The Auk 120(3):1–XXX, 2003

INFLUENCE OF CHICK MASS AND DATE AT DEPARTURE FROM THE COLONY ON ADULT CHARACTERISTICS IN A PRECOCIAL SEABIRD: THE ANCIENT MURRELET (*SYNTHLIBORAMPHUS ANTIQUUS*)

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ABSTRACT.—I investigated the effect of mass and date of departure of Ancient Murrelet (*Synthliboramphus antiquus*) chicks reared at two colonies in Haida Gwaii, British Columbia, on aspects of their adult biology. Chicks were captured, banded, and weighed while departing from their natal colony at two to three days old, during 1984–1998. Adults were recaptured at the same colonies during the breeding seasons of 1986–2000. Just under 1% of 13,055 chicks were recaptured as adults. Chicks that were heavier than average at colony departure were recaptured as adults at a younger age and were heavier as breeders than lighter chicks. However, chick departure mass did not affect adult mass of birds recaptured as nonbreeders. The date at which chicks left the colony had no effect on either adult mass or age at recapture. Correlation between chick mass at colony departure and adult mass as a breeder is rarely reported and is difficult to explain. However, if chick mass is determined by reproductive investment on the part of the parents and adult mass is a measure of reproductive investment by the individual, the correlation suggests that degree of parental investment could be a heritable trait. *Received 10 May 2002, accepted 14 April 2003.*

RÉSUMÉ.—J'ai étudié l'effet du poids et de la date au moment de quitter le nid chez des oisillons de Guillemot à cou blanc (*Synthliboramphus antiquus*) élevés dans deux colonies de Haida Gwaii, Colombie-Britannique, sur différents aspects de leur biologie adulte. Les oisillons ont été capturés, marqués et pesés au moment de quitter leur colonie de naissance à l'âge de 2-3 j, au cours de la période 1984-1998. Les adultes étaient recapturés dans les mêmes colonies au cours des saisons de reproduction de 1986-2000. Un peu moins de 1% des 13 055 oisillons ont été recapturés une fois adulte. Les oisillons qui étaient plus lourds que la moyenne au moment de quitter la colonie étaient recapturés à en tant qu'adulte reproducteur plus précocement et avec un poids plus lourd que les oisillons plus légers. Néanmoins, le poids des oisillons à leur départ n'affectait pas le poids adulte des oiseaux recapturés en tant que non reproducteur. La date à laquelle les oisillons quittaient la colonie n'avait pas d'effet ni sur le poids adulte, ni sur l'âge au moment de la recapture. La corrélation entre le poids des oisillons à leur départ de la colonie et le poids à l'âge adulte et en tant que reproducteur est rarement mentionnée et elle est difficile à expliquer. Néanmoins, si le poids est déterminé par l'investissement dans la reproduction pour les parents et la poids adulte est une mesure de cette investissement par l'individu, la corrélation suggère que le degré de l'investissement parental pourrait être un trait d'héritabilité.

UNDERSTANDING THE ROLE of egg size and consequent nestling mass in determining fitness is a key to understanding the evolution of egg size in birds. The role of egg size and laying date in determining subsequent survival and fitness of offspring has been investigated for a number of bird species (Ricklefs 1984, Williams 1994). Date of hatch often has a significant effect on subsequent survival (Martin 1987, Price et al. 1988, Brown and Brown 1999). However, reported effects of egg size and hatchling mass have been variable, sometimes correlating with offspring growth and survival to fledging (Birkhead and Nettleship 1982, Galbraith 1988, Bolton 1991, Hipfner and Gaston 1999), but sometimes becoming insignificant within a few days of hatching (e.g. Brook 1986, Ollason and Dunnet 1986, Amundsen and Stockland 1990, Reid and Boersma 1990, Meathrel et al. 1993). The extent to which condition at different stages of nestling growth affects adult condition in birds has been

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studied for only a few species (Cooke et al. 1995, Spear and Nur 1994, Christensen 1999). So far, hatchling mass has been found to have little effect on adult mass.

The Ancient Murrelet (*Synthliboramphus antiquus*) is a small member of the family Alcidae in which nestlings are not fed on land but leave their nest site at two to three days old and accompany their parents at sea during the growth period (Sealy 1976, Jones et al. 1987). As part of that unusual development strategy, Ancient Murrelets lay the largest egg, relative to their body size, of any flying bird (Sealy 1975, Gaston 1992). The egg has an exceptionally large component of yolk (Birkhead and Gaston 1988). The very large size of the egg and yolk provide the chick with substantial lipid reserves at colony departure. Those probably are essential to early survival (Duncan and Gaston 1988, 1990). Because each egg constitutes a larger reproductive investment for Ancient Murrelets than for most birds, we might expect hatchling size to be more influential on subsequent growth and survival than is the case for other birds.

Gaston (1997) showed that, unlike most seabirds (Brook 1991, Harris et al. 1992, Spear and Nur 1994), Ancient Murrelet chicks leaving the colony later in the season do not suffer a lower survival than those leaving early: in some years late chicks survive better. In addition, mass of chicks at colony departure has a significant effect on their subsequent survival, a finding not observed so far for other auks (Hedgren 1981, Harris et al. 1992). Here, I investigate effects of chick departure date and mass at departure from the natal colony on features of adult biology: age at first recapture (assumed to be linked to age at first breeding), and adult body mass. Effects of nestling characteristics on features of adult biology can only be studied when many banded nestlings of known mass are recaptured as adults. Data of that sort are available for few species, and a link between hatchling characteristics and adult mass or age at recruitment has not been previously demonstrated for seabirds.

Age at first recapture is likely to be negatively correlated with fitness, if earlier colony return is linked to earlier recruitment into the breeding population (Newton 1989a, Partridge 1989). If adult mass is an index of body condition, then it may be positively correlated with fitness: there is some evidence that adult body mass may be critical to reproduction in the Ancient Murrelet (Gaston and Jones 1989). Hence, influences of chick departure mass on adult capture dates and body mass may illustrate links between parental investment (timing of breeding, egg size, and nest attendance) and subsequent offspring fitness.

METHODS

Ancient Murrelet chicks were captured while departing from two breeding colonies in Laskeek Bay, Queen Charlotte Islands, British Columbia (for details of location, see Gaston 1992), by means of plastic fences that guided them to trapping stations near the shore. Stations were operated nightly throughout the departure period of the chicks at Reef Island ("RI", 1985–1989, 1995, 1997, ~5,000 breeding pairs; Gaston 1994a) and East Limestone Island ("ELI", 1990–1997, ~1,200 breeding pairs), so that most chicks departing from certain areas of each colony were captured (Gaston et al. 1988). Departure periods varied from 30 to 33 days at Reef Island and from 23 to 38 days at East Limestone Island (Gray 2001), except in the "El Niño year" of 1998, when the spread of departure dates was 48 days (Gaston and Smith 2001). The period over which 90% of chicks were captured varied from 15 to 25 days.

Chicks captured were banded, weighed on a 50 g spring balance (±0.5 g), and released to the sea, usually within 10 min of capture. Chicks left the colony between 2230 and 0400 hours. All chicks departing on a given night were assigned the same departure date: that of the preceding day (hence, night of 19 or 20 May = 19, etc.). In most years, some chicks were also banded in burrows before departure. Because mass changes rapidly in the one to three days before departure (Gaston 1992), those chicks (two of those recaptured as adults) were not included in analyses of departure mass, but their departure date was assumed to have been the day after banding and was included in other analyses. As a trend towards earlier departures has been detected over the course of the study (A. J. Gaston pers. obs.), date at colony departure was also analyzed as deviations from the colony median for that year (termed "relative departure date").

Adult Ancient Murrelets were trapped at RI during the breeding seasons of 1985–1989, 1995, 1997, and 1999 and at ELI in 1989–2000. Several methods were used: birds were removed from burrows during daytime at about the time of hatching; some were trapped on the surface by spotlighting them and catching them by hand or with a dip-net; some were trapped by means of large plastic "knock-down" nets which intercepted the birds as they departed the colony in flight, not tangling them, but causing them to fall to the ground, where they were picked up by a waiting field crew. Most adult birds captured were weighed on a 300 g spring balance (±1 g) and their bill depth was measured immediately posterior to the gonys, using vernier calipers (±0.1 mm, that measurement is the best discriminator of sex in the species; Gaston 1994b). The abdomen was examined for the presence of a brood patch. When fully developed, that measures 20–25 mm maximum diameter (Gaston 1990). Masses of three adults that were >3 SD above the mean for breeders were omitted because of the likelihood that they were carrying oviduct eggs when weighed (Gaston 1992).

Breeding status was assessed in two ways: all birds trapped prior to 15 April were considered to have bred in that year (>80% of all adults trapped <15 April and subsequently recaptured later in the season possessed fully developed brood patches at the second capture; Gaston 1992). In addition, birds caught after 15 May (date by which >90% of clutches were complete) with a brood patch >19 mm maximum diameter were considered to be breeding, whereas those with a brood patch <10 mm were considered to be nonbreeders in that year. Birds with brood patches of intermediate size, and those trapped between 16 April and 15 May with brood patches <19 mm across, were unclassified. All birds captured while incubating had brood patches >19 mm; hence, those without brood patches in mid-May and later were certainly nonbreeders (see Gaston 1990 for details and justification). Two birds were recovered as predation remains: measurements and breeding status could not be obtained from those. For birds trapped more than once as adults, only information from the first capture was included in analyses.

Age was assessed solely on the basis of the year of banding as nestlings. Ancient Murrelets begin to breed at two to four years old—mostly at three or four (Gaston 1990). I used age at first capture as an index of age at first return. Clearly, not all birds were trapped in the first year that they visited the colony. However, I have assumed that if a bird visited the colony in a given year, the likelihood of its recapture was independent of its characteristics as a chick (mass, date of departure). Because the two- and three-year-old age classes include both breeders and nonbreeders, recaptures at those two ages were combined to compare measurements and mass of what would likely be first-time breeders with nonbreeders of similar age.

Bivariate analyses were conducted using the regression procedure of STATISTICA 5.0. Analyses involving more than one independent variable were performed using the GLM Type III procedure of SAS. Unless otherwise stated, all analyses apply to the sample of birds banded as chicks and recaptured as adults (first recapture only). No significant differences in means of variables analyzed were found between colonies, except for chick mass (see below). Probability tests that proved significant for the combined data for both colonies were re-run separately for each colony: in all cases, differences (sign) and trends (sign, slope) were similar, although probabilities were not always significant at $\alpha < 0.05$. Consequently, data from both colonies were combined in all analyses other than those involving chick mass, for which results are reported separately by colony.

RESULTS

Intercolony effects.—One hundred and thirty-one Ancient Murrelet chicks banded at departure during 1984–1998 were recaptured as adults up to the summer of 2000 (1.0% of the total: RI 6,274, ELI 6,781). Ages at first recapture ranged from 1 to 12 years, with 49% being caught first at 2 years, 21% at 3 years, and only three (2%) at >8 years. Eighty-five of those recaptured were reared at ELI and 46 at RI. Thirteen ELI chicks were recaptured at RI, and six RI chicks at ELI. Chick date of departure, and adult mass and bill depth, did not differ between the two colonies, but there was a small difference in chick mass at departure (Table 1). There were no differences between chicks recaptured at their natal colony and those recaptured at the other colony (all $P > 0.1$). Consequently, data for philopatric and nonphilopatric chicks were combined in subsequent analyses.

Chick mass and date of departure.—As found in an earlier analysis (Gaston 1997), there was a negative relationship between mass at colony departure of those chicks recaptured as adults

TABLE 1. Chick mass and date of colony departure and adult mass at recapture of Ancient Murrelets banded as chicks at two breeding colonies in Haida Gwaii.

		Reef Island			East Limestone Island				
Variable	Breeding status	Mean	SD	*n*	Mean	SD	*n*	*t*	*P*
Chick mass (g)		27.1	2.1	42	27.9	2.2	80	2.08	0.04
Departure date (days from 1 May)		25.3	6.4	46	24.1	5.6	74	1.34	0.18
Adult mass (g)	Breeder	191.5	10.3	10	197.7	9.2	23	0.51	0.61
	Nonbreeder	181.0	12.7	33	182.2	10.2	46	0.38	0.71

and their actual and relative dates of departure (both actual and relative dates, $R^2 = 0.105$, $n = 121$, $P < 0.001$). That is similar to findings for all departing chicks (Gaston 1992). However, the slope of the regression of mass on relative departure date for those chicks recaptured as adults (–0.153 ± 0.035 g per day; Fig. 1) was significantly greater than that for all chicks (–0.065 ± 0.005, $P < 0.001$) and also greater than the slope in any individual year (maximum slope in 16 colony years, –0.112 g per day, mean –0.070 ± 0.025 g per day), which suggests that date of departure had an effect on selection in relation to mass. All colony year slopes intersected that for chicks recaptured as adults. Hence, among chicks recaptured as adults, those that departed early tended to be heavier than average, whereas those that departed late tended to be lighter. However, because both slopes and intercepts varied among years and individual year samples for chicks recaptured as adults were small, it was not possible to separate year and date effects.

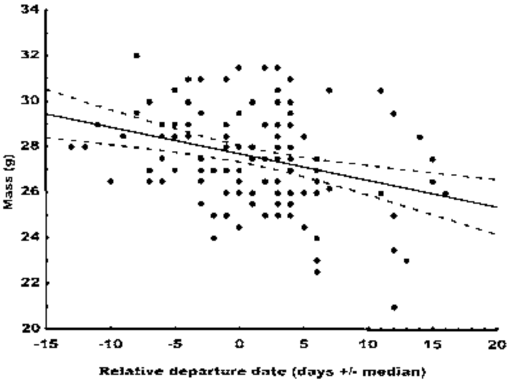

FIG. 1. Departure mass of chicks retrapped as adults, in relation to their relative date of departure from the colony (days ± median date of departure for a given year).

Effect on age at recapture.—Adults recaptured as breeders and nonbreeders did not differ in actual or relative dates at which they had departed from the colony as chicks, or in their actual mass at departure (all $P > 0.1$). Breeding birds two and three years old were heavier as chicks than nonbreeders of the same age but showed no significant difference in relative departure date (Table 2). In addition, for all breeders, there was a negative correlation between chick mass and age at recapture, the effect being similar for both colonies (Fig. 2, Table 3). That was not found for nonbreeders (Table 3). Nor was there any correlation with actual or relative departure dates for either breeders or nonbreeders. When age of adults at recapture was examined in relation to breeding status, chick relative departure date and mass, and interactions among independent variables, departure mass, breeding status, and the interaction status × departure mass all contributed significantly to the model (Table 4). The significant interaction term shows that the relationship differed between breeders and nonbreeders. The resulting model for breeders was age (years) = 14.18 – 0.35 × departure mass (g).

Effects on adult mass.—There was no correlation between adult mass and date of recapture for either breeders or nonbreeders ($P > 0.1$). Adult mass was not correlated with mass as chicks, or with actual or relative date of colony departure. However, when breeders and nonbreeders were considered separately, there was a positive correlation between adult and chick mass for breeders, with trends similar at both colonies (Table 3, Fig. 3), but not for nonbreeders (Table 3).

Adults trapped as breeders were heavier than those trapped as nonbreeders (breeders 195.4 ± 9.9 g, $n = 37$; nonbreeders 181.8 ± 9.3 g,

TABLE 2. Mass and date of departure of chicks that did or did not breed at two and three years old.

Variable	Breeding status	Mean	SD	n	t	P
Mass (g) — both islands	Breeders	29.2	2.06	9	2.38	0.020
	Nonbreeders	27.4	2.12	73	–	–
Reef Island	Breeders	29.7	1.53	3	2.39	0.024
	Nonbreeders	27.0	1.86	27	–	–
East Limestone Island	Breeders	28.9	2.38	6	1.20	0.24
	Nonbreeders	27.7	2.26	46	–	–
Relative departure date (days ± median)	Breeders	–0.40	5.5	10	–0.87	0.39
	Nonbreeders	1.18	5.42	77	–	–

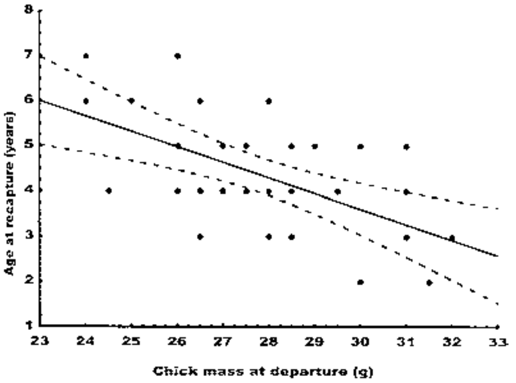

FIG. 2. Age of breeders at first recapture in relation to their mass as chicks at departure from the colony.

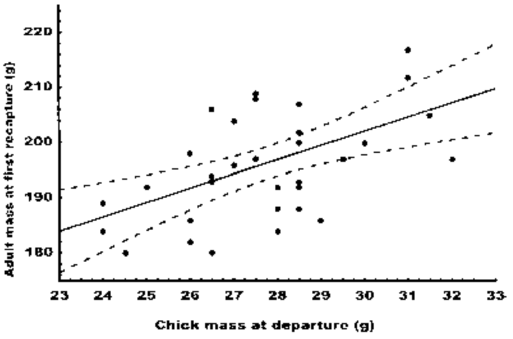

FIG. 3. Mass of breeders at first recapture in relation to their mass as chicks at departure from the colony.

$n = 82$; $t = 7.69$, $P < 0.001$). There was no effect of age on mass for nonbreeders ($R^2 < 0.01$, df = 76, $P = 0.55$); but for breeders, there was a significant negative correlation between age and mass ($R^2 = 0.119$, df = 34, $P = 0.039$). When the single, outlying, 12-year-old was omitted, the relationship was much closer ($R^2 = 0.290$, df = 33, $P = <0.001$; Fig. 4). Applying GLM models to the dependent variable adult mass with age, breeding status, chick mass, and relative departure date as independent variables, two very similar models could be fitted. In the first model, age, breeding status, and the interaction status × age contributed significantly ($R^2 = 0.39$; Table 5). Model for breeders only was mass (g) = 210.03 – 3.18 × age (years).

When age was omitted from the model, status, chick departure mass and the interaction status × departure mass all contributed significantly to the model ($R^2 = 0.41$; Table 5). The model indicated a very small slope for nonbreeders. It appears that the correlation between age at recapture and chick departure mass (Table 3) prevents distinguishing between the two models. However, the significant interaction terms status × age and status × departure mass indicate that the effect is expressed differently for breeders and nonbreeders. Because nonbreeders in a given year will presumably become breeders later, and because there is no increase in measurements with age (A. J. Gaston unpubl. data), the fact that the relationship differs between the two breeding status groups presumably indicates that differences in mass relate to variation in the size of reserves maintained for breeding, rather than to size per se.

DISCUSSION

Intercolony effects.—The two study islands are only 6 km apart and departing chicks from both colonies move rapidly into the same waters of Hecate Strait immediately after departure (Duncan and Gaston 1990). There was no sig-

TABLE 3. Regression analyses for adult mass and age at recapture on chick departure mass.

		Mass (g)			Age (years)		
Colony	Breeding status	R^2	P	n	R^2	P	n
Colonies Combined	Nonbreeder	<0.01	0.67	75	<0.01	0.303	78
	Breeder	0.292	0.001	34	0.119	0.04	36
	Breeder (excluding 12 year old)	0.302	0.001	33	0.290	0.001	35
East Limestone Island	Nonbreeder	<0.01	0.771	47	<0.01	0.52	49
	Breeder	0.177	0.040	24	0.070	0.29	24
Reef Island	Nonbreeder	0.04	0.314	28	<0.01	0.76	29
	Breeder	0.484	0.025	10	0.339	0.08	10

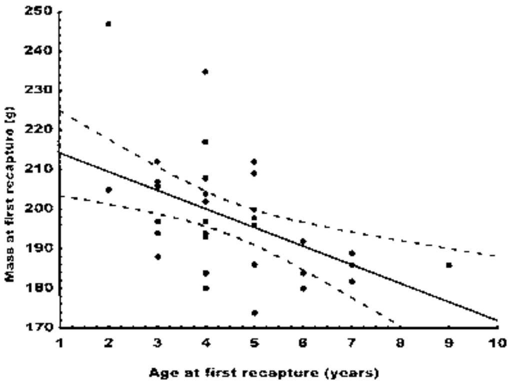

FIG. 4. Mass of breeding adults in relation to age at first recapture.

nificant interyear or intercolony variation in egg volume during the years of banding (A. J. Gaston unpubl. data). Hence, we would not expect any difference in selection operating on chicks from the two colonies: in fact, no difference between the two study colonies was found in any of the trends described. That was despite temporal overlap between banding at the two colonies being small (1995, 1997 only).

Are recaptures representative?—The small proportion of chicks recaptured as adults raises the question of how representative that sample is likely to be. Approximately 50–100 birds that had not been trapped previously as adults were caught annually at ELI during the study period, among a colony of ~1,200 breeding pairs at the start of the study (Gaston 1994b). Assuming a nonbreeding population of ~600, that suggests annual captures of 1.5–3% of the population. Because most birds not captured previously were nonbreeders, we can probably assume that ~5% of nonbreeders were captured annually. On that assumption, recapturing 1% of departing chicks suggests the return of ~20% of those banded—not far from the survival rate required for a stable population (27% to age 2; Gaston 1990). The recapture sample was trapped almost entirely within three small subsections of the colony selected for convenience of siting flight nets: there is no apparent reason why birds captured at those sites should not be representative of the whole population. In addition, no difference was detected between birds trapped at the natal colony and those trapped on the other island, which suggests that philopatric individuals did not differ physically from emigrants.

TABLE 4. Results of GLM analysis of age at recapture in relation to chick mass, departure date, and breeding status (after nonsignificant variables were discarded).

Source	df	MSE	*F*	*P*
Breeding status	1	21.05	29.67	<0.001
Departure mass	1	10.15	14.31	<0.001
Status × departure mass	1	14.57	20.54	<0.001
Error	105	0.71	–	–

TABLE 5. Results of GLM analysis of mass at recapture in relation to chick mass and departure date, age and breeding status (after nonsignificant variables were discarded).

Source	df	MSE	*F*	*P*
Including age				
Breeding status	1	2163.21	25.12	<0.001
Age	1	7.59	0.09	0.77
Status × age	1	608.63	7.07	0.009
Error	105	86.13	–	–
Omitting age				
Breeding status	1	333.22	4.19	0.043
Departure mass	1	941.69	11.85	<0.001
Status × departure mass	1	533.56	6.71	0.011
Error	105	79.5	–	–

Chick mass and date of departure.—The difference in slope of the relationship between chick mass and departure date between all chicks weighed at colony departure and those recaptured as adults suggests that selection against lighter chicks was greater among those departing from the colony early in the season than those leaving later. Given that water temperatures encountered by departing chicks are lowest for those leaving early in the season, it is possible that size of energy reserves is more critical for them than for chicks departing later. A tendency for higher survival among late-departing chicks was noted earlier (Gaston 1997). If conditions for survival improve as the season progresses, the effect of departure mass on survival may decline, resulting in little difference between distribution of departure mass for all chicks and that for the sample recaptured. My results were consistent with that hypothesis.

Recruitment.—We know from the examination of many incubating adults that birds that were incubating when captured would have exhibited brood patches >19 mm across (Gaston 1990). By the same token, birds without brood patches by mid-May were very unlikely to have bred that year, as by that date incubation had commenced for >98% of the population in all years except the El Niño year of 1998 (Gaston and Smith 2001). On the other hand, we cannot be certain that some nonbreeders did not acquire large brood patches: the existence of some birds with intermediate-sized patches suggests that the brood patches of nonbreeders sometimes approached those of breeders. In the following discussion, I assume that all birds with >19 mm brood patches were breeding, but it is possible that a few may not have been. However, any that were not breeding were sufficiently advanced in their hormonal preparations for breeding to develop full-sized brood patches and that, in itself, constitutes a noteworthy distinction from birds defined as nonbreeders by my criteria.

Chicks that were heavier than average when departing from the colony were more likely to begin breeding at two or three years old than lighter chicks. In several other seabirds, there is a difference between sexes in the mean age at first breeding, with females starting to breed at a younger age than males (Adelie Penguin [*Pygoscelis adeliae*], Ainley et al. 1983; Red-billed Gull [*Larus novaehollandiae*], Mills 1989; Thick-billed Murre [*Uria lomvia*], Gaston et al. 1994). However, variation in proportion of males and females probably did not explain the observed difference in chick mass at departure between breeding and nonbreeding two- and three-year-olds, because there was no significant difference in bill depth at three years old (breeders 6.96 ± 0.16 mm, nonbreeders 6.86 ± 0.38 mm; $F = 0.54$, df = 1 and 28, $P = 0.47$): bill depth is the main measurement discriminating the two sexes (Gaston 1994b). If females predominated among young breeders, we would expect the bill depth of breeders to be smaller than that of nonbreeders.

A younger age at first breeding improves both lifetime reproductive success (Woolfenden and Fitzpatrick 1984, Newton 1989a) and intrinsic rate of population increase (O'Donald 1983, Partridge 1989), provided that subsequent survival is not affected. Hence, having chicks that depart from the colony weighing more than average apparently confers a fitness advantage in the Ancient Murrelet that has not been recognized for other birds (Cooke et al. 1995, Daan and Tinbergen 1997).

Adult mass.—The lack of correlation between chick mass and adult mass for nonbreeders (a larger sample than breeders) suggests that the correlation observed for breeding birds does not relate to body size, but to the amount of fat reserves that breeders carry while breeding (Gaston and Jones 1989). If a correlation between chick mass and adult size was the cause, we should expect to find the same correlation for breeders and nonbreeders. There was no correlation between bill depth and adult mass for a large sample of breeders of unknown age ($n = 560$, $P > 0.1$; A. J. Gaston unpubl. data). That and previous findings that the sexes did not differ in mass while breeding (Gaston 1994b) make it unlikely that variation in the sex ratios of birds trapped could be involved in observed mass trends. Rather, variation in breeding mass may be related to foraging skill or effort, to reproductive investment, or to both (Mills 1989, Wendeln and Becker 1999).

The mass of hatchling auks is strongly related to egg mass (Birkhead and Nettleship 1984, Duncan and Gaston 1988) and the mass of Ancient Murrelet chicks at colony departure relates both to egg size and to the length of time spent in the burrow, determined by the frequency of visits by the nonbrooding parent (Gaston 1992). Like adult mass, those characteristics may be related to parental foraging effort, or skill, or to reproductive effort. Hence, the correlation between chick mass at departure and their subsequent mass as breeding adults could be an expression of the heritability of such traits.

Conclusion.—The correlation between chick mass and mass of breeding adults cannot be explained by selection operating during colony departure. It appears that heavy chicks bred earlier and at a higher mass than lighter chicks. Both of those characteristics are likely to affect lifetime reproductive success, and hence fitness (Newton 1989b, Fitzpatrick and Woolfenden 1989, Wendeln and Becker 1999).

Typically, traits with a strong influence on fitness have a low heritability (Gustafsson 1986, Price and Liou 1989, Cooke et al. 1995). However, reproductive effort, either in terms of energy reserves stored or frequency of colony visits, is widely believed to have evolved as an evolutionary trade-off. If environmental conditions fluctuate from year to year and on longer timescales, as is characteristic of north-east Pacific marine ecosystems (Ainley and Boekelheide 1990, Sydeman et al. 1991), the most successful balance of reproductive investment and future survival may vary over a wide range and on a variety of timescales, reducing stabilizing selection on the trait, and allowing substantial variability within populations. Under those conditions, persistence of heritability in traits closely related to the determination of fitness may be possible. However, the argument that correlations detected were caused by the inheritance of traits related to parental investment is tenuous. It is discussed here only to encourage further work on the issue.

Effects of chick mass on adult fitness needs to be investigated for other species. Although some of the relationships detected are surprising and puzzling, the potential influence of chick condition on later adult fitness requires a cautious approach to the use of reproductive success alone as a measure of fitness (Spear and Nur 1994).

Acknowledgments

I thank the following who worked with me in the field at Reef Island for their enthusiasm and dedication: C. Eberl, K. Heise, I. Jones, A. Lawrence, K. Moore, D. Noble, D. Powell, S. Smith, Y. Turcott, and K. Woo. I also thank the directors, camp supervisors, and volunteers of the Laskeek Bay Conservation Society who contributed enormously to the work by carrying out most of the banding program at East Limestone Island: special thanks go to J. Brown, V. Collins, J. Fournier, C. French, J. Gray, R. Kelly, and J. Smith. B. Collins carried out the GLM analyses and B. Collins, R. Dunn, M. Hipfner, P. Blancher, E. Murphy, D. Nettleship, and two anonymous referees contributed useful comments on earlier drafts.

Literature Cited

Ainley, D. G., and R. J. Boekelheide. 1990. Seabirds of the Farallon Islands. Stanford University Press, Stanford, California.

Ainley, D. G., R. E. LeResche, and J. L. Sladen. 1983. Breeding Biology of the Adelie Penguin. University of California Press, Berkeley, California.

Amundsen, T., and J. N. Stockland. 1990. Egg size and parent quality influence nestling growth in the Shag. Auk 107:410–413.

Birkhead, T. R., and A. J. Gaston. 1988. The composition of Ancient Murrelet eggs. Condor 90: 965–966.

Birkhead, T. R., and D. N. Nettleship. 1982. Adaptive significance of egg size and laying date in Thick-billed Murres. Ecology 63: 300–306.

Birkhead, T. R., and D. N. Nettleship. 1984. Egg size, composition and offspring quality in some Alcidae (Aves: Charadriiformes). Journal of Zoology (London) 202:177–194.

Bolton, M. 1991. Determinants of chick survival in the Lesser Black-backed Gull: Relative contributions of egg size and parental quality. Journal of Avian Biology 60:949–960.

Brook, M. de L. 1986. Manx Shearwater chicks: Seasonal, parental and genetic influences on the chick's age and weight at fledging. Condor 88:324–327.

Brook, M. de L. 1991. The Manx Shearwater. T. and A.D. Poyser, London.

Brown, C. R., and M. B. Brown. 1999. Fitness components associated with laying date in the Cliff Swallow. Condor 101:230–245.

Christensen, T. K. 1999. Effects of cohort and individual variation in duckling body condition on survival and recruitment in the Common Eider *Somateria mollissima*. Journal of Avian Biology 30:302–308.

Cooke, F., R. F. Rockwell, and D. B. Lank. 1995. The Snow Geese of La Perouse Bay. Oxford University Press, Oxford.

Daan, S. and J. M. Tinbergen. 1997. Adaptation of life-histories. Pages 311–333 *in* Behavioural Ecology, 4th ed. (J. R. Krebs, and N. B. Davies, Eds.). Blackwell, Oxford.

Duncan, D. C., and A. J. Gaston. 1988. The relationship between precocity and body composition in some neonate Alcids. Condor 90:718–721.

Duncan, D. C., and A. J. Gaston. 1990. Movements of Ancient Murrelet broods away from a colony. Studies in Avian Biology 14:109–113.

Fitzpatrick, J. W., and Woolfenden, G. E. 1989. Florida Scrub Jay. Pages 201–218 *in* Lifetime Reproduction in Birds (I. Newton, Ed.). Academic Press, London.

Galbraith, H. 1988. Effects of egg size and composition on the size, quality and survival of Lapwing *Vanellus vanellus* chicks. Journal of Zoology (London) 214:383–398.

Gaston, A. J. 1990. Population parameters of the Ancient Murrelet. Condor 92:998–1011.

Gaston, A. J. 1992. The Ancient Murrelet. T. and A. D. Poyser, London.

Gaston, A. J. 1994a. Status of the Ancient Murrelet, *Synthliboramphus antiquus*, in Canada and the effects of introduced predators. Canadian Field-Naturalist 108:211–222.

Gaston, A. J. 1994b. Ancient Murrelet (*Synthliboramphus antiquus*). *In* The Birds of North America, no. 132 (A. Poole, and F.

Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Gaston, A. J. 1997. Mass and date at departure affect the survival of Ancient Murrelet *Synthliboramphus antiquus* chicks after leaving the colony. Ibis 139:673–678.

Gaston, A. J., L. N. de Forest, G. Donaldson, and D. G. Noble. 1994. Population parameters of Thick-billed Murres at Coats Island, NWT, Canada. Condor 96:935–948.

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., I. L. Jones, and D. G. Noble. 1988. Monitoring Ancient Murrelet breeding populations. Colonial Waterbirds 11:58–66.

Gaston, A. J., and J. L. Smith. 2001. Changes in oceanographic conditions off northern British Columbia (1983–1999) and the reproduction of a marine bird: The Ancient Murrelet (*Synthliboramphus antiquus*). Canadian Journal of Zoology 79:1735–1742.

Gray, J. 2001. East Limestone Island camp: Report for the 2000 field season. Laskeek Bay Research 10:9–15.

Gustafsson, L. 1986. Lifetime reproductive success and heritability: Empirical support for Fisher's fundamental theorem. American Naturalist 128:761–764.

Harris, M. P., D. J. Halley, and S. Wanless. 1992. The post-fledging survival of young guillemots *Uria aalge* in relation to hatching date and growth. Ibis 134:335–339.

Hedgren, S. 1981. Effects of fledging weight and timing of fledging on survival of guillemot *Uria aalge* chicks. Ornis Scandinavica 12:51–54.

Hipfner, J. M., and A. J. Gaston. 1999. The relationship between egg size and posthatching development in the Thick-billed Murre. Ecology 80: 1289–1297.

Jones, I. L., J. B. Falls, and A. J. Gaston. 1987. Colony departure of family groups of Ancient Murrelets. Condor 89:940–943.

Martin, T. E. 1987. Food as a limit on breeding birds: A life-history perspective. Annual Review of Ecology and Systematics 18: 453–487.

Meathrel, C. E., J. S. Bradley, R. D. Wooler, and R. J. Skira. 1993. The effect of parental condition on egg size and reproductive success in Short-tailed Shearwaters *Puffinus tenuirostris*. Oecologia 93:162–164.

Mills, J. A. 1989. Red-billed Gull. Pages 387–404 *in* Lifetime Reproduction in Birds (I. Newton, Ed.). Academic Press, London.

Newton, I. 1989a. Synthesis. Pages 441–469 *in* Lifetime Reproduction in Birds (I. Newton, Ed.). Academic Press, London.

Newton, I. 1989b. Sparrowhawk. Pages 279–296 *in* Lifetime Reproduction in Birds (I. Newton, Ed.). Academic Press, London.

O'Donald, P. J. 1983. The Arctic Skua. Cambridge University Press, Cambridge, United Kingdom.

Ollason, J., and G. M. Dunnet. 1986. Relative effects of parental performance and egg quality on breeding success of fulmars *Fulmarus glacialis*. Ibis 128:290–296.

Partridge, L. 1989. Lifetime reproductive success and life-history evolution. Pages 421–440 *in* Lifetime Reproduction in Birds (I. Newton, Ed.). Academic Press, London.

Price, T., and L. Liou. 1989. Selection on clutch size in birds. American Naturalist 134:950–959.

Price, T., M. Kirkpatrick, and S. J. Arnold. 1988. Directional selection and the evolution of breeding date in birds. Science 240:798–799.

Reid, W. V., and P. D. Boersma. 1990. Parental quality and selection on egg size in the Megallanic Penguin. Evolution 44:1780–1786.

Ricklefs, R. E. 1984. Components of variance in the measurements of nestling European Starlings (*Sturnus vulgaris*) in southeastern Pennsylvania. Auk 101:319–333.

Sealy, S. G. 1975. Egg size of murrelets. Condor 77: 500–501.

Sealy, S. G. 1976. Biology of nesting Ancient Murrelets. Condor 78:294–306.

Spear, L., and N. Nur. 1994. Brood size, hatching order and hatching date: Effects of four life-history stages from hatching to recruitment in Western Gulls. Journal of Animal Ecology 63:283–298

Sydeman, W. J., J. F. Penniman, T. M. Penniman, P. Pyle, and D. G. Ainley. 1991. Breeding performance in the Western Gull: Effects of parental age, timing of breeding and year in relation to food availability. Journal of Animal Ecology 60: 135–149.

Wendeln, H., and P. H. Becker. 1999. Effects of parental quality and effort on the reproduction of common terns. Journal of Animal Ecology 68: 205–214.

Williams, T. D. 1994. Intraspecific variation in egg size and egg composition in birds: Effects on offspring fitness. Biological Reviews 68:35–59.

Woolfenden, G. E., and J. W. Fitzpatrick. 1984. The Florida Scrub-Jay: Demography of a cooperative breeding bird. Princeton University Press, Princeton, New Jersey.

Associate Editor: D. Nettleship