

BIOMETRICS AS PREDICTORS OF CHICK AGE IN EUROPEAN STORM PETRELS *HYDROBATES PELAGICUS*

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ABSTRACT

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Hatching dates for seabird chicks are often unknown, though they are of key utility for monitoring breeding timing, success, and chick fitness. Biometric measurements of known-age chicks can be used to construct growth curves for estimating the ages of chicks of unknown age. Such growth curves can be of particular use in species whose nesting attempts are not readily observed, such as in burrow-nesting species. However, comprehensive growth curves for chicks are not available for many seabird species. Here we use data collected in two breeding seasons on Mousa, Shetland, United Kingdom, to produce growth rate curves for the burrow-nesting European Storm Petrel *Hydrobates pelagicus*. We analyse data on body mass, and wing and tarsus length measurements, of known-age chicks. Importantly, all models account for individual-level variation in growth rates. Body mass and tarsus length increased consistently with age until *ca.* 40 d, after which body mass decreased and tarsus growth plateaued as chicks approached fledging size. We provide estimates of age and their associated body mass, tarsus length, and wing length across the full range of biometric measurements modelled. Age estimates derived from these biometrics will facilitate the ageing of storm petrel chicks to within *ca.* 3–6 d for birds up to around 65 d old. Obtaining multiple biometric measurements from individuals, and/or using multiple biometric types, may further refine these estimates.

Key words: biometrics, growth curve, growth rates, Hydrobatidae, physiology, Procellariiformes

INTRODUCTION

Determining the age of chicks can provide a useful measure of breeding timing, from which inferences can be made about the favourability of local environmental conditions. Chick age may also indicate the likelihood of fledging success when chicks are estimated to be older than the minimum fledging age (Minguez & Oro, 2003). In addition, chick age facilitates the back-calculation of hatching dates, which are key fitness indicators at both the individual and population levels (Hatchwell, 1991). Chick age may be determined through frequent nest observations to identify hatching dates of chicks directly. An approximation of chick age may also be obtained from measurements of morphological features known to correlate with age, either as single or combined measurements, such as wing length, body mass, and tarsus length (Benson & Piatt, 2003; Huin & Prince, 2000). However, acquiring high resolution growth rate data that can be used to generate growth curves and predictive equations to reliably age chicks requires intensive preliminary studies. Consequently, biometric growth curves to age chicks are not available for many seabird species.

In burrow-nesting species, such as storm petrels, monitoring breeding attempts can be difficult because incubating adults are not readily observed. Therefore, monitoring the breeding of burrow-nesting species typically requires multiple visits to individual nests throughout a breeding season. Growth curves of phylogenetically related burrow-nesting species may show similar trends and relationships (Bedolla-Guzmán et al., 2017; Mauck & Ricklefs, 2005). However, species-specific growth

curves are required for accurate back-calculation of age because physiological characteristics, climatic conditions, and overall body size vary between and even within species (Mauck & Ricklefs, 2005).

Growth rates of chicks have been quantified for several storm petrel species using biometric measurements to allow the back-calculation of chick age and the estimation of hatching and laying dates (Boersma & Parrish, 1998; Fiske et al., 2013). However, for the European Storm Petrel *Hydrobates pelagicus* (hereafter ‘storm petrel’), there are currently no published growth curves and associated equations that allow chick age to be estimated from body mass, wing length, or tarsus length, or that compare the relative utility of these three measures. Both Scott (1970) and Bolton (1995) present growth curves for storm petrel body mass, and Scott (1970) additionally provides growth curves for wing length. However, neither study provides equations for estimating chick age from these biometric measurements, and neither includes growth curves for tarsus length. Consequently, estimates of storm petrel chick age, and subsequent inferences on breeding timing and its relationship with extrinsic factors, remain relatively coarse.

To address the lack of chick growth equations that can be readily used to estimate chick age in studies of the storm petrel, we reanalysed data collected in the early 1990s of chick body masses, tarsus length, and wing length. From these data, we derived formulae for back-calculating chick age from each biometric measure and determined the maximum age at which these estimates are reliable.

METHODS

Data Collection

To determine the relationship between chick age and tarsus length in the European Storm Petrel, we used data collected from chicks of known hatching date on Mousa, Shetland (60°00'N, 01°11'W), during 1992 and 1993. All chicks were monitored through to fledging. On Mousa, storm petrels breed in boulder beaches, scree, abandoned buildings, and structures such as stone walls. Storm petrels lay a one-egg clutch and can rear a maximum of one chick per breeding season, which remains in the nest for *ca.* 65 d until fledging.

Storm petrel nests can be hard to access because birds nest in small crevices reached by narrow, winding access routes. Extreme care is required when accessing nests to avoid damaging these fragile structures, as even minor disturbance may alter the access route and prevent a bird from reaching their nest. To facilitate easy and safe monitoring of breeding attempts by the petrels on Mousa, a number of nest boxes were installed in stone walls on the island in the early 1990s (Bolton, 1996). Nesting attempts in nest boxes and accessible natural sites were monitored intensively in both years of data collection for this study, and hatching dates were recorded for all chicks.

Body mass was measured to the nearest 0.1 g using digital scales ($n = 1,631$ observations). Chick's tarsus length was measured to the nearest 0.1 mm using dial callipers ($n = 1,600$ observations), and wing lengths were measured to the nearest 1 mm using a wing rule ($n = 587$ observations). The minimum tarsus length was recorded, defined as the distance between the foot and the notch of the "knee" (Redfern & Clark, 2001). Wing length was measured as the maximum chord length and was recorded only in 1993 in chicks aged 25 d or older, after primary feather growth had started. For many chicks, biometric measurements were recorded repeatedly prior to fledging (Table 1; Appendix 1, available on the website). All measurements were taken by the same individual in both years.

Statistical Analysis

All analysis was undertaken in R statistical software version 4.3 (R Core Team, 2024). For each biometric measure, we tested whether a linear, quadratic, logistic, Richards, or Gompertz curve produced the best model fit through comparison of AIC scores and R^2 values. We incorporated a random effect of 'individual ID' in each case to account for individual-level variation in growth rates.

Linear and quadratic models were run in the R package "lme4" (Bates et al., 2001). All logarithmic, Gompertz, and Richards curve

models were run using the R package "saemix" (Comets et al., 2017), with model formulae following those described in Boedeker (2021).

The logistic curve took the following form:

$$G_t = \text{Lower Asymptote}_i + \frac{\text{Total Growth}_i}{1 + e^{-\text{Approach}_i(t - \text{Timing}_i)}} + u_{i,t}$$

The Richards curve took the following form:

$$G_t = \text{Lower Asymptote}_i + \frac{\text{Total Growth}_i}{(1 + s_i \cdot e^{-\text{Approach}_i(t - \text{Timing}_i)})^{\frac{1}{s_i}}} + u_{i,t}$$

The Gompertz curve took the following form:

$$G_t = \text{Lower Asymptote} * \text{Total Growth}_i * e^{-e^{-\text{Approach}_i(t - \text{Timing}_i)}} + u_{i,t}$$

where G_t is the 'growth measure' at time t , Lower Asymptote_i is the lower asymptote for individual ' i ', Total Growth_i is the total change in the growth measure for individual ' i ', Approach is the rate of growth to the upper asymptote for individual ' i ', Timing_i is the age of individuals at the inflection point, s_i , and $u_{i,t}$ is the residual for individual i at time t .

Because data were collected over two breeding seasons, *Year* was also included as a fixed term in all models. However, this effect was non-significant in all cases, and model fit was improved when it was excluded. Consequently, this term is not included in final models (ΔAIC for models including *Year* as a fixed term: mass = +8.5, tarsus = +43.6, wing length = +20.1).

To model the relationship between chick age and body mass, we used a quadratic polynomial because this produced the best model fit ($R^2 = 0.83$; ΔAIC relative to the next-best model = 12.7, simple linear model).

We used a Richards curve to model the relationship between chick age and tarsus length ($R^2 = 0.99$; ΔAIC relative to the next best performing model, Gompertz = 86).

Lastly, we used a Gompertz curve to model the relationship between chick age and wing length ($R^2 = 0.99$; ΔAIC to the next best performing model, Richards = 0.96).

RESULTS

Summary of Biometric Data

For context, the relationships among the three biometric measures are presented in Fig. 1. Tarsus length was strongly correlated with chick body mass and moderately correlated with wing length (Fig. 1; body mass: $cor = 0.92_{df=91}$, $p < .01$; wing length: $cor = 0.43_{df=72}$, $p < .01$). The relationship between body mass and tarsus length plateaued beyond a tarsus length of *ca.* 23 mm. In contrast, body mass was not significantly related to wing length ($p = .09$).

Growth Rates

For all three biometric measurements, initial growth was broadly linear, although all biometrics ultimately followed a non-linear relationship with age (Fig. 2).

TABLE 1

Number of biometric measurements (body mass, tarsus length, and wing length) obtained from chicks in each study year^a

Year	Biometric		
	Body mass (g)	Tarsus length (mm)	Wing length (mm)
1992	28 (2)	28 (2)	n/a
1993	86 (5)	86 (5)	75 (0)
Total	114	114	75

^a Values in brackets indicate the number of chicks without repeated biometric measurements in a given year.

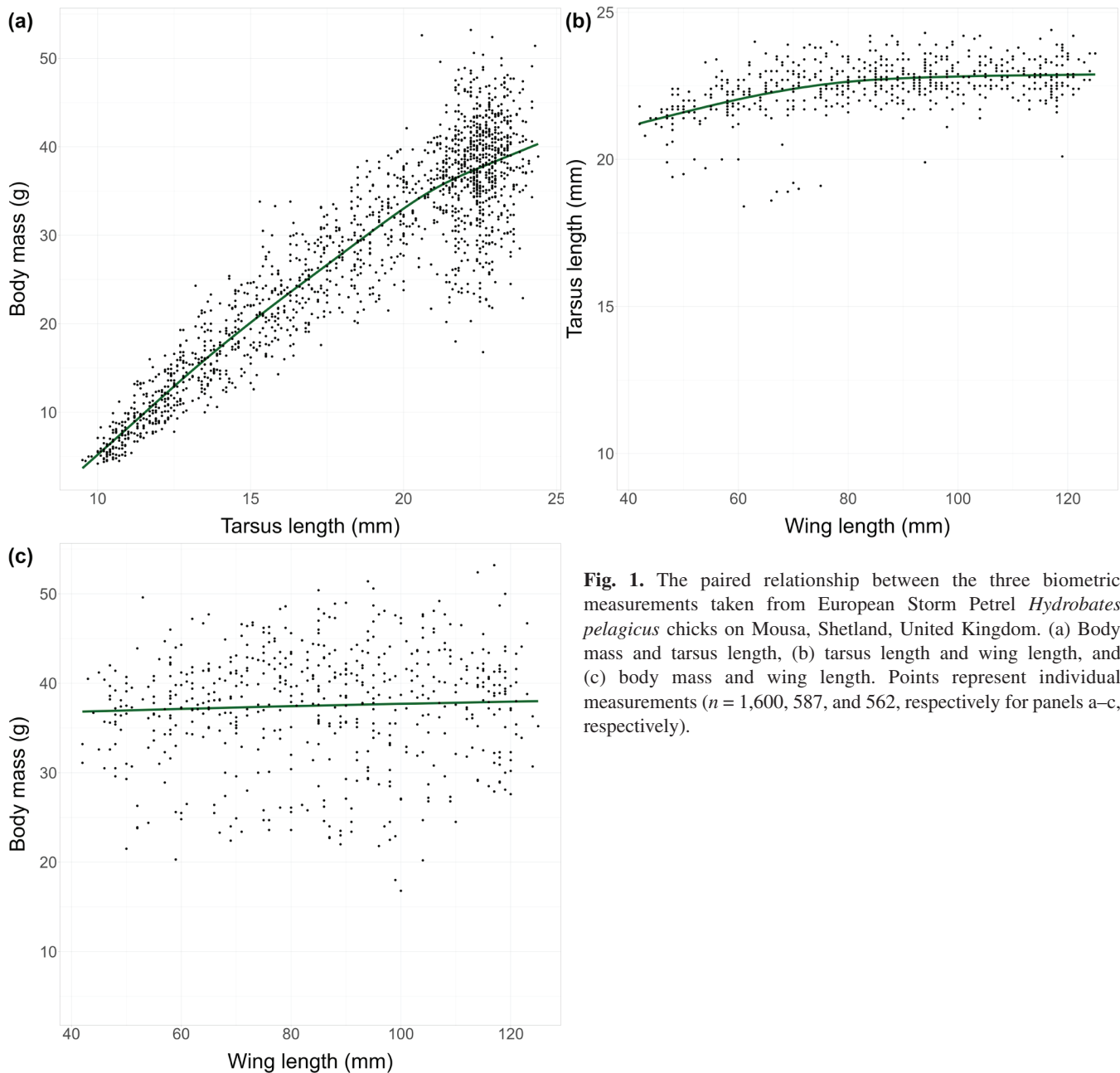


Fig. 1. The paired relationship between the three biometric measurements taken from European Storm Petrel *Hydrobates pelagicus* chicks on Mousa, Shetland, United Kingdom. (a) Body mass and tarsus length, (b) tarsus length and wing length, and (c) body mass and wing length. Points represent individual measurements ($n = 1,600, 587$, and 562 , respectively for panels a–c, respectively).

There was a broadly linear relationship between chick body mass and age until *ca.* 30 d of age (body mass = 34.6 g; Fig. 2a). Beyond *ca.* 30 d of age, the rate of increase in body mass slowed and the relationship between body mass and age became non-linear. From *ca.* 49 d of age onward, body mass showed a negative relationship with age. Furthermore, once chicks reached a body mass of *ca.* 30 g, the quadratic nature of the relationship meant that body mass could no longer be used as a reliable predictor of age because the equation yielded two viable solutions of the equation (i.e., two possible age estimates for a given mass). The associated standard error in estimated ages derived from body mass increased markedly from *ca.* 25 ± 4 d to ± 7 d of age, largely as a consequence of the quadratic relationship. The relationship of chick age and body mass can be described with the following formula, and ages can be estimated reliably for chicks with body masses up to 30 g when the plus-minus term is considered a '+':

$$\text{Age (days)} = 49.35 \pm \frac{\sqrt{2.46 - 0.0613(\text{Body mass (g)})}}{-0.0306}$$

The relationship between chick tarsus length and age was curvilinear, reaching a plateau in growth from *ca.* 50 d of age. As with body mass, the standard error of age estimates derived from tarsus lengths increased markedly, from *ca.* 25 ± 3 d of age to ± 7 d thereafter. Chick ages may be estimated from tarsus length using a Richards curve, described using the formula below. In the formula, G is the observation for an individual ' i ' at time ' t '. Population averages for the model parameters were 9.7 for the lower asymptote, 13.13 for total growth, 0.13 for the rate of approach to the upper asymptote at the point of inflection, 0.92 for the symmetry parameter, and 19.07 for the age at which the rate of change in growth was the greatest. Each parameter was subject to individual-level variation ' i ', and ' u ' represents the residual

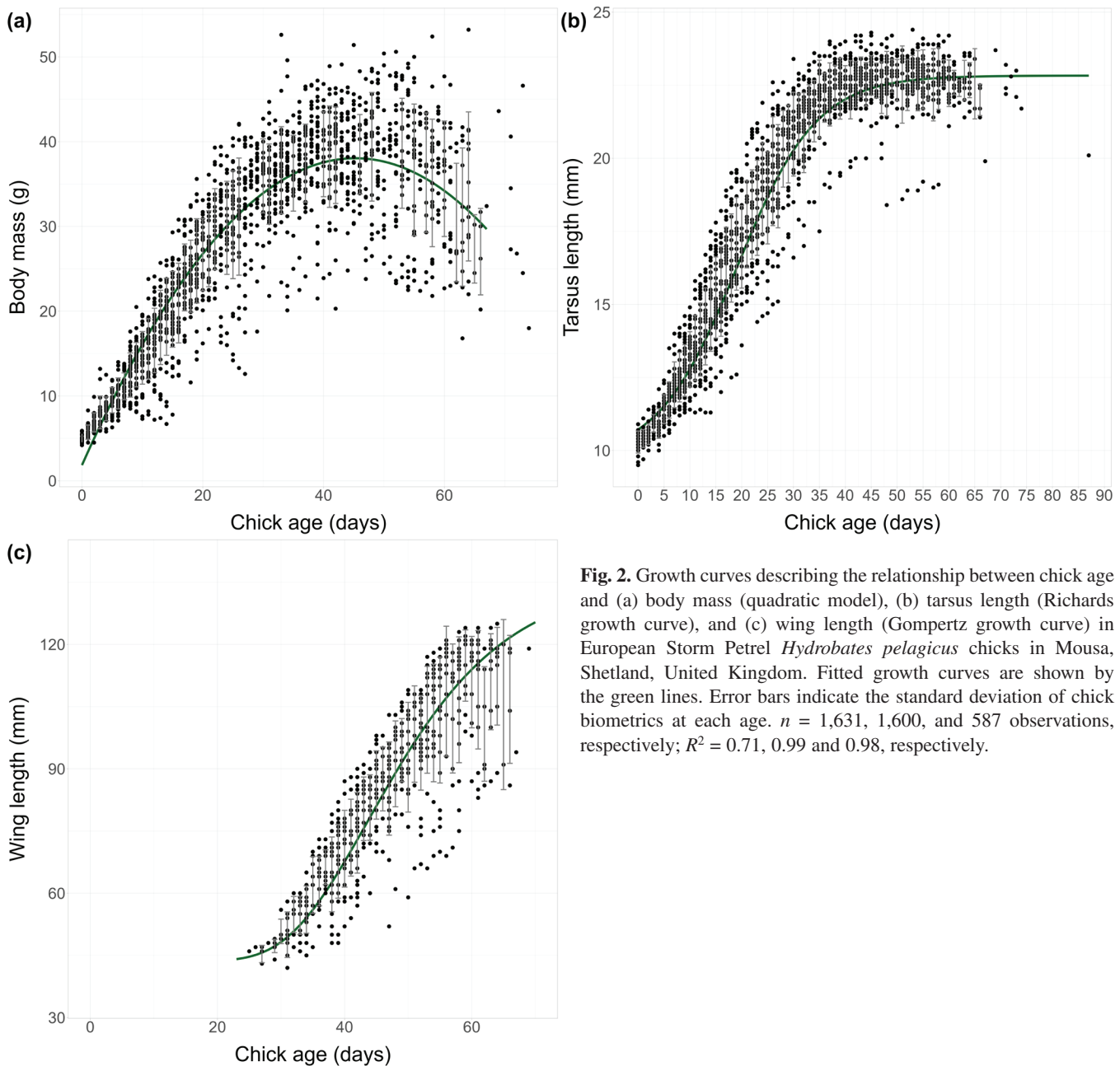


Fig. 2. Growth curves describing the relationship between chick age and (a) body mass (quadratic model), (b) tarsus length (Richards growth curve), and (c) wing length (Gompertz growth curve) in European Storm Petrel *Hydrobates pelagicus* chicks in Mousa, Shetland, United Kingdom. Fitted growth curves are shown by the green lines. Error bars indicate the standard deviation of chick biometrics at each age. $n = 1,631$, $1,600$, and 587 observations, respectively; $R^2 = 0.71$, 0.99 and 0.98 , respectively.

error for individual ' i ' at time ' t ', where t denotes chick age in days (Fig. 2b):

$$G_{i,t} = 9.7_i + \frac{13.13_i}{(1 + 0.92_i \cdot e^{-0.13_i(t-19.07_i)})^{0.92}} + u_{i,t}$$

The above equation can then be approximated and rearranged to solve for ' t ' (chick age, d):

$$t = 19.07 - \frac{1}{0.13} \ln\left(\frac{\left(\frac{13.13}{Tarsus\ Length - 9.7}\right)^{0.92} - 1}{0.92}\right)$$

The relationship between chick wing lengths and age was also curvilinear but did not reach a plateau across the ages measured. The standard error of age estimates derived from wing length

remained relatively consistent until *ca.* 50 d of age, after which it increased from an average of ± 3 d to ± 6 d. Wing length followed a Gompertz growth curve (Fig. 2c). Accordingly, chick age may be estimated from wing length with the formula below. In the formula, G represents the wing length for an individual ' i ' at time ' t ' (where t is chick age, d). Population averages provided for the model parameters were 43.62 for the lower asymptote, 92.34 for total growth, 0.08 for the rate of approach to the upper asymptote at the point of inflection, and 43.78 for the age at which the rate of change in growth was greatest. Each parameter was subject to individual-level variation ' i ', and ' u ' represents the residual error for individual ' i ' at time ' t ', where t denotes the age in days (Fig. 2c):

$$G_t = 43.62 * 92.34_i * e^{-e^{0.08_i(t-43.73_i)}} + u_{i,t}$$

The above equation can then be approximated and rearranged to solve for 't' (chick age, d):

$$t = 43.73 + 12.5 \ln[-\ln(\frac{\text{Wing Length}}{4027.9})]$$

Predicted ages corresponding to a range values for each of the three biometric measures are provided in Table 2. As shown, the growth rate of chicks decreased with age; consequently, age estimates for older chicks are subject to greater imprecision than those for younger chicks (Table 2). Larger-format versions of all growth curves, presented at finer increments to improve readability, are provided in Appendix 2.

DISCUSSION

We quantified the relationship between three chick biometric measures and age in European Storm Petrels up to 65 d, or fledging. Body mass increased consistently with age until *ca.* 40 d, after which chicks lost mass. Tarsus length increased non-linearly with age until *ca.* 40 d, after which growth approached a plateau. Wing length also showed a logistic relationship with age but did not reach a plateau within the age range measured. Overall age estimates derived from tarsus length and body mass were most precise for younger chicks, with chicks < 25 d old assigned ages with an average uncertainty of ± 3 –4 d. Thereafter, chicks could be aged to within ± 7 d using tarsus length until *ca.* 40 d of age, beyond which tarsus length could not be used to estimate age reliably. In contrast, wing length could be used to estimate the age of chicks from *ca.* 25 d to fledging (*ca.* 65 d), although the associated error increased from ± 3 d for chicks < 50 d, to about ± 6 d for older chicks. Consequently, measurements of body mass, tarsus length, and wing length provide a useful, though relatively imprecise, measure of their age. If multiple measurements are obtained from the same chick, the variation in the relationship between age and each biometric measurement may yield a range of potential age estimates. In particular, repeated measurements of tarsus length over multiple time points may increase confidence in derived ages; where a single measurement gives a range of potential ages, obtaining one or more additional measurements may help refine age estimates further where measures fall in between the age estimates provided in Table 1.

Chicks of several storm petrel and other procellariiform species increase in body mass until shortly before fledging, after which body mass decreases until fledging (Albores-Barajas et al., 2015; Bolton, 1995; Scott, 1970). Our data show the same pattern, which somewhat limits the utility of body mass alone as an indicator of age. Once body mass exceeds 30 g, the range of possible ages becomes relatively broad (*ca.* 23–65+ d of age). Consequently, our analyses suggest that tarsus length, wing length, or a combination of both provides a more useful means of ageing chicks across their development. In Wilson's Storm Petrel *Oceanites oceanicus*, tarsus length was also found to be the most useful and reliable method to age chicks (Quillfeldt & Peter, 2000). Both wing length and tarsus length were found to be the most useful and consistent biometrics for ageing chicks in several other storm petrel species and followed the same growth pattern (Bedolla-Guzmán et al., 2017; Fiske et al., 2013; Mauck & Ricklefs, 2005). Tarsus length reaches adult size (*ca.* 19.6–24.3 mm; Demongin, 2016) well before fledging, resulting in the observed growth plateau. In contrast, wing length may continue

to increase until fledging, reaching 116–134 mm in adults (this study; Bedolla-Guzmán et al., 2017; Demongin, 2016; Fiske et al., 2013). Therefore, wing length may provide the most reliable biometric measurement for ageing storm petrel chicks from mid-development onward, though combining multiple metrics or obtaining repeated measurements over time may further improve the precision of age estimates. Some studies have shown that storm petrel chicks that survive to 25 d of age are very likely to fledge. Minguez & Oro (2003) found that 94% of chick mortality occurred before 25 d age. Therefore, estimating a chick's age as > 25 d from tarsus or wing length may provide a reliable estimate of fledging probability. However, age-specific survival likelihood may vary between years and regions.

The greater confidence in assigned ages for chicks up to *ca.* 25 d of age, for all biometrics assessed here, also indicates that these biometrics could be used to estimate breeding success without requiring repeated visits by researchers throughout the *ca.* 65-d fledging period (Davis, 1957; Scott, 1970). Consequently, a single visit to a nest containing a chick estimated to be > 25 d old may provide a useful broad estimate of breeding success.

The growth rate of chicks may be influenced by changes in prey availability and climatic factors, both of which may vary inter-annually and affect fledging success (Benowitz-Fredericks et al., 2006; Hunt & Hunt, 1976; Sauve et al., 2023). In years where extrinsic conditions are less favourable, growth rates may be slower (Mauck & Ricklefs, 2005). Consequently, growth rate curves derived solely from years with favourable conditions, and faster growing chicks, may predict chick age less accurately than those developed from data spanning a wider range of potential growth rates (Watson et al. 2021). Because the data in this study were collected in only two breeding seasons, they are unlikely to encompass the full range of possible growth trajectories across each biometric measurement. However, a relatively large number of individual chicks were measured in both years, irrespective of whether they later fledged successfully, and therefore the data should capture a broad range of growth rates. Watson et al. (2021) also investigated growth rates in storm petrels at the same colony as this study in two later study years and reported growth curves of similar shape for all three biometric measures. The tarsus and wing length curves closely resembled those identified in this study, suggesting that these two metrics provide robust and consistent estimates of chick age across years. In contrast, the curve for body mass showed greater inter-annual variation, both within Watson et al. (2021) and relative to the current study, likely reflecting the greater sensitivity of body mass to annual variation in local environmental conditions.

Growth rates may also vary with latitude, limiting the application of growth rates derived in one region to other populations (Jakubas et al., 2014). However, growth patterns in European Storm Petrels have been shown to be consistent across a range as large as the North Atlantic (Minguez, 1996). Given that the breeding range of storm petrels is largely limited to western Europe (Snow & Perrins, 1998), the growth curves presented here are likely to be broadly applicable throughout the species' range. Further work investigating the relationships between chick growth rates and breeding success across regions would help establish the broader applicability of these models. Notably, this study accounted for repeated measurements from individual chicks, thereby incorporating individual variation in growth trajectories, an important source of variation that has largely

TABLE 2
Chick body mass, tarsus length, and wing length, and their associated mean predicted ages
across the range of potential measurements for which models were appropriate

Body mass (g)	Estimated age (d)	Tarsus length (mm)	Estimated age (d)	Wing length (mm)	Estimated age (d)
10	0	10.7	0	< 45	< 25
4	1	10.8	1	45	25
6	2	11.0	2	45	26
7	3	11.1	3	46	27
9	4	11.3	4	46	28
10	5	11.5	5	47	29
11	6	11.7	6	48	30
13	7	12.0	7	49	31
14	8	12.2	8	51	32
15	9	12.5	9	52	33
16	10	12.8	10	54	34
18	11	13.1	11	56	35
19	12	13.4	12	58	36
20	13	13.8	13	60	37
21	14	14.2	14	63	38
22	15	14.6	15	65	39
23	16	15.0	16	68	40
24	17	15.4	17	70	41
25	18	15.8	18	73	42
26	19	16.2	19	76	43
27	20	16.7	20	78	44
28	21	17.1	21	81	45
29	22	17.5	22	84	46
30+	23+	17.9	23	86	47
		18.3	24	89	48
		18.7	25	92	49
		19.0	26	94	50
		19.4	27	96	51
		19.7	28	99	52
		20.0	29	101	53
		20.3	30	103	54
		20.5	31	105	55
		20.8	32	107	56
		21.0	33	109	57
		21.2	34	111	58
		21.4	35	112	59
		21.5	36	114	60
		21.7	37	115	61
		21.8	38	117	62
		21.9	39	118	63
		22.0	40	119	64
		22.1	41	121	65
		22.2	42		
		22.3	43–44		
		22.4	45–46		
		22.5	47–48		
		22.6	49–51		
		22.7	52–58		
		22.8	59+		

been overlooked in previous studies. As a result, the growth rate estimates produced here may supersede any previous estimates that did not account for repeated measurements of individuals.

Overall, we present equations for estimating the age of storm petrel chicks from body mass, tarsus length, and wing length. Although all three biometric measures may be used to estimate chick age, tarsus length is likely to be the single most useful measure for chicks up to about 40 d of age (tarsus length < 20 mm), after which wing length provides a more reliable estimate. Using the equations presented here, a single biometric measurement can be used to estimate chick age. Consequently, hatch date may be estimated and, where chicks are estimated to be > 25 d old during a nest visit, breeding success can be broadly inferred. Multiple visits to nests with chicks may then refine estimated ages further and allow comparative estimates of the rate of chick growth to be made to infer the quality of extrinsic conditions.

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The authors declare no conflicts of interest.

ETHICS STATEMENT

All procedures were conducted under the appropriate licences and land access permissions.

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