

## Mass and date at departure affect the survival of Ancient Murrelet *Synthliboramphus antiquus* chicks after leaving the colony

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I compared the timing of colony departure and body mass of 53 Ancient Murrelet *Synthliboramphus antiquus* chicks that were retrapped as adults in Haida Gwaii, British Columbia, with those of 3992 chicks not retrapped. If the probability of recapture is a measure of survival, survival was related to both mass and date. Chicks that left the colony at 26 g or less had a lower chance of survival than heavier chicks, and those that left after the median date of departure survived better in some years than those that left earlier. The effect of date was not related to a seasonal change in departure mass because chick mass declined with departure date. I suggest that, because of heavy adult mortality during breeding, the timing of breeding in the Ancient Murrelet is based on a compromise between the optimum dates for chick and adult survival. This is in contrast to evidence from other, nonprecocial, seabirds.

Variation in the survival of young birds after leaving the nest may affect parental fitness and hence alter assumptions based on measures of reproductive success that terminate at the end of the nest phase (Spear & Nur 1994). Because post-fledging survival is difficult to measure, especially in marine birds, the mass of chicks at departure from the nest has been used as an index of their condition. Mass at departure has been implicitly assumed to be related to subsequent survival (Gaston 1985, Cairns 1987). Moreover, mass at departure, or some related measure of condition (e.g. growth rate, weight at a given age), frequently shows a negative correlation with timing of breeding (i.e. date of laying, hatching). These observations lead to the general conclusion that, among most single-brooded species, good-quality breeders lay early and produce heavier chicks and hence are more likely to contribute to the next generation than breeders that lay later (Ryder 1980, Reid 1988).

Among seabirds, a correlation between the mass or growth rate of chicks and their subsequent survival has been demonstrated for the Manx Shearwater *Puffinus puffinus* (Perrins *et al.* 1973), Herring Gull *Larus argentatus* (Nisbet & Drury 1972), Western Gull *Larus occidentalis* (Spear & Nur 1994) and Cape Gannet *Morus capensis* (Jarvis 1974). However, no such correlation has been found in auks (Harris *et al.* 1992) despite the fact that mass at departure frequently declines with date of hatching (Razorbill *Alca torda*, Lloyd 1979; Guillemot *Uria aalge*, Hedgren 1979; Brunnich's Guillemot *Uria lomvia*, Gaston & Nettleship 1981; Cassin's Auklet *Ptychoramphus aleuticus*, Ainley *et al.* 1990; Puffin *Fratercula arctica*, Harris & Rothery 1985). Post-fledging survival was found to be negatively correlated with date

of hatching in some years for Guillemots at the Isle of May, Scotland. However, survival of young was not affected by chick growth rate at the colony (Harris *et al.* 1992).

I report here on the effects of departure date and mass on the probability that Ancient Murrelet *Synthliboramphus antiquus* chicks will be retrapped as adults at their natal colony. Ancient Murrelets breed in burrows up to 400 m from the sea. After hatching, the young leave the burrow at 1–4 days old, without having been fed, and walk to the shore at night (Sealy 1976, Shibaev 1978, Jones *et al.* 1987a). On reaching the sea, they rendezvous with their parents by mutual recognition of calls (Jones *et al.* 1987b). During the first 18 h after leaving the colony, they travel nonstop to reach offshore feeding areas (Duncan & Gaston 1990), and they are then reared at sea by their parents for about 6 weeks before fledging. The apparent necessity for a lengthy period of travel on leaving the colony may make the size of energy reserves at departure critical to subsequent survival (Duncan & Gaston 1990).

### METHODS

Chicks were trapped nightly throughout the breeding season in 1985–1987 at Reef Island and in 1990–1992 at East Limestone Island, both in Haida Gwaii (Queen Charlotte Islands), British Columbia (for details of these colonies, see Gaston 1992). Trapping was conducted by means of plastic fences that guided chicks to ringing stations situated close to the shore (Gaston *et al.* 1988). Ringing stations were operated nightly from before chicks started to leave the col-

**Table 1.** Mass (g) of Ancient Murrelet chicks at departure from the colony in relation to date of departure

Colony and year	Regression formula			P	n	Mean (g)	s.d.
	Slope $\pm$ s.e.	Intercept $\pm$ s.e.	$r^2$				
Reef Island							
1985	-0.112 $\pm$ 0.032	30.63 $\pm$ 1.91	0.052	<0.01	235	27.7	1.7
1986	-0.087 $\pm$ 0.011	29.86 $\pm$ 0.30	0.081	<0.01	734	27.5	2.1
1987	-0.102 $\pm$ 0.012	30.12 $\pm$ 0.29	0.053	<0.01	775	27.5	1.6
All chicks retrapped	-0.166 $\pm$ 0.044	32.08 $\pm$ 1.36	0.382	<0.01	25	27.9	1.7
East Limestone Island							
1990	-0.100 $\pm$ 0.012	30.31 $\pm$ 2.44	0.069	<0.01	867	27.8	2.5
1991	-0.018 $\pm$ 0.007	27.56 $\pm$ 1.93	0.013	<0.05	589	27.3	2.2
1992	-0.018 $\pm$ 0.021	27.11 $\pm$ 2.14	0.001	n.s.	643	26.9	2.4
All chicks retrapped	-0.139 $\pm$ 0.179	31.38 $\pm$ 2.28	0.029	n.s.	22	27.8	2.2

ony (about 3 h after sunset) to 2 h after the last chick had been captured or to 02.00 h, whichever came first. Ringing operations began before the first chicks were expected to leave the colony in all years except 1985, when they began on 15 May, about 5 days after the earliest chicks departed. Operations ceased after the first night each season on which no chicks were captured.

Chicks were ringed on capture and weighed to the nearest 0.5 g on a Pesola spring balance. They were released at the water's edge within 5 min of capture. Observations through an image-intensifying nightoscope suggested that their subsequent behaviour was normal; they reunited successfully with their parents (Gaston *et al.* 1988).

In 1986–1989 at Reef Island and in 1989–1994 at East Limestone Island, adult Ancient Murrelets were trapped on the forest floor at night by means of dip nets. All captures were examined for rings and the ring numbers of retraps were recorded.

The effect of chick mass on recapture probability was modelled with the use of the logistic regression procedure of Statistix 4.0 (Analytical Software). All  $\chi^2$  comparisons with 1 d.f. include Yates' correction. Probabilities involving multiple comparisons were calculated as  $P/n$ , where  $n$  is the number of pairwise comparisons.

## RESULTS

At Reef Island 286–937 chicks and at East Limestone Island 562–873 chicks were ringed annually, of which more than 90% were weighed. Median dates of departure varied from 23 to 28 May. Annual mean mass at departure ranged from 26.9 g (1992) to 27.8 g (1990). At both islands in all years, the mass of chicks at ringing was negatively correlated with their date of departure, although the effect was not significant at East Limestone Island in 1992 (Table 1).

During the 2–4 years subsequent to ringing (1986–1989, 1991–1994), 1.55% ( $n = 1935$ ) of chicks ringed at Reef Island and 1.04% ( $n = 2110$ ) of chicks ringed at East Lime-

stone Island were retrapped as adults, either at their colony of origin or at the other colony (three Reef Island chicks were retrapped as nonbreeders at East Limestone Island in 1989). Most birds were retrapped as 2-year-olds (73% of those ringed at Reef Island, 64% at East Limestone Island).

### The effect of departure date

For chicks ringed at Reef Island, there was no evidence that departure date had any effect on the probability of recapture as an adult; we recaptured 15 of those that departed before and 14 of those that departed after the median date of departure (chicks departing at the median date were excluded). At East Limestone Island, only five chicks recaptured as adults had originally departed before the median date, compared with 17 that departed later (binomial  $P < 0.01$ ; difference between colonies  $\chi^2_1 = 8.71$ ,  $P < 0.01$ ; Table 2). No interyear variation was detectable. The number of retrapped chicks that departed before the median date of departure was greater than the number that departed later only in 1985. The combined distribution of recapture probability in relation to timing of departure suggests that there may be some advantage in leaving during the peak of departures (Fig. 1).

### The effect of mass at departure

At Reef Island, the proportion of chicks that were retrapped as adults increased significantly with departure mass (unweighted logistic regression coefficient =  $0.239 \pm 0.103$ , d.f. = 1691,  $P < 0.03$ , probability of model fit = 1.0; Fig. 2). Only 0.2% ( $n = 517$ ) of those weighing less than 26 g at departure were recaptured, compared with 2.1% ( $n = 1178$ ) for those weighing 26 g or more ( $\chi^2_1 = 7.19$ ,  $P < 0.01$ ). Corresponding percentages at East Limestone Island were 0.7% ( $n = 578$ ) and 1.7% ( $n = 1198$ ;  $\chi^2_1 = 1.79$ , n.s.; Fig. 2); the relationship of mass to recapture probability using logistic regression was not significant for the East Limestone Island sample.

**Table 2.** Numbers of Ancient Murrelet chicks recaptured in relation to their date of departure from the colony

Colony and year	Median departure date <sup>a</sup>	3-day periods from median departure								
		-4	-3	-2	-1	0	+1	+2	+3	+4
Reef Island										
1985	25 <sup>b</sup>			2	3	3		1		
1986	27	1			1	1		4		1
1987	23			2	4	2	3	1	1	
Totals		1		4	8	6	3	6	1	1
East Limestone Island										
1990	23					4	4			1
1991	23					4	6			
1992	22				1		1	1		
Totals					1	8	11	1		1
Grand totals		1		4	9	14	14	7	1	2

<sup>a</sup> All median dates refer to the day preceding the night of departure (e.g. 23 = night of 23/24 May).

<sup>b</sup> Based on chicks trapped; because of late start to trapping, true median = 24.

When only the chicks retrapped as adults were considered, the departure mass of those ringed at Reef Island showed a significant negative correlation with date of departure ( $r_{23} = -0.62$ ,  $P < 0.01$ ; Fig. 3a). The slope of the regression was significantly steeper than that for chicks weighed at departure at Reef Island ( $t_{1693} = 2.91$ ,  $P < 0.01$ ). No significant correlation between mass and date at departure was found for chicks ringed at East Limestone Island ( $r_{20} = 0.17$ , n.s.; Fig. 3b).

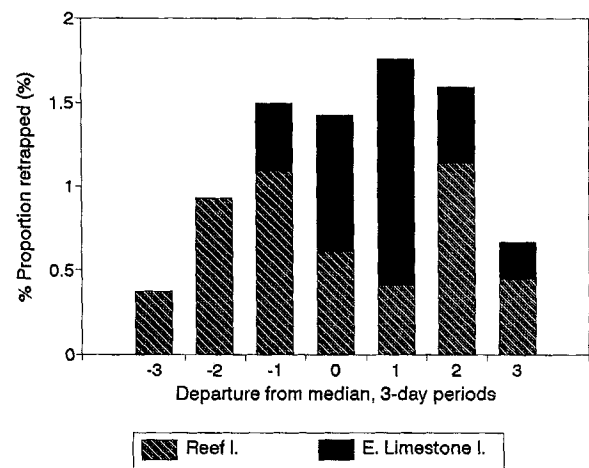
## DISCUSSION

Because of the very low overall retrap rate (<2%), the present results need to be interpreted cautiously. I have argued elsewhere (Gaston 1990) that a large proportion of Ancient Murrelets prospect colonies other than the one where they were reared. Because the majority of birds were retrapped at 2 years old, few were likely to have been breeding when retrapped (only two 2-year-old retraps had complete brood patches). If the date or mass at colony departure affects the dispersal behaviour of the birds, and hence the probability that they will prospect at other colonies, the proportion of retraps may not correspond to relative survival rates. However, the subsequent discussion assumes that the probability of retrapping birds is a measure of the proportion surviving, the most parsimonious explanation with present information and one that has been made by other investigators dealing with similar data (Perrins *et al.* 1973, Harris & Rothery 1985, Harris *et al.* 1992).

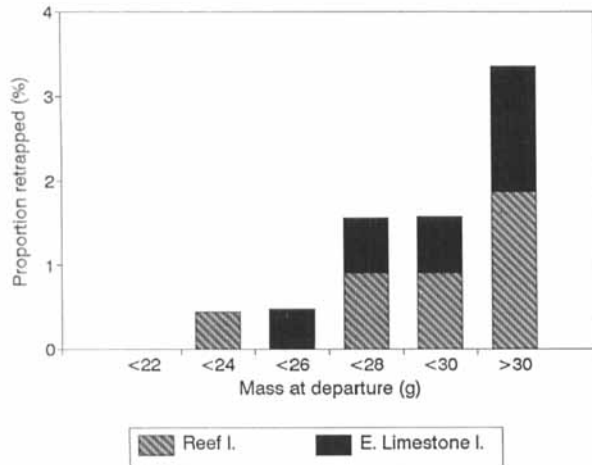
The observation that the probability of survival increased with increased departure mass for Reef Island chicks is not surprising because of the demands of travel immediately after leaving the colony. At departure, chicks averaging 27

g in mass have a lipid index (lipid mass/lean dry mass) of 0.41 (lipid 32% of dry mass), giving them sufficient energy reserves for a maximum of 48 h of activity before they need to be fed (Duncan & Gaston 1988, 1990). Gaston (1992) showed that chicks lose more than 3 g daily where they remain in the burrow and suggested that the length of time elapsing between hatching and departure may be an important determinant of departure mass. The results presented here suggest that the lightest chicks probably leave the colony with insufficient energy reserves to survive.

The relationship between date of departure and subsequent recapture probability did not support the idea that early chicks survive better than those reared later. At Reef



**Figure 1.** Proportion of Ancient Murrelet chicks retrapped as adults in relation to date of departure from the colony. Shaded = Reef Island, solid = East Limestone Island.



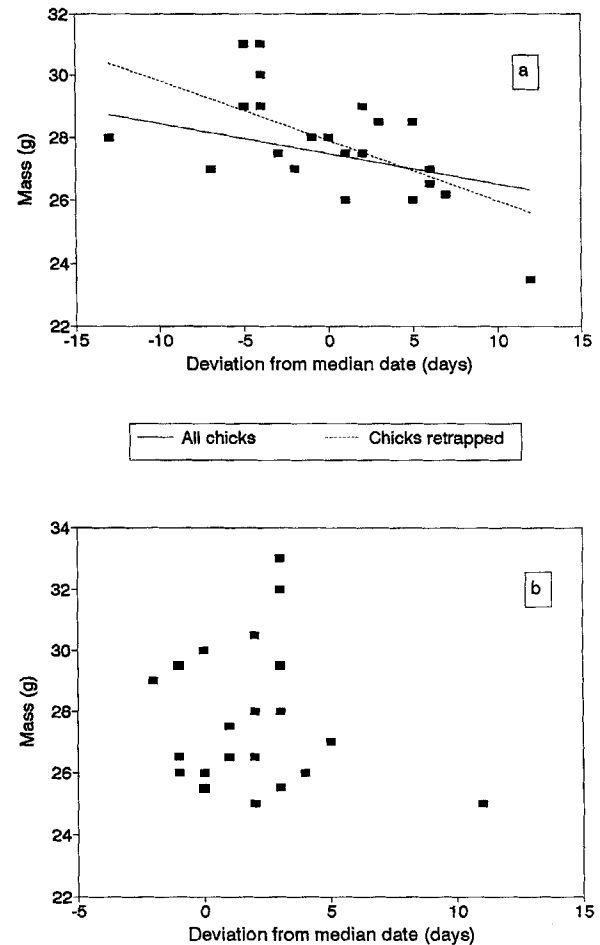
**Figure 2.** Proportion of Ancient Murrelet chicks retrapped as adults in relation to mass at departure from the colony. Shaded = Reef Island, solid = East Limestone Island.

Island, no effect was detectable, while at East Limestone Island, the reverse occurred. In most years, conditions for chick survival apparently improved as the season progressed.

Without simultaneous trapping on both islands, and with only a small sample of years for each, I cannot estimate the degree to which the intercolony difference was caused by interyear variation. Because the two islands are only 6.5 km apart and chicks from both colonies almost certainly disperse into the same waters for the rearing period, it is difficult to understand how colony-specific variation in survival after colony departure could arise. However, for the present, distinction between intercolony and interyear effects is not possible.

Late-departing chicks were retrapped more often than those departing early, despite the fact that earlier chicks tended to be heavier at departure than those hatched later. Consequently, the effects of mass and date appear to have operated independently, at least at East Limestone Island. The observation that, at Reef Island, the regression of departure mass on date for retrapped chicks had a steeper negative slope than the corresponding regression for all chicks weighed at departure suggested that mass may have affected the survival rate more for early than for late chicks (by increasing the proportion of heavy chicks among survivors departing from the colony in the early part of the season).

In 1985, the only year for which early chicks were recaptured more often than late chicks, the negative slope of the regression of chick mass on date of departure was the highest recorded. Chicks that departed more than 3 days after the median date were lighter than in any other year, including 1988, 1989 and 1993 (Gaston 1992:fig. 13.4 and unpubl.), so that later chicks were, compared with other years, exceptionally light. It is possible that, in 1985, the



**Figure 3.** Ancient Murrelet chick mass in relation to date of colony departure for Ancient Murrelet chicks retrapped as adults. (a) Chicks from Reef Island; (b) Chicks from East Limestone Island. Solid line = regression for all chicks at Reef Island, dashed line = regression for Reef Island chicks retrapped as adults.

disadvantage of a low departure mass overrode whatever advantage is normally gained by late departure.

If the survival of chicks after colony departure improves as the breeding season progresses, we need to explain why Ancient Murrelets breed so early (along with Cassin's Auklet, they are the earliest laying auks in British Columbia; Campbell *et al.* 1990).

Lack (1954) proposed that birds time their breeding to coincide with the optimum period for chick rearing. This theory, modified to take account of the fact that laying at the optimal time is sometimes constrained by food availability, holds for a wide variety of bird species (Perrins 1970, 1996). However, the theory depends on there being no variation in the cost of reproduction in relation to the time of year (Williams 1966). In the case of the Ancient Murrelet, breeders suffer heavy mortality at the colony from avian and mammalian predators, sufficient to give them an unusually low adult survival rate for a seabird (Gaston 1990). Colony

visits by Ancient Murrelets are strictly nocturnal. Because many of their predators are diurnal (Peregrine Falcon *Falco peregrinus*, Raven *Corvus corax*, Bald Eagle *Haliaeetus leucocephalus*; Vermeer & Lemon 1986, Rodway *et al.* 1988), nocturnality probably is mainly a predator-avoidance strategy (Jones *et al.* 1990, Gaston 1992).

At the latitude of Reef Island (53°N), Ancient Murrelets come to land for only about 3 h in midsummer (mainly non-breeders at that date; Jones *et al.* 1990). The behaviour of family parties at departure from the colony requires that breeders call loudly and persistently on the ground for up to 20 min, following which the parents await the chicks on the sea, close inshore (Jones *et al.* 1987a). I suggest that the timing of breeding of Ancient Murrelets at the latitude of Haida Gwaii is adjusted to avoid taking the chicks to sea in late June because of the attendant risk of predation inherent in the departure process. Pairs leaving in mid-May have a 2–3-h longer period of darkness in which to complete the departure and put some distance between themselves and land.

Among 32 records of timing of breeding for Ancient Murrelets listed by Gaston (1992), with peaks of chick departure ranging from late April (Yellow Sea) to early August (Sea of Okhotsk), none gave a peak of chick departures between 10 June and 5 July, which suggests that Ancient Murrelets adjust their timing of breeding to avoid taking their young to sea in midsummer. Hence, the timing of breeding in the Ancient Murrelet may represent a compromise between selection for predator avoidance by adults on the one hand and the availability of adequate feeding conditions for rearing chicks on the other. An interesting test of this hypothesis would be to examine the survival of chicks from colonies where departure occurs post-solstice. At these colonies, chicks might show a more typical pattern of survival in relation to departure date, with early chicks surviving better than later ones.

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