

POPULATION PARAMETERS OF THE ANCIENT MURRELET¹

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Abstract. Banding and retrapping of adult Ancient Murrelets (*Synthliboramphus antiquus*) and chicks at Reef Island, in the Queen Charlotte Islands, British Columbia was carried out over 6 years. The breeding status of adults was determined by inspecting brood patches, or by finding birds with eggs or chicks, or was based on the date of capture. Retrapping of breeders gave an estimate of annual survival of 77%, lower than estimates for other alcids. Reproductive success under undisturbed conditions was measured in 2 years, and averaged 1.54 chicks per breeding pair per year; unusually high for an alcid. Nonbreeders visiting the colony were mainly in their second or third year, and breeding probably begins in the third or fourth year. Three birds reared on Reef Island were retrapped at a nearby colony, and many prospectors visiting Reef Island must have originated from several other colonies. The high mortality of adult Ancient Murrelets on their breeding colonies could explain the evolution of their precocial departure strategy.

Key words: Ancient Murrelet; *Synthliboramphus antiquus*; demography; reproductive success; age at first breeding; survival.

INTRODUCTION

Little information is available on the demography of the Ancient Murrelet *Synthliboramphus antiquus*, apart from an estimate of reproductive success by Vermeer and Lemon (1986), and some tentative predictions concerning the age at first breeding by Sealy (1976). To aid in the management of the Ancient Murrelet population in British Columbia, the Canadian Wildlife Service has attempted recently to estimate critical population parameters by banding hatchlings and adult birds at a colony in the Queen Charlotte Islands Archipelago.

Ancient Murrelets are confined to the temperate and subarctic waters of the North Pacific. They feed in continental shelf waters, usually out of sight of land (Wahl 1975, Vermeer and Rankin 1984, Briggs et al. 1987). Ancient Murrelet chicks, in common with their congeners, but unlike all other seabirds, are never fed at the colony. Instead, the two chicks which comprise most broods leave at night, 2-4 days after hatching, travel out to sea, and are fed by their parents until fully grown to about 6-8 weeks old (Sealy 1976, Litvinenko and Shibaev 1987, Jones et al. 1987). Because precocity is unusual among seabirds, the

existence of this strategy among the *Synthliboramphus* murrelets has led to speculation about its adaptive significance (Lack 1968, Sealy 1976).

Whatever the evolutionary significance of the precocial behavior of young Ancient Murrelets, it gives the species the potential to rear a brood of two chicks. Members of the genus *Synthliboramphus* usually lay a clutch of two eggs. All other alcids, except the inshore-feeding *Cephus* spp., have a clutch size of one (Lack 1968, Sealy 1973). The same applies to practically all other flying, offshore-feeding seabirds, because the distance that they must travel to find food precludes delivering it at a rate sufficient to provision more than one chick during the period of maximum demand for food (Ashmole 1963, Goodman 1974, Asbirk 1979, Ricklefs 1983, Pennycuik et al. 1984).

Theoretical treatments of life history tactics suggest that different demographic parameters should be interrelated (Williams 1966, Goodman 1974, Stearns 1976) and a negative relationship between fecundity and adult survival has been demonstrated for North American game birds by Zammuto (1986), and for all birds by Gaillard et al. (1989). If the Ancient Murrelet differs from other alcids in demographic characteristics other than clutch size, then these demographic differences may have contributed to its peculiar life-history strategy. In this paper I report the results of the recent Canadian Wildlife Service study of population parameters for the species and assess the likelihood that the pre-

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social departure of the chicks is related to demographic constraints.

METHODS

Research was conducted at Reef Island, British Columbia (52°52'N, 131°31'W) during the breeding seasons of 1984–1989. The island is 4 km long and 1.6 km across at the widest point, lies about 7 km from the main islands of the archipelago, and is densely forested with coniferous trees. Ancient Murrelets nest over about 39.5 ha, at a density of about 126 occupied burrows per ha (Gaston et al. 1988, Rodway et al. 1988). The population, of about 5,000 pairs, appears to be stable at present (unpubl. observ.).

In 1984 and 1985 we investigated reproductive success by inspecting burrows regularly for eggs and chicks, but this caused desertions (Gaston et al. 1988). In 1986 fieldwork began after the incubation of many clutches had started, so data from that year was not used to assess reproductive success. In 1987 we inspected burrows on 22 or 23 April, and again on 11 May, 17 May, and every 3 days thereafter, but some desertions still occurred. Consequently, in 1988 and 1989, we fitted nest chambers with thermometer probes to monitor breeding (Gaston and Powell 1989). As inspection hatches had been dug in previous years for practically all nest chambers, we could use the probes without causing additional disturbance to the burrows. We inspected burrows directly after 29 days of incubation, by which time most eggs were pipping. The small number of desertions at this stage of breeding were probably the result of our disturbance. The nests involved were omitted from estimates of reproductive success. Only those estimates of reproductive success obtained in 1988 and 1989 are considered representative of natural conditions.

Some chicks became trapped by difficult terrain en route to the sea, or were attacked by Saw-whet Owls *Aegolius acadicus*, deer mice *Peromyscus* sp., or other predators. A few were taken by large fish close to shore. Mortality from these causes was estimated by making boat surveys at first light up to 16 km from the colony to locate family parties and count the number of chicks in each. Because the two chicks in a brood do not remain in contact while making their way to the sea (Jones et al. 1987), we assumed that losses of chicks from the same brood occurred independently.

We captured adult Ancient Murrelets on the surface for banding as they arrived at the colony at night; others were removed from their burrows for banding during the 2-day period between the hatching and departure of their chicks. Only a few adults removed from the burrow at this stage of breeding deserted subsequently (3 of 221), although those few removed during incubation in 1984 all did so (Gaston et al. 1988). We examined the majority of birds captured for the presence of brood patches (the Ancient Murrelet has two lateral brood patches, each measuring about 20–25 mm across when fully developed), or eggs about to be laid (the egg makes a conspicuous bulge in the lower abdomen). The birds were weighed to ± 1 g on a Pesola spring balance and the wing length was measured (maximum chord ± 1 mm). Not all information was recorded for all birds, hence sample sizes for different measurements vary somewhat. Birds were subsequently classified into AHY (all after hatching year), nonbreeders, and breeders (see below).

In all years we banded some chicks before they left the burrow, but larger numbers were captured in 1985–1989 by using plastic fences to funnel departing chicks to a collecting point where they were banded and released to the sea (Gaston et al. 1988). By stationing catchers at the collecting point throughout the period of departures, all the chicks leaving a certain portion of the colony (Fig. 1) were captured in 1986–1989. The same method was used in 1985, though for only part of the season. The catchment area of the fences was delineated by observing where chicks banded in burrows and recaptured at the collecting point had come from. The number of burrows in the catchment area was estimated in 1989 using circular quadrats of 100 m² evenly spaced on a 50-m grid covering the entire catchment area. An additional chick-catching area was used periodically in 1987 and 1988, contributing to the total of chicks banded, but not included in the assessment of total numbers produced in the catchment area. In 1985 we recorded several cases of deer mice attacking chicks near the collecting point. This was eliminated by trapping mice in the area of the funnels. No other evidence was obtained that the funnels affected predation rates during departure.

Adult survival was estimated from retrapping data using the regression method (Furness 1978, Kampp 1982), and the SURGE program for PCs based on the modification of Cormack's (1964)

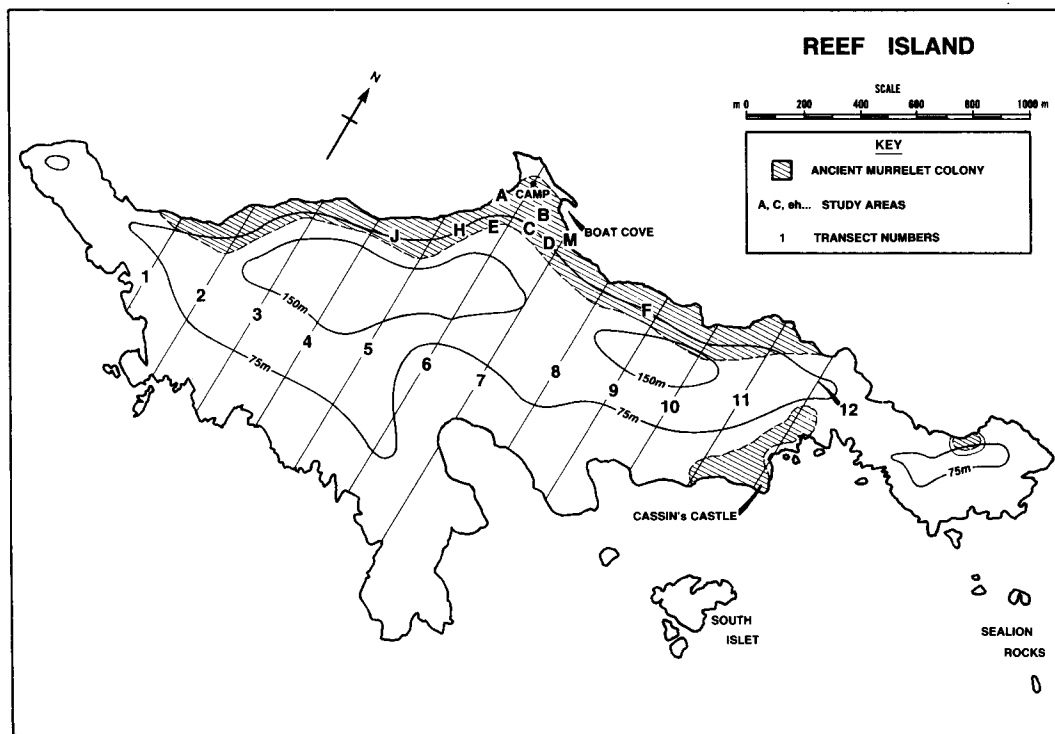


FIGURE 1. Map of Reef Island and surroundings.

capture-recapture method by Clobert and Lebreton (1985). The SURGE program allows survival to be estimated separately for different years after capture, and provides estimates of how the probability of recapture varies among years (Lebreton and Clobert 1986, Clobert et al. 1987).

In 1984–1985 we did practically all trapping in areas B, D, and E (Fig. 1). In 1986 the trapping area was extended to include areas C and M. In 1987, and subsequently, trapping was carried out over the areas used in earlier years, plus area K. At area F birds were captured in burrows in all years, but surface trapping was carried out only in 1988 and 1989. We trapped at area J in 1989 only. Surface captures at the last two sites were omitted from all analyses, except those involving movements within the colony.

The regression method for estimating survival relies on an equal likelihood of retrapping birds surviving from any earlier year. Because the trapping area was expanded in the course of the study, I have included only retrapping data from 1987 onwards, when the trapping area remained sta-

ble. For the sake of consistency, I have used the same years for the analysis of birds retrapped in burrows, although all burrows known to have been used were investigated in all subsequent years. To investigate whether birds banded at Reef Island were visiting other colonies, additional trapping on the surface was carried out on a colony of about 1,000 pairs on East Limestone Island, 5.6 km to the west of Reef Island, in 1989.

Evidence of predation on adult Ancient Murrelets, in the form of feather piles and wings, was abundant on Reef Island. Similar signs have been observed frequently on all Ancient Murrelet colonies in the Queen Charlotte Islands (Rodway et al. 1988). It proved impossible to quantify this predation, because predators and subsequent scavengers removed some remains from the colony area, and may have redistributed others within the colony. Minimum estimates of numbers of adults killed in 1989 were obtained from counts of wings on 42 100-m² plots, evenly distributed through the colony, and amounting to a sample of 1% of the colony area.

TABLE 1. Brood-patch development of females trapped with oviductal eggs (all years).

Date	Maximum diameter of brood patch (mm)		
	0	1-10	>10
<10 April	15	0	0
10-30 April	15	15	28
>30 April	3	0	13

RESULTS

BROOD PATCHES

At the beginning of egg laying, in early April, the majority of females trapped with oviductal eggs showed no signs of brood patches. By the end of egg laying, in the first half of May, the majority had a brood patch at least half-grown (Table 1). The interval between the laying of first and second eggs is 7-8 days (Sealy 1976, pers. observ.) and the development of the brood patch apparently takes place during this interval, so that by the start of incubation (usually 1-2 days after the laying of the second egg [Gaston and Powell 1989]) most females probably have a more-or-less complete brood patch. Sealy (1976) reached a similar conclusion. The timing of brood-patch development in the male is not known, but presumably it occurs at about the same time. Among birds trapped with chicks, all but one out of 77 had fully developed brood patches, so the brood patch does not regress significantly before departure from the colony. Only one bird was trapped on the colony, in the same year, after its brood had departed, out of 310 banded with chicks in all years. The brood patch was partly refeathered, but was still clearly detectable. It appears that few breeders return to the colony after the successful completion of breeding.

Among birds trapped on the surface, the proportion with brood patches rose to about 50% by late April, then fell somewhat and thereafter hovered around 30-40% until observations ceased (Fig. 2). Among birds trapped without a brood patch before 15 April, and retrapped after 12 May in the same year, 30/37 (81%) had fully developed brood patches when examined for the second time. If we assume that some of those which did not have brood patches when retrapped had attempted to breed, but never started to incubate (see below), then it appears that most birds present on the colony before mid-April attempted to breed that year. The majority

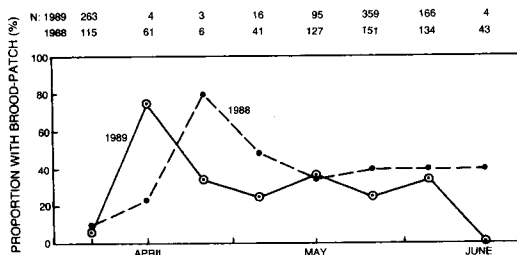


FIGURE 2. Proportions of birds trapped with brood patches in relation to time of year.

of birds trapped after the cessation of egg laying (about mid-May in all years) on which brood patches were either incompletely developed, or absent, were presumably nonbreeders, although some may have been failed breeders.

On the basis of the information obtained on brood patches I treated the following categories of birds as breeders: birds trapped on the colony before 15 April; birds trapped in burrows, accompanied by chicks on the surface, or having oviductal eggs; birds trapped with a fully developed brood patch (>19 mm maximum diameter). I judged that birds trapped for the first time after 12 May in any year, and with a brood patch less than 11 mm across, were not going to breed in that year (one exception was detected, see below). Birds not meeting the criteria for either breeders or nonbreeders were not assigned a definite breeding status, and were not included in any analyses. These amounted to only 4% ($n = 1,334$) of all birds not considered breeders.

STATUS OF BREEDERS AND NONBREEDERS WHEN RETRAPPED IN LATER YEARS

Out of 31 birds trapped as nonbreeders and retrapped the next season, 21 (68%) were breeders when retrapped, according to the above criteria. Out of 11 retrapped 2 years later, all but one (91%) were breeding. The corresponding figures for birds trapped on the surface as breeders were 90/95 (95%) and 60/61 (98%). Considering that some failed breeders may have been classified as nonbreeders, it seems likely that Ancient Murrelets breed every year once they have begun to do so. During the period 1987-1989 (see Methods) 28/672 (4.2%) birds trapped as nonbreeders were retrapped in the following year, compared to 56/417 (13.4%) breeders trapped on the surface ($\chi^2 = 31.0$, $P < 0.001$).

TABLE 2. Areas of banding and retrapping for birds captured as breeders (upper) and nonbreeders (lower). Numbers in boldface represent retrapped birds in non-adjacent areas. The small contiguous areas C and D were lumped to make all areas roughly the same size.

Area of retrapping	Area of banding						
	B	C/D	E	F	H	K	M
B	5	4	1				
C/D		84	3			4	1
E			38				
F				30			
H					2		
K						21	
M							36
<hr/>							
B	2						
C/D	2	12					
E		2	3				
F				1			
H							
K		1				10	
M		2				3	12

MOVEMENTS WITHIN THE COLONY

Ninety percent ($n = 286$) of retraps of birds banded as AHY were caught in the same area where they had been banded (Table 2). Significantly more nonbreeders (22%, $n = 51$) were retrapped away from their area of banding than breeders (8%, $n = 235$; $\chi^2 = 8.11$, $P < 0.005$). If we consider only those birds trapped in areas not con-

TABLE 3. Years of banding of birds retrapped in subsequent years.

Year banded	Total banded	Year recaptured				
		1985	1986	1987	1988	1989
All breeders						
1984	125	27	4	0	5	6
1985	137		7	18	16	10
1986	124			18	16	17
1987	132				16	17
1988	274					36
Trapped in burrows only						
1984	17	1	1	0	0	1
1985	26		5	11	7	6
1986	15			4	1	0
1987	20				4	5
1988	25					11
Nonbreeders						
1984	32	3	1	1	1	0
1985	78		2	1	3	4
1986	70			3	3	2
1987	289				13	7
1988	313					12
All AHY						
1984	188	35	5	2	8	8
1985	246		9	19	22	14
1986	172			21	19	18
1987	443				31	26
1988	588					52

tiguous with their banding area the difference is greater (nonbreeders 14%, breeders 1%; $\chi^2 = 19.25$, $P < 0.001$). At two catching areas separated from the others by more than 400 m (F and J), no birds banded elsewhere as AHYs were retrapped among 106 birds captured in 1988 and 1989 (the only years when birds were trapped on the surface in these areas). No birds banded on Reef Island as AHY were retrapped on Limestone Island. The site fidelity, particularly of the breeding birds, means that estimates of survival rates were not greatly influenced by emigration to other parts of the colony.

ANNUAL SURVIVAL OF BREEDERS

Banding and retrapping data on which the survival analyses were based are given in Table 3. The regression of the proportion of breeders (\log_{10}) retrapped on the number of years elapsing since banding has a slope of -0.124 giving an estimate of 75% annual survival, with 95% confidence interval 69–82% (Table 4, Fig. 3). If only birds trapped in burrows are considered, the estimated survival is 67%, with broader confidence limits,

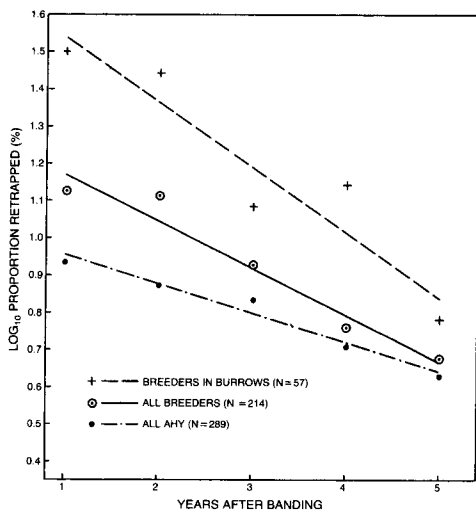


FIGURE 3. Proportion of Ancient Murrelets recaptured as adults in relation to the number of years elapsed since banding.

TABLE 4. Regression estimates of adult annual survival.

Sample	Regression slope (±95% confidence interval)	Annual survival (±95% confidence interval)	r ²
All recapture years			
All breeders	-0.123 (0.087-0.163)	0.75 (0.69-0.82)	0.95
Breeders in burrows	-0.175 (0.090-0.259)	0.67 (0.55-0.82)	0.88
All captures	-0.078 (0.057-0.100)	0.84 (0.77-0.88)	0.96
Omitting first year after capture			
All breeders	-0.147 (0.108-0.186)	0.69 (0.65-0.78)	0.97
Breeders in burrows	-0.194 (0.054-0.334)	0.64 (0.46-0.88)	0.84
All captures	-0.086 (0.054-0.118)	0.82 (0.76-0.88)	0.95

and if all retrapped birds are considered, 84% (95% confidence interval 79-88%). The slope of the corresponding regression for nonbreeders does not differ significantly from 0 and hence no useful estimate is possible.

The SURGE estimate based on the figures in Table 3 gives an annual survival of 69.0%, if interyear variation is ignored. If survival is estimated separately for the first year after capture and for subsequent years, the estimates are 47.4% and 76.7%, both estimates falling outside the 95% confidence limits for the other (Table 5). This suggests that the chance of retrapping a bird in the first year after banding was lower than in subsequent years, perhaps because the disturbance caused by capture affected the probability that an individual would visit the colony the following year. The estimate for survival in subsequent years is very close to that obtained by the regression method. Data for birds retrapped in burrows only were inadequate for use with SURGE.

The SURGE program estimates the probabil-

ity of recapture by year (Table 5). The highest estimate for recaptures (1985, 0.49) and the lowest (1986, 0.11) fall outside the 95% confidence limits for the other 3 years, which are all fairly similar. These interyear differences in recapture probabilities reflect changes in catching operations. In 1984 and 1985 practically all trapping was confined to one small area, giving the high recapture rate observed. In 1986 the catching area was expanded and trapping in the previous banding area was less intensive. In 1987 the area was again expanded, but with increased effort overall. The catching area remained fairly similar, with a further slight increase of effort, in 1988 and 1989. The evidence from recapture probabilities justifies limiting the recapture data used in the regression analysis to the years 1987-1989.

Because, according to the SURGE analysis, the apparent survival of birds in their first year after capture is lower than in subsequent years, I reanalyzed the regression data omitting the first year after capture. The resulting regression slopes,

TABLE 5. SURGE estimates of adult survival and recapture probabilities (version SURGE 4.0).

Parameter	Estimate	Minimum	Maximum	SE
Survival				
Breeders, first year	0.474	0.365	0.585	0.057
other years	0.767	0.666	0.845	0.046
all years combined	0.691	0.612	0.759	0.038
All AHY, first year	0.355	0.284	0.432	0.038
other years	0.819	0.720	0.889	0.043
Recapture probabilities				
Breeders, (divided into first and later years)				
1985	0.494	0.310	0.680	0.099
1986	0.105	0.056	0.188	0.033
1987	0.247	0.171	0.342	0.044
1988	0.303	0.217	0.404	0.048
1989	0.327	0.238	0.429	0.049

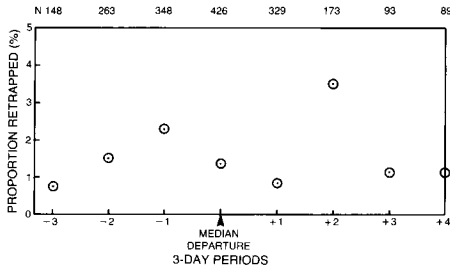


FIGURE 4. Proportion of birds banded as chicks that were retrapped in relation to their date of departure from the colony.

based on only four data points, were all steeper than those based on all 5 years of recapture, giving lower survival estimates (Table 4).

CHANGES IN BURROW OCCUPANCY

In 14 cases the identity of both breeders in a particular burrow was known in more than one season. In the eight cases where the two seasons were consecutive three pairs remained unchanged, four had changed one member, and in the other burrow both members of the pair had changed. Hence 10/16 (62%) had definitely survived. After 2 years one burrow contained the same pair, while two had changed one member. In each of the three cases separated by more than 2 years, one member had changed. Out of 58 birds trapped in burrows and retrapped in burrows in later years, 13 (22%) were in a different burrow. Two cases were recorded of pairs breeding together in different burrows in different years (distances moved 2.5 and 10 m). In one case, two previously paired birds were found breeding separately in a later year. Although the data on changes in pair composition are too few to provide an estimate of survival, the relatively high rate of changes in membership indicates, either that divorce is common, or mortality is high.

RETRAPPED BIRDS BANDED AS CHICKS

We retrapped 2 1-year-old (1Y), 21 2-year-old (2Y), 6 3-year-old (3Y) and 1 4-year-old (4Y) birds (Table 6). Two of these birds appeared to be breeding when recaptured, a 2Y caught on 23 May 1989 with a complete brood patch, and a 3Y caught on 22 May 1988 without a brood patch and again on 6 June 1988 with a fully developed brood patch. The latter bird had apparently initiated breeding very late in the season, as might be expected for a first-time breeder

TABLE 6. Numbers of chicks banded and numbers retrapped in subsequent years.

Year banded	Total banded	Year recaptured			
		1986	1987	1988	1989
1985	328	1	4	3	1
1986	720		0	5	3
1987	1,070			1	12
1988	1,256				0

(Ryder 1980). This indicates that a few birds identified by my criteria as nonbreeders actually may have bred that year. Otherwise, only the single 4Y showed any signs of a brood patch (an incomplete one, 10 mm width). A 3Y, trapped on 7 April 1988, qualified as a breeder based on the date of capture. Apart from this bird, the earliest date of capture of a bird banded as a chick was 12 May.

Recapture rates as a proportion of chicks banded were 0.06% ($n = 3,374$) for 1Ys, 0.99% ($n = 2,118$) for 2Ys, 0.57% ($n = 1,048$) for 3Ys, and 0.30% ($n = 328$) for 4Ys. Recapture rates for 2Ys varied from 0.69% for the 1986 cohort in 1988 to 1.22% for the 1985 cohort in 1987. The mean recapture rate over the 3 years available was $1.01 \pm 0.28\%$, giving an upper 95% confidence limit of 1.91% (Table 6). Three of the 12 2Ys retrapped in 1989 were caught on East Limestone Island, the only birds banded at Reef Island to be retrapped there, out of 250 captured. The 2Ys constituted 1.6% ($n = 183$) of nonbreeders captured on East Limestone Island. This proportion did not differ significantly from the proportion of 2Ys among nonbreeders captured at Reef Island in 1989 (2.2%, $n = 412$, comparing colonies $\chi^2 = 0.19$, ns).

The mean departure weight of chicks which were retrapped as AHYs was 27.7 ± 1.63 g ($n = 25$), compared with mean chick departure weights over the whole season of 28.0 g in 1985, 27.5 g in 1986, 27.5 g in 1987, and 26.3 g in 1988. Hence, it appears that the likelihood of retrapping a chick was not greatly affected by its weight at departure from the colony. There was no tendency for chicks banded early in the season to be retrapped more often than those banded later (Fig. 4).

WEIGHTS AND WING LENGTHS

The weights of breeding Ancient Murrelets varied both within and among years. The highest

weights occurred at the start of incubation, when means varied from 217–238 g among years. Lowest weights (201–208 g) were recorded for birds with chicks, at which point there was no significant interyear variation. Gaston and Jones (1989) provide full details of weight changes in breeders. The mean weight of nonbreeders trapped in all years was 184.6 ± 11.64 g ($n = 924$). The upper 95% confidence limit for the mean (185.4 g) falls well below the mean weight of breeders at any stage in the season. The mean weight of nonbreeding 2Ys retrapped at the colony was 180.1 ± 7.37 g ($n = 20$), not significantly different from that of all nonbreeders. The 2Y breeder weighed 247 g. The mean weight of nonbreeding 3Ys was 197.5 ± 13.59 g ($n = 4$), significantly heavier than the nonbreeding 2Ys ($t = 3.64$, $P < 0.01$) and all nonbreeders ($t = 2.21$, $P < 0.05$). The two 3Y breeders weighed 212 and 203 g. The 4Y weighed 204 g. Sealy (1976), who collected AHY Ancient Murrelets at sea, did not find any difference in weight between breeders and nonbreeders, but found that breeders had longer wings.

The mean wing length of breeders in my study was 140.2 ± 3.25 mm ($n = 533$), while that of nonbreeders was significantly shorter, 138.08 ± 3.20 mm ($n = 859$) ($t = 11.84$, $P < 0.001$). The mean wing length of 2Ys was 137.7 ± 3.12 mm ($n = 21$), which was not significantly different from that of all nonbreeders, but was significantly shorter than that of breeders ($t = 4.80$, $P < 0.01$). The mean wing length of 3Ys was 139.3 ± 2.80 mm ($n = 6$), closer to that of breeders than that of nonbreeders, but not significantly different from that of 2Ys, all nonbreeders, or all breeders. Sealy (1976) considered that nonbreeders differed from breeders in bill measurements, but his figures do not support the contention and I found no difference between these two classes in either culmen length or bill depth (unpubl. data).

REPRODUCTIVE SUCCESS

Practically all clutches where incubation had begun were of two eggs (286/298, 96%, Table 7), and most broods consisted of two chicks at departure (154/168, 92%). Egg color and pattern suggested that the small number of clutches including more than two eggs were the product of more than one female. In all years, a few eggs were found laid on the surface. These may have been laid by females without burrows, or by females which did have a burrow, but failed to

locate it on the night in question. This may explain some or all of the single-egg clutches.

Out of 336 eggs incubating for at least 30 days, 322 (96%) hatched. The three desertions which occurred after hatching were probably due to our interference (Gaston and Powell 1989). Under natural conditions practically all chicks that hatch apparently survive to depart from the burrow in the normal way.

In 1988 and 1989, when incubation was followed using the temperature probes, 76% and 88% of pairs, respectively, succeeded in departing with at least one chick. Most failures involved desertions before incubation had begun, which occurred at 10–28% of burrows in different years. Such desertions accounted for 8/10 failures in 1988 and 5/6 in 1989. Overall reproductive success was 1.46 and 1.60 chicks/pair (Table 7).

Within the catchment area of the chick-trapping funnels (6.15 ha) 29 census plots contained 44 burrows (137.9 ± 33.8 SE burrows/ha), yielding an estimate of 848 burrows. The mean burrow-occupancy rate for the colony in 1985 was 63% ($n = 59$). Numbers of chicks captured at the catching points operated throughout the season were as follows: 1986, 712; 1987, 955; 1988, 987; 1989, 900. If occupancy was similar in all years, 534 pairs would have bred in the catchment area, yielding estimates of 1.33, 1.81, 1.85, and 1.68 chicks departing per breeding pair. Some of the interyear variation presumably derives from changes in occupancy rates, but the fluctuations appear to be modest and suggest that productivity in excess of 1.2 chicks per pair is normal at Reef Island.

BROOD SIZE AT SEA ON THE DAY FOLLOWING DEPARTURE

Family parties leaving the colony travel rapidly out to sea, and most are more than 6 km away by dawn (Duncan and Gaston 1990). By that time they have scattered and it is very hard to find them (cf. Sealy 1976). We attempted to locate family parties at dawn in all years except 1984, finding 10 in 1985, four in 1986 and 1987, and two in 1988 and 1989. All but three of the 22 parties included two chicks, one party was of three, and the other two were of one. The group of three chicks was probably the result of at least one chick attaching itself to the wrong parents. The proportion of parties including two chicks (86%) does not differ significantly from the proportion at departure from the burrow (92%, χ^2

TABLE 7. Reproductive success of Ancient Murrelets at Reef Island.

Parameter	Year						Totals
	1984	1985	1986	1987	1988	1989	
Clutch size							
1	4	0	1	0	1	2	8
2	47	61	45	47	40	46	286
3 or 4	0	2	0	0	0	2	4
Mean clutch size	1.92	2.05	1.98	2.00	1.98	2.00	1.99
Brood size at departure							
1	0	0	2	2	2	8	14
2	9	31	22	27	29	36	154
Mean brood size	2.00	2.00	1.92	1.93	1.94	1.82	1.92
Eggs incubated 30+ days	20	62	48	58	62	86	336
No. hatched	18	62	46	56	60	80	322
% hatched	90	100	96	97	97	93	96
Nests deserted without incubation	6	6	—	13	8	5	38
% deserted	12	10	—	28	20	10	15
Chicks departing per pair	—	—	—	—	1.46	1.60	1.54

= 0.81, ns), and suggests that losses between the chicks leaving the burrow and making a rendezvous with their parents are relatively low. If the chance of a chick being lost is independent of the chance of its brood-mate being lost, then the chance of both chicks being lost from the same brood can be assumed to be very low.

PREDATION ON ADULTS

Our quadrat counts of predation remains revealed five wings, which extrapolated to 500 adult Ancient Murrelets over the entire colony area. In addition, Ancient Murrelets made up 50% ($n = 16$) of prey items collected near two Peregrine Falcon *Falco peregrinus* nests on the island over the 6 years of the study. Nelson and Myres (1976) estimated that a pair of falcons killed 1,000 murrelets a year. The Reef Island falcons may have fed partly on murrelets from other colonies nearby, so their take of Reef Island murrelets was unknown, but presumably must have amounted to several hundred birds per year.

We also found evidence of substantial predation by the two pairs of Ravens *Corvus corax* resident on Reef Island, in the form of piles of wings and pellets containing Ancient Murrelet feathers close to the nests. This amounted to a minimum of 50 adults per year, which were not included in the wing survey. Bald Eagles *Haliaeetus leucocephalus* also preyed on murrelets. One was flushed from a fresh corpse, a band from a breeding adult murrelet was recovered from an

eagle pellet, and other eagle pellets contained murrelet feathers. Eagles and ravens could have scavenged one another's kills, and Northwestern Crows *Corvus caurinus* could have scavenged from either, or taken murrelets directly.

A conservative appraisal of evidence for predation suggests that between 500–1,000 adult Ancient Murrelets were killed on, or near, the colony in 1989, amounting to 5–10% of the breeding population. Comparison with casual observations carried out in earlier years suggested that this was a typical level of predation at Reef Island. Similar systematic counts of predation remains on Limestone Island suggested a higher level of predation there (pers. observ.).

DISCUSSION

ADULT SURVIVAL

Both methods used to estimate adult survival suggest a mean annual survival rate of less than 0.8, which is very low for a pelagic seabird (Croxall and Gaston 1988). For all breeders, probably the most homogeneous sample, annual survival was 0.75 according to the regression analysis and 0.69 according to SURGE. The process of dropping the first year after capture from the analysis (estimating it separately in the case of SURGE) had the opposite effect on the two estimates, causing the SURGE estimate to rise to 0.77, and the regression estimate to fall to 0.69. The SURGE result, which makes more detailed use

of the data, should be closer to the true survival rate. Consequently, I use the SURGE estimate for the second and subsequent years after capture (0.77) in further calculations.

AGE OF NONBREEDERS

The majority of nonbreeding birds was probably 2Ys because: (1) a greater proportion of this age class was retrapped than any other, and (2) the wing lengths and weights of nonbreeders were closer to those of 2Ys than 3Ys. At least one 2Y was probably breeding, as were 2/6 3Ys. The fact that more than half the nonbreeders trapped in 1 year were classified as breeders when trapped the following year, and more than 90% 2 years later, suggests that most birds spent only 1 or 2 years as nonbreeders. A few birds visited the colony as 1Ys, but the proportion of 2Ys trapped was 16× as high as the proportion of 1Ys, so 1Ys probably make up only a small proportion of nonbreeders at the colony. Hence, most birds must begin to breed in their third or fourth year. Thereafter, it appears that the majority breed every year, as few birds caught as breeders were retrapped subsequently as nonbreeders.

Sealy (1976) also considered that most nonbreeders visiting the colony were in their second year, although he did not have any birds of known age in his study. The lack of any difference in weight between breeders and nonbreeders in Sealy's study is puzzling. However, his birds were mainly collected at sea, whereas mine were trapped on arrival at the colony. Consequently, my sample of breeders consisted mainly of birds carrying sufficient reserves to undertake several days of incubation (Gaston and Jones 1989), whereas Sealy's were presumably a random sample of off-duty breeders.

REPRODUCTIVE SUCCESS

Two other studies in the Queen Charlotte Islands, provide data on reproductive success for Ancient Murrelets under conditions of minimal disturbance by the investigators. At Frederick Island in 1980 and 1981, Vermeer and Lemon (1986) recorded breeding success on the basis of inspections made only late in the incubation period. Their study pairs reared 1.48 and 1.69 chicks/pair in the two seasons. These figures may exaggerate reproductive success slightly, because they presumably omit any burrows where eggs disappeared early in incubation (only a small number at Reef Island). In 1982, Rodway and

Lemon (Rodway et al. 1988) made a small number of visits to 25 burrows at Dodge Point, Lyell Island, and found an overall reproductive success of 1.44 chicks/pair. In both studies, as at Reef Island in 1988 and 1989, most failures occurred due to desertion, with no evidence for most clutches that incubation was ever begun. At Reef Island, where we knew from our temperature probes how many days each clutch was incubated, incubation was never initiated for most deserted clutches. The information available strongly suggests that, under undisturbed conditions, Ancient Murrelets in the Queen Charlotte Islands rear about 1.5 chicks per breeding pair per year.

Two other studies mention the size of broods of young Ancient Murrelets soon after departure from the colony, although neither attempted to count them on the first day. Guiget (1953) saw eight family groups in Queen Charlotte Sound on 13 June, all including two young. At that date the chicks could have been several weeks old. Sealy and Campbell (1979) reported 10 families, eight two-chick and two one-chick, off the Queen Charlotte Islands. Assuming that broods do not amalgamate, these observations suggest that chick survival immediately after departure from the colony is high.

POPULATION DYNAMICS

If we assume that half of the population first breeds at 3 years of age, and the rest at 4 years of age, that all continue to breed annually thereafter, and that the survival of nonbreeders from the age at which they return to the colony is similar to that of breeders, we can estimate the survival of 2-year-olds from departure to return (S_2) for a stable population. Using the estimates presented here for the annual survival of breeders (S_b , 0.77), and the annual production of young at departure from the colony (r , 0.77 females per female breeder), gives:

$$S_2 = \frac{(1 - S_b) \times 2}{r \times (S_b) \times (1 + S_b)} = 0.44.$$

The 95% confidence limits for the survival estimate of breeders (0.67–0.84) give limits of 0.27–0.77 for S_2 . The upper limit of 77% survival from colony departure to 2 years, based on the lower limit of 67% adult survival, appears unlikely, given the very young age of the chicks at departure. Because mortality of breeders at this and other colonies is high (Vermeer et al. 1984, Rod-

way et al. 1988, this study), the survival of pre-breeders up to the time they begin to visit the colony may be higher than that of breeders, in which case the lower limit of 27% survival from departure to 2 years may be nearer the truth.

To estimate the age structure of the population during the breeding season, and hence what proportion of the AHY population is actually breeding, I have assumed that half of the mortality occurring between departure and 2 years (using the value for S_2 of 0.44) happens before the first spring. In that case, at the start of breeding, there will be 0.55 1Ys, 0.34 2Ys, 0.26 3Ys, and 0.20 4Ys for every breeder of the previous year, of which 0.77 remain. New recruits to the breeding population consist of 0.13 3Ys and 0.10 4Ys. Hence 26% of the population is made up of 1Ys which do not visit the colony, 27% of nonbreeding 2Ys, 3Ys, and 4Ys and 47% of breeders 3 or more years old. If the mortality of pre-2Y birds is concentrated mainly in the period immediately after leaving the colony, which seems likely, the proportion of 1Ys may be lower, but the ratio of nonbreeders to breeders among birds visiting the colony remains unaffected.

The capture on East Limestone Island of several birds banded at Reef Island as chicks shows that some nonbreeders prospect a variety of colonies before deciding where to breed. The proportion of banded birds among nonbreeders trapped at Reef Island supports this. The census of burrows, and the number of chicks trapped, both suggested that about 534 pairs (P_b) bred within the catchment area of the chick-trapping funnels. In 1989, 12 birds banded as chicks in 1986 and 1987 were recaptured on Reef Island (C), out of 595 nonbreeders (NB), presumably mainly 2Ys and 3Ys. We can estimate the total number of pairs involved in producing the nonbreeders (N_p) from which the Reef Island sample was trapped (the source population) as follows:

$$N_p = \frac{P_b \times NB}{C} = 26,477 \text{ pairs.}$$

The nearest colonies to Reef Island are those on the Limestone Islands (ca. 1,000 pairs, 6.5 km away), and at Dodge Point, Lyell Island (ca. 11,000 pairs, Rodway et al. 1988), about 15 km away. Otherwise, the nearest colonies are more than 30 km away, at Ramsay, House, and Agglomerate islands in Juan Perez Sound. The es-

timated size of the source population supplying potential recruits to Reef Island suggests that population exchange may extend at least as far as Juan Perez Sound. This has implications for their conservation, because it may enable Ancient Murrelet populations to shift between colonies through the differential establishment of prospectors. Conversely, some colonies could persist in the face of heavy predation, and act as population sinks, something which appears to be happening at the Limestone Islands, where predation remains amounted to more than 50% of the estimated breeding population in 1989 (unpubl. data).

PREDATION OF ADULTS

The number of adult murrelets killed by predators at Reef Island could not be accurately quantified. Even the identity of the main predator(s) is unknown. Peregrine Falcons in the Queen Charlotte Islands apparently take most Ancient Murrelets at sea, while feeding or staging (Nelson 1977). Both of the falcon nests, and all their perching and plucking posts on Reef Island, were situated outside the Ancient Murrelet colony. Hence, most predation remains found within the colony were presumably left by other predators, of which ravens and Bald Eagles were the most likely.

Figures for rates of predation by natural predators are available for very few alcid populations. This is probably partly because such predation is hard to quantify, but most certainly because predation on adults is usually not conspicuous. On Dun, in the St. Kilda Islands, Harris (1980) found that gulls killed 1.5% of breeding Atlantic Puffins *Fratercula arctica* annually. However, this appears to be unusually high for a puffin colony (Harris 1984). Predation on adult Thick-billed Murres *Uria lomvia* at Digges Island, Canada amounted to less than 1% of the breeding population annually (Gaston et al. 1985). These examples suggest that predation on adult Ancient Murrelets at Reef Island is relatively high. Among seabirds breeding in the Queen Charlotte Islands, Ancient Murrelets appear to suffer the highest level of predation, judging from the frequency of predation remains on their colonies (Rodway et al. 1988). Our own estimate of adult mortality at the colony suggests that it comprises a significant proportion of total annual mortality; not less than 20%.

THE DEPARTURE STRATEGY

Lack (1968) speculated that Ancient Murrelet feeding areas were too far from the colony for provisioning chicks at the nest to be a viable strategy. Sealy (1972, 1973, 1976), who obtained evidence that some breeders fed not far from their breeding sites during the incubation period, suggested that their food was patchily dispersed and hence very unpredictable to locate. He considered that precocity had evolved to avoid the risk that the parents would be unable to find unpredictable patches on daily foraging trips. Sealy stated (1976): "The ecological advantage alone of taking the young to the food source adequately accounts for this [precocial] strategy. . . ."

It would be equally true of any offshore feeding alcid, or for that matter any seabird, that taking the chicks to the feeding area would eliminate the time and energy devoted to provisioning journeys. However, most seabirds have reduced their provisioning journeys by reducing their clutch size, a route that *Synthliboramphus* has not taken. This major difference requires explanation.

Difficulty in provisioning the chick is accepted as an explanation for the departure of *Uria* and *Alca* chicks from their breeding colonies while still less than a third of adult weight (Lack 1968, Birkhead and Harris 1985, Gaston 1985, Ydenberg 1989). However, adults of these genera, which apparently approach the upper limit of wing loading for flying birds (Greenwalt 1962), are severely constrained by a small load-carrying capacity (Birkhead and Harris 1985, Ydenberg 1989). The Ancient Murrelet has a much lower wing loading than the murrelets (1.02 g cm⁻² vs. 1.69 for *U. lomvia*, 2.06 for *U. aalge* [Livezey 1988]) and hence should be capable of carrying proportionately larger loads. It is difficult, therefore, to view the departure strategy of *Synthliboramphus* as an extreme example of adaptation to the same constraints of those under which *Uria* and *Alca* evolved. Moreover, if the food supply is patchy, taking the chicks to sea is a poor strategy, as the searching ability of the parents is then limited by the swimming speed of their chicks. In fact, it is a prerequisite of the precocial strategy that food be fairly easy to find, within a short distance of the colony, and some broods, at least, are fed not far away (Duncan and Gaston 1990).

The estimated annual survival of breeding An-

cient Murrelets, at between 0.67 and 0.84, is lower than has been observed for any other alcid (Hudson 1985, Croxall and Gaston 1988), or any other pelagic seabird (Croxall and Gaston 1988). In order to survive in the face of such high mortality, a high reproductive rate is needed, and this requires the potential to rear more than one offspring per year. The normal annual productivity, about 1.5 chicks per breeding pair, is the highest regularly recorded for any alcid, although similar productivity has been recorded for a few populations of Black Guillemots *Cepphus grylle* (Harris and Birkhead 1985). As an offshore feeder, and nocturnal colony visitor, the Ancient Murrelet presumably could not provision two semiprecocial chicks adequately.

I propose that the precocial departure of Ancient Murrelet chicks evolved in response to high adult mortality. This necessitated maintaining a clutch size greater than one. At the same time, because a significant fraction of mortality was caused by predation at the breeding colony, adaptations which reduced the number of colony visits made each year were selected for. The unique compromise of *Synthliboramphus* was to maintain the two-egg clutch typical of the Cephphini, but for the chicks to become precocial. This hypothesis envisages that the precocial murrelets derived directly from an inshore-feeding alcid with a two-egg clutch, evolving their peculiar precocial strategy as they extended their foraging range offshore, while suffering continuous heavy adult mortality. Their present combination of traits enables them to maintain large populations in areas, such as the Queen Charlotte Islands, where predators are numerous.

Several important features of Ancient Murrelet breeding behavior (nocturnal colony visits, long incubation shifts) can be interpreted as adaptations designed to minimize predation (Jones 1985, Jones et al. 1990). None of the other offshore-feeding alcids, whether fish-, or plankton-feeders, normally have such long incubation shifts. Heavy predation on adult Xantus' (*S. hypoleucos*) and Japanese (*S. wumizusume*) murrelets on their breeding grounds has also been documented (Higuchi 1979, Murray et al. 1983).

The idea that predation on the breeding grounds played a role in the evolution of precocity in murrelets was specifically rejected by Sealy (1973). Ydenberg (1989) suggested that predation on nestlings might be important, but the view that

the risk to adults might be a factor in the evolution of precocity has not been put forward hitherto.

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LITERATURE CITED

- ASBIRK, S. 1979. The adaptive significance of the reproductive pattern in the Black Guillemot, *Cephus grylle*. Vidensk. Medd. Dan. Naturhist. Foren. 141:29-80.
- ASHMOLE, N. P. 1963. The regulation of numbers of tropical oceanic birds. Ibis 103:458-473.
- BIRKHEAD, T. R., AND M. P. HARRIS. 1985. Ecological adaptations for breeding in the Atlantic Alcidae, p. 205-231. In D. N. Nettleship and T. R. Birkhead [eds.], The Atlantic Alcidae. Academic Press, Orlando, FL.
- BRIGGS, K. T., W. B. TYLER, D. B. LEWIS, AND D. R. CARLSON. 1987. Bird communities at sea off California: 1975-1983. Stud. Avian Biol. 11:1-74.
- CLOBERT, J., AND J. D. LEBRETON. 1985. Dependence de facteurs de milieu dans les estimations de taux de survie par capture-recapture. Biometrics 41: 1031-1037.
- CLOBERT, J., J. D. LEBRETON, AND D. ALLAINE. 1987. A general approach to survival rate estimation by recaptures, or resightings, of marked birds. Ardea 75:133-142.
- CORMACK, R. M. 1964. Estimates of survival from the sightings of marked animals. Biometrika 51: 429-438.
- CROXALL, J. P., AND A. J. GASTON. 1988. Patterns of reproduction in high-latitude northern- and southern-hemisphere seabirds. Proc. XIX Int. Ornithol. Congr. (1986):1176-1194.
- DUNCAN, D. C., AND A. J. GASTON. 1990. Movements of Ancient Murrelet broods away from a colony. Stud. Avian Biol. 11:1-74.
- FURNESS, R. W. 1978. Movements and mortality rates of Great Skuas ringed in Scotland. Bird Study 25: 229-238.
- GAILLARD, J. M., D. PONTIER, D. ALLAINÉ, J. D. LEBRETON, J. TROUVILLIEZ, AND J. CLOBERT. 1989. An analysis of demographic tactics in birds and mammals. Oikos 56:59-76.
- GASTON, A. J. 1985. Development of the young in the Atlantic Alcidae, p. 319-354. In D. N. Nettleship and T. R. Birkhead [eds.], The Atlantic Alcidae. Academic Press, Orlando, FL.
- GASTON, A. J., D. K. CAIRNS, R. D. ELLIOTT, AND D. G. NOBLE. 1985. A natural history of Digges Sound. Can. Wildl. Serv. Rep. Ser. 46:1-63.
- GASTON, A. J., I. L. JONES, AND D. G. NOBLE. 1988. Monitoring Ancient Murrelet breeding populations. Colonial Waterbirds 11:58-66.
- GASTON, A. J., AND I. L. JONES. 1989. The relative importance of stress and programmed anorexia in determining mass loss by incubating Ancient Murrelets. Auk 106:653-658.
- GASTON, A. J., AND D. W. POWELL. 1989. Natural incubation, egg neglect, and hatchability in the Ancient Murrelet. Auk 106:433-438.
- GOODMAN, D. 1974. Natural selection and a cost ceiling on reproductive effort. Am. Nat. 108:247-268.
- GREENWALT, C. H. 1962. Dimensional relationships for flying animals. Smithsonian Misc. Coll. 144:1-46.
- GUGET, C. J. 1953. An ecological study of Goose Island, British Columbia, with special reference to mammals and birds. Occas. Pap. B.C. Prov. Mus. 10:1-78.
- HARRIS, M. P. 1980. Breeding performance of puffins *Fratricula arctica* in relation to nest density, laying date and year. Ibis 122:193-209.
- HARRIS, M. P. 1984. The Puffin. T. and A. D. Poyser, Calton, United Kingdom.
- HARRIS, M. P., AND T. R. BIRKHEAD. 1985. Breeding ecology of the Atlantic Alcidae, p. 155-204. In D. N. Nettleship and T. R. Birkhead [eds.], The Atlantic Alcidae. Academic Press, Orlando, FL.
- HIGUCHI, Y. 1979. Breeding ecology and distribution of the Japanese Crested Murrelet. Aquatic Biol. 1: 20-24.
- HUDSON, P. J. 1985. Population parameters for the Atlantic Alcidae, p. 233-261. In D. N. Nettleship and T. R. Birkhead [eds.], The Atlantic Alcidae. Academic Press, Orlando, FL.
- JONES, I. L. 1985. Structure and function of vocalizations and related behaviour of the Ancient Murrelet (*Synthliboramphus antiquus*). M.Sc. thesis, Univ. of Toronto, Toronto, Canada.
- JONES, I. L., J. B. FALLS, AND A. J. GASTON. 1987. Colony departure of family groups of Ancient Murrelets. Condor 89:940-943.
- JONES, I. L., A. J. GASTON, AND J. B. FALLS. 1990. Factors affecting colony attendance by Ancient Murrelets. Can. J. Zool. 68:433-441.
- KAMPP, K. 1982. Den Kortnaebbede lomvie *Uria lomvia* i Gronland—vandringer, mortalitet og beskydning: en analyse af 35 ars ringmaerkninger. Specialerapport til Naturvidenskabelig Kandidatexamen ved Kobenhavns Universitet, Kobenhavns.
- LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.
- LEBRETON, J. D., AND J. CLOBERT. 1986. User's manual for program SURGE. C.E.P.E./C.N.R.S., Montpellier.

- LITVINENKO, N. M., AND YU. V. SHIBAEV. 1987. The Ancient Murrelet—*Synthliboramphus antiquus* (Gm.): reproductive biology and raising of young, p. 72–84. *In* N. M. Litvinenko [ed.], *Rasprostraneniye i biologiya morskikh ptits Dal'nego Vostoka* (Distribution and biology of seabirds of the Far East). Far Eastern Science Centre of the USSR Academy of Sciences, Vladivostok, USSR.
- LIVEZEY, B. C. 1988. Morphometrics of flightlessness in the Alcidae. *Auk* 105:681–698.
- MURRAY, K. G., K. WINNETT-MURRAY, Z. A. EPPLEY, G. L. HUNT, JR., AND D. B. SCHWARTZ. 1983. Breeding biology of the Xantus' Murrelet. *Condor* 85:12–21.
- NELSON, R. W. 1977. Behavioural ecology of coastal peregrines (*Falco peregrinus pealei*). Ph.D.diss., Univ. of Calgary, Calgary, Canada.
- NELSON, R. W., AND M. T. MYRES. 1976. Declines in populations of Peregrine Falcons and their seabird prey at Langara Island, British Columbia. *Condor* 78:281–293.
- PENNYCUICK, C. J., J. P. CROXALL, AND P. A. PRINCE. 1984. Scaling of foraging radius and growth rate in petrels and albatrosses (Procellariiformes). *Ornis Scand.* 15:145–154.
- RICKLEFS, R. E. 1983. Some considerations of the foraging energetics of pelagic seabirds. *Stud. Avian Biol.* 8:84–94.
- RODWAY, M. S., M.J.F. LEMON, AND G. W. KAISER. 1988. British Columbia seabird colony inventory: report #1—east coast Moresby Island. Tech. Rep. Ser. No. 50. Can. Wildl. Serv., Pacific and Yukon Region, British Columbia.
- RYDER, J. P. 1980. The influence of age on the breeding biology of colonial nesting seabirds, p. 153–168. *In* J. Burger, B. L. Olla, and H. E. Winn [eds.], *Behaviour in marine animals*. Vol. 4: Marine birds. Plenum Press, New York.
- SEALY, S. G. 1972. Adaptive differences in breeding biology in the marine bird family Alcidae. Ph.D.diss., Univ. of Michigan, Ann Arbor.
- SEALY, S. G. 1973. Adaptive significance of post-hatching developmental patterns and growth rates in the Alcidae. *Ornis Scand.* 4:113–121.
- SEALY, S. G. 1976. Biology of nesting Ancient Murrelets. *Condor* 78:294–306.
- SEALY, S. G., AND R. W. CAMPBELL. 1979. Post-hatching movements of young Ancient Murrelets. *Western Birds* 10:25–30.
- STEARNS, S. 1976. Life-history tactics: a review of the ideas. *Q. Rev. Biol.* 51:3–47.
- VERMEER, K., AND LEMON, M. 1986. Nesting habits and habitats of Ancient Murrelets and Cassin's Auklets in the Queen Charlotte Islands, British Columbia. *Murrelet* 67:33–44.
- VERMEER, K., S. G. SEALY, M. LEMON, AND M. RODWAY. 1984. Predation and potential environmental perturbances on Ancient Murrelets nesting in British Columbia, p. 757–770. *In* J. P. Croxall, P.G.H. Evans, and R. W. Schreiber [eds.], *Status and conservation of the world's seabirds*. International Council for Bird Preservation Technical Publication No. 2.
- VERMEER, K., AND RANKIN, L. 1984. Pelagic seabird populations in Hecate Strait and Queen Charlotte Sound: comparison with the west coast of the Queen Charlotte Islands. *Can. Tech. Rep. Hydrography and Ocean Sciences* No. 52.
- WAHL, T. R. 1975. Seabirds in Washington's offshore zone. *Western Birds* 6:117–134.
- WILLIAMS, G. C. 1966. Natural selection, the cost of reproduction, and a refinement of Lack's principle. *Am. Nat.* 100:687–690.
- YDENBERG, R. C. 1989. Growth-mortality trade-offs and the evolution of juvenile life-histories in the Alcidae. *Ecology* 70:1494–1506.
- ZAMMUTO, R. M. 1986. Life histories of birds: clutch size, longevity and body mass among North American game birds. *Can. J. Zool.* 64:2739–2749.