuals arriving early in the night (less than three hours after sunset) are likely breeders arriving to relieve their mate from incubation duties or lead their chick to the ocean, whereas the proportion of non-breeders arriving increases with time after sunset (Gaston 1992). I predicted that the relationship between colony arrivals and light and weather conditions would differ with time after sunset, but would decrease during 1) moonlit, bright nights with minimal cloud cover and 2) poor weather conditions (high wind and waves), although birds arriving early in the night (three to four hours after sunset) would be less likely to be influenced by environmental conditions than those arriving later. Further, I predicted that, if radar and observation counts are comparable, using either to test the relationship between arrivals and environmental conditions would yield similar results.

STUDY AREA

Langara Island (54°12′N, 133°01′W) is located at the northern tip of Haida Gwaii, British Columbia. The densely forested Ancient Murrelet breeding colony site, situated on the northeastern tip of Langara Island (McPherson Point), is used by approximately 24 000 breeding pairs (Gaston 1992, Regehr *et al.* 2006, 2007). Although I occasionally heard a Leach's Storm-petrel *Oceanodroma leucorhoa* during observations, and a small pocket of Cassin's Auklets *Ptychoramphus aleuticus* nest nearby (see Regehr *et al.* 2006), abundance of these species is very low (pers. obs.). In Haida Gwaii, the peak of chick departures and prospector activity occurs during late May and early June (pers. obs., Gaston 1992).

METHODS

I monitored colony attendance using direct observations of individuals arriving on the colony and counts of radar targets.

Colony observations

I counted arriving and departing individuals (identified by the presence of wing beats entering the colony site from the ocean or leaving the colony site, flying toward the ocean) in 30-min intervals between 22h30 and 04h30 (all times Pacific Daylight Time) each night 18 May–18 June 2006 and 12 May–11 June 2007. Counts were completed by observers sitting silently in the colony with no artificial light using two tally counters (one for arrivals and one for departures). Observers counted only clear wing beats for which the direction (entering the forest from the ocean or leaving toward the ocean) could be easily discerned (i.e. individuals within an approximate 20 m radius of the observation point, resulting in an observation area of ~0.001 km^2). Each night, two observers completed counts in 30-min intervals of counting and resting, so that when one observer was counting the other was resting. I present colony arrivals as the total number of individuals counted in 60-min intervals for comparison with environmental variables, as data for wind speed and wave height are available only for 60-min intervals.

RADAR OBSERVATIONS

I counted radar targets adjacent to McPherson Point, Langara Island, using a Furuno FR810D (9410 MHz, 10 kW) marine radar (Furuno Electric Company Ltd. Japan), with a 2.0 m antenna, powered by two 12 V DC batteries. The radar unit was placed on a platform ~30 cm off the ground on a grassy slope with an unobstructed view of the ocean at McPherson Point (54°14′N, 132°58′W). The antenna beam was tilted upwards by 25°, and an adjustable aluminum anti-clutter screen was mounted on the beam's lower edge. Both the sea and rain scatter suppressors were turned all the way down, and at the start of the season gain was set to maximize sensitivity to signals and minimize noise. Once set, the gain was not changed for the duration of all observations in each year. The radar unit was set to detect to 0.5 nautical miles (0.8 km)

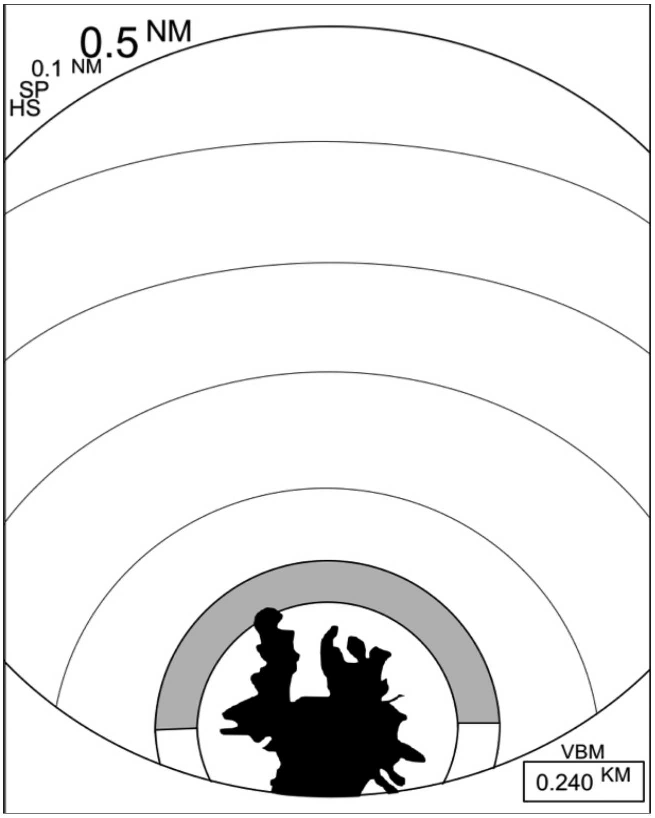

Fig. 1. Depiction of the marine radar display, showing the land (black) and my observation area (gray shaded area) where targets were counted during one 9-min interval every half hour at Langara Island, BC, in 2006 and 2007.

and zoomed to display 1 km directly ahead of the unit (Fig. 1); the adjustable ring was set at 240 m. All counts were made within this 240 m ring in one 9-min interval each half hour, resulting in an observation area of ~0.05 km^2. Counts of radar targets occurred between 23h00 and 03h39 in one 9-min interval, beginning at each half hour during 2 June–19 June 2006 and 12 May–11 June 2007. Observers completed a count of all targets detected using tally counters for each sweep of the antenna and noted the total number counted at the end of each 9-min interval. Counts were not performed during rain or when seas were rough, as it was difficult to distinguish targets from rain and sea scatter. For comparison with counts from colony observations, I estimated arrivals by calculating a per-minute rate from the 9-min counting interval, multiplied by 60 min. This total was then multiplied by the proportion of birds arriving at the colony (i.e. total number of birds flying toward the colony divided by the total number of birds counted flying toward the colony and the ocean) counted during colony observations to obtain an estimated number of targets arriving at the colony site.

Light conditions and weather variables

I examined colony attendance in relation to seven competing models (composed of four light and weather variables) and one intercept-only null model (for a total eight models, Appendix 1, available on the website). Variables of interest were 1) time after sunset in hours; 2) moon absence, calculated as the proportion of the moon absent during the night, accounting for moon phase and time of moon rise and set, where 0 represents full moon present and 1 no moon present; 3) cloud cover, recorded at the end of each 60-min observation interval as the proportion of sky free of clouds, where 0 represents no clouds and 1 full cloud cover; 4) wind speed in meters per second; and 5) wave height in meters. Moon set and rise times were downloaded from the Astronomical Applications Department of the US Naval Department website (http://aa.usno/navy.mil/index.php), and weather information was downloaded for the central Dixon Entrance weather buoy (buoy 46145; located at 54°22′N, 132°27′W from the National Data Buoy Center website (http://www.ndbc.noaa.gov). Counts were continued in all weather conditions, but I included data (for both observation and radar counts) with wind speeds <18.0 m/s only, when counts would not be affected by wind noise. I omitted data for two hours after sunset because of low sample size.

STATISTICAL ANALYSIS

All statistical analyses were performed in the R Studio Environment (R ver. 3.2.4; R Core Team 2016) using a generalized linear mixed model (*glmmADMB* package; Fournier *et al.* 2012) with a maximum-likelihood fitting method, negative binomial distribution, and log-link function. I used an information theoretic approach to evaluate statistical relationships and ranked models using Akaike's information criterion for small sample sizes (AICc), correcting for over-dispersion by including an estimate of model deviance for the global model ($\hat{\Phi}$ = model deviance/df; quasi-AICc [QAICc]). QAICc weights (*wi*) were used to evaluate model likelihood (Burnham & Anderson 2002).

TABLE 1
Candidate model set describing correlation between counts of arriving Ancient Murrelets at the colony and estimated radar targets arriving at the colony (n = 93, $\hat{\Phi}$ = 0.78)

Candidate model	K	QAICc	ΔQAICc	*wi*
Global model	6	1992.34	0.00	1.00
Null	5	2074.37	82.03	0.00

To evaluate the relationship between observed arrivals and estimated radar arrivals, I considered two *a priori* candidate models: a global model with one explanatory variable (observed count of colony arrivals) and one intercept-only null model. In both cases, Julian day and year were included as random effects. To evaluate the relationship between Ancient Murrelet arrivals at the colony and environmental variables, I used two separate generalized linear mixed models. The first evaluated the relationship between observer-counted arrivals and environmental variables, and the second, between estimated radar counts and environmental variables. In both analyses, I considered eight *a priori* candidate models composed of five explanatory variables of interest (Appendix 1). I included Julian day as a random effect in all models, including the null models. I present results of both models as a second measure to evaluate accuracy of estimated radar counts. Results are given as mean ± 95% confidence intervals.

RESULTS

Radar observations

During 2006 and 2007 at Langara Island, I simultaneously estimated observed colony arrivals and radar targets near the island for 93 60-min intervals over 27 d. Ancient Murrelet observed colony arrivals ranged between five and 52 individuals per 60-min interval (mean 23 ± 2 birds/h), while estimated radar targets approaching the island ranged between 183 and 5 760 targets/h (mean 2 410 ± 283 targets/h).

The top supported model from my candidate set explaining the relationship between estimated radar targets and observed Ancient Murrelet colony arrivals received all of the weight (100%) among candidate models and included the term "observed colony arrivals," suggesting a statistically meaningful relationship between the two variables (Table 1, Fig. 2). Parameter estimates and standard errors show a positive relationship between estimated radar targets and

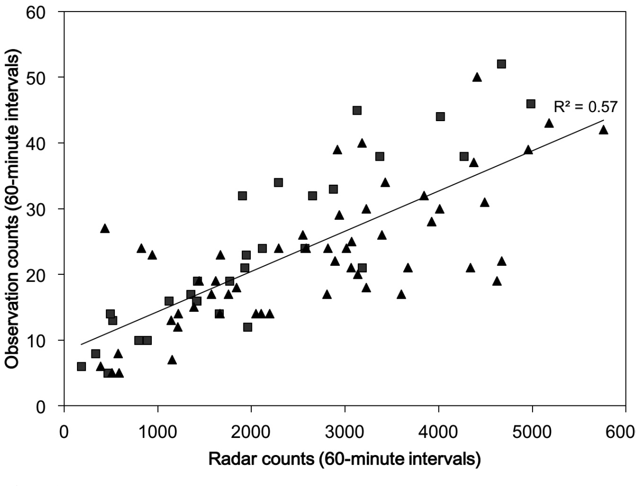

Fig. 2. Correlation between estimated radar target counts and observations of arriving Ancient Murrelets at McPherson Point, Langara Island in 2006 and 2007.

observed colony arrivals, in which estimated radar targets were 95 times higher than observed colony arrivals (Table 2).

Colony arrivals and environmental variables

During 2006 and 2007 at Langara Island, my sample of observed Ancient Murrelet colony arrivals with complete weather and light condition information included 188 60-min intervals over 50 d (177 60-min intervals between three and six hours after sunset; Appendix 2, available on the website). My sample of estimated radar arrivals with complete weather and light condition information included 93 60-min intervals over 27 d (Appendix 3, available on the website). Ancient Murrelet observed colony arrivals at Langara ranged from no arrivals to 52 individuals/h (mean 18 ± 2 birds/h), much lower than arrivals estimated according to the radar targets (mean 2 410 ± 283 targets/h, range: 183–5 760). Most birds arrived between 00h30 and 01h30 (approximately four to five hours after sunset; Fig. 3).

In both analyses, the top five ranked candidate models were the same, but the top ranked candidate models that received virtually all of the weight among models in both data sets were different (Table 3). Both analyses suggest that the interactions between time after sunset and environmental conditions (particularly light conditions) are important predictors of Ancient Murrelet colony arrivals. Parameter estimates and standard errors show that colony arrivals were highest four hours after sunset; the interactions between time after sunset and moon absence, and between time after sunset and cloud cover, were most important three hours after sunset; and weather conditions (wind speed and wave height) did not have a large influence on colony arrivals (although wave height three hours after sunset was an important predictor for observed colony arrivals; Tables 4, 5).

TABLE 2
Terms in the top candidate model describing correlation between estimated radar targets and observation counts of arriving Ancient Murrelets in 2006 and 2007 (n = 93)

Parameter	Parameter likelihood, summed Akaike weight *(wi)*	Parameter estimate	SE[a]
Intercept	1.00	6.53	0.17
Radar	1.00	0.05	0.01

[a] SE = standard error.

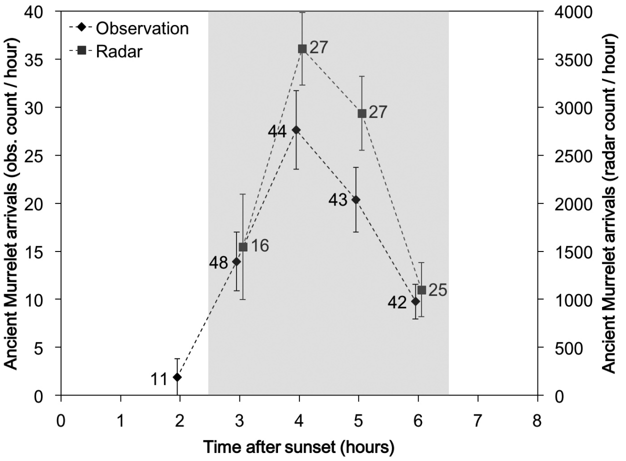

Fig. 3. Summary of Ancient Murrelet arrivals by hour and time after sunset (in hours). Data within the gray box are those included in the analyses. Counts are shown as means ± 95% CI with sample sizes.

DISCUSSION

Daily patterns of colony attendance are an important aspect of seabird ecology, but monitoring colony attendance of nocturnal species can be challenging. Here, I examined the effectiveness of monitoring Ancient Murrelet colony arrivals using marine radar and found a strong correlation between the number of radar targets counted and the number of Ancient Murrelets counted by observers in the colony, with estimated radar target counts being ~95 times higher than observer counts. This large difference is likely the result of the proportionally larger area covered by the radar (~50 times larger) and the possibility of individuals (particularly non-breeders) flying over the area but not landing. Furthermore, my hypothesis that patterns of colony attendance are related to environmental conditions (i.e. light and weather), and that this relationship changes with time after sunset, was supported. For both observation and estimated radar counts, the top supported models suggested that interactions between time after sunset and environmental conditions (particularly light conditions) were important predictors of colony arrivals. Contrary to my prediction, light conditions and, to a lesser extent, wave height were most important for individuals arriving three hours after sunset. Although the relationship varied with time after sunset, individuals arriving later than three hours after sunset did not seem to be influenced by environmental conditions.

Marine radar

Marine radar has been widely used to monitor bird migration, populations, and collision risk with human structures (e.g. Plonczkier & Simms 2012, Cooper *et al.* 2006, Diehl *et al.* 2003),

TABLE 3
Top five candidate models describing Ancient Murrelet colony arrivals at Langara Island in 2006 and 2007

Candidate model	K	QAICc	ΔQAIC	*wi*
Observation counts (n = 177, ($\hat{\Phi}$ = 0.90)				
Global model	26	1432.97	0.00	0.92
Time[a] and light[b]	18	1437.90	4.93	0.08
Time	6	1450.14	17.17	0.00
Time and weather[c]	14	1454.89	21.92	0.00
Weather	5	1518.71	85.74	0.00
Radar counts (n = 93, ($\hat{\Phi}$ = 1.04)				
Time and light	19	1471.53	0.00	0.93
Time and weather	15	1477.53	6.00	0.05
Time	7	1479.68	8.15	0.02
Global model	27	1482.03	10.50	0.00
Weather	6	1552.39	80.86	0.00

[a] Hours after sunset.
[b] Moon absence and cloud cover.
[c] Wind speed and wave height.

but only a few studies have used marine radar to monitor seabirds at a colony (e.g. Hamer *et al.* 2005, Lilliendahl *et al.* 2003, Bertram *et al.* 1999). Assessing populations of nocturnal burrow-nesting seabirds is logistically difficult, and many studies use burrow contents to estimate colony area and size (e.g. Ambagis 2004). However, these methods do not provide information on patterns of colony attendance, which is an important metric in the general biology of a species and for the design and implementation of many conservation practices. Here, I evaluated the usefulness of marine radar to monitor colony attendance of Ancient Murrelets at McPherson Point, Langara Island, comparing radar estimates of attendance with those counted by observers. I predicted a correlation between radar counts and observer counts, with radar counts being higher likely because this method surveys a larger area. Further, I predicted that, if radar and observation counts are comparable, using either to evaluate the influence of time after sunset and environmental conditions on arrivals would yield similar results (although there was a large difference in sample size between the two methods). My results support both of these predictions, suggesting that marine radar is an effective tool to monitor Ancient Murrelet colony arrivals.

The colony at McPherson Point is made up almost entirely of Ancient Murrelets, thus, my results suggest that, at a single-species colony, marine radar is an effective monitoring tool. Studies have shown that it is possible to distinguish among species when using

TABLE 4
Terms in the top candidate model describing Ancient Murrelet colony arrivals at Langara Island in 2006 and 2007 (n = 177)

Parameter[a]	Parameter likelihood	Parameter estimate	SE[b]
Intercept	1.00	2.15	0.98
Time after sunset (3 h)	1.00	-2.98	1.18
Time after sunset (4 h)	1.00	1.82	0.98
Time after sunset (5 h)	1.00	1.73	0.95
Moon absence	1.00	0.08	0.86
Cloud cover	1.00	-0.58	0.93
Wind speed (m/s)	0.92	0.01	0.02
Wave height (m)	0.92	-0.10	0.39
Time after sunset (3 h) × Moon absence	1.00	4.14	1.16
Time after sunset (4 h) × Moon absence	1.00	-0.08	0.90
Time after sunset (5 h) × Moon absence	1.00	-0.73	0.88
Time after sunset (3 h) × Cloud cover	1.00	5.02	1.19
Time after sunset (4 h) × Cloud cover	1.00	0.28	0.93
Time after sunset (5 h) × Cloud cover	1.00	-0.13	0.91
Time after sunset (3 h) × Wind speed	0.92	0.02	0.02
Time after sunset (4 h) × Wind speed	0.92	-0.03	0.02
Time after sunset (5 h) × Wind speed	0.92	-0.02	0.02
Time after sunset (3 h) × Wave height	0.92	-1.43	0.42
Time after sunset (4 h) × Wave height	0.92	-0.53	0.39
Time after sunset (5 h) × Wave height	0.92	-0.27	0.40
Moon absence × Cloud cover	1.00	0.56	0.94
Time after sunset (3 h) × Moon absence × Cloud cover	1.00	-5.16	1.27
Time after sunset (4 h) × Moon absence × Cloud cover	1.00	-0.53	1.00
Time after sunset (5 h) × Moon absence × Cloud cover	1.00	0.02	1.00

[a] Categorical variable time after sunset (6 h) set to 0 in all models.
[b] SE = standard error.

TABLE 5
Terms in the top candidate model describing Ancient Murrelet colony arrivals at Langara Island in 2006 and 2007 (n = 93)

Parameter[a]	Parameter likelihood	Parameter estimate	SE[b]
Intercept	1.00	5.30	0.59
Time after sunset (3 h)	1.00	-2.57	2.25
Time after sunset (4 h)	1.00	2.30	0.55
Time after sunset (5 h)	1.00	2.27	0.54
Moon absence	0.93	2.08	0.63
Cloud cover	0.93	1.32	0.63
Time after sunset (3 h) × Moon absence	0.93	2.24	2.38
Time after sunset (4 h) × Moon absence	0.93	-1.62	0.61
Time after sunset (5 h) × Moon absence	0.93	-1.60	0.58
Time after sunset (3 h) × Cloud cover	0.93	3.81	2.31
Time after sunset (4 h) × Cloud cover	0.93	-0.62	0.59
Time after sunset (5 h) × Cloud cover	0.93	-0.89	0.58
Moon absence × Cloud cover	0.93	-1.71	0.67
Time after sunset (3 h) × Moon absence × Cloud cover	0.93	-3.55	2.46
Time after sunset (4 h) × Moon absence × Cloud cover	0.93	1.25	0.69
Time after sunset (5 h) × Moon absence × Cloud cover	0.93	1.10	0.67

[a] Categorical variable time after sunset (6 h) set to 0 in all models.
[b] SE = standard error.

marine radar (e.g. Day and Cooper 1995, Hamer *et al*. 2005). However, these studies have generally been completed at colony sites with relatively low density, where observers can distinguish species using the size of the radar target and/or track individuals to assess flight speed and pattern. Additional research, likely including automation of counting and evaluating target size, flight speed, etc., need to be completed at medium- and high-density multi-species colonies to assess the effectiveness of distinguishing among species and the accuracy of those counts. Furthermore, during high-activity periods each night, I was unable to distinguish arrivals from departures (although with newer radar systems this may not be an issue). I needed to use the ratio of arriving and departing individuals from my observer counts to estimate arrivals from the total number of targets counted. Completing both types of counts is redundant. If the purpose of using marine radar is to avoid the need for observer colony counts, the issue of identifying arriving and departing individuals needs to be resolved.

Colony attendance in relation to light and weather variables

At Reef Island (~150 km south of Langara Island), Gaston (1992) found that the proportion of Ancient Murrelets arriving at the colony with brood patches (i.e. breeders) was ~80% between 23h00 and 00h00 (about three hours after sunset) and this proportion dropped to ~40% by 01h00 (four hours after sunset) and to ~25% by 02h00 (five hours after sunset). Assuming this relationship holds true for birds at the McPherson Point colony on Langara Island, I expected differences in colony attendance behavior related to time and environmental conditions. Non-breeding birds (i.e. those arriving later in the evening) are not tied to a colony for reproductive obligations and should make colony attendance decisions based on predation risk and ability to effectively communicate with conspecifics. Breeding birds (i.e. those arriving early in the evening), on the other hand, would make colony attendance decisions based upon their current reproductive effort. Further, Jones et al. (1990) suggested that Ancient Murrelets require some light to navigate the forest while also requiring sufficient darkness to avoid predation. Additionally, they suggested that inclement weather (i.e. heavy cloud cover and windy conditions) decreased visibility in the densely forested colony sites in Haida Gwaii, discouraging Ancient Murrelets from attending colony sites by making breeding sites more difficult to find and increasing the risk of injury due to collision with tree branches. My results support both of these accounts.

Light conditions

Jones et al. (1990) found that Ancient Murrelet vocal activity at Reef Island was related to moonlight, with more calls being recorded during moonless than moonlit periods. For arrivals, Jones et al. (1990) found that this relationship was less apparent, except when heavily overcast conditions were excluded, hinting at an important interaction between cloud cover and moonlight, as indicated by my results. Expanding on this and Gaston's work at Reef Island (Gaston 1992), I was interested in whether colony attendance by Ancient Murrelets was related to the interaction between light conditions and the amount of time since sunset. As predicted, I found that Ancient Murrelet colony arrivals were strongly related to moonlight and cloud cover conditions and that this relationship varied with time. Specifically, my results show a strong negative relationship between light conditions and arrivals three hours after sunset (when most arriving individuals are breeders) and an increasing weakening of this relationship four or more hours after sunset, when >60% of individuals arriving would be non-breeders.

If light conditions (i.e. moon absence and cloud cover) are an important driver of colony arrivals, I would expect ambient sunlight to amplify the relationship. During my sample of nights, the darkest time occurred during nautical twilight (astronomical twilight is not reached in Haida Gwaii during the spring and summer). On average, nautical twilight began at 23h29 (two hours after sunset; range 22h34–00h17) and ended at 02h12 (five hours after sunset; range 01h29–03h05). Thus, in my sample, ambient light was highest six hours after sunset and lowest three to four hours after sunset. If light conditions are an important driver of colony arrivals, and conditions are darkest three to four hours after sunset, I would expect colony arrivals to be highest during those times, as my results show. Further, if light conditions are the driving factor behind colony attendance, the relationship between arrivals and light conditions at three and four hours after sunset should be similar, and those at five and six hours after sunset should also be similar (but different from those three and four hours after sunset). Conversely, my results show differences in the relationships with light conditions at all times (although general patterns do suggest an effect of ambient light), suggesting another factor, such as age class, is driving colony arrivals.

Weather conditions

In many cases, the presence of nocturnal burrow-nesting seabirds at breeding colonies is evident by the cacophony of calls. Ancient Murrelets typify this finding; they have at least nine distinct vocal displays that show unusually locatable and individually distinctive characteristics (Jones *et al*. 1989). Audio cues are used for conspecific attraction (Major & Jones 2011) and during family group departures, when adults lead chicks from breeding burrows to the ocean with a series of distinctive calls (Jones *et al.* 1987). However, increased ambient noise associated with increased wind speed and breaking waves could result in difficulty locating the site and limit communication. Thus, I predicted colony arrivals would be influenced by weather conditions (specifically wave height and wind speed) adjacent to the colony. Similar to light conditions, I predicted this relationship would be stronger four or more hours after sunset. However, I found that the interaction between time after sunset and wind speed was not an important predictor of arrivals but that wave height (for observation counts only) was an important predictor. The observation that wind speed was not an important predictor may be related to my omitting all observations recorded during wind speeds higher than 18 m/s. This was done because observers had difficulty counting arrivals over wind noise and because the high amount of scatter on the radar screen limited counts. I suspect that including higher wind speeds may have given different results. Additionally, radar counts were also stopped during high waves, again because of scatter on the radar screen. However, observation counts continued during all wave heights. This is likely the reason that my analysis using observation colony counts shows wave height as an important predictor of colony attendance, whereas my analysis using radar did not. As technology improves, it may be possible to continue radar surveys in a wider range of wind speeds and wave heights. Once again, the finding that birds arriving early in the night are most influenced by wave height was unexpected and contrary to my predictions. It is possible that this relationship is due to vital communication between adults and chicks while family groups are departing, rather than to birds locating the colony and colony social interactions by non-breeders (the majority of whom arrive later in the night). This work encompassed only the few weeks surrounding hatching and colony departures, when colony activity peaks and a large number of non-breeders are visiting the colony (Jones *et al.* 1987, Jones *et al.* 1990). Future work might involve observations over the course of an entire breeding season to evaluate changes in arrival behavior of Ancient Murrelets.

Overall, this study found that marine radar is an effective tool to monitor a single-species colony of nocturnal burrow-nesting seabirds and supports Jones et al.'s (1990) findings that colony arrivals are related to light and weather conditions and that this relationship changes with time. Following the work at Reef Island by Gaston (1992), and assuming that the majority of early arrivals (three hours after sunset) are breeders and the majority of late arrivals (more than four hours after sunset) are non-breeders, my results suggest that breeders and non-breeders make colony attendance decisions based on different environmental conditions. Contrary to my predictions, I found that breeders are influenced most by light and weather conditions, while those arriving more than four hours after sunset (the majority of whom are non-breeders) seem to attend the colony irrespective of most light and weather conditions. Future work should focus on whether these changes are, in fact, due to differences related to breeding and non-breeding or simply to ambient light and timing.

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