

WING LENGTH AND MASS AT FLEDGING PREDICT LOCAL JUVENILE SURVIVAL AND AGE AT FIRST RETURN IN TUFTED PUFFINS

KYLE W. MORRISON^{1,4}, J. MARK HIPFNER^{1,2}, CARINA GJERDRUM³, AND DAVID J. GREEN¹

¹Centre for Wildlife Ecology, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia V5A 1S6, Canada

²Canadian Wildlife Service, RR1 5421 Robertson Rd., Delta, British Columbia V4K 3N2, Canada

³Canadian Wildlife Service, 45 Alderney Drive, Dartmouth, Nova Scotia B2Y 2N6, Canada

Abstract. In long-lived species, juvenile survival and the age at which individuals begin the process of recruitment have important consequences for individual fitness and population growth. We investigated how characteristics of fledglings (mass, wing length, and date) influenced the local survival of juveniles and age at first return to the natal breeding colony of two annual cohorts of the Tufted Puffin (*Fratercula cirrhata*) at Triangle Island, British Columbia. Although both cohorts were produced in years when nestlings grew quickly and had high mass at fledging, only 8% of banded nestlings from the 1999 cohort, but 43% of nestlings from the 2000 cohort, were resighted up to 2008. Age at first return of the 2000 cohort averaged one year younger than that of the 1999 cohort. In addition to the cohort effect, we found that the local survival of juveniles increased strongly with wing length at fledging, providing an ultimate explanation for puffin nestlings' preferential allocation of energy and nutrients to wing growth over mass growth. Mass and date at fledging had detectable, but much weaker, effects on survival. Conversely, nestlings' age at first return decreased strongly with mass at fledging, weakly with wing length at fledging. Ours is the first study to report an effect of characteristics at fledging on juvenile survival and age at first return in an alcid whose offspring receive no parental care after they leave the nest site.

Key words: adaptive growth, Alcidae, cohort effect, early conditions, *Fratercula cirrhata*, recruitment, seabird, Tufted Puffin.

La Longitud del Ala y el Peso al Momento de Emplumar Predicen la Supervivencia Local de los Jóvenes y la Edad al Tiempo del Primer Regreso en *Fratercula cirrhata*

Resumen. En especies de vida larga, la supervivencia de los jóvenes y la edad a la que los individuos inician el proceso de reclutamiento tienen consecuencias importantes para la adecuación individual y para el crecimiento poblacional. Investigamos cómo las características de los volantones (peso, longitud del ala y fecha) influenciaron la supervivencia local de los jóvenes y la edad a la cual regresaron por primera vez a la colonia de anidación natal en dos cohortes anuales de *Fratercula cirrhata* en la isla Triangle, Columbia Británica. Aunque ambas cohortes se produjeron en años en los que los pichones crecieron rápidamente y presentaron un peso alto al emplumar, sólo el 8% de los pichones anillados en la cohorte de 1999 y el 43% de aquellos de la de 2000 fueron vueltos a observar hasta el 2008. La edad a la que las aves de la cohorte de 2000 regresaron por primera vez fue, en promedio, un año menor que la edad de las de la cohorte de 1999. Además del efecto de la cohorte, encontramos que la probabilidad de supervivencia de aves jóvenes locales aumentó fuertemente con la longitud del ala al emplumar, lo que provee una explicación de base para la asignación preferencial de energía y nutrientes al crecimiento de las alas y no al aumento de peso en esta especie. El peso y la fecha de emplumamiento tuvieron efectos detectables, pero mucho más débiles, sobre la supervivencia. De modo contrario, la edad de los jóvenes al momento de su primer regreso disminuyó fuertemente con el peso al momento de emplumamiento y débilmente con la longitud del ala al emplumar. Este es el primer estudio que documenta un efecto de las características de los volantones sobre la supervivencia de las aves jóvenes y su edad al tiempo del primer regreso en un álcido con crías que no reciben cuidado parental después de abandonar el sitio de anidación.

INTRODUCTION

Demographic modeling suggests adult survival is the most important trait affecting population trajectories of long-lived species, including many seabirds (Newton 1991). However, juvenile survival, i.e., survival between departure from the nest until return to the breeding area, may affect the dynamics of

seabird populations more strongly during periods when adult survival is relatively constant (Lee et al. 2008). Age at recruitment is another demographic characteristic that can have large effects on individual fitness (Kruger 2005) and rate of population growth (Porter and Coulson 1987). Age at recruitment varies by individual, population, and year, but the individual (Becker and Bradley 2007) and environmental (Reid et

Manuscript received 2 December 2008; accepted 22 May 2009.

⁴E-mail: kwmorris@sfu.ca

The Condor, Vol. 111, Number 3, pages 433–441. ISSN 0010-5422, electronic ISSN 1938-5422. © 2009 by The Cooper Ornithological Society. All rights reserved. Please direct all requests for permission to photocopy or reproduce article content through the University of California Press's Rights and Permissions website, <http://www.ucpressjournals.com/reprintInfo.asp>. DOI: 10.1525/cond.2009.080099

al. 2003) factors that underlie this variation remain poorly understood. Therefore, long-term studies examining factors that affect juvenile survival and age at recruitment are important to our understanding of population processes.

Conditions early in life can have consequences for juvenile survival and age at recruitment (Lindstrom 1999, Metcalfe and Monaghan 2001). In birds, two factors that often affect both processes are mass at fledging and fledging date (Monros et al. 2002, Ludwigs and Becker 2006). Mass at fledging is often positively correlated with probability of local recruitment, which is often assumed to reflect juvenile survival (Perrins et al. 1973, Green and Cockburn 2001). The positive association between fledging mass and juvenile survival may be due to heavier fledglings having greater endogenous reserves to draw upon after they leave the nest when they have to feed themselves but lack critical foraging skills (Weimerskirch et al. 2000). As for fledging date, in many avian species offspring raised early in the season are more likely to survive than those raised later (Harris et al. 1992, Catry et al. 1998). Juvenile survival may decline with date either because food availability declines through the season or because parents breeding earlier in the year are of higher quality and provide more food to offspring (Verhulst and Nilsson 2008).

Although heavier fledglings may be more likely to survive, growth in mass is only one component of nestling development that might affect juvenile survival. The “adaptive growth” hypothesis predicts that selection drives nestlings to preferentially allocate limited resources to maintain growth of structures most important to maximizing survival (O'Connor 1977). The importance of skull, bill, and wing growth to survival of juvenile birds is suggested by the minimal sensitivity of these elements to food restriction (Boag 1987, Øyan and Anker-Nilssen 1996, Dahdul and Horn 2003). Skull size reflects development of the central nervous system, while bill size and wing length may aid juvenile survival by increasing foraging efficiency and favoring successful fledging (Birkhead 1977, Øyan and Anker-Nilssen 1996).

In addition to being more likely to survive to recruitment, larger and better-developed fledglings may be younger at recruitment (Sedinger et al. 1995, Gaston 2001). This correlation suggests that mass at fledging reflects individuals' quality (Ludwigs and Becker 2006) or condition at recruitment (Sedinger et al. 1995). If slower growth or low fledgling mass results in decreased condition later in life (Metcalfe and Monaghan 2001), then light fledglings may be constrained or restrain themselves from breeding at an early age (Curio 1983). A nestling's hatching and fledging date can also affect its age at recruitment. Young hatched and fledged early may recruit at a younger age because they are dominant over late fledglings in accessing food resources after fledging (Spear and Nur 1994).

We used an information-theoretic approach (AIC) to examine how year (cohort), as well as mass, date, and wing length at fledging influenced local juvenile survival and the

age at which individuals first return to their natal colony in two cohorts of the Tufted Puffin (*Fratercula cirrhata*). Like most long-lived seabirds, Tufted Puffins spend their juvenile period entirely at sea and attend breeding colonies for a period of one or more years before recruiting (Piatt and Kitaysky 2002). This “prospecting” period dictates that an individual's age at first return to the colony usually differs from its age at recruitment. Because the two are positively correlated (Porter 1990, Halley et al. 1995, Ludwigs and Becker 2002), however, age at first return likely influences age at recruitment. Tufted Puffins lay a single-egg clutch, so neither differences among offspring in parental investment nor sibling competition are confounding factors affecting their fledging mass, date, or wing length (Sydeman and Emslie 1992). Puffins become fully independent of their parents when they fledge, so that we can expect their condition at that time to influence local juvenile survival and age at first return. We predict that Tufted Puffins that fledge with a higher weight, longer wings, and at an earlier date will survive at a higher rate and return to their natal breeding colony at a younger age.

METHODS

STUDY AREA

In the 1980s, Triangle Island, British Columbia, Canada (50° 52' N, 129° 05' W), supported ~26 500 breeding pairs of Tufted Puffins, making it the largest breeding colony south of Alaska (Rodway et al. 1990). We studied a subcolony of about 12 000 pairs on Puffin Rock in 1999 and 2000, years with cold water and high productivity (Mackas et al. 2007) that ranked within the top 3 of 11 years in terms of fledging success and growth rate at this site (Gjerdrum et al. 2003).

FIELD PROCEDURES

From June to August in 1999 and 2000 we removed nestling puffins from burrows and measured them (tarsus, mass, wing chord) every 5 days until they were 40 days old and every 2 days thereafter (Gjerdrum 2004). Mass was measured to the nearest 1 g (for masses <100 g) or 2 g (for masses >100 g) with Pesola spring scales. We measured the length of the flattened wing from the wrist to the wing tip (± 1 mm). We banded each nestling at about age 40 days with a size-6 U.S. Fish and Wildlife Service steel band on one leg and an individually coded two-digit alphanumeric plastic color band on the other. Mass at fledging was defined as the last mass measured before the bird disappeared, provided it was at least 40 days of age (Vermeer and Cullen 1979). We defined a nestling's date of fledging as the day before its burrow was found empty. We assumed nestlings missing before 40 days of age were dead rather than fledged and excluded them from the analyses.

From mid-April to the end of August 2002–2008, as weather permitted, we observed Puffin Rock systematically

for ≥ 2 hr daily to resight banded puffins at their natal subcolony. We made observations at various times of day through a 20–60 \times spotting scope from a blind with good visibility of one third of the area of the subcolony on Puffin Rock. The observed area included the slopes where nestlings had been banded, as well as a peripheral rocky cliff edge where we resighted young puffins in gatherings of their fellow prospectors (Wehle 1980). We made observations on 46 to 123 days per year. In some years observation effort was low because the puffins abandoned the colony mid-season (2003 and 2007) or because the field crew arrived late (end of May in 2008). However, the resighting effort in 2007 and 2008 resulted in high probabilities of resighting for a separate sample of adult puffins, 0.86 ± 0.11 (95% CI) and 0.98 ± 0.12 , respectively (Morrison 2009).

Alphanumeric combinations on the bands were never illegible, and we never resighted birds that had lost an alphanumeric band or a steel band, suggesting low rates of band wear and band loss. We reduced the probability of including misread band combinations by having observers record only band combinations of which they were certain. There is no reason to expect that band wear, band loss, or the misreading of bands are related to cohort, fledging mass, date, or wing length, so these potential sources of bias should not have altered our results. Alcids' natal philopatry is generally high (Crespin et al. 2006, Sandvik et al. 2008), but any emigration will cause us to underestimate the true rate of juvenile survival. Because we lack information on natal philopatry and therefore can not include probability of resighting in our estimate of juvenile survival, we actually measured return rate. We assume that return rate does not vary by cohort or with mass, date, or wing length at fledging and is therefore an unbiased index to juvenile survival. To make this distinction explicit, we refer to juvenile survival as *local* juvenile survival.

STATISTICAL ANALYSIS

We used an information-theoretic approach to model selection to evaluate factors that influenced local juvenile survival and age at first return. We included four explanatory variables in our models: year and date, mass, and wing length at fledging. We did not include year-interaction terms because of the very low number of puffins resighted from one of the cohorts. Therefore, our candidate model set for each analysis included 16 biologically plausible models, which included all additive combinations of explanatory variables, plus a null model.

Following the methods outlined by Burnham and Anderson (2002), we calculated Akaike's information criterion for small sample sizes (AIC_c) for all models, along with associated parameters. We calculated \hat{c} for the analysis of juvenile survival with logistic regression from the global model by using the formula $\hat{c} = \chi^2/df$, where χ^2 is Pearson's chi squared and df is the degrees of freedom. We did not need to correct the response variable for juvenile survival for overdispersion ($\hat{c} = 0.92$). We present correlation-coefficient (R^2) values from

multiple regression for each of the general linear models of the juvenile-survival analysis as a measure of the proportion of variance in the probability of local juvenile survival explained by the independent variables. We also calculated the difference between each model and the best-fitting model (Δ_i), as well as Akaike weights (w_i). We estimated the relative importance of each variable by summing the Akaike weights across all competing models in which the variable occurred. We used model-averaged parameter estimates to assess the size of the effect and thus biological significance of each parameter. We estimated the unconditional standard error (SE) of each parameter directly by considering only the subset of models that included the parameter of interest. We calculated 95% confidence intervals with the formula $95\% \text{ CI} = 1.96 \times \text{SE}$.

We fitted logistic regression models to the juvenile-survival dataset in SAS 9.1 (SAS Institute 2003) by using PROC GENMOD with a binomial-error distribution and the logit-link function. General linear models were fitted to the data on age at first return with the "Fit (Y X)" linear-regression application in SAS 9.1. AIC_c values were calculated manually, after Burnham and Anderson (2002). All means are presented $\pm 95\%$ confidence interval unless otherwise stated.

RESULTS

We measured and banded 63 and 70 nestling puffins that survived to fledge in 1999 and 2000, respectively. The birds' mean mass at fledging in both years was similar ($475 \text{ g} \pm 21$ vs. $502 \text{ g} \pm 13$), ranging (both years pooled) from 42 to 92% of adults' mean mass on Triangle Island ($721 \text{ g} \pm 62 \text{ SD}$, $n = 10$; Piatt and Kitaysky 2002). In both cohorts the mean wing length at fledging was similar ($151 \text{ mm} \pm 2$ in 1999 and $153 \text{ mm} \pm 2$ in 2000) and ranged from only 64 to 79% of the adults' mean wing length ($209 \text{ mm} \pm 5 \text{ SD}$, $n = 10$; Piatt and Kitaysky 2002). As expected, mass and date at fledging were inversely related ($R^2 = 0.49$, Fig. 1); mass and wing length at

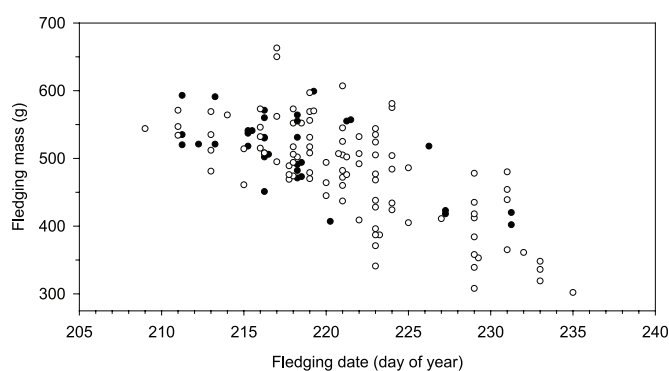


FIGURE 1. Fledging date (day of year) in relation to mass (g) at fledging of Tufted Puffin nestlings banded ($n = 133$) at Triangle Island, British Columbia in 1999 and 2000. Solid circles represent individuals that were resighted; empty circles represent individuals that were not resighted.

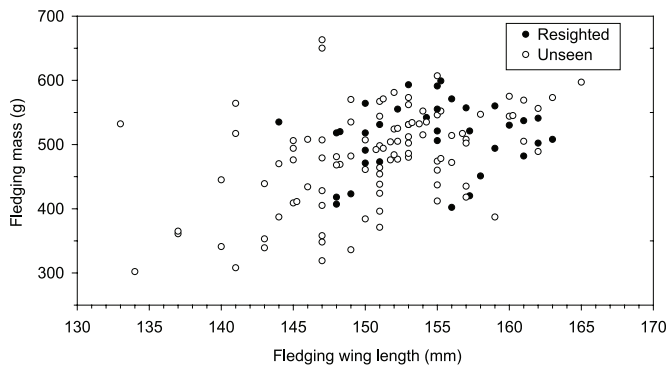


FIGURE 2. Wing length (mm) at fledging in relation to mass (g) at fledging of Tufted Puffins nestlings banded ($n = 133$) at Triangle Island, British Columbia in 1999 and 2000. Solid circles represent individuals that were resighted; empty circles represent individuals that were not resighted.

fledging were positively correlated, although less strongly ($R^2 = 0.20$, Fig. 2); wing length and date at fledging were only weakly correlated ($R^2 = 0.09$).

Of the 133 puffins we banded, we resighted 35 (26%) at their natal subcolony from 2002 to 2008 (Fig. 1 and 2). Of the nestlings resighted from either cohort, we saw 17 in one year only, and of these 17, we saw eight only once. Seven other individuals seen only once in the first year of resighting, were seen subsequently in multiple years. Fourteen puffins in our dataset were resighted in three or more years. These patterns of resighting suggest that some of the individuals we observed were transient prospectors at first resighting and that others went on to recruit to their natal colony.

LOCAL JUVENILE SURVIVAL

The best-supported model for local juvenile survival included only year and wing length at fledging (Table 1), and importance values (both ≥ 0.90) and parameter estimates confirmed that both factors had strong effects (Table 2). Local survival of the 2000 cohort (30 of 70) was much greater than that of the 1999 cohort (5 of 63), and the predicted probability of survival increased from 0.01 to 0.22 in 1999 and from 0.13 to 0.67 in 2000 over the range of wing lengths at fledging observed in each year. The two other strongly supported models ($\Delta_i < 2$, Burnham and Anderson 2002) again included year and wing length at fledging and additionally included effects of either mass or date at fledging (Table 1). However, the addition of each term did little to improve the fit of their respective models, as evidenced by only slight increases in log-likelihood values over that of the best-supported model (Table 1). Local survival was positively related to mass at fledging and negatively related to fledging date, although both terms had low importance values, 0.34 and 0.32 respectively, and unconditional standard errors that were larger than their parameter estimates (Table 2), suggesting their effects were weak.

TABLE 1. Support for logistic regression models predicting local juvenile survival of the 1999 and 2000 cohorts of the Tufted Puffin on Triangle Island, British Columbia, in relation to cohort (YEAR), fledging date (FDATE), fledging mass (FMASS), and fledging wing length (FWING). K is the number of parameters in the model, $\log(L)$ is the log-likelihood value, AIC_c is Akaike's information criterion adjusted for small sample size, Δ_i is the difference in AIC_c value from that of the top model (i.e., lowest AIC_c), and w_i is the Akaike weight; $n = 133$ nestlings. Except for the null model, only models with $\Delta_i < 10$ are shown.

Model	$\log(L)$	K	Δ_i	w_i
YEAR + FWING ^a	-61.37	3	0.00	0.41
YEAR + FWING + FMASS	-60.99	4	1.37	0.21
YEAR + FWING + FDATE	-61.00	4	1.39	0.21
YEAR + FWING + FMASS + FDATE	-60.91	5	3.36	0.08
YEAR + FMASS	-63.77	3	4.81	0.04
YEAR + FDATE	-64.21	3	5.68	0.02
YEAR	-65.27	2	5.70	0.02
YEAR + FMASS + FDATE	-63.69	4	6.76	0.01
NULL	-76.65	1	26.41	0.00

^aTop model; $AIC_c = 128.93$.

AGE AT FIRST RETURN

The age at first return of the 35 resighted individuals ranged from 3 to 7 years (Fig. 3). The best-supported model included effects of year and mass at fledging (Table 3), and the importance values of each factor (0.80 and 0.68, respectively; Table 4) further indicated both had strong effects. Offspring from the 2000 cohort first returned at average age (4.0 ± 0.3 years) younger than those from the 1999 cohort (5.0 ± 1.0 years). The predicted age at first return decreased substantially as mass at fledging increased, from 6.0 to 4.5 years in 1999 and from 4.7 to 3.6 years in 2000 over the range of masses recorded at fledging in each year. The only other strongly supported model ($\Delta_i < 2$) included wing length at fledging in addition to year and mass at fledging (Table 3). Wing length at fledging had only a weak, negative effect on age at first return, given its intermediate importance value (0.40) and parameter estimate that was smaller than its unconditional standard error (Table 4). Fledging date was not included in any strongly supported model and had a low importance value (0.33; Table 4).

TABLE 2. Importance values, model-averaged parameter estimates and associated unconditional standard errors (SE) and 95% confidence intervals (95% CI) explaining local juvenile survival of the 1999 and 2000 cohorts of the Tufted Puffin on Triangle Island, British Columbia. The year 2000 was used as the reference category. See Table 1 for explanation of parameters.

Parameter	Importance	Estimate	SE	95% CI
Intercept		-13.4797	10.8654	21.2961
YEAR	1.00	-2.0768	1.0232	2.0055
FMASS	0.34	0.0012	0.0039	0.0076
FDATE	0.32	-0.0119	0.0781	0.1530
FWING	0.90	0.0993	0.0466	0.0913

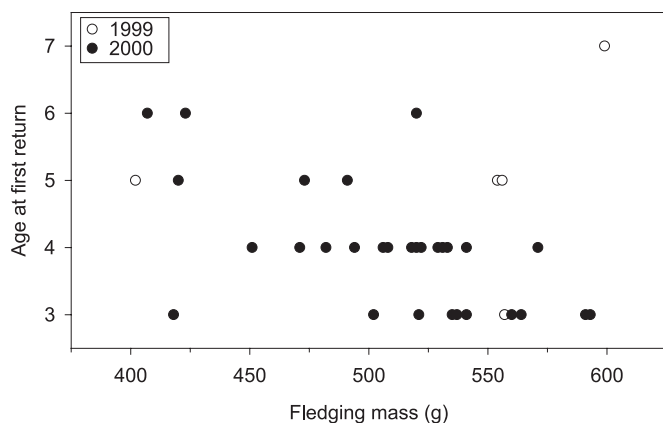


FIGURE 3. Age at first return to the natal breeding colony in relation to mass (g) at fledging of Tufted Puffins resighted at Triangle Island, British Columbia from the 1999 and 2000 cohorts ($n = 35$).

DISCUSSION

As predicted, puffins that fledged with a greater wing length were more likely to survive to return to their natal colony. There was also a weak, but detectable, tendency for increased survival rates among offspring that fledged heavier and earlier. Heavier fledglings and those with a greater wing length also returned to their natal colony at a younger age. However, annual (cohort) effects, which we did not expect given that nestlings of both cohorts grew rapidly, were the strongest effects on both local juvenile survival and age at first return. Contrary to prediction, we found little evidence of an effect of fledging date on age at first return.

LOCAL JUVENILE SURVIVAL

Cohort effects on local juvenile survival have been well documented in other seabird species (Harris et al. 1994, Sandvik et al. 2008) and are usually attributed to climatic effects on food availability or quality (Kitaysky et al. 2006, Frederiksen et al. 2008) or to direct mortality from severe weather. Given that the lipid content of the nestlings' diet in both years appeared similar (Gjerdrum 2001), the low survival of the 1999 cohort cannot be easily attributed to a "junk-food" diet (Romano et al. 2006, Kitaysky et al. 2006). Likewise, severe storms were apparently no more common in the northeast Pacific in the winter of 1999–2000 than in that of 2000–2001, on the basis of wave-height data recorded by buoys at sea (Bromerski et al. 2005, Menendez et al. 2008).

Puffins that fledged with longer wings were more likely to survive to return to their natal colony. Nestling alcid, including Tufted Puffins, fed a restricted diet during early development gain mass at greatly retarded rates, but the wing's growth rate is less affected (Øyan and Anker-Nilssen 1996, Romano et al. 2006, Benowitz-Fredericks et al. 2006, Sears and Hatch 2008). Likewise, as we found with the Tufted Puffin, Hipfner and Gaston (1999) found the mean mass at fledging of the Atlantic Puffin (*Fratercula arctica*; 50–80% of adult mass) varied much more by colony and year than did wing lengths at fledging (80–85% of adult size). Preferential allocation of energy and nutrients toward wing growth in alcid nestlings has been hypothesized to be an adaptive growth strategy (O'Connor 1977, Øyan and Anker-Nilssen 1996). Long wings may enable fledglings to reach the ocean when they depart the colony and to increase their diving and

TABLE 3. Support for general linear models predicting age at first return of the 1999 and 2000 cohorts of the Tufted Puffin at Triangle Island, British Columbia; $n = 35$ resighted individuals. SSE is the sum of squared error of each model, and R^2 is the multiple regression correlation coefficient. See Table 1 for explanation of parameters and other results presented.

Model	SSE	K	Δ_i	w_i	R^2
YEAR + FMASS ^a	27.93	4	0.00	0.29	0.26
YEAR + FMASS + FWING	26.47	5	0.86	0.19	0.29
YEAR + FMASS + FDATE	27.87	5	2.66	0.08	0.26
YEAR	32.97	3	3.24	0.06	0.12
YEAR + FWING	30.68	4	3.28	0.06	0.18
FDATE	33.15	3	3.43	0.05	0.12
YEAR + FDATE	30.81	4	3.44	0.05	0.18
YEAR + FMASS + FWING + FDATE	26.42	6	3.71	0.05	0.30
YEAR + FWING + FDATE	28.93	5	3.96	0.04	0.23
FWING + FDATE	31.62	4	4.34	0.03	0.16
FMASS	34.08	3	4.40	0.03	0.09
NULL	37.54	2	5.39	0.02	0.00
FMASS + FDATE	32.65	4	5.46	0.02	0.13
FMASS + FWING	32.81	4	5.63	0.02	0.13
FWING	35.61	3	5.94	0.02	0.05
FMASS + FWING + FDATE	31.32	5	6.74	0.01	0.17

^aTop model; $AIC_c = 1.44$.

TABLE 4. Importance values, model-averaged parameter estimates, and associated unconditional standard errors (SE) and 95% confidence intervals (95% CI) explaining age at first return of the 1999 and 2000 cohorts of the Tufted Puffin at Triangle Island, British Columbia. The year 2000 was used as the reference category. See Table 1 for explanation of parameters.

Parameter	Importance	Estimate	SE	95% CI
Intercept		6.9632	8.0906	15.8575
YEAR	0.80	0.9342	0.5502	1.0784
FMASS	0.68	-0.0047	0.0042	0.0083
FDATE	0.33	0.0104	0.0566	0.1110
FWING	0.40	-0.0183	0.0434	0.0851

foraging efficiency once at sea (Birkhead 1977, Hedgren 1981, Hipfner and Gaston 1999), thus increasing their chances of surviving. Our results provide an ultimate explanation for the results of earlier studies demonstrating preferential allocation to wing growth in puffins.

Low wing loading (body mass/wing area) could be important to successful colony departure in alcids (Barrett and Rikardsen 1992). Although we did not measure wing area to evaluate the effect of wing loading on local juvenile survival, our results indicate positive effects of both wing length and, to a lesser extent, mass at fledging on local juvenile survival, suggesting that minimization of wing loading is of lesser importance to the survival of juvenile puffins than having both long wings and being heavy at fledging.

In some other seabirds, nestlings that fledge at a heavier mass and at an earlier date are more likely to survive to return to their natal colony (Perrins et al. 1973, Harris et al. 1992, Ludwigs and Becker 2006), but in the Tufted Puffin we found these effects to be weak. The weak positive effect of mass at fledging on local juvenile survival might reflect the importance of large energy reserves buffering fledglings against food shortage during the critical period when they must learn to forage on their own (Weimerskirch et al. 2000). In pursuit-diving seabirds like puffins, learning to forage is a lengthy process that can be a key determinant of juvenile survival (Daunt et al. 2007). Early fledglings may have had slightly higher survival rates because they had more time to gain foraging efficiency before the onset of winter food shortages and severe weather (Harris et al. 1994).

Previous authors have suggested that in alcids the timing of fledging is driven by differences in growth rates and survival that can be expected in the nest and on the ocean (Ydenberg 1989, Ydenberg et al. 1995) or by the importance of reaching a critical minimum wing length before fledging (Hipfner and Gaston 1999, Deguchi et al. 2004). Our results support a positive effect of mass at fledging on juvenile survival, a critical assumption of the Ydenberg models, but also highlight the importance of including wing length at fledging in any consideration of the fledging decision of alcid nestlings.

Previous studies examining effects of fledging mass and date on local juvenile survival of other alcid species have produced inconsistent results (Harris et al. 1992, Hedgren 1981, Lloyd 1979, Harris and Rothery 1985, Gaston 1997). Only one of these other studies considered an alcid that is independent at fledging, whose characteristics at fledging should most strongly reflect survival probability. Null effects of date and condition on local juvenile survival in the Atlantic Puffin could be attributed to weak selection pressure resulting from near optimal conditions and a short migration distance to wintering grounds (Harris and Rothery 1985), low sample sizes of birds confirmed to have fledged, or a higher proportion of missed individuals through a protocol of recapture rather than resighting. In addition, our results suggest that the lack of clear effects of fledging mass or date on local juvenile survival in other alcid species could be the result of these studies not considering the importance of wing length at departure.

An alternative explanation of our results is that there is a bias in favor of resighting individuals that fledged with longer wings, heavier mass, or at an earlier date because they are more likely to recruit to their natal colony (Spear et al. 1998, Prevot-Julliard et al. 2001). Our resighting protocol should account for this possibility because our study site is the largest puffin colony in a large area (Piatt and Kitaysky 2002) and is likely to attract prospecting individuals (Serrano et al. 2003). No banded puffins were resighted at Sartine Island, the largest neighboring puffin colony (6000 pairs; Rodway 1991), over a 4-day survey in 2006. Furthermore, because our protocol was not dependent on individuals recruiting, it provided a better estimate of actual local juvenile survival since seabirds usually return first to their natal colony before emigrating or recruiting in subsequent years (Spear et al. 1998, Bradley et al. 1999, Dittmann et al. 2005). Our findings could also be explained by a difference between the sexes in wing length or mass at fledging and natal philopatry (Sagar and Horning 1998). However, no sexual difference is apparent in natal philopatry of the Atlantic Puffin (Harris 1983), and in the Rhinoceros Auklet (*Cerorhinca monocerata*, actually a puffin) the difference between sexes in wing lengths and masses at fledging is negligible (Addison et al. 2008).

AGE AT FIRST RETURN

We found a strong effect of cohort on age at first return that was unexpected given that both cohorts we studied were similarly strong (Gjerdrum et al. 2003), so we can only speculate as to its cause. The delay in age at first return of the 1999 cohort relative to the 2000 cohort may be related to the different environmental conditions that each cohort faced at its time of return. None of the 1999 cohort returned at the age of 4 years in 2003, a year of mild El Niño conditions when widespread breeding failure and colony abandonment at Puffin Rock (Hipfner et al. 2007) suggested food availability was low. Likewise, colony attendance of prospecting

Thick-billed Murres (*Uria lomvia*) decreases when food availability is low (Gaston and Nettleship 1982). In contrast, the puffins' breeding success on Triangle Island was much higher in 2004 (Hipfner et al. 2007), when half of the resighted individuals from the 2000 cohort first returned at the age of 4 years.

Puffins with a greater mass at fledging returned to their natal colony at a younger age than lighter fledglings. Although we know of no other studies relating characteristics at fledging to age at first return, some studies considering age at recruitment have found a similar effect of fledgling mass or size (Gaston 2003, Cam et al. 2003). The literature suggests that poor conditions early in life may constrain or restrain individuals from breeding at an earlier age because their condition reduces the potential net benefit of an early breeding attempt (Curio 1983). In the context of the current study, heavy fledglings appear to reach the condition at which the benefits of returning to begin the recruitment process outweigh the associated costs of breeding at a younger age. A restricted nestling diet (associated with a lighter mass at fledging) results in stunting of adult tarsus size in Tufted Puffins (Kitaysky 1999) and Rhinoceros Auklets (Sears and Hatch 2008), evidence long-term consequences of poor early development that may affect age at first return.

This study is the first to show an effect of wing length or mass at fledging on local juvenile survival or age at first return to the natal breeding colony of a semi-precocial alcid, while at the same time adding to the growing body of literature that demonstrates the importance of conditions early in life on fitness of birds (Lindstrom 1999). We found strong evidence that puffins with longer wings at fledging had higher local juvenile survival, whereas puffins that were heavier at fledging first returned to the natal colony at a younger age. Future studies should consider evaluating the effects of characteristics at fledging on age at first return, as in this study, in addition to age at recruitment. An examination of whether mass or wing length at fledging affects the quality of the mate or breeding site obtained and future reproductive success would also be informative as to the long-term consequences of variation in birds' condition at fledging.

ACKNOWLEDGMENTS

We are very grateful to a number of people for assistance in the field, especially M. Sorensen, J. Havelaar, L. Pollock, J. Ryder, and G. Yanega. Thanks to the British Columbia Ministry of Environment Lands and Parks for providing the permit to work on Triangle Island (Anne Vallée Ecological Reserve) and to the Canadian Coast Guard, West Coast Helicopters, J. Higham, M. Court, and C. Smith for providing essential logistical support. Our research was conducted under a scientific permit from the Canadian Wildlife Service and an animal-care permit from Simon Fraser University (SFU). This research was funded by the Natural Sciences and Engineering Research Council of Canada, Centre for Wildlife Ecology at Simon Fraser University, and the Canadian Wildlife Service. Additional support was provided to CG. and KWM. by SFU graduate fellowships and to KWM by an SFU C. D. Nelson Memorial Graduate

Entrance Scholarship. We thank two anonymous reviewers for their constructive reviews and D. Esler, B. Smith, N. Dulvy, P. Baird, R. Ydenberg, and S. Jamieson for helpful discussion and comments on previous drafts.

LITERATURE CITED

- ADDISON, B., A. S. KITAYSKY, AND J. M. HIPFNER. 2008. Sex allocation in a monomorphic seabird with a single-egg clutch: test of the environment, mate quality, and female condition hypotheses. *Behavioral Ecology and Sociobiology* 63:135–141.
- BARRETT, R. T., AND F. RIKARSEN. 1992. Chick growth, fledging periods and adult mass-loss of Atlantic Puffins *Fratercula arctica* during years of prolonged food stress. *Colonial Waterbirds* 15:24–32.
- BECKER, P. H., AND J. S. BRADLEY. 2007. The role of intrinsic factors for the recruitment process in long-lived birds. *Journal of Ornithology* 148:S377–S384.
- BENOWITZ-FREDERICKS, Z. M., A. S. KITAYSKY, AND C. W. THOMPSON. 2006. Growth and allocation in captive Common Murre (*Uria aalge*) chicks. *Auk* 123:722–734.
- BIRKHEAD, T. R. 1977. Adaptive significance of nestling period of Guillemots *Uria aalge*. *Ibis* 119:544–549.
- BOAG, P. T. 1987. Effects of nestling diet on the growth and adult size of Zebra Finches (*Poephila guttata*). *Auk* 104:155–166.
- BRADLEY, J., B. M. GUNN, I. J. SKIRA, AND R. D. WOOLLER. 1999. Age-dependent prospecting and recruitment to a breeding colony of Short-tailed Shearwaters *Puffinus tenuirostris*. *Ibis* 141:277–285.
- BROMERSKI, P. D., D. R. CAYAN, AND R. E. FLICK. 2005. Wave spectral energy variability in the northeast Pacific. *Journal of Geophysical Research-Oceans* 110:C03005–C03011.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, NY.
- CAM, E., J. MONNAT, AND J. E. HINES. 2003. Long-term fitness consequences of early conditions in the kittiwake. *Journal of Animal Ecology* 72:411–424.
- CATRY, P., N. RATCLIFFE, AND R. W. FURNESS. 1998. The influence of hatching date on different life-history stages of Great Skuas *Catharacta skua*. *Journal of Avian Biology* 29:299–304.
- CRISPIN, L., M. P. HARRIS, J-D. LEBRETON, AND S. WANLESS. 2006. Recruitment to a seabird population depends on environmental factors and on population size. *Journal of Animal Ecology* 75:228–238.
- CURIO, E. 1983. Why do young birds reproduce less well? *Ibis* 125:400–404.
- DAHDUL, W. M., AND M. H. HORN. 2003. Energy allocation and postnatal growth in captive Elegant Tern (*Sterna elegans*) chicks: responses to high- versus low-energy diets. *Auk* 120:1069–1081.
- DAUNT, F., V. AFANASYEV, A. ADAM, J. P. CROXALL, AND S. WANLESS. 2007. From cradle to early grave: juvenile mortality in European Shags *Phalacrocorax aristotelis* results from inadequate development of foraging proficiency. *Biology Letters* 3:371–374.
- DEGUCHI, T., A. TAKAHASHI, AND Y. WATANUKI. 2004. Proximate factors determining age and mass at fledging in Rhinoceros Auklets (*Cerorhinca monocerata*): intra- and interyear variations. *Auk* 121:452–462.
- DITTMANN, T., D. ZINSMEISTER, AND P. H. BECKER. 2005. Dispersal decisions: Common Terns, *Sterna hirundo*, choose between colonies during prospecting. *Animal Behaviour* 70:13–20.
- FREDERIKSEN, M., F. DAUNT, M. P. HARRIS, AND S. WANLESS. 2008. The demographic impact of extreme events: stochastic weather

- drives survival and population dynamics in a long-lived seabird. *Journal of Animal Ecology* 77:1020–1029.
- GASTON, A. 2003. Influence of chick mass and date at departure from the colony on adult characteristics in Ancient Murrelets (*Synthliboramphus antiquus*), a precocial seabird. *Auk* 120:818–826.
- 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. 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.
- GASTON, A. J., AND D. N. NETTLESHIP. 1982. Factors determining seasonal changes in attendance at colonies of the Thick-billed Murre (*Uria lomvia*). *Auk* 99:468–473.
- GJERDRUM, C. 2001. Nestling growth and parental provisioning of Tufted Puffins (*Fratercula cirrhata*) on Triangle Island, British Columbia. M.Sc. thesis, Simon Fraser University, Burnaby, BC.
- GJERDRUM, C. 2004. Parental provisioning and nestling departure decisions: a supplementary feeding experiment in Tufted Puffins (*Fratercula cirrhata*) on Triangle Island, British Columbia. *Auk* 121:463–472.
- GJERDRUM, C., A. M. J. VALLEE, C. C. ST. CLAIR, D. F. BERTRAM, J. L. RYDER, AND G. S. BLACKBURN. 2003. Tufted Puffin reproduction reveals ocean climate variability. *Proceedings of the National Academy of Sciences, USA* 100:9377–9382.
- GREEN, D. J., AND A. COCKBURN. 2001. Post-fledging care, philopatry and recruitment in Brown Thornbills. *Journal of Animal Ecology* 70:505–514.
- HALLEY, D. J., M. P. HARRIS, AND S. WANLESS. 1995. Colony attendance patterns and recruitment in immature Common Murres (*Uria aalge*). *Auk* 112:947–957.
- HARRIS, M. P. 1983. Biology and survival of the immature puffin *Fratercula arctica*. *Ibis* 125:56–73.
- HARRIS, M. P., AND P. ROTHERY. 1985. The post-fledging survival of young puffins *Fratercula arctica* in relation to hatching date and growth. *Ibis* 127:243–250.
- 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.
- HARRIS, M. P., S. T. BUCKLAND, S. M. RUSSELL, AND S. WANLESS. 1994. Post-fledging survival to breeding age of Shags *Phalacrocorax aristotelis* in relation to year, date of fledging and brood size. *Journal of Avian Biology* 25:268–274.
- HEDGREN, S. 1981. Effects of fledging weight and time of fledging on survival of Guillemot *Uria aalge* chicks. *Ornis Scandinavica* 12:51–54.
- HIPFNER, J., M. R. CHARETTE, AND G. S. BLACKBURN. 2007. Subcolony variation in breeding success in the Tufted Puffin (*Fratercula cirrhata*): association with foraging ecology and implications. *Auk* 124:1149–1157.
- HIPFNER, J. M., AND A. J. GASTON. 1999. Timing of nest departure in the Thick-billed Murre and Razorbill: tests of Ydenberg's model. *Ecology* 80:587–596.
- KITAYSKY, A. S. 1999. Metabolic and developmental responses of alcid chicks to experimental variation in food intake. *Physiological and Biochemical Zoology* 72:462–473.
- KITAYSKY, A. S., E. V. KITAISKAIA, J. F. PIATT, AND J. C. WINGFIELD. 2006. A mechanistic link between chick diet and decline in seabirds? *Proceedings of the Royal Society B* 273:445–450.
- KRUGER, O. 2005. Age at first breeding and fitness in Goshawk *Accipiter gentilis*. *Journal of Animal Ecology* 74:266–273.
- LEE, D. E., C. L. ABRAHAM, P. M. WARZYBOK, R. W. BRADLEY, AND W. J. SYDEMAN. 2008. Age-specific survival, breeding success, and recruitment in Common Murres (*Uria aalge*) of the California Current system. *Auk* 125:316–325.
- LINDSTROM, J. 1999. Early development and fitness in birds and mammals. *Trends in Ecology and Evolution* 14:343–348.
- LLOYD, C. 1979. Factors affecting breeding of Razorbills *Alca torda* on Skokholm. *Ibis* 121:165–176.
- LUDWIGS, J., AND P. H. BECKER. 2002. The hurdle of recruitment: influences of arrival date, colony experience and sex in the Common Tern *Sterna hirundo*. *Ardea* 90:389–399.
- LUDWIGS, J., AND P. H. BECKER. 2006. Individual quality and recruitment in the Common Tern *Sterna hirundo*. *Acta Zoologica Sinica* 52 (Supplement):96–100.
- MACKAS, D. L., S. BATTEN, AND M. TRUDEL. 2007. Effects on zooplankton of a warmer ocean: recent evidence from the northeast Pacific. *Progress in Oceanography* 75:223–252.
- MENENDEZ, M., F. J. MENDEZ, I. J. LOSADA, AND N. E. GRAHAM. 2008. Variability of extreme wave heights in the northeast Pacific Ocean based on buoy measurements. *Geophysical Research Letters* 35:L22607.
- METCALFE, N., AND P. MONAGHAN. 2001. Compensation for a bad start: grow now, pay later? *Trends in Ecology and Evolution* 16:254–260.
- MONROS, J. S., E. J. BELDA, AND E. BARBA. 2002. Post-fledging survival of individual Great Tits: the effect of hatching date and fledging mass. *Oikos* 99:481–488.
- MORRISON, K. W. 2009. Demographic consequences of early development and extreme climate events for alcids on Triangle Island, British Columbia. M.Sc. thesis, Simon Fraser University, Burnaby, BC.
- NEWTON, I. 1991. The role of recruitment in population regulation. *Acta Congressus Internationalis Ornithologici* 20:1689–1699.
- O'CONNOR, R. J. 1977. Differential growth and body-composition in altricial passerines. *Ibis* 119:147–166.
- ØYAN, H. S., AND T. ANKER-NILSSEN. 1996. Allocation of growth in food-stressed Atlantic Puffin chicks. *Auk* 113:830–841.
- PERRINS, C., M. P. HARRIS, AND C. K. BRITTON. 1973. Survival of Manx Shearwaters *Puffinus puffinus*. *Ibis* 115:535–548.
- PIATT, J. F., AND A. S. KITAYSKY. 2002. Tufted Puffin (*Fratercula cirrhata*), no 708. In A. Poole and F. Gill [EDS.], *The birds of North America*. Birds of North America, Inc., Philadelphia.
- PORTER, J. M. 1990. Patterns of recruitment to the breeding group in the Kittiwake *Rissa tridactyla*. *Animal Behaviour* 40:350–360.
- PORTER, J. M., AND J. C. COULSON. 1987. Long-term changes in recruitment to the breeding group, and the quality of recruits at a Kittiwake *Rissa tridactyla* colony. *Journal of Animal Ecology* 56:675–689.
- PREVOT-JULLIARD, A., R. PRADEL, R. JULLIARD, V. GROSBOIS, AND J. LEBRETON. 2001. Hatching date influences age at first reproduction in the Black-headed Gull. *Oecologia* 127:62–68.
- REID, J. M., E. M. SIGNAL, S. SIGNAL, D. I. MCCrackEN, AND P. MONAGHAN. 2003. Environmental variability, life-history covariation and cohort effects in the Red-billed Chough *Pyrrhocorax pyrrhocorax*. *Journal of Animal Ecology* 72:36–46.
- RODWAY, M. S., M. J. F. LEMON, AND K. R. SUMMERS. 1990. British Columbia seabird colony inventory: report #4—Scott Islands. Canadian Wildlife Service, Pacific and Yukon Region, British Columbia, Technical Report Series 86.
- RODWAY, M. S. 1991. Status and conservation of breeding seabirds in British Columbia. International Council for Bird Preservation Technical Publication 11:43–102.
- ROMANO, M., J. F. PIATT, AND D. D. ROBY. 2006. Testing the junk-food hypothesis on marine birds: effects of prey type on growth and development. *Waterbirds* 29:407–414.

- SAGAR, P. M., AND D. S. J. HORNING. 1998. Mass-related survival of fledgling Sooty Shearwaters *Puffinus griseus* at the Snares, New Zealand. *Ibis* 140:329–331.
- SANDVIK, H., K. E. ERIKSTAD, P. FAUCHALD, AND T. TVERAA. 2008. High survival of immatures in a long-lived seabird: insights from a long-term study of the Atlantic Puffin (*Fratercula arctica*). *Auk* 125:723–730.
- SAS INSTITUTE. 2003. SAS/STAT user's guide. Version 9.1. SAS Institute, Inc., Cary, NC.
- SEARS, J., AND S. A. HATCH. 2008. Rhinoceros Auklet developmental responses to food limitation: an experimental study. *Condor* 110:709–717.
- SEDINGER, J. S., P. L. FLINT, AND M. S. LINDBERG. 1995. Environmental influence on life-history traits: growth, survival, and fecundity in Black Brant (*Branta bernicla*). *Ecology* 76:2404–2414.
- SERRANO, D., J. L. TELLA, J. A. DONAZAR, AND M. POMAROL. 2003. Social and individual features affecting natal dispersal in the colonial Lesser Kestrel. *Ecology* 84:3044–3054.
- SPEAR, L., AND N. NUR. 1994. Brood size, hatching order and hatching date: effects on four life-history stages from hatching to recruitment in Western Gulls. *Journal of Animal Ecology* 63:283–298.
- SPEAR, L. B., P. PYLE, AND N. NUR. 1998. Natal dispersal in the Western Gull: proximal factors and fitness consequences. *Journal of Animal Ecology* 67:165–179.
- SYDEMAN, W., AND S. D. EMSLIE. 1992. Effects of parental age on hatching asynchrony, egg size and third-chick disadvantage in Western Gulls. *Auk* 109:242–248.
- VERHULST, S., AND J. NILSSON. 2008. The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding. *Philosophical Transactions of the Royal Society B—Biological Sciences* 363:399–410.
- VERMEER, K., AND L. CULLEN. 1979. Growth of Rhinoceros Auklets and Tufted Puffins, Triangle Island, British Columbia. *Ardea* 67:22–27.
- WEHLE, D. H. S. 1980. The breeding biology of the puffins: Tufted Puffin (*Lunda cirrhata*), Horned Puffin (*Fratercula corniculata*), Common Puffin (*F. arctica*), and Rhinoceros Auklet (*Cerorhinca monocerata*). Ph.D. dissertation, University of Alaska, Fairbanks, AK.
- WEIMERSKIRCH, H., D. BARBRAUD, AND P. LYS. 2000. Sex differences in parental investment and chick growth in Wandering Albatrosses: fitness consequences. *Ecology* 81:309–318.
- YDENBERG, R. C. 1989. Growth mortality trade-offs and the evolution of juvenile life histories in the Alcidae. *Ecology* 70:1494–1506.
- YDENBERG, R. C., R. W. CLARK, AND A. HARFENIST. 1995. Intraspecific fledging mass variation in the Alcidae, with special reference to the seasonal fledging mass decline. *American Naturalist* 145:412–433.