

COMPARISON OF OFFSPRING GROWTH MODELS IN ATLANTIC PUFFINS *FRATERCULA ARCTICA*

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ABSTRACT

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Growth of morphological traits in the offspring of many seabirds, including Atlantic Puffins *Fratercula arctica*, has typically been characterized by linear models despite displaying nonlinear patterns. We assessed the fit of six typical avian growth models to measurements of puffling mass, wing length, and tenth primary length. Across all three biometrics, the first- and second-best performing models were nonlinear (i.e., quadratic, logistic, extreme value function); these models were then used to generate separate growth curves for individual pufflings and extract easily interpretable and comparable parameter estimates. We recommend the reported models in future studies incorporating metrics of puffling growth and encourage the use of this methodology to explore nonlinear growth patterns across avian species.

Key words: avian growth, biometrics, nonlinear models, parameter estimates, puffins

INTRODUCTION

Offspring growth analysis is a well-studied component of avian biology. Typically, growth is described by plotting a biometric measure against age, fitting a regression model to the data, and estimating or extracting parameter estimates (Ricklefs, 1967, 1976). Historically, several models have been selected as candidates for postnatal growth, including the logistic, Gompertz, von Bertalanffy, and extreme value function (EVF) models (Ricklefs, 1968, 1973; Tjørve & Tjørve, 2010).

Offspring growth parameters can function as life history descriptors across species (Starck & Ricklefs, 1998), as well as indicators of the overall health and well-being of individuals (Karkach, 2006). Chick growth has also been linked to broader ecological phenomena, such as marine prey availability (Lyons & Roby, 2011) and population health (i.e., density-related growth depression; Hunt et al., 1986). Patterns of chick growth differ among species and within species as a function of geographic location, phenology, nutrition, and genetics (Ricklefs, 1968). Growth analysis in seabirds is particularly interesting because seabirds (1) have much lower growth rates compared to other avian species and (2) are some of the only species in which offspring mass can surpass adult mass (Ricklefs, 1968). Several aspects of seabird biology have been associated with these growth patterns, including the relatively long chick-rearing period, low clutch size, and heavy reliance on flight for foraging (Ricklefs, 1968).

Like other seabirds, Atlantic Puffin *Fratercula arctica* chicks (hereafter: pufflings) exhibit a typified growth pattern, although there is considerable inter-individual variation in the shapes of these curves. After hatch, pufflings regularly increase in mass until reaching a peak at ~70% of the adult body mass (~270 g), which

is achieved 24–28 d post-hatch (Harris & Wanless, 2011). After this point, they decline in mass for the next 7–10 d until fledging. In contrast to mass, structural measurements such as wing length increase regularly with age, reaching a maximum at fledging or even post-fledging. Wing and bill length are thus considered better indicators of age, although growth curves for these traits are colony-specific (Harris & Wanless, 2011). It is important to note, however, that these patterns assume ideal growth conditions, and offspring growth may be delayed, extended, or otherwise altered in years of low food availability or otherwise poor conditions (Harris & Wanless, 2011; Øyan & Anker-Nilssen, 1996). Therefore, typical growth models may not be applicable to curves representing poorly nourished offspring (Ricklefs, 1968), despite concerted interest in relating chick growth to feeding conditions (i.e., Baillie & Jones, 2003; Fitzsimmons et al., 2017).

Regimes for measuring puffling mass and wing length growth in the field are fairly standardized. Typically, pufflings are measured less frequently during the initial “linear” growth period of 25–30 d (e.g., every 10 d) and more frequently as they approach fledging (e.g., every day, or every three to five days). This technique is used to more precisely identify the linear component of growth, from which the slope can be derived as the linear growth rate. Few studies assessing puffling growth have considered the nonlinear portion of the curve, although many include additional measures independent of the growth curve’s shape (e.g., fledging mass). On the Isle of May, Great Britain, puffling growth has been measured consistently from 1974–2010 and described according to peak mass, fledging mass/wing length, and linear growth rate (Harris & Rothery 1985; Harris & Wanless 2011). Similarly, a study by Archer and Taylor (2009) on Sule Skerry, Scotland, during 1982–2005 assessed fledging mass, mass/wing length ratios, and mean daily increases in mass

and wing length. Harris (1978) and Harris *et al.* (1998) presented annual mean fledging masses from their studies on St. Kilda, Scotland, 1973–1996, and Kress *et al.* (2017) measured mass/wing length ratios on three colonies in Maine, USA, 1993–2009. Several other studies rely on these parameters to make short-term inferences (Ashcroft, 1979; Baillie & Jones, 2003), draw long-term conclusions (Harris & Wanless 2011; Scopel *et al.*, 2019), or compare between experimental groups (Cook & Hamer 1997; Harris & Rothery 1985). More recently, simple or mixed effects linear regressions have been fit over a specified temporal window to obtain growth rates (Baillie & Jones, 2003; Barrett, 2015; Cook & Hamer, 1997; Dahl *et al.*, 2005; Diamond, 2021; Fitzsimmons, 2018; Olsen, 2021; Øyan & Anker-Nilssen, 1996) or mean weights of age classes (Baillie & Jones, 2003; Eilertsen *et al.*, 2008; Johnsen *et al.*, 1994). While Starck and Ricklefs (1998) provide nonlinear growth rate constants from several studies on Atlantic pufflings (*i.e.*, Ashcroft, 1979; Harris, 1976; Harris & Rothery, 1985; Pearson, 1968), only one of these studies reports puffling growth as nonlinear (Barrett *et al.*, 1987; logistic growth). For the remaining studies, nonlinear parameters must have been derived from the original data or from reported linear parameter estimates. To our knowledge, Barrett *et al.* (1987) represents the only comparison of nonlinear candidate models in pufflings to date (but see Rodway [1997] for use of nonlinear modeling to estimate age from wing length).

Employing an accurate and reliable method of measuring growth is essential to our understanding of population viability and success. Several of the previously listed studies have discussed changes in puffling growth over time, reporting a decline of 7–9 g in average daily mass gain (Harris & Wanless, 2011), a 15% reduction in fledging mass (Harris *et al.*, 1998), and a decrease in mass/wing length ratio by 0.0305 units. These reports contribute to our understanding of Atlantic Puffin population decline in the North Atlantic and may support their classification as Vulnerable on the IUCN Red List (BirdLife International, 2018).

In this study, we assess the fit of multiple nonlinear candidate models to puffling measurements taken over the course of the chick-rearing period. We expand Barrett *et al.*'s (1987) study on Norwegian colonies by evaluating puffling growth in the western North Atlantic, considering two additional nonlinear candidate models, and fitting curves to individual puffling measurements. Throughout this paper, we provide detailed explanations to enhance the reproducibility of our methodology in future studies. Our approach provides a precise assessment of individual growth variation, which, while broadly useful, may be particularly suited for work examining specific behavioral, morphological, or environmental correlates of offspring condition.

METHODS

Ethics

The procedures in this study were approved by the Animal Care Committee of Memorial University of Newfoundland (AUP 19-02-DW and associated amendments). Federal permission to conduct research was approved by a Migratory Bird Research permit (SC4061) and the Canadian Bird Banding Office (Permit holder: 10926). Provincial permission to access Witless Bay Ecological Reserve and sample birds was obtained from the government of Newfoundland and Labrador (WBER 2022-24).

Study site

This study was conducted on Gull Island in the Witless Bay Ecological Reserve of Newfoundland and Labrador, Canada (47°15'45.54"N, -52°46'18.73"W). The Atlantic Puffin colony on Gull Island is one of the largest in the western North Atlantic, with ~120,000 breeding pairs according to a 2012 population survey (Wilhelm, 2017). At colonies of this size, and assuming little variation in food availability, we might expect depressed offspring growth rates due to intraspecific competition (Hunt *et al.*, 1986). More recent population estimates, however, indicate that this colony is still growing and not food-limited (S. Wilhelm, personal communication, November 2023).

Field methods: hatch date

As part of a broader study investigating the predictors of puffling growth, 58 burrows were monitored during the 2022 breeding season. On 13 June and 24 June 2022, occupied burrows were identified using a burrowscope (EMS2021 Gopher Tortoise Camera System with infrared detection; Environmental Management Services, Canton, Georgia, USA) and marked if an egg was present. From 24 June until 20 July 2022 (*i.e.*, hatching period), burrows were checked with a burrowscope every three to five days for evidence of hatching. Nine of the 58 burrows were discovered empty before a puffling hatched, so data are available for only 49 burrows. Hatch date was determined based on burrow contents at each visit. If a burrow contained a puffling on a given visit and an egg on the previous visit, the hatch date was considered to be the midpoint between the visits (Baillie & Jones, 2003). If the puffling appeared wet, the hatch date was designated as the date of the current visit. If a burrow contained an egg, the burrow was re-checked after three to five days. However, if the puffling appeared to be hatching (*i.e.*, cracks or holes in the egg), the hatch date was designated as the date after the current visit, and the burrow was re-checked during the next visit to confirm the presence of a puffling.

Field methods: puffling morphometric data collection

Once a puffling hatched, we attempted to collect morphometric data at least five times for each individual. Pufflings were measured three times during the linear growth period (~10-, 20-, and 30-d post-hatch), and every three to six days thereafter until they reached typical fledging size (wing length \geq 130 mm). We did not visit thereafter to limit plot disturbance and reduce the probability of inducing premature fledging (Rodway *et al.*, 1996). For the first visit, we handled the puffling only if the parents were confirmed with the infrared camera as not present in the burrow. Pufflings were extracted carefully from the burrow, occasionally with the aid of rubber-tipped tongs. At each capture, mass was measured with a 600 g Pesola to the nearest 5 g, flattened wing chord length was measured with a stopped ruler to the nearest millimeter, and the stage of development was noted. Once the pufflings had pin feathers on their wings, the length of the tenth primary (*i.e.*, the longest, not including the downy tip; hereafter, p10) was measured with a 100 mm stopped ruler to the nearest millimeter. These metrics were chosen because they represent classic measures of size, as well as structural and feather development. On the last visit, pufflings with wing chords $>$ 125 mm were banded with a Canadian Wildlife Service (CWS) stainless steel band.

We were unable to measure ten pufflings because of the depth or complexity of the burrow. Twelve additional burrows were empty at

the first check, and in two cases the puffling was discovered dead. Empty burrows may not necessarily reflect puffling mortality, as some burrows could not be properly assessed because the adults had dug deeper after disturbance and/or capture. Many of the adults in our sample were captured as part of a complimentary study on parental coloration and offspring growth. Two additional pufflings were excluded because their burrows connected with the burrows of other monitored offspring and were therefore assumed to be the same individuals. Full data were collected for 15 individuals, and partial data were collected for eight additional individuals.

Model selection for chick growth

To generate metrics of chick growth, six different growth models were evaluated for mass, wing length, and p10 length. Each model was assessed using averages of the response variable (mass, wing length, or p10 length) at each age point to avoid pseudoreplication. The linear and quadratic models represent classic systems of equations that may be relevant to growth. The logistic, Gompertz, extreme value function (EVF), and von Bertalanffy models are considered typical postnatal growth models across many avian taxa and are taken from the analysis by Tjørve and Tjørve (2010) (Appendix 1, available on the website).

The best model was chosen for each metric of chick growth based on comparison of the corrected Akaike's Information Criterion (AICc), which is useful for comparing models generated from relatively small sample sizes. We ran the models with and without the last data point of the oldest recorded individual in our dataset, who was estimated to be 58 days old on the last capture date (i.e., five days older than the next observation). However, the AICc values of the two sets of models followed the same ranking order, so only results from the models including the outlier are presented here. In each case, the model with the lowest AICc was selected as the preferred model. Following Tjørve and Tjørve's (2010) approach, the preferred model was compared to the model with the second-lowest AICc value to determine the probability that we selected the better model of the two:

$$\text{probability} = e^{\text{AICc}(\text{preferred model}) - \text{AICc}(\text{second model})} / 2.$$

Chick growth parameters

Once the preferred models were selected for each growth metric, curves were fitted separately to each individual. We excluded pufflings that were sampled fewer than three times for a given biometric; therefore, of the 23 measured individuals, we generated mass and wing length growth curves for 18 individuals and p10 growth curves for 15 individuals.

Growth curves were generated using the *nlsList* function in the "nlme" package, grouping by individual ID and estimating variance separately for each growth curve (Pinheiro *et al.*, 2022). For pufflings with three or four measurements for a given biometric, growth curves could sometimes not be generated with *nlsList* due to either a near-perfect fit of the data or incompatibility with the model type. In such cases, we used the *nls* function in the "nlme" package to separately generate curves using fixed upper limits of $a = 0$ for mass (i.e., concave-down quadratic function), $K = 164$ mm for wing length, and $K = 82$ mm for p10 length (Pinheiro *et al.*, 2022; Tjørve & Tjørve, 2010). Tjørve and Tjørve (2010) recommend fixing upper asymptotes to average adult values in the population

if free asymptotes produce unrealistic estimates. Because pufflings are smaller than adults in every dimension at fledging, we used average adult values as an upper asymptotic limit rather than a fixed asymptote. For wing length, we used an upper limit of 164 mm based on the average wing length of 463 adult puffins in Witless Bay, Newfoundland. Because we did not have adult measurements of tenth primaries, we used half the wing length (82 mm) as the upper limit, which is just slightly higher than the largest value generated from *nlsList* (78 mm). The curves were then visually assessed to determine if the model properly fit the data.

For logistic and EVF models, four informative parameters could be extracted from the growth curves: growth rate constant (r , dimensionless measure describing how growth rate changes over time), normalized growth rate constant (r/K , scaled by asymptotic size and important for comparisons across colonies with different maximum sizes), the y -value at the inflection point (y_i), and the asymptotic value (K). For the quadratic model, the quadratic constant (a) and the maximum value (y_{max}) were extracted as analogs to the growth rate constant (r) and the asymptotic value (K), respectively. To evaluate the potential for historical comparison with parameters extracted from the linear portion of the curve, we investigated the relationship between the nonlinear growth constant and the linear growth rate. The key difference between these two parameters lies in how they represent growth. The nonlinear growth rate constant captures how fast the puffling grows initially, with higher values indicating more rapid initial growth, whereas the linear growth rate treats the puffling as growing consistently over time, with higher values indicating consistent rapid growth. Pearson correlations between nonlinear growth constants (r in logistic and EVF models; a in quadratic models) and linear growth rates were assessed to determine if a conversion factor could be calculated from a linear regression.

RESULTS

The pufflings for which we had full data ($n = 15$) were last sampled at a mean age of 45.7 d (standard deviation [SD] = 5.6, range = 39.0–58.5) and a median age of 44.0 d. Although this estimate lies at the upper limit of the normal fledging period for puffins (38–44 d; Harris & Wanless, 2011), longer fledging periods seem to be more common in recent decades (i.e., Isle of May fledging periods increased from 39–40 d in the 1970s to 42–46 d in the 2000s). This trend may, however, be limited to eastern North Atlantic colonies, as fledging periods on Machias Island have remained constant at ~45 d, including in poor condition years (i.e., heat waves; Major *et al.*, 2021). A fledging period of 45 d is similar to the mean in our sample, perhaps reflecting regional or colony differences in typical fledging periods. Indeed, estimates from the late 1990s at another western North Atlantic colony, Gannet Islands, Labrador, are consistent with these values (mean = 44.8 ± 2.2 d, range = 41–48 d; Baillie, 2001). While the average fledging period in our sample aligns with recent estimates from the western North Atlantic, the upper limit of our range falls well outside the norm. We may also have underestimated fledging age across our sample because we did not confirm fledging after pufflings reached typical fledging size. Taken together, this may indicate that our site experienced a mildly poor chick-rearing year. However, breeding success estimates from this year on Gull Island point to a good chick-rearing year (80.4%, fledged chicks/burrow; Zabala Belenguer, 2023). Because these breeding success plots were not located adjacent to our study site, we cannot determine whether the prolonged fledging periods we observed were the result of our

activities or due to small-scale variations across the island, such as habitat differences (e.g., Nettleship, 1972; Rodway *et al.*, 1998).

The preferred chick growth model differed between the three biometric measurements. The quadratic model was preferred for mass, the logistic model for wing length, and the extreme value function (EVF) model for p10 length (Table 1, Fig. 1). The EVF model was the only model to appear as either the preferred or second-best model for all three measures of chick growth, but it clearly represented structural growth better than mass gain (Fig. 1).

Typically, the best model is supported over another model if the difference in AICc is > 8 ; models with ΔAICc of 4–7 may be plausible alternatives, and models with ΔAICc of 0–2 should be considered practically equivalent (Burnham *et al.*, 2011). As expected, when the ΔAICc was small, as was the case for wing length and p10, the probability that the best model was selected dropped well below 50% (Table 1). Although there is considerable uncertainty in model selection in these cases, only the results from the preferred models are reported here, as they likely yield similar results to those from the second-best models. Additionally, all three preferred models fit the overall pattern of puffling growth well (adjusted [adj.] $R^2 = 0.64\text{--}0.96$). Importantly, the linear model was clearly not supported for any of the biometrics based on our AICc criteria.

Parameter estimates could be calculated for most individuals using the *nlsList* function (Fig. 2; Table A1 in Appendix 2, available on the website). There were nine cases for which growth curves could not be successfully generated with *nlsList* and were separately fit with the *nls* function. Based on visual inspection of the curves, realistic estimates (i.e., fit the curve shape) were created in five of these cases, and unrealistic, distorted curves (*sensu* Ricklefs, 1968) were created in two cases. In the remaining two instances, the upper limit constraint could not be met. These four instances of unrealistic and unbound curves were excluded from our final dataset, yielding final sample sizes of 18 for wing length, 17 for mass, and 12 for p10 length (Table A1 in Appendix 2).

There was a significant correlation between the nonlinear growth rate constant (r) and linear growth rate for wing length only ($r(15) = -0.61$, $P = .009$). We used a linear regression to derive a conversion equation connecting the two methods (nonlinear constant = $-0.038 \times \text{linear rate} + 0.246$).

DISCUSSION

Our analysis shows that the growth of Atlantic Puffin offspring follows a nonlinear pattern across multiple biometrics. We assessed the fit of a linear model and five nonlinear candidate models to daily average values of mass, wing chord, and p10 length. Both the preferred and second-best models for all three metrics were nonlinear. Specifically, mass was best fit by the quadratic model, wing length by the logistic model, and p10 length by the EVF model.

This study was conducted in a single population during a single breeding season. While it is plausible that the selected models provide the best fit to puffling growth data across different years and populations, this should not be presumed. Indeed, there can be considerable variation in growth regimes as a function of prey availability (e.g., Fitzsimmons *et al.*, 2017) and environmental conditions (e.g., Gjerdrum *et al.*, 2003). For instance, mass in poor food years tends to plateau around fledging with little to no weight loss at the end of the nestling period, mirroring asymptotic models more closely than the quadratic model (Barrett *et al.*, 1987). It is also possible that we did not capture typical growth patterns in this colony, as we recorded locally low breeding success and some instances of prolonged fledging periods. We therefore recommend adopting our proposed methodology to explore the fit of candidate models before drawing broader conclusions about puffling growth curves.

Nevertheless, in our study sample, the selected models produced realistic curves for most individual chick growth patterns. There were only four cases in which the chosen model did not fit an individual's measurements, typically because the data did not

TABLE 1
Atlantic Puffin *Fratercula arctica* chick growth model selection based on corrected AIC values

Biometric	Rank	Model	Adjusted R^2	AICc	AICc weight	ΔAICc	Probability best model
mass	1	Quadratic	0.64	540.95	0.70	—	82.75%
	2	EVF	0.61	544.46	0.12	3.51	
	3	Logistic	0.60	545.38	0.08	4.43	
	4	Gompertz	0.60	546.10	0.05	5.16	
	5	von Bertalanffy	0.60	546.51	0.04	5.56	
	6	Linear	0.36	570.41	0.00	29.47	
wing length	1	Logistic	0.96	378.11	0.54	—	29.40%
	2	EVF	0.95	378.81	0.38	0.70	
	3	Gompertz	0.95	382.57	0.06	4.45	
	4	von Bertalanffy	0.95	385.38	0.01	7.26	
	5	Quadratic	0.95	388.29	0.00	10.17	
	6	Linear	0.90	417.81	0.00	39.70	
p10	1	EVF	0.86	237.26	0.29	—	11.77%
	2	Logistic	0.85	238.05	0.25	0.250	
	3	Gompertz	0.85	238.36	0.17	1.10	
	4	Quadratic	0.85	238.44	0.16	1.18	
	5	von Bertalanffy	0.85	238.81	0.13	1.55	
	6	Linear	0.81	247.75	0.00	10.49	

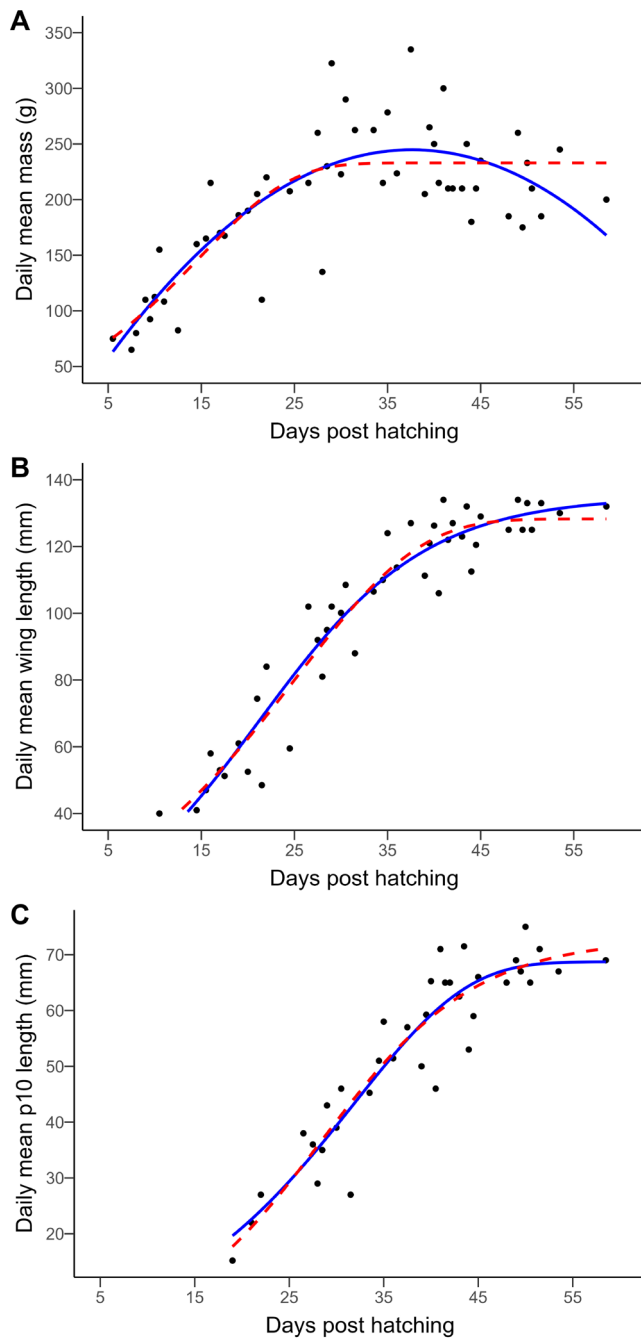


Fig. 1. Growth models for chicks of Atlantic Puffins *Fratercula arctica*. Each point represents the mean value at the given age across the study sample. Blue solid lines represent preferred models for each biometric, and red dashed lines represent second-best models for each biometric. (A) Mass growth curves with the quadratic model as preferred ($adj. R^2 = 0.64$) and extreme value function (EVF) model as second-best ($adj. R^2 = 0.61$). (B) Wing length growth curves with the logistic model as preferred ($adj. R^2 = 0.96$) and EVF model ($adj. R^2 = 0.95$) as second-best. (C) Tenth primary (p10) length growth curves with the EVF model ($adj. R^2 = 0.86$) as preferred and logistic model ($adj. R^2 = 0.85$) as second-best.

visually align with the curve. This was mostly a consequence of too few observations (i.e., four or fewer) and seemed especially likely to occur in the absence of measurements toward the end

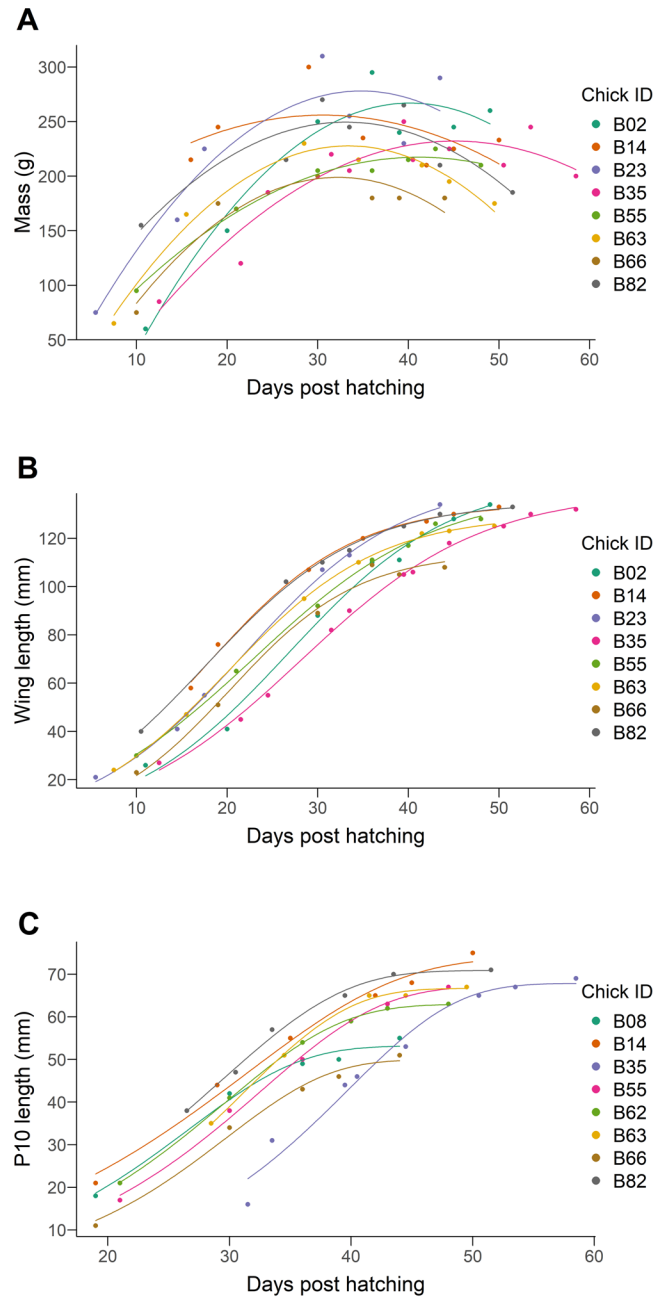


Fig. 2. Individual growth curves of Atlantic Puffin *Fratercula arctica* chicks generated by the *nlsList* function. For each biometric, samples from eight pufflings with the most measurements were chosen for visual display. (A) Quadratic growth curves for mass, (B) logistic growth curves for wing length, and (C) extreme value function (EVF) growth curves for tenth primary (p10) length.

of the chick-rearing period. For example, the single puffling for which a mass growth curve could not be calculated had five measurements (i.e., presumably sufficient), but the last weight measurement was taken at day 32. Similarly, the single puffling for which a wing length growth curve could not be estimated had only three measurements, with the last observation on day 30. These measurements are just outside the range of the linear growth period, which extends until day 25–30 in puffins (Harris & Wanless,

2011). Nearly all other individuals were measured at least once after day 35, providing a more complete picture of the post-linear growth period. Thus, we recommend that in future measurements of puffling growth, researchers should pay special attention to this period. For most studies on growth in Atlantic Puffins, pufflings were measured more frequently as they approached fledging, and our results provide support for such visitation regimes. Specifically, to balance accurate procurement of growth data with the negative effects of researcher disturbance, we suggest that pufflings be measured three to four times in the first 30 d after hatching and every three to five days thereafter until fledging. However, we also recommend that researchers include control plots adjacent to their study plots to assess the impact of this visitation regime on breeding success. When conducting studies unrelated to offspring growth at particularly sensitive colonies, a less intensive visitation regime is likely to be more suitable.

Another reason that the selected growth model could not be fit to an individual puffling was the inability of the asymptote to remain below the upper limit. In cases where data are truncated towards the end of the chick-rearing period, Tjørve & Tjørve (2010) suggested using fixed upper asymptotes based on adult mean morphometric values as a way to prevent the generation of unrealistic curves. We adapted this recommendation to our study species by employing upper asymptotic limits whenever there was a high risk of generating unrealistic growth curves (i.e., fewer than five measurements). These constraints ensured that only realistic growth curves were calculated. We did not fix the asymptote at a specific value because doing so can reduce model fit (Tjørve & Tjørve, 2010) and is particularly unsuitable for species that fledge at smaller sizes than adults, such as puffins. Therefore, we recommend using upper asymptotic limits in future studies of postnatal avian growth.

Our parameter estimates for wing and tenth primary feather length are easily extractable and interpretable. The growth rate and normalized growth rate constants, as well as the inflection point and asymptotic values, can be procured from most of our candidate nonlinear growth models. The growth rate constant is perhaps the most recognizable parameter and, as such, conversions between the logistic, Gompertz, and von Bertalanffy models have been calculated to allow for direct comparison (Ricklefs, 1968, 1973). The quadratic model is the one nonlinear curve under consideration using different parameters, and in our sample, puffling mass gain was clearly quadratic. We defined the mass's asymptotic value as the maximum value on the curve, roughly corresponding to asymptotic values of other nonlinear curves such as logistic and EVF growth. We also considered the quadratic constant a an analog of the growth rate constant r , as it influences both the concavity and width of the parabola based on the sign and value, respectively. While we acknowledge that this lack of comparability represents a limitation of our methodology, we maintain that the quadratic model is important to consider, as it was undoubtedly the best model for puffling mass gain.

Most studies to date have reported peak values and growth rates during the linear phase of growth (i.e., linear growth rates) for each biometric. The asymptotes calculated from nonlinear curves roughly correspond to peak values and can therefore be readily compared to historical data. In contrast, the growth rate parameters from nonlinear models are fundamentally different than linear growth rate. Most notably, the nonlinear growth constant is dimensionless, whereas linear growth rate is measured as daily change in size. This

limits the possibility of directly comparing nonlinear parameter estimates to historical, linear growth rate values. However, for wing growth, we found a significant correlation between the nonlinear growth constant and linear growth rate, permitting calculation of a conversion factor. We caution against the use of this conversion factor, however, without broader comparison of its utility in larger datasets spanning multiple years and populations. Instead, if the historical data are available, we recommend exploring the fit of nonlinear curves to original puffling measurements and calculating nonlinear growth rate constants where applicable, as in the summary of avian growth parameters presented by Starck and Ricklefs (1998). Otherwise, the only remaining option for parameters without conversion factors is to compare linear growth rates, either by linearizing the nonlinear curves or assessing growth rate within the linear portion of the curve (i.e., until 25–30 d of age).

We have shown that nonlinear growth curves can be used to characterize puffling growth. Although our approach is not a new methodology, it differs from most of the Atlantic Puffin literature, where puffling growth has been measured during the linear period only. Nonlinear growth parameters may provide additional detail that the linear phase of growth has not yet detected. We recognize that our approach is more time-intensive and potentially invasive, which may not make it suitable for all studies, especially those conducted in sensitive colonies where puffling growth is not the focus. However, it also has the potential to reveal new insights into the determinants of offspring success—an endeavor that is more important than ever for this threatened species. We hope that our study provides not only a framework for using nonlinear growth models in pufflings, but also a methodological playbook for successfully selecting and fitting curves to any postnatal avian growth dataset.

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REFERENCES

- Archer, M. G., & Taylor, R. C. (2009). Fledging weights of Atlantic Puffins *Fratercula arctica* on Sule Skerry, Scotland, with reference to a relatively poor season in 2005. *Seabird*, 22, 1–8. <https://doi.org/10.61350/sbj.22.1>
- Ashcroft, R. E. (1979). Survival rates and breeding biology of puffins on Skomer Island, Wales. *Ornis Scandinavica*, 10(1), 100–110. <https://doi.org/10.2307/3676349>
- Baillie, S. M. (2001). *Atlantic puffin response to changes in capelin abundance in Newfoundland and Labrador: An inter-colony and inter-decade comparison*. [Master's dissertation, Memorial University of Newfoundland]. Memorial University Research Repository.
- Baillie, S. M., & Jones, I. L. (2003). Atlantic puffin (*Fratercula arctica*) chick diet and reproductive performance at colonies with high and low capelin (*Mallotus villosus*) abundance. *Canadian Journal of Zoology*, 81(9), 1598–1607. <https://doi.org/10.1139/z03-145>

- Barrett, R. T. (2015). Atlantic Puffin *Fratercula arctica* chick growth in relation to food load composition. *Seabird*, 28, 17–29. <https://doi.org/10.61350/sbj.28.17>
- Barrett, R. T., Anker-Nilssen, T., Rikardsen, F., Valde, K., Røv, N., & Vader, W. (1987). The food, growth and fledging success of Norwegian puffin chicks *Fratercula arctica* in 1980–1983. *Ornis Scandinavica*, 18(2), 73–83. <https://doi.org/10.2307/3676842>
- BirdLife International. (2018). *Fratercula arctica*. IUCN Red List of Threatened Species 2018: e.T22694927A132581443. Retrieved December 2, 2024, from <https://doi.org/10.2307/IUCN.UK.2018-2.RLTS.T22694927A132581443.en>
- Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, 65, 23–35. <https://doi.org/10.1007/s00265-010-1029-6>
- Cook, M. I., & Hamer, K. C. (1997). Effects of supplementary feeding on provisioning and growth rates of nestling puffins *Fratercula arctica*: Evidence for regulation of growth. *Journal of Avian Biology*, 28(1), 56–62. <https://doi.org/10.2307/3677094>
- Dahl, H. K., Barrett, R. T., & Rolf, I. T. (2005). Effects of supplementary feeding on provisioning and growth rates of Atlantic puffin *Fratercula arctica* chicks in North Norway. *Atlantic Seabirds*, 7(3), 133–143.
- Diamond, A. W. (2021). Seabirds in a changing ocean: An overview of 20 years of research and monitoring on Machias Seal Island, Bay of Fundy, Canada. *Proceedings of the Nova Scotian Institute of Science*, 51(2), 354–409. <https://doi.org/10.15273/pnsis.v51i2.11165>
- Eilertsen, K., Barrett, R. T., & Torstein, P. (2008). Diet, growth and early survival of Atlantic Puffin (*Fratercula arctica*) chicks in North Norway. *Waterbirds*, 31(1), 107–114. [https://doi.org/10.1675/1524-4695\(2008\)31\[107:DGAESO\]2.0.CO;2](https://doi.org/10.1675/1524-4695(2008)31[107:DGAESO]2.0.CO;2)
- Fitzsimmons, M. G. (2018). *Sex-specific behavioural and physiological responses of breeding Atlantic puffins (Fratercula arctica) and their chicks to fluctuating prey abundance*. [Doctoral dissertation, Memorial University of Newfoundland], Memorial University Research Repository.
- Fitzsimmons, M. G., Rector, M. E., McKay, D. W., & Storey, A. E. (2017). High growth and low corticosterone in food-supplemented Atlantic puffin *Fratercula arctica* chicks under poor foraging conditions. *Marine Ecology Progress Series*, 565, 217–226. <https://doi.org/10.3354/meps11999>
- Gjerdrum, C., Vallée, A. M. J., St. Clair, C. C., Bertram, D. F., Ryder, J. L., & Blackburn, G. S. (2003). Tufted puffin reproduction reveals ocean climate variability. *Proceedings of the National Academy of Sciences*, 100(1), 9377–9382. <https://doi.org/10.1073/pnas.1133383100>
- Harris, M. P. (1976). Lack of a ‘desertion period’ in the nestling life of the puffin *Fratercula Arctica*. *Ibis*, 118(1), 115–118. <https://doi.org/10.1111/j.1474-919X.1976.tb02016.x>
- Harris, M. P. (1978). Supplementary feeding of young puffins, *Fratercula arctica*. *Journal of Animal Ecology*, 47(1), 15–23. <https://doi.org/10.2307/3919>
- Harris, M. P., Murray, S., & Wanless, S. (1998). Long-term changes in breeding performance of Puffins *Fratercula arctica* on St. Kilda. *Bird Study*, 45(3), 371–374. <https://doi.org/10.1080/00063659809461109>
- Harris, M. P., & Rothery, P. (1985). The post-fledging survival of young puffins *Fratercula arctica* in relation to hatching date and growth. *Ibis*, 127(2), 243–250. <https://doi.org/10.1111/j.1474-919X.1985.tb05059.x>
- Harris, M. P. & Wanless, S. (2011). *The Puffin*. Bloomsbury Publishing. <https://doi.org/10.1675/063.035.0220>
- Hunt, G. L., JR., Eppley, Z. A., & Schneider, D. C. (1986). Reproductive performance of seabirds: The importance of population and colony size. *The Auk*, 103(2), 306–317. <https://doi.org/10.1093/auk/103.2.306>
- Johnsen, I., Erikstad, K. E., & Sæther, B.-E. (1994). Regulation of parental investment in a long-lived seabird, the puffin *Fratercula arctica*: An experiment. *Oikos*, 71(2), 273–278. <https://doi.org/10.2307/3546276>
- Karkach, A. S. (2006). Trajectories and models of individual growth. *Demographic Research*, 15(12), 347–400. <https://doi.org/10.4054/DemRes.2006.15.12>
- Kress, S. W., Shannon, P., & O’Neal, C. (2017). Recent changes in the diet and survival of Atlantic puffin chicks in the face of climate change and commercial fishing in midcoast Maine, USA. *FACETS*, 1(1), 27–43. <https://doi.org/10.1139/facets-2015-0009>
- Lyons, D. E., & Roby, D. D. (2011). Validating growth and development of a seabird as an indicator of food availability: Captive-reared Caspian Tern chicks fed ad libitum and restricted diets. *Journal of Field Ornithology*, 82(1), 88–100. <https://doi.org/10.1111/j.1557-9263.2010.00311.x>
- Major, H. L., Durham, S. E., Fana, N., Rivers, J. E., & Diamond, A. W. (2021). Contrasting phenological and demographic responses of Atlantic Puffin (*Fratercula arctica*) and Razorbill (*Alca torda*) to climate change in the Gulf of Maine. *Elementa: Science of the Anthropocene*, 9(1), 00033. <https://doi.org/10.1525/elementa.2021.00033>
- Nettleship, D. N. (1972). Breeding success of the common puffin (*Fratercula arctica* L.) on different habitats at Great Island, Newfoundland. *Ecological Monographs*, 42(2), 239–268. <https://doi.org/10.2307/1942264>
- Olsen, M. (2021). *The effect of climate variability and prey abundance on chick growth in a subarctic Atlantic puffin (Fratercula arctica) colony*. [Master’s dissertation, University of Bergen]. Bergen Open Research Archive.
- Øyan, H. S., & Anker-Nilssen, T. (1996). Allocation of growth in food-stressed Atlantic puffin chicks. *The Auk*, 113(4), 830–841. <https://doi.org/10.2307/4088861>
- Pearson, T. H. (1968). The feeding biology of seabird species breeding on the Farne Islands, Northumberland. *Journal of Animal Ecology*, 37(3), 521–552. <https://doi.org/10.2307/3073>
- Pinheiro, J., Bates, D., Debroy, S., Sarkar, D., EISPACk authors, Heisterkamp, S., Van Willigen, B., Ranke, J., R Core Team. (2022). Package “nlme” (Version 3.1-160). CRAN. <https://svn.r-project.org/R/packages/trunk/nlme/>
- Ricklefs, R. E. (1967). A graphical method of fitting equations to growth curves. *Ecology*, 48(6), 978–983. <https://doi.org/10.2307/1934545>
- Ricklefs, R. E. (1968). Patterns of growth in birds. *Ibis*, 110(4), 419–451. <https://doi.org/10.1111/j.1474-919X.1968.tb00058.x>
- Ricklefs, R. E. (1973). Patterns of growth in birds. II. Growth rate and mode of development. *Ibis*, 115(2), 177–201. <https://doi.org/10.1111/j.1474-919X.1973.tb02636.x>
- Ricklefs, R. E. (1976). Growth rates of birds in the humid new world tropics. *Ibis*, 118(2), 179–207. <https://doi.org/10.1111/j.1474-919X.1976.tb03065.x>
- Rodway, M. S., Montevecchi, W. A., & Chardine, J. W. (1996). Effects of investigator disturbance on breeding success of Atlantic puffins *Fratercula arctica*. *Biological Conservation*, 76(3), 311–319. [https://doi.org/10.1016/0006-3207\(94\)00118-9](https://doi.org/10.1016/0006-3207(94)00118-9)
- Rodway, M. S. (1997). Relationship between wing length and body mass in Atlantic puffin chicks. *Journal of Field Ornithology*, 68(3), 338–347.

- Rodway, M. S., Chardine, J. W., & Montevecchi, W. A. (1998). Intra-colony variation in breeding performance of Atlantic Puffins. *Waterbirds*, 21(2), 171–184. <https://doi.org/10.2307/1521904>
- Scopel, L., Diamond, A., Kress, S., & Shannon, P. (2019). Varied breeding responses of seabirds to a regime shift in prey base in the Gulf of Maine. *Marine Ecology Progress Series*, 626, 177–196. <https://doi.org/10.3354/meps13048>
- Starck, J. M., & Ricklefs, R. E. (1998). *Avian growth and development: Evolution within the altricial-precocial spectrum*. Oxford University Press. <https://doi.org/10.1093/oso/9780195106084.001.0001>
- Tjørve, K. M. C., & Tjørve, E. (2010). Shapes and functions of bird-growth models: How to characterise chick postnatal growth. *Zoology*, 113(6), 326–333. <https://doi.org/10.1016/j.zool.2010.05.003>
- Wilhelm, S. (2017). *CWS: Waterbird colony database (Atlantic region)*. OBIS Canada Digital Collections. http://ipt.iobis.org/obiscanada/resource?r=cws_atlantic_colonydbase
- Zabala Belenguer, R. (2023). *Estimating breeding status in Atlantic puffin colonies across Newfoundland: A methodological comparison*. [Master's dissertation, Memorial University of Newfoundland]. Memorial University Research Repository.
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