

## Factors affecting colony attendance by Ancient Murrelets (*Synthliboramphus antiquus*)

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We studied factors influencing variation in nightly levels of activity (birds arriving and vocalizing) and numbers of birds staging offshore at a colony of Ancient Murrelets at Reef Island, British Columbia, during 1984, 1985, and 1986. Activity was restricted to the hours of darkness and extremely variable in magnitude from night to night. The rate of entry into burrows tended to decrease, and the amount of vocalization and numbers of birds at the staging area increased during the nesting season. We detected an underlying 4-day cyclical pattern of attendance. Nightly variability of activity at the colony was affected by moonlight and weather conditions. Since activity, particularly vocalization, was reduced on moonlit nights, we suggest that nocturnal colony attendance is a strategy to avoid diurnal predators in this species. The largest numbers of birds were present and vocalizing at the colony on calm moonless nights. Weather conditions explained a substantial proportion of the night to night variability in murrelet activity. Among weather variables, wind speed had the most consistent effect and was particularly important in 1985. Both short-term, i.e., of a particular night, and long-term, i.e., over the previous 3 days, conditions influenced activity. Our observations suggest that direct weather effects at the colony may be more important than weather effects related to foraging conditions. Interyear differences in activity may have resulted from the interaction of weather and general foraging conditions.

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Nous avons étudié les facteurs de variation de l'activité nocturne (arrivées et émissions de vocalises) et le nombre d'oiseaux au lieu de rassemblement d'une colonie d'Alques à cou blanc, au large des côtes de l'île Reef, Colombie-Britannique, en 1984, 1985 et 1986. L'activité était limitée aux heures d'obscurité et son importance était extrêmement variable d'une nuit à l'autre. Durant la période de nidation, le pourcentage de fréquentation des terriers avait tendance à diminuer alors que l'importance des vocalises et le nombre d'oiseaux au lieu de rassemblement avait tendance à augmenter. Nous avons pu percevoir que la présence des oiseaux suivait un cycle de 4 jours. La variabilité de l'activité nocturne au point de rassemblement était fonction de la lune et des conditions climatiques. L'activité, particulièrement l'émission de cris, était réduite au cours des nuits bien éclairées et il est probable que la présence à la colonie la nuit soit une stratégie qui permette d'éviter les prédateurs diurnes chez cette espèce. C'est au cours des nuits calmes sans lune qu'il y avait le plus grand nombre d'oiseaux à la colonie et que l'émission de cris était le plus intense. Les conditions climatiques étaient responsables d'une grande proportion de la variabilité de l'activité d'une nuit à l'autre. Parmi ces conditions, la vitesse du vent était celle qui avait l'influence la plus soutenue et ses effets se sont avérés particulièrement remarquables en 1985. Les conditions à court terme (une nuit en particulier) et les conditions à plus long terme (celles qui ont prévalu au cours des 3 jours précédents) influençaient toutes l'activité. Nos observations indiquent que l'influence des conditions climatiques à la colonie semble se faire plus par action directe que par le biais de leur action sur les conditions de recherche de nourriture. Les différences interannuelles de l'activité résultent cependant probablement de l'interaction entre les conditions climatiques et les conditions générales de quête de nourriture.

[Traduit par la revue]

### Introduction

When and for how long a seabird visits its breeding colony is crucial to its reproductive success and survival. An individual's attendance at the colony must commence at the correct time for it to initiate or reestablish a relationship with a mate and so that the young hatch at a time that maximizes their chance of subsequent survival (Lack 1968; Perrins 1970). Within the nesting season, time spent at the colony may be limited by the unpredictable time requirements of foraging far from the colony and by the risk of predation at the colony, each of which may be affected by weather conditions or other environmental variables. Temporal variation in activity at a seabird colony should thus reflect the activities of individual members, each acting in relation to these factors in a way that maximizes their fitness. In

this study, we examined the night to night and seasonal variation in activity (vocal and other behaviour and numbers of birds present) at a colony of Ancient Murrelets (*Synthliboramphus antiquus*) at Reef Island in the Queen Charlotte Islands of British Columbia in relation to environmental factors.

Ancient Murrelets are small, colonial, burrow-nesting alcids. In British Columbia, they nest on conifer-forested slopes within a few hundred meters of the sea, usually on small islands. They are active aboveground at the colony at night during their brief nesting season (April, May, and early June). Breeding pairs incubate their clutch of two for about 32 days in 2- to 4-day shifts, then accompany the precocial young to the sea a few days after hatching (Sealy 1976; Jones *et al.* 1987a, 1987b). On active nights at the colony, large numbers of murrelets perch in trees and on stumps and perform a variety of conspicuous vocal displays. Nonbreeders visit the colony late in the season to prospect for mates and nest sites.

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Cody (1973) suggested that nocturnal colony attendance of some alcids (e.g., Rhinoceros Auklet, *Cerorhinca monocerata*; Cassin's Auklet, *Ptychoramphus aleuticus*; Ancient Murrelet; and Xantus' Murrelet, *Synthliboramphus hypoleucus*) is a means of avoiding diurnal predators. However, factors relating to foraging ecology (e.g., a necessity for feeding during daylight hours) could also be important for some species (Manuwal 1974). If the predation avoidance hypothesis to explain nocturnality is valid, activity should decrease when the benefits of nocturnal activity are reduced, for example on bright moonlit nights, and the nighttime activity period should contract as the night gets shorter during the nesting season. If the daylight foraging hypothesis alone is responsible for nocturnal colony attendance, activity would be predicted to be independent of moon phase and nighttime light intensity. Moonlight avoidance has been documented in species with mainly diurnal predators, such as Cassin's Auklets (Manuwal 1974), and several nocturnal Procellariiformes, including Manx Shearwaters, *Puffinus puffinus* (Storey and Grimmer 1986) and Leach's Storm Petrels, *Oceanodroma leucorhoa* (Watanuki 1986). We studied the effect of moonlight and nighttime light intensity on the activities of Ancient Murrelets and their predators to evaluate the hypothesis that nocturnality functions as a mean to avoid predators.

A number of studies have investigated the relationship between attendance at alcid colonies and weather conditions (Birkhead 1977; Manuwal 1974; Slater 1980; Gaston and Nettleship 1981). Weather conditions could affect activity at the colony in two ways. In the short term, inclement weather on a particular night could decrease activity at the colony by interfering with murrelet navigation within the complex forest habitat of the colony, or by rendering vocal advertising displays inaudible and thus ineffective. In the long term, weather over several days could affect levels of activity at the colony through its influence on murrelet foraging success. Gaston and Nettleship (1982) hypothesized that food availability is the primary factor determining colony attendance levels in Thick-billed Murres (*Uria lomvia*). Like murres, Ancient Murrelets are thought to forage far from their colonies on patchy prey (Sealy 1976), which would likely be more difficult to locate in rough weather. Thus, weather on the days preceding a particular night could indirectly determine the level of activity at the colony by its effect on the energetic condition of the murrelet population. We investigated the relative influences of short- and long-term weather conditions on activity at the colony to evaluate these predictions.

In summary, the objectives of our study were (i) to look for and investigate the significance of seasonal trends in levels of activity at the colony; (ii) to investigate the effect of moonlight and nighttime light levels on activity at the colony to evaluate hypotheses about the function of nocturnal colony attendance; and (iii) to investigate the influence of weather conditions on activity at the colony and evaluate the relative importance of weather's effect on foraging conditions or conditions at the colony.

### Methods

Observations were made at Reef Island (52°52'N 1131°31'W), a 3 km long island in the Queen Charlotte Islands archipelago of British Columbia. Approximately 5000 pairs of murrelets nest on the island, most along the steep forested slopes of the north shore. The density of occupied burrows in the colony averaged about 125 per hectare in 1985 (A. J. Gaston, unpublished data). The nesting slopes are densely forested with Sitka spruce (*Picea sitchensis*) and Western hemlock

(*Tsuga heterophylla*) and have little undergrowth, a habitat similar to that found in other Ancient Murrelet colonies of the Charlottes (Vermeer *et al.* 1984).

To investigate the night to night and seasonal variation in attendance and activity we made observations at a study plot located in a dense part of the colony at an elevation of about 100 m. Activity was monitored by two means: a nightly observation period and a count of burrows entered. Nightly observations were made from a small canvas blind placed at the bottom centre of the 30 × 40 m plot. The plot's amphitheatrelike topography made it suitable for consistent monitoring of murrelet activities within a restricted area. The monitoring was conducted from April 17 to June 21, 1984, and from April 7 to June 15, 1985. Murrelet activities were quantified by continuously listening from the blind and noting the events of each 10-min period on a compact cassette recorder. The monitoring period began each night before the arrival of the first murrelet and continued for 10 (1984) or 15 (1985) 10-min intervals following the first arrival. To document the activities of murrelets for all hours of darkness we extended the monitoring period until the last departures from the plot at dawn on 13 nights in 1984.

Counts of the following activities were noted for each 10-min interval: (i) arrivals of murrelets on the plot; (ii) calls (chirrup) on the plot; (iii) songs (song chirrup) on the plot; and (iv) departures of murrelets from the plot. Activities were noted to be on the plot when they occurred within the ground boundaries and above the plot to about 1.5 times the height of the trees (ca. 45 m). The identification of events as either arrivals or departures was straightforward as each is accompanied by distinctive wing sounds and noises of collision with vegetation. Arrivals were defined as approaches from outside the colony and involved steep descents through the forest canopy. Departures involved a rapid acceleration seawards, leaving the colony directly. Murrelets making short flights under the forest canopy on and (or) off the plot were not scored as arrivals or departures. The vocalizations were classified as either short spontaneous chirrup calls or the more complex song, which consists of chirrups and other elements incorporated into an extended vocalization (Jones 1985; Jones *et al.* 1989).

Because natural noise could have affected our ability to score murrelet activities, we were careful to note the listening conditions regularly. Monitoring periods with poor listening conditions caused by high wind, precipitation, or wave action were excluded from further analysis. Fortunately, the topography of the plot allowed most murrelet activity to be scored in all but the most severe weather conditions.

In 1985, light intensity was recorded at the beginning of each 10-min interval of the monitoring. To measure the light, the observer viewed a series of similar patterns of black bars of decreasing size on a white plexiglass card laid on the ground in front of the blind. As light intensity decreased the patterns became unresolvable in succession, starting with the smallest. Thus an index of ambient light intensity was obtained for each interval by noting the number assigned to the smallest resolvable pattern.

We measured activity at 80 selected burrows, most occupied by breeding pairs, on the same plot monitored at night. Plastic strips (4.5 × 1.0 × 0.05 cm) were positioned in the burrow entrances in such a manner as to be knocked over or moved by birds entering or leaving. The burrows were numbered for identification and checked each morning. To avoid disturbance, we did not excavate or otherwise tamper with burrows on the study plot. We checked for evidence of occupancy (e.g., fresh eggshells, feathers, droppings, and nighttime vocalizations) for all burrows. In a separate study on a nearby area, most instances where strips were knocked down at occupied burrows occurred simultaneously with a change in the incubating adult (A. J. Gaston, unpublished).

To determine the timing of breeding, we regularly checked a sample of burrows ( $n = 51$  in 1984 and  $n = 63$  in 1985) away from the activity plot for the presence of eggs or chicks. In 14 burrows the adults were marked with fluorescent paint on their flank or back to measure 38 incubation shifts in 1984 and 125 shifts in 1985. Also, at other areas of the colony, 135 birds were captured in 1984 and 234 in 1985 to check

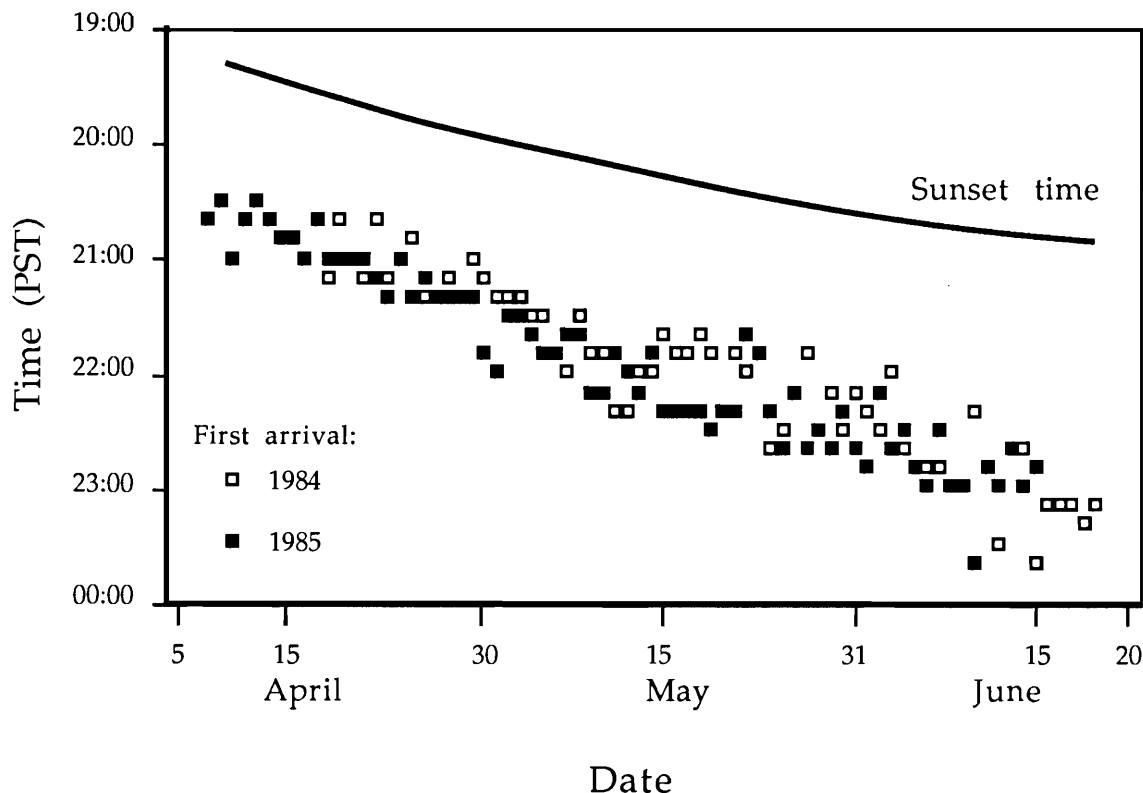


FIG. 1. The time of arrival of the first murrelet at the study plot, each night, in relation to sunset during April, May, and June of 1984 and 1985. Murrelets tended to arrive earlier in 1985.

for the presence of brood patches and estimate the relative numbers of breeding and nonbreeding birds present.

To quantify the daily variation in numbers of birds at their nearby staging area, we made counts each evening between 8 May and 15 June 1985, and 7 May and 14 June 1986. The staging area lay 1.5–3.5 km to the north of Reef Island and was observed from a low cliff, using a 25 $\times$  magnification telescope. A 5-min count of all murrelets flying through the field of view was made each evening about 3 h before the first arrivals at the colony. Counts were restricted to flying birds because of the difficulty of observing birds resting on the sea. The counts of flying birds provide a useful index of numbers of birds staging because of the murrelets' habit of making frequent short flights around the staging area.

To assess seasonal trends, we compared levels of activity and vocalization with the stages of the nesting season graphically and using nonparametric tests. To check for consistent periodic night to night variation in activities, we looked for autocorrelation of arrival, vocalization, and burrow entry counts (i.e., correlation of activity counts with counts made 1–10 days previously). We assessed the effect of moonlight by comparing counts of activities made during moonlit periods with preceding and following moonless periods. For the 1985 season, simple regression was used to compare each evening's arrival, chirrup, and burrow entry counts with the mean light intensity during the monitoring period. We investigated the large night to night variation in numbers of birds arriving and vocalizing at the colony with weather variables of 1984 and 1985, using partial correlation to assess the independent effects of each weather variable and multiple regression to measure the combined effect of the weather variables on murrelet activities. Except for percent cloud cover, which was estimated from Reef Island, weather data were obtained from a nearby weather station (Sandspit, 40 km to the north). Since weather could affect the ability of the birds to forage and thus have long-term significance, we checked to see if mean weather conditions over the 3 days prior to a particular night were associated with activity at the colony. Three-day means were chosen because this was the most

frequent incubation shift length and was thus likely to represent a typical time period available to murrelets for foraging.

## Results

Ancient Murrelets arrived and departed the colony throughout the night, but these activities peaked in the first and last 90 min of each evening. Activity at the colony lasted for over 6 h during nights in April, but for only about 2.5 h by mid-June, owing to the short period of darkness at that time. The first arrivals at the colony on each night occurred about 90 min after sunset, tracking the onset of nearly complete darkness under the forest canopy through the nesting season (Fig. 1). We never saw a murrelet aboveground during daylight hours, or before complete darkness fell each night, despite hundreds of hours spent in the colony. However, comparison of identical dates showed that first arrivals occurred significantly earlier in 1984 than 1985. Of 40 nights monitored in both years, first arrival time was earlier in 1985 on 30 nights (binomial,  $P = 0.008$ ).

The numbers of birds arriving each night varied greatly in both 1984 and 1985 (Fig. 2). In both years, the highest numbers of arrivals were recorded during the laying period while the largest numbers of chirrup calls were counted during the family departure period (periods of the breeding cycle were inferred from the timing of clutch initiations in study burrows and departures of family groups; see below). However, the seasonal pattern of activity was quite different between years. In 1984, there were several nights with spectacularly high levels of activity during the laying period, while there was only a single similar night in 1985 (Fig. 2). Furthermore, we detected very little activity in 1984 during the period following the departure of most breeders (June 10–20, Fig. 2), whereas it was a period of intense activity in 1985 (5–15 June, Fig. 2). We recorded

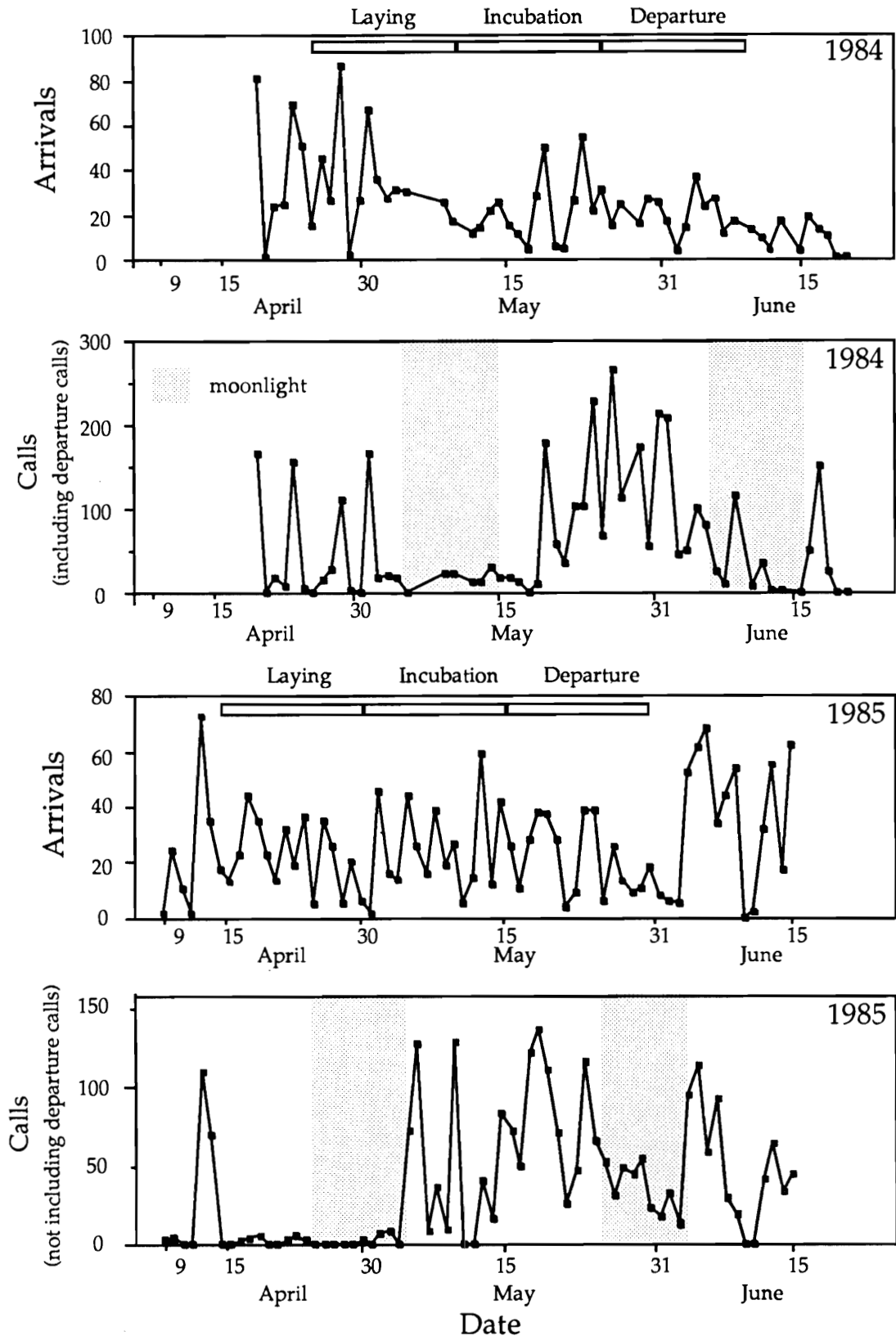


FIG. 2. Nightly counts of arrivals and calls made at the study plot in 1984 and 1985 in relation to the stages of the nesting cycle and moonlight periods. The timing of activity peaks in relation to the nesting cycle differed between years.

large numbers of calls during the departure period of 1984 (maximum of 265 calls/100 min), but fewer calls during this period in 1985 (maximum of 150 calls/100 min). However, there was generally less activity at the colony in 1984 than 1985.

Numbers of arrivals, chirrup calls, song chirrups, and activity at the staging area were all significantly intercorrelated (Table 1). However, the number of burrows entered was independent of chirrup calling and activity at the staging area. Counts of

TABLE 1. Spearman rank correlations among colony activity variables and staging area counts

	Chirrup call count		Song chirrup count		Burrows entered		Flyby count	
	1984	1985	1984	1985	1984	1985	1984	1985
Arrival count	0.809**	0.609**	na	0.639**	0.388**	0.518**	na	0.591**
Chirrup call count			na	0.764**	0.169	0.238	na	0.758**
Song chirrup count					na	0.406**	na	0.557**
Burrows entered count							na	0.135

NOTE: Spearman rank correlation test significance: \*,  $P < 0.05$ ; \*\*,  $P < 0.005$ . In 1984,  $n = 63$  nights, and in 1985,  $n = 67$  nights; na: information not recorded in 1984.

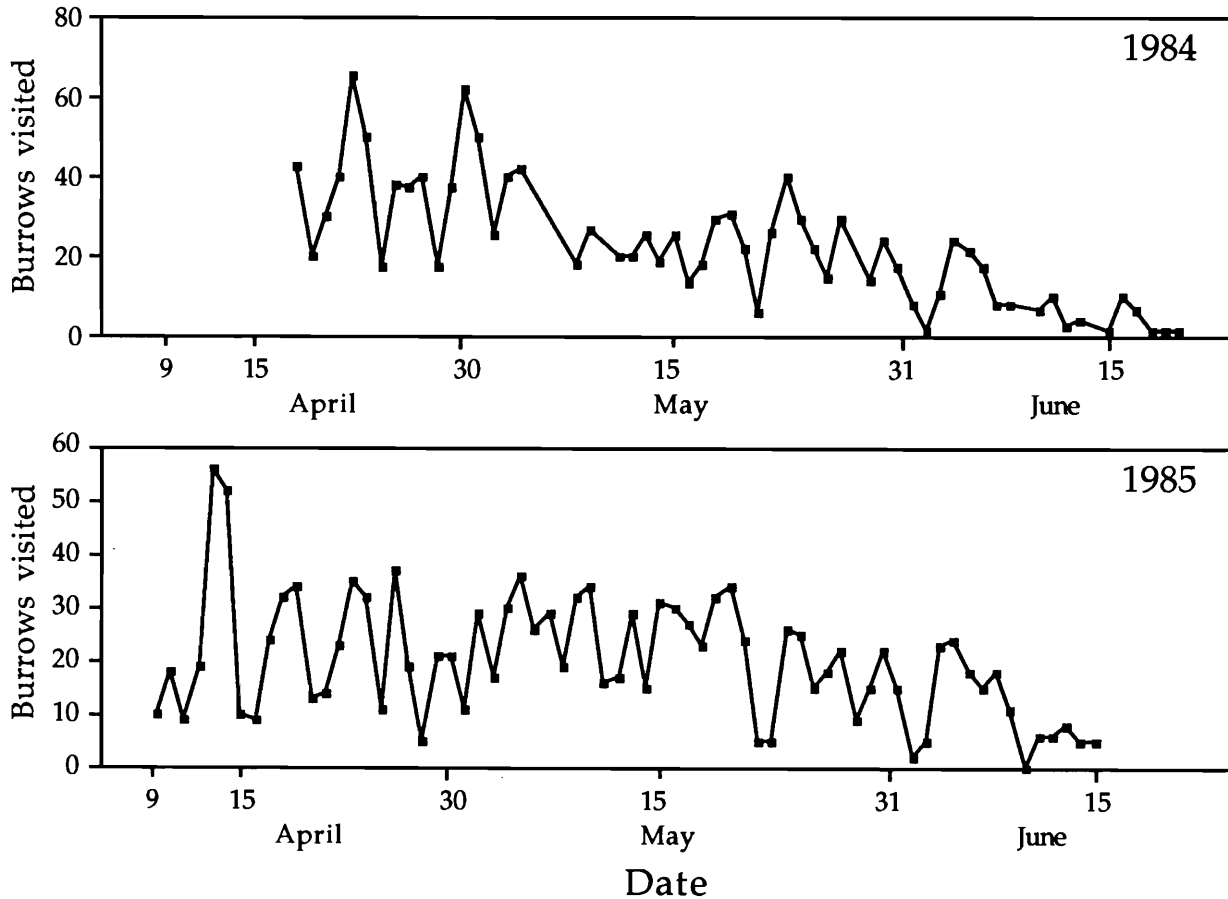


FIG. 3. Counts of burrows visited at the study plot in 1984 and 1985.

burrows entered decreased through the season in both 1984 and 1985 (Fig. 3). Activity at the staging area increased through the season in both 1985 and 1986.

Night to night variation in activity, as measured from counts of arrivals, calls, and burrows entered, involved the regular occurrence of nights with very high levels of activity. In a repeated pattern, these “peak” nights were followed by several with very low levels of activity. Peak nights were sometimes followed by a single night with virtually no activity (e.g., 20 and 29 April 1984, and 11 May 1985, Fig. 2). Early in the season of 1984, five conspicuous activity peaks were spaced 2–4 days apart (Fig. 2). Virtually all active burrows on the study plot were visited on each of several early season peak nights in 1984 and 1985. Autocorrelation analysis demonstrated a consistent pattern of peak counts of burrows entered every 4th night (i.e., the count of burrows visited tended to be significantly correlated

with counts made 4 days previously, but not 2 or 3 days previously; Fig. 4). There was no consistent periodicity for counts of arrivals or vocalizations.

Laying of first eggs was spaced over about 35 days in 1984 and 1985; so, the last eggs were laid about the time of the first chick departures from the study plot. However, we were able to define three consecutive 15-day periods in 1984 and 1985 that contained over 80% of laying, incubation, and family departures; thus, activity levels could be compared with stages of the nesting cycle (Fig. 2). In 1984, arrival counts were higher in the laying period than in the incubation and departure periods (Mann-Whitney  $U$ -tests,  $P < 0.05$ , following significant result of Kruskal-Wallis test for heterogeneity among periods). There was no significant differences in arrival counts among different stages of the nesting season in 1985. Similarly, counts of burrows entered were significantly higher in the laying period in

TABLE 2. The effects of moonlight periods on arrivals and calling at the colony (Mann-Whitney *U*-tests)

	Arrivals				Calls			
	Moonlit $\bar{X}(N = 10)$	Moonless $\bar{X}(N = 20)$	<i>Z</i>	<i>P</i>	Moonlit $\bar{X}(N = 10)$	Moonless $\bar{X}(N = 20)$	<i>Z</i>	<i>P</i>
1984	17.6	31.25	2.159	<0.05	14.9	76.5	2.156	<0.05
1985	17.4	25.9	1.542	>0.1	1.7	23.9	2.181	<0.05

NOTE: Comparisons of activity during 10-day moonlit periods with the preceding and following 10-day moonless periods.

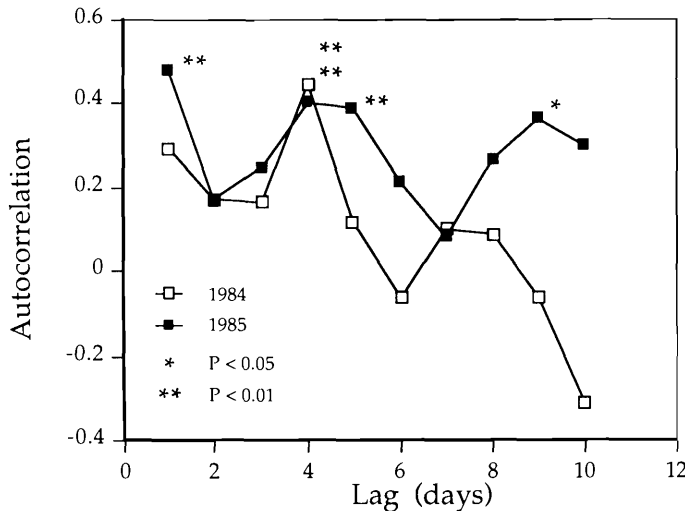


FIG. 4. Correlations of counts of burrows visited with counts made 1–10 days previously. The number of burrows entered on a particular night was significantly correlated with the count made 4 days previously in both 1984 and 1985, evidence that a 4-day cycle was operating.

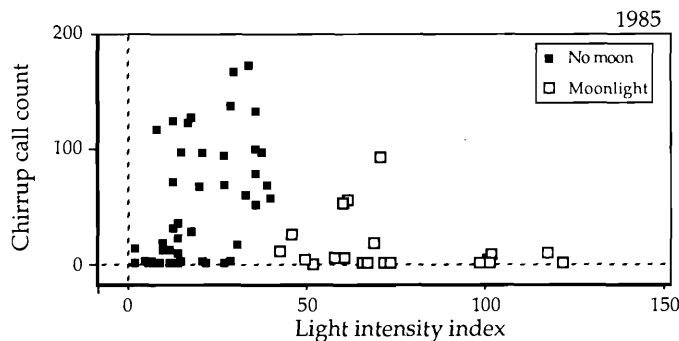


FIG. 5. The relationship of call count to mean light intensity recorded during all nightly monitoring periods in 1985 ( $R^2 = 0.061$ ,  $p < 0.05$ ,  $N = 68$ ). Counts of calls during moonlit periods were significantly lower than moonless periods at the same stage of the nesting cycle (Mann-Whitney *U*-test,  $P < 0.05$ , Table 2).

1984 (Mann-Whitney *U*-tests,  $P < 0.05$ ), but no differences were apparent in 1985 (Kruskal-Wallis,  $P > 0.05$ ). Counts of chirrup calls were higher in the departure period than in the laying and incubation periods in 1984 (Mann-Whitney *U*-tests,  $P < 0.05$ ) and increased significantly with each stage of the season in 1985 (Mann-Whitney *U*-tests,  $P < 0.05$ ). The highest counts of song-chirrup were made in the incubation period of 1985 (Mann-Whitney *U*-tests,  $P < 0.05$ ), the only year singing was monitored. Activity at the staging area was monitored in

1985 and 1986 and was significantly higher in the departure period (Mann-Whitney *U*-tests,  $P < 0.05$ ) in both years

Activity was greatly reduced on moonlit nights, vocalization being particularly affected. On clear nights, with the moon overhead, calling was virtually nonexistent at the colony. This tendency was reflected in counts of chirrup calls made during the evening monitoring periods: more calls were recorded on moonless than in moonlit periods in mid-season, during both 1984 and 1985 (Mann-Whitney *U*-tests,  $P < 0.05$ , Table 2; Fig. 5 illustrates the effect in 1985). Arrivals appeared to be less affected, because the differences in arrival counts between all moonlit and moonless periods were significant in 1984 only (Mann-Whitney *U*-test,  $0.1 > P > 0.05$ ). However, when nights with heavy overcast conditions were excluded from the sample of moonlit nights, a reduction in arrivals was apparent (Mann-Whitney *U*-test,  $P < 0.05$ ). During moonlit periods, the arriving birds appeared to enter their burrows immediately and few birds were heard flying about in the treetops. An anecdotal observation suggests that moonlight could have a nearly instantaneous effect on activity: on several dark nights, when the moon was concealed in dense cloud, murrelet vocal and other activity would suddenly cease when the moon was revealed by occasional patches of clear sky. There was a significant inverse relationship between the mean light intensity recorded during each evening watch period and murrelet activities (Fig. 5,  $R^2 = 0.061$ ,  $P < 0.05$ ,  $N = 68$ ). It is possible that light intensity becomes important at some critical level, which is exceeded during moonlit conditions.

Weather conditions influenced the level of activity at the colony in several ways, the most striking being a reduction in activity to virtually nil during storms. For example, fewer than five arrivals and almost no calls were recorded during the seven nights in the 1984 and 1985 seasons with stormy conditions ( $>55$  km/h mean wind speed and associated heavy rain). As with moonlight, a short period of poor weather, such as a brief rain shower on an otherwise fine night, resulted in immediately reduced vocal and other activity. We found significant Spearman rank correlations among weather variables in both 1984 and 1985. Not unexpectedly, precipitation was correlated with wind and both were inversely related to barometric pressure (Table 3). Regression analyses indicated that weather variables accounted for significant proportions of the night to night variability in arrivals and burrow visitation in 1984, and in arrivals, calls, songs, activity at the staging area, and burrow visitation in 1985 (Table 4). Because there were significant correlations among weather variables, partial correlation analysis was used to assess the independent effects of each weather variable (e.g., the effect of wind speed on arrivals, holding all other weather variables constant). Few individual weather variables showed significant effects when their correlations

TABLE 3. Spearman rank correlations among weather variables

	Cloud	3-Day cloud	Pressure	3-Day pressure	Wind	Precipitation	3-Day precipitation
1984							
3-Day cloud	0.632*						
Pressure	-0.288*	-0.437*					
3-Day pressure	-0.110	-0.379*	0.799*				
Wind	0.227	0.476*	-0.422*	-0.325*			
3-Day wind	0.074	0.461*	-0.371*	-0.486*	0.749*		
1985							
3-Day precipitation						0.655*	
Pressure						-0.463*	-0.295
3-Day pressure			0.648*			-0.537*	-0.655*
Wind			-0.394*	-0.301		0.387*	0.341
3-Day wind			-0.353	-0.502*	0.689*	0.472*	0.571*

NOTE: Spearman rank correlation test significance: \*,  $P < 0.05$ ; in 1984,  $n = 63$  nights, and in 1985,  $n = 68$  nights.

TABLE 4. Partial correlations showing the independent effect of each weather variable on murrelet activity measures, and the coefficients of multiple determination ( $R^2$ ) for the multiple regression of each activity variable, including all weather variables, and including only single-day weather variables

Weather	Activity measures									
	Arrivals		Calls		Burrows		Song		Flybys	
	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>
1984, $n = 57$ days										
1. Cloud	-0.121	>0.2	-0.010	>0.5	-0.073	>0.5				
2. 3-Day cloud	-0.004	>0.5	+0.017	>0.5	-0.014	>0.5				
3. Pressure	+0.017	>0.5	-0.001	>0.5	+0.001	>0.5				
4. 3-Day pressure	-0.118	>0.2	+0.001	>0.5	-0.155	>0.2				
5. Wind	-0.006	>0.5	-0.049	>0.5	-0.079	>0.5				
6. 3-Day wind	+0.097	>0.5	+0.025	>0.5	+0.154	>0.2				
$R^2$ , all variables (1-6)	0.204	0.007	0.012	0.511 ns	0.275	0.001				
$R^2$ , 1-day variables only (1,3,5)	0.107	0.110 ns	0.040	0.535 ns	0.039	0.167 ns				
1985, $n = 68$ days										
1. Precipitation	-0.020	>0.5	-0.023	>0.5	-0.068	>0.5	-0.051	>0.5	-0.005	>0.5
2. 3-Day precipitation	+0.054	>0.5	-0.004	>0.5	-0.001	>0.5	+0.045	>0.5	+0.019	>0.5
3. Pressure	+0.079	>0.5	+0.156	>0.2	+0.008	>0.5	-0.058	>0.5	-0.012	>0.5
4. 3-Day pressure	-0.044	>0.5	+0.072	>0.5	-0.035	>0.5	+0.081	>0.5	+0.007	>0.5
5. Wind	-0.352	<0.005*	-0.353	<0.005*	-0.086	>0.5	-0.202	>0.1	-0.482	<0.001*
6. 3-Day wind	+0.161	>0.2	+0.048	>0.5	+0.136	>0.2	+0.003	>0.5	+0.010	>0.5
$R^2$ , all variables (1-6)	0.458	<0.001	0.414	<0.001	0.260	<0.001	0.276	<0.004	0.440	<0.001
$R^2$ , 1-day variables only (1,3,5)	0.293	<0.001	0.431	<0.001	0.053	>0.05	0.239	<0.001	0.449	<0.001

NOTE: ns, not significant.

with other variables were accounted for. For example, in 1984, none of the partial correlations of individual weather variables was significant, although the combined weather variables explained significant proportions of the variability in arrivals and burrow visitation (Table 4, 1984). However, in 1985, partial correlations of wind speed with arrivals, calling, and activity at the staging area were significant (Table 4), indicating that wind was the most important weather factor affecting colony attendance. Barometric pressure was likely of indirect importance since it would appear to have no obvious direct effect on murrelet foraging or other activities. The signs of the partial correlations suggest that murrelet activity was reduced during poor weather, particularly in windy conditions. When included in the regression, the 3-day mean weather variables add significantly to the proportion of the variability in activity

explained by the same night variables alone, except for calls and staging area activity in 1985 (Table 4). This suggests that murrelet activity on a particular night is affected by long- as well as short-term weather conditions. The correlations of 3-day means of wind speed with activity variables in 1984 and 1985 were all positive, suggesting that murrelet activity at the colony may be greater following windy periods. At Reef Island, high winds and precipitation were associated with low barometric pressure (significant rank correlations, Table 3) and weather conditions changed rapidly (weak correlations of weather with that of the 3 previous days). There was more precipitation in 1984 than in 1985, but no significant differences in mean wind speed or barometric pressure.

There were interyear differences in reproductive phenology and performance that are relevant to the interpretation of

weather effects. Ancient Murrelets at Reef Island bred earlier in 1985 than in 1984 (median date of clutch completion: 28 April 1984, 21 April 1985). Several observations suggest that conditions for breeding were better in 1985 than in 1984: eggs were heavier (1985  $\bar{X} = 46.7 \pm 3.29$  g; 1984  $\bar{X} = 43.8 \pm 3.17$  g;  $t$ -test,  $P < 0.001$ ) and incubation shifts were shorter (1985  $\bar{X} = 2.31 \pm 1.02$  days; 1984  $\bar{X} = 3.11 \pm 0.83$  days;  $t$ -test,  $P < 0.001$ ). Furthermore, breeders captured at the start of the season were heavier in 1985 than in 1984 (Gaston and Jones 1990).

In both years, large numbers of birds without brood patches (nonbreeders) began to appear in the colony midway through the incubation period. Of 13 birds performing the typical 'song' vocalization display that were examined late in the incubation period, only one had a brood patch and all were males (6 sexed by dissection and 7 sexed by external measurements; Jones 1985), indicating that nonbreeders are responsible for most of the vocal activity at that time.

### Discussion

Ancient Murrelets exhibit colony attendance behaviour with greater temporal variation in colony activity than has been described for any 'diurnal' alcid species. Murrelet activity on successive nights at any stage of the season may differ by as much as an order of magnitude, greater variability than that described for most other alcids, and their colonies may appear nearly abandoned for several nights at a stretch in the middle of the breeding season. Highly variable activity early in the season, as was noted in April 1984 at Reef Island, is also found in Common Murres, *Uria aalge* (Birkhead 1978), Thick-billed Murres (Netherlands 1981), Razorbills, *Alca torda* (Lloyd 1975), Atlantic Puffins, *Fratercula arctica* (Harris 1984), and Dovekies, *Alle alle* (Salomonsen 1951). Ancient Murrelets appear to show greater night to night variability in colony activity than the day to day variability of these species, possibly because of the relatively short, nighttime activity periods. Regularly spaced peaks of activity, with a periodicity similar to that recorded in Ancient Murrelets, have been reported for Common Murres (5–6 days; Birkhead 1978), Razorbills (2–7 days; Corkhill 1971), and Common Puffins (4–7 days; Harris and Birkhead 1985). The peak nights of the Ancient Murrelet prelaying and laying periods may involve attendance at the colony by most of the breeding population, with both members of many pairs present.

Nonbreeding Ancient Murrelets have a big effect on the seasonal pattern of activity at the colony and the offshore staging area. For example, an influx of birds without brood patches into the colony about midway through the incubation period was coincident with an increase in nightly call counts and counts of birds on the staging area. Increased rates of calling through the chick departure period were noted in both years (Jones *et al.* 1987), even when the calls of adults to their chicks during colony departure were excluded. As we have shown, much of the vocalization late in the season was attributable to nonbreeding males. A similar increase in vocalization occurs with the influx of nonbreeding Manx Shearwaters into colonies during the chick-rearing period (James 1985). Vocalization during peak nights early in the season was attributable to breeding birds, because most birds trapped in the colony before the influx of nonbreeders had full brood patches when caught again during the incubation period (A. J. Gaston, unpublished data).

Several of our observations suggested that murrelets restricted their activities at the colony to periods of the lowest light intensity. For example, vocalization and other murrelet activi-

ties were reduced on moonlit nights and nightly activity commenced at a predictable interval after sunset, and only when there was nearly complete darkness below the forest canopy. This behaviour is a prediction of the predation avoidance hypothesis, but not of the daylight foraging hypothesis, so we suggest that nocturnal colony activity of Ancient Murrelets functions for predator avoidance. Whether murrelet requirements for daytime foraging play a role in the timing of activity at the colony will only be revealed by further study of the foraging ecology of this species.

At Reef Island, several predator species may have been significant in restricting murrelet activity. Bald Eagles (*Haliaeetus leucocephalus*) were observed flying about in and near the colony on moonlit nights, and are known to prey on murrelets at night elsewhere (Vermeer *et al.* 1984; M. Rodway and M. Lemon, personal communication). We found murrelet carcasses and eagle pellets containing murrelet remains, presumably from birds captured at the colony, under eagle roost trees. Peregrine Falcons (*Falco peregrinus*) also preyed on Ancient Murrelets at Reef Island, as they do elsewhere (Nelson and Myres 1976). Among alcids, reduced colony attendance during moonlit periods has been reported for one other species, the Cassin's Auklet (Manuwal 1974). Manuwal found that moonlight was associated with reduced numbers of arrivals, and particularly vocalizations, and implicated Western Gulls (*Larus occidentalis*) in nighttime predation. Gull predation has also been suggested to relate to reduced activity on moonlit nights by Leach's Storm Petrels (Watanuki 1986) and Manx Shearwaters (Storey and Grimmer 1986).

Murrelet activity at Reef Island was reduced by poor weather conditions, particularly wind. Drastically reduced colony attendance during gales and highest attendance in fair weather has also been documented for Common Murres (Birkhead 1978), Razorbills (Corkhill 1971), and Black Guillemots, *Cepphus grylle* (Petersen 1981). Nighttime weather conditions at the colony may have an instantaneous influence on activity, while several days of poor weather might influence the level of activity by affecting foraging conditions and thus the condition of colony members. Clearly, weather had both short- and long-term associations with murrelet activity levels at Reef Island.

Current weather conditions in the colony may have influenced activity in two ways. First, the level of environmental noise associated with wind and precipitation could interfere with murrelet vocal displays and thus discourage calling, since we noted that murrelets ceased vocalizing immediately coincident with short periods of poor weather on otherwise suitable nights. Second, weather may influence activity by reducing visibility and thereby discouraging murrelets from entering or flying about in the colony. Visibility was greatly reduced in the colony in poor weather, with precipitation and fog reducing light levels at the forest floor to near complete darkness. We noted unusually frequent collisions of birds with vegetation and found disoriented birds in the colony in these conditions (personal observation), evidence that murrelet navigation was impaired.

There are two possible explanations for the long-term (i.e., 3 days prior) weather effects. One is that weather affects the foraging success of the murrelet population, so that a period of poor weather changes the proportion of the population that must remain at sea another day rather than return to the colony to exchange incubation duties or perform other activities. Poor weather (i.e., heavy seas, high winds, and poor visibility) could reduce foraging success (Birkhead 1977) and increase energetic

expenditure either by dispersing or driving prey deeper, or make surface clues to the presence of food (e.g., other feeding murrelets) more difficult to locate. Another possibility is that several days of poor weather with reduced attendance at the colony result in an influx on the first night with fair weather. Our observations are more consistent with the latter hypothesis, since the partial correlations suggest that activity was increased slightly after poor weather (e.g., all activities showed a positive correlation with 3-day mean wind speed in 1984 and 1985, Table 4). However, none of the partial correlations of activity with 3-day weather means was significant.

Weather effects and some aspects of breeding biology differed between 1984 and 1985. In 1984, activity at the colony was less associated with weather. In 1985, weather conditions explained a greater proportion of the night to night variability of activity and short-term weather (e.g., wind speed) was particularly important. A possible explanation is that, since in 1984 foraging conditions were poor (as indicated by the later timing of breeding, lower weights of breeders, and smaller egg size), the weather's influence was small compared with that of the generally poorer foraging conditions in that year. In 1985, when reproductive performance and likely the condition of the birds was better, short-term weather showed strong effects, possibly because murrelets could choose to visit the colony whenever the conditions on a particular night were suitable. Larger numbers of nonbreeders were active at the colony in 1985 during the last half of the season compared with 1984. This subpopulation, lacking the need to store energy for 3-day incubation shifts, may be more affected by short-term weather at the colony than the breeders. We therefore suggest that interyear differences in activity may have resulted from the interaction of weather and general foraging conditions.

We found that the activity of Ancient Murrelets at Reef Island varied from night to night, among seasons, and among years. Weather, moonlight, and an underlying 4-day cycle were each responsible for part of this variability in activity. These findings are relevant to the design of monitoring techniques for this species, because indices of population sizes and trends of seabirds are usually derived from counts of birds attending colonies. Counts are usually taken during periods of the lowest day to day variability in colony attendance, when they will most reflect the breeding population. In Ancient Murrelets, the extreme night to night variation and inconsistent seasonal variation in counts of arrivals and calls appear to preclude their usefulness for population indexing (Gaston *et al.* 1988). Burrow arrivals, as indicated by tags knocked down, appear to be a more promising technique, if carried out over periods of >7 days (Gaston and Collins 1987; Gaston *et al.* 1988). However, vocalizations do appear to be a useful means of locating low density nesting areas in nighttime surveys.

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