RELATIONSHIP BETWEEN WING LENGTH AND BODY MASS IN ATLANTIC PUFFIN CHICKS

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Abstract.—Ages of Atlantic Puffin (*Fratercula arctica*) chicks are sometimes estimated by comparing their wing lengths with a sample of known-aged chicks from the same colony. The technique is reliable if the rate of wing growth is unaffected by variation in nutrition. Recent studies suggest that wing growth may respond to food supply. I investigated variation in wing length in relation to chick age and mass during a period of reduced food availability. Wing length was correlated with mass at all chick ages, and wing growth over a 4-d interval was related to change in mass over the same interval at most ages. Variation in wing length and differences between estimated and actual ages increased with age. Average ages of chicks between 5–50-d old were estimated satisfactorily, but estimates for chicks growing faster or slower than average were biased. Measurements from a representative sample of contemporary, known-aged chicks are required to provide reliable, average age estimates. Large potential errors for individual chicks poses problems for studies investigating individual behavior.

RELACIÓN ENTRE LARGO DE ALA Y MASA CORPORAL EN PICHONES DE FRATERCULA ARTICA

Sinopsis.—Las edades de pichones de *Fratercula artica* son a veces estimadas al comparar el largo de sus alas con una muestra de pichones de una edad conocida en la misma colonia. La técnica es confiable si la tasa de crecimiento del ala no es afectada por variación en la nutrición. Estudios recientes sugieren que el crecimiento del ala puede responder a la provisión de alimento. Investigué la variación en el largo de ala con relación a la edad del pichon y a su masa corporal durante un período de reducción en la disponibilidad de alimento. El largo del ala se correlacionó con la masa en todas las edades de los pichones, y el crecimiento del ala a través de un intérvalo de 4 días se relacionó con cambios en masa a través del mismo intérvalo en la mayoría de las edades. La variación en el largo de ala y las diferencias entre las edades estimadas y actuales aumentaron con la edad. Las edades promedios de pichones entre 5 y 50 días de nacidos se estimaron satisfactoriamente, pero estimados para pichones creciendo más velozmente o más lentamente que el promedio fueron viciados. Se requieren medidas de una muestra representativa de pichones contemporáneos de edad conocida para proveer estimados de edad promedio confiables. El gran potencial de errar al estimar edades de pichones individuales plantea problemas para estudios investigando la conducta individual.

Knowledge of the ages of chicks is important in studies of comparative reproductive performance, feeding ecology, and life-history strategies (e.g., Galbraith 1983, Murphy et al. 1991, Nettleship 1972, Ydenberg 1989). Obtaining accurate hatching dates is time consuming and can cause desertion and disruption of breeding efforts (Gaston et al. 1988, Harris 1984, Pierce and Simons 1986, Rodway et al. 1996) and mortality of eggs and chicks (Ellison and Cleary 1978). Effects of disturbance are undesirable for the birds and may distort study results (Brown and Morris 1994, Pierce and Simons 1986). Methods of estimating chick ages from morphological measurements have been developed to alleviate these problems (Elowe and Payne 1979, Gilliland and Ankney 1992, Harris

1984, Kirkham and Montevecchi 1982, Mineau et al. 1982). Such techniques generally assume that growth rates of selected body parts are independent of changes in nutrition (e.g., Coleman and Fraser 1989).

Wing length has been used to estimate chick ages given a reference growth curve from known age chicks at a particular colony (Barrett and Rikardsen 1992, Harris 1984). Several researchers have shown that the rate of wing growth in alcid chicks is unaffected by nutrition; others have found correlations between wing length and mass at certain ages (Gaston 1985). In the puffin, *Fratercula arctica,* wing length at fledging is not related to fledging mass (Anker-Nilssen 1987, Barrett et al. 1987, Nettleship 1972), and the growth rate of the wing has not responded to supplementary feeding of the chick (Harris 1978, Hudson 1979). Tschanz (1979) found that the growth of most body parts was retarded in 4–14-d-old starving chicks. He recommended tarsus and middle-toe length as the best aging criteria up to 14 d, as their growth was least affected. He was unable to determine how nutrition affected wing length because all poorly nourished chicks died before the start of feather development. Anker-Nilssen (1987) found that growth rates of culmen and tarsus were dependent on food supply and culmen lengths at fledging were shorter in poor years than in good ones. Wing lengths at fledging were similar across years, suggesting that during periods of food shortage, chicks will selectively allocate growth to the wings at the cost of other body parts (Anker-Nilssen 1987). Anker-Nilssen measured wing length throughout the nestling period only in one year and was unable to compare growth rates among years.

Fledging periods for puffins have ranged from 39–83 d at a single colony (Nettleship 1972). This suggests that there is large variation in the growth rate of the wing if wing length is constant at fledging. I investigated how growth is allocated to the wing over a range of nutritional conditions as part of a larger study on intracolony variability of breeding performance of Atlantic Puffins on Great Island in 1992 and 1993. My objectives were (1) to describe the variation in wing length with age, (2) to determine how chick mass and changes in mass are related to wing length and growth, and (3) to determine the accuracy and precision of age estimates based on wing measurements. My hypothesis was as follows. A minimum-sized wing is required for fledging and chicks will not fledge until their wings reach that minimum (Barrett and Rikardsen 1992). The growth rate of the wing, and other body parts, has an upper limit set by physiological constraints (Carrier and Auriemma 1992, Gaston 1985) and that growth rate is maintained with normal or supplementary feeding. Below that limit the growth rate is responsive to food supply, allowing the chick to vary its rate of development and survive periods of low food availability.

METHODS

The study was conducted on Great Island (47°11'N, 52°46'W), Newfoundland from 23 May–31 Aug. 1992 and from 6 Jun.–30 Aug. 1993. The

island has been described in detail by Nettleship (1972), Pierotti (1982), and Rodway (1994). In 1992, nine study plots containing 20 burrows each were distributed systematically at three different locations around the island (north, east, and south) and in three different habitats (maritime slope, maritime level, and inland slope) at each location. This minimized biases caused by intracolony differences in breeding performance (Harris 1980, Nettleship 1972, Rodway 1994). Burrows were checked to determine occupancy during incubation, and active burrows were checked every 4 d from just before hatching to fledging. The midpoint between checks was considered the hatching date unless chicks were observed hatching. Thus, hatching dates were known within 2 d for all chicks and exactly for a smaller sample that had just hatched when checked. Chicks were weighed to the nearest 1 g using Pesola spring balances, wing lengths (maximum flattened chord) were measured to the nearest 1 mm with a stopped ruler, and culmen and tarsus lengths to the nearest 0.1 mm using vernier calipers. Near fledging, measurements were taken every 2 d.

In 1993, one plot of 84 burrows was established in maritime level habitat on the south side of the island. Burrows were not disturbed during incubation and hatching dates were estimated by observing when food was first delivered to each occupied burrow. Observations were maintained from dawn to dusk every 4 d and during the peak feeding times from 0600–0800 h every second day throughout the hatching period. Thus, first feedings were known within 4 d for all chicks and within 2 d for most chicks, since an average of 86% of chicks that were fed on all day watches were fed during the 2-h peak feeding period (Rodway, unpubl.). Chicks were assumed to be 1-d-old when they were first fed (Harris 1984). Chicks were measured 30 d after their first feeding, again 9 d later, and then every 1–2 d near fledging. The same measurements were taken as in 1992, except tarsus, which was not measured.

Standard growth curves (Ricklefs 1968) were fit to wing-growth data for known-age chicks using nonlinear least squares regression (program NONLIN in SYSTAT; Wilkinson 1990). Of 20 known-age chicks only 8 survived to fledging. Distorted growth curves made curve fitting inappropriate for two slow-growing survivors (Ricklefs 1968) and measurements from the remaining six were used to fit growth curves. A logistic equation gave marginally lower residual sum of squares ($r^2 = 0.982$ vs. 0.977 for Gompertz and 0.974 for von Bertalanffy) and the best estimate of asymptotic size (Rodway, unpubl.). Parameter estimates were used to generate an inverse form of the logistic equation following Mineau et al. (1982) to estimate age from wing length.

Linear regression was used to analyze relationships between wing length and mass at specific chick ages. Each analysis used one measure per chick to meet the assumption of independence. Residuals from all analyses were inspected to insure that assumptions of normality and homoscedasticity were satisfied. Tolerance for type I error was set at 5% for all tests. Means are quoted ± 1 SD.

RESULTS

Wing length at fledging averaged 145 ± 4 mm (n = 69) in 1992 and 144 ± 5 mm (n = 24) in 1993 and was not related to age at fledging (r^2 = 0.03, $F_{1,44}$ = 1.11, P = 0.30). There was a weak negative relationship between wing length at fledging and date of fledging (r^2 = 0.04, $F_{1,92}$ = 4.01, P = 0.048). Wing length was related to mass at fledging (r^2 = 0.13, $F_{1,92}$ = 13.43, P < 0.001) and at all chick ages (r^2 = 0.34–0.74, P < 0.001 for all regressions). The strength of the relationship between wing length and mass peaked at 14 d of age and was weakest just after hatching (Fig. 1). Growth of the wing was positively related to change in mass at most ages, especially during the first 2 wks (Fig. 1).

There was considerable variation in wing length at specific ages. At age 30–31 d, wing length ranged from 77–127 mm (Fig. 2). Differences in mass explained 63% of the variation in wing length at that age ($F_{1,79}$ = 136.36, P < 0.001). Age to reach a wing length of 120 mm varied from 30–60 d (Fig. 2).

Errors in age estimation for individual chicks increased with age (Fig. 3). Ages of slow-growing chicks 50–60-d old were under-estimated by as much as 25 d. Ages were over-estimated for chicks that fledged in less than 45 d and under-estimated for chicks that took longer than 60 d to fledge (Fig. 4). Wing growth was retarded in slow-growing chicks (Fig. 4).

Average estimated ages were biased for chicks < 5-d old (mean difference between estimated and actual ages = 1.6 ± 1.2 d) and for chicks > 50-d old (mean difference = −10.3 ± 9.1 d; Fig. 3). Between 5–50-d old, average estimated ages and actual ages for chicks that fledged were similar (mean difference = −0.1 ± 4.9 d). After 5 d of age, ages of chicks that died were consistently under-estimated (Fig. 3).

Growth rates were higher at south than at north and east locations (Rodway, unpubl.) affecting the accuracy of age estimates at those locations. At age 30–31 d, estimates differed from actual ages by 1.5 ± 2.2 d at south, −1.7 ± 5.0 d at north, and −2.2 ± 3.3 d at east location ($F_{2,44}$ = 4.95, P = 0.012).

Growth of culmen and tarsus were similar to wing length in relation to fledging age and mass. Lengths of culmen and tarsus at fledging were not related to fledging age (r^2 = 0.00, $F_{1,21}$ = 0.08, P = 0.78; and r^2 = 0.04, $F_{1,21}$ = 0.86, P = 0.36, respectively) and were related to mass at fledging (r^2 = 0.42, $F_{1,21}$ = 15.29, P = 0.001; and r^2 = 0.18, $F_{1,21}$ = 4.66, P = 0.043, respectively). As with wing length, culmen and tarsus growth were retarded in slow-growing chicks.

DISCUSSION

Growth rates of wing, culmen, and tarsus varied and depended on the nutritional state of the chick as indicated by mass and changes in mass. Similar relationships have been illustrated by Anker-Nilssen (1987), Barrett et al. (1987), Barrett and Rikardsen (1992), and Tschanz (1979). Correlations between mass and wing length also have been reported for
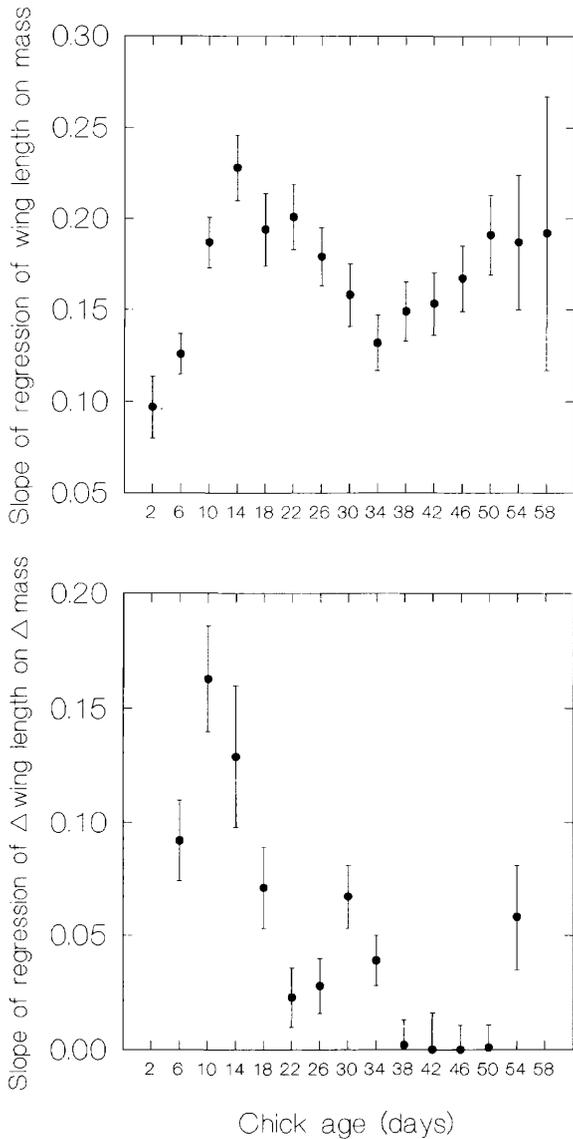
FIGURE 1.   Regression coefficients ± SE for regressions of wing length on mass and change in wing length on change in mass at different ages for Atlantic Puffin chicks on Great Island in 1992. Changes in wing length and mass were calculated over each 4-d measurement interval. Ages given on abscissas represent the third day of 4-d age categories. Sample size was 70 at age 2 d and was reduced to 7 by age 58 d as chicks died or fledged.
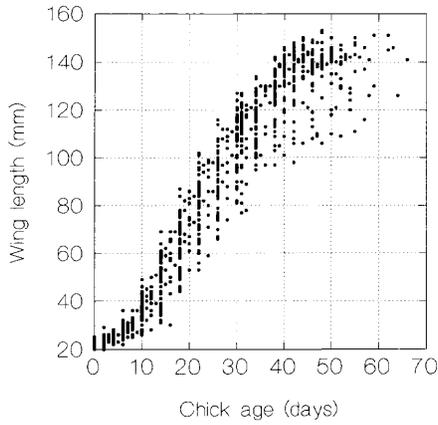
FIGURE 2.   Variation in wing length with age of Atlantic Puffin chicks on Great Island in 1992 and 1993.
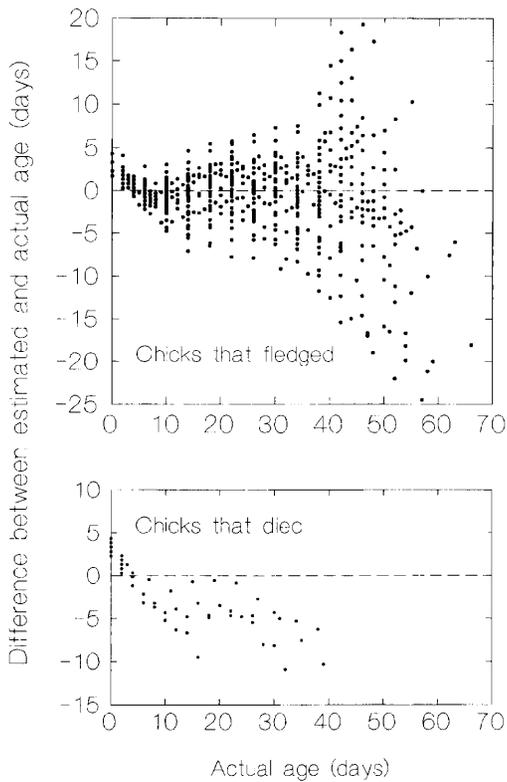

FIGURE 3.   Differences between estimated and actual ages for Atlantic Puffin chicks that fledged and that died on Great Island in 1992.
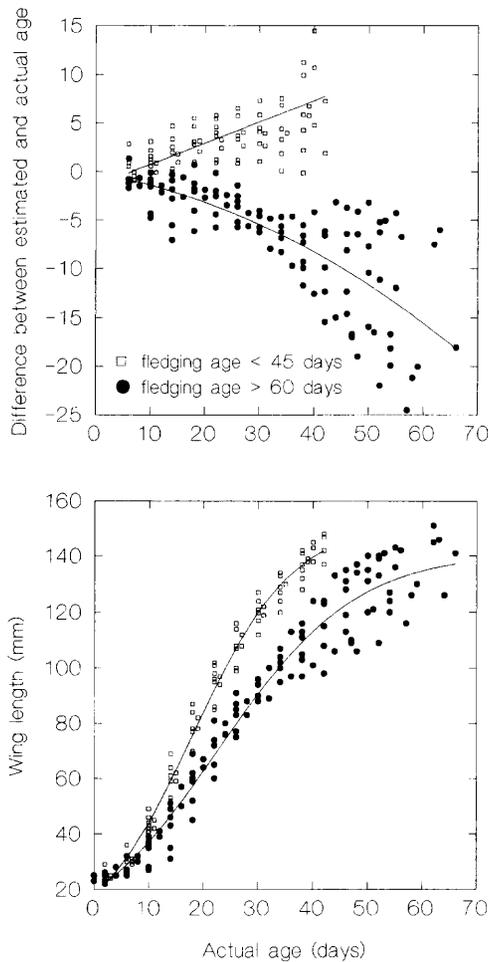
FIGURE 4. Comparison of age estimation errors and wing growth for Atlantic Puffin chicks
    that fledged in < 45 d and > 60 d on Great Island in 1992.

Thick-billed Murres (*Uria lomvia*; Birkhead and Nettleship 1981, Gaston
and Nettleship 1981) and Dovekies (*Alle alle*; Stempniewicz 1980). Growth
was protracted over the nestling period and resulted in similar sizes at
fledging independent of fledging age.

Wing length at fledging was related to mass at fledging, in contrast to
results of previous studies (Anker-Nilssen 1987, Barrett et al. 1987, Net-
tleship 1972). Researchers in past studies analyzed group differences be-
tween year or habitat categories and did not investigate the relationship
between wing length and mass at fledging for individual chicks. A positive
relationship between wing length and mass suggests that some chicks may
be choosing to fledge at smaller sizes when provisioning by parents is

poor (Ydenberg 1989). The tendency for wing length at fledging to decrease with fledging date supports this idea because feeding conditions near the colony deteriorate later in the season (Carscadden 1984, Piatt 1990), and chicks may do better at sea away from the colony. Variations in patterns of provisioning over the nestling period imply unique decisions for each individual and may help explain the lack of relationships found for group comparisons as well as between wing length at fledging and fledging age. Considering wing loading, lighter chicks also may be capable of fledging at a smaller wing size than heavy chicks.

Average ages of a larger sample of chicks between 5–50-d old could be estimated satisfactorily using a logistic growth curve derived from only six known-age chicks. Results with only six chicks may have been partly fortuitous but do suggest that a small, representative sample of contemporary, known-aged chicks will provide unbiased estimates of average age in a particular season (Anker-Nilssen 1987). Harris (1984) recommends a sample size of 20. Intra-colony differences among north, east, and south locations stress the importance of a representative sample (Gaston 1985). Extrapolations of growth data across years for aging purposes are probably unreliable during periods of fluctuating food supplies when average growth rates vary (Anker-Nilssen 1987, Barrett et al. 1987, Barrett and Rikardsen 1992).

Precision of age estimates was poor and accuracy for most individuals decreased as they got older. This is not a serious problem if only average estimates are desired, but does present difficulties for investigations of individual behaviour requiring known chick ages (e.g., Clark and Ydenberg 1990, Ydenberg 1989). If individual ages are needed, aging should be performed when chicks are as young as possible, but trade-offs between accuracy of age estimates and disturbance during hatching or brooding, which may affect breeding success, distort attendance and feeding behaviour, and compromise study results, need to be considered.

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