# Who’s Coming Home? Shorter Early-Life Telomeres Predict Return to the Natal Colony in an Arctic Seabird

**Jingqi Corey Liu**[1,*]
**Olivier Chastel**[1]
**Christophe Barbraud**[1]
**Claus Bech**[2]
**Pierre Blévin**[3]
**Paco Bustamante**[4]
**Børge Moe**[5]
**Elin Noreen**[2]
**Frédéric Angelier**[1]
[1]Centre d’Etudes Biologiques de Chizé, CNRS–La Rochelle Université, UMR 7372, F-79360 Villiers-en-Bois, France; [2]Department of Biology, Norwegian University of Science and Technology, NO-7491 Trondheim, Norway; [3]Akvaplan-niva AS, Fram Centre, NO-9296 Tromsø, Norway; [4]Littoral Environnement et Sociétés, UMR 7266, CNRS–La Rochelle Université, 2 rue Olympe de Gouges, F-17000 La Rochelle, France; [5]Norwegian Institute for Nature Research, Division of Arctic Ecology, NO-9296 Tromsø, Norway

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## ABSTRACT

In wild animals, the length of their telomeres, the noncoding DNA sequences protecting the ends of chromosomes, in early life has been shown to predict their performance (e.g., survival, reproduction) later in life. However, literature has reported mixed relationships between telomere length (TL) and individual performance, possibly because many previous studies overlooked the effects of the resource-modulated trade-off between growth and telomere maintenance. We investigated the effects of early-life conditions (e.g., sibling competition [one or two chicks] and trophic level [nitrogen isotopic values]) on the TL of black-legged kittiwake (*Rissa tridactyla*) chicks while accounting for the growth-TL trade-off. We also tested whether early-life TL was related to their return probability to the natal colony within 6 yr after fledging (a proxy of survival to adulthood). Although there was no strong evidence for direct effects of the early-life conditions on TL, we found that in broods of two chicks, larger individuals tended to receive a higher-trophic-level diet and have shorter telomeres. This suggests that sibling competition might have imposed stronger resource constraints on the chicks, making them prioritize the limited resources toward growth at the expense of TL. Surprisingly, we found that chicks with shorter telomeres were more likely to return to their colony, whereas body size was not related to return probability, suggesting that TL may be a more comprehensive predictor of return probability than body size. Therefore, our study supports that early-life TL can be a predictor of later-life performance, but it should be used with caution when considering the effect of the resource allocation trade-off with growth, which can influence the direction of prediction.

*Keywords:* telomeres, early-life conditions, seabirds, survival, fitness, black-legged kittiwakes, brood size, nitrogen isotopic value.

## Introduction

Some individuals perform better than others by showing better survival and reproduction, giving rise to fitness variation between individuals (Wilson and Nussey 2010; Cam et al. 2016). As such, it is important to study the source of this interindividual variation in performance to further our understanding of fitness-driven processes like population dynamics and evolutionary responses to changing environments (Nussey et al. 2007; Uller 2008; Noble et al. 2018). However, measuring individual performance in terms of survival and lifetime reproductive success is often time consuming and costly (McGraw and Caswell 1996), especially in long-lived vertebrates, because it requires longitudinal monitoring of individuals for several years or decades. As a result, studies have often relied on the use of fitness-related traits to circumvent this issue (e.g., body condition [Wilder et al. 2016], foraging behavior [Crossin et al. 2014], endocrine levels [Angelier et al. 2010]). However, many of these traits reflect only certain physiological aspects of the individual state, which may be relevant to individuals’ fitness in specific environmental conditions but not necessarily in the long run (Angelier et al. 2010; Sorenson et al. 2017; Mellado et al. 2024). In search of a more reliable fitness proxy, traits underlying cellular functioning seem to be good candidates because cellular functioning lays the foundation of all organismal activities and thus may better integrate different aspects of the individual state.

Telomere length (TL) has been suggested as such an integrative measurement of biological individual states (Haussmann

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[*]Corresponding author; email: jingqi.liu@cebc.cnrs.fr.

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et al. 2003; Monaghan and Haussmann 2006; Barrett et al. 2013). Telomeres are DNA-protein complexes at the ends of chromosomes containing highly conserved, tandemly repeated nucleotide sequences (Blackburn 2005). They protect the genome from damage, such as degradation, erroneous recombination, and incomplete replication caused by the end-replication problem, which also shortens telomeres with cell replication (Blackburn 2005). Telomere shortening can be accelerated by oxidative stress (von Zglinicki 2002; Armstrong and Boonekamp 2023), which may increase with chronological age (Finkel and Holbrook 2000; Marasco et al. 2017) and environmental stressors (Reichert and Stier 2017; Angelier et al. 2018; Chatelain et al. 2020). When telomeres shorten to a critical threshold, cell senescence may be triggered, which can lead to organismal senescence when accumulated (Campisi 2005; Campisi and di Fagagna 2007; Armanios and Blackburn 2012). Given its role in maintaining cellular health and functioning, TL has been linked to organismal performance. For example, long telomeres were found to be correlated with better survival and higher reproductive success in vertebrates (e.g., Plot et al. 2012; Fairlie et al. 2016; Wilbourn et al. 2018; Angelier et al. 2019; Eastwood et al. 2019; van Lieshout et al. 2019; Heidinger et al. 2021; Chik et al. 2024). However, such correlations were found to be missing or even reversed in some studies (e.g., Wood and Young 2019; Pepke et al. 2022*a*; see Wilbourn et al. 2018; Eastwood et al. 2023; Badás et al. 2025), questioning the reliability of this molecular proxy of individual performance.

To understand the link between TL and individual performance, many studies have focused on early-life conditions (e.g., Boonekamp et al. 2014; Eastwood et al. 2019; Salmón et al. 2021; Marasco et al. 2022). Telomere shortening is usually the most drastic during early life (i.e., growth and developmental period), possibly due to rapid cell replication for growth (Hall et al. 2004; Heidinger et al. 2012; Marasco et al. 2022). Studies have found that many environmental stressors during this critical period are associated with shorter telomeres (e.g., Angelier et al. 2018; van Lieshout et al. 2021, 2022; Eastwood et al. 2022). Similarly, harsh early-life conditions can lead to lower adult survival or fecundity (Briga et al. 2017; Cooper and Kruuk 2018; Wilson and Burley 2024). Hence, early-life conditions may be a key factor in the relevance of TL as an individual performance predictor.

Some early-life stressors have been found to affect both early-life TL and later-life performance. For instance, nutritional stress during growth can have a carryover effect on adult survival (Lindström 1999; Metcalfe and Monaghan 2001; Monaghan 2007). Such stress can be induced by food shortage under harsh environmental conditions or in low-quality habitats, which were found to be associated with shorter early-life telomeres in birds (Gómez et al. 2021) and mammals (van Lieshout et al. 2022). Inversely, nutritional supplementation could slow down telomere shortening during the developmental period (Cram et al. 2017). Sibling competition can cause not only nutritional constraints (Benhaiem et al. 2012; Wojczulanis-Jakubas et al. 2023; Oelze et al. 2024) but also physiological stress that can accelerate telomere shortening (Herborn et al. 2014; Gil et al. 2020). Passerine and seabird nestlings raised in experimentally enlarged broods were found to have shorter telomeres (e.g., Costanzo et al. 2017; Young et al. 2017; Gil et al. 2020; Voirin et al. 2023) and lower later-life survival and fecundity (Saino et al. 2018). The assumptions of positive relationships among early-life conditions, TL, and later-life performance are widely accepted (e.g., McLennan et al. 2016; Mizutani et al. 2016). However, few studies have simultaneously investigated the relationships of these three elements, and their results are more complicated than expected. Jackdaw nestlings (*Corvus monedula*) in enlarged broods had shorter telomeres, but their TL did not predict recruitment or adult survival (Boonekamp et al. 2014). In Seychelles warblers (*Acrocephalus sechellensis*), van de Crommenacker et al. (2022) found, counterintuitively, shorter telomeres in nestlings living in better environmental conditions and no association between short telomeres and poor future performance.

Such complex results may be due to the resource allocation trade-off between growth and telomere maintenance (hereafter, growth-TL trade-off; Monaghan and Ozanne 2018). With limited resources, especially in adverse conditions, some individuals may prioritize body size growth to maximize immediate survival at the expense of TL (Stier et al. 2014; Badás et al. 2023), as a large body size is often crucial for the survival of young animals (Ronget et al. 2018). Such benefits from growth may compensate for the negative telomeric cost in early life, potentially leading to dissociation or a negative association between early-life TL and individual performance (Vedder et al. 2017; van de Crommenacker et al. 2022). As the intensity of this growth-TL trade-off may be accentuated in harsh environmental conditions (Stier et al. 2014; McLennan et al. 2016) and vary among species (Parolini et al. 2015; Badás et al. 2023), it should be considered to better explain the complicated relationships of TL with early-life conditions and individual performance in different contexts.

Here, we used a cohort of black-legged kittiwake (*Rissa tridactyla*; hereafter, kittiwake) chicks from Svalbard in the high Arctic to test whether TL is influenced by early-life conditions (brood size and trophic level). Then we investigated whether early-life TL is related to body size and whether it can predict individual performance or, more specifically, the return probability to the natal colony. The kittiwake is a long-lived species that shows natal philopatry (Coulson 2011), making this species appropriate for studying the long-term effects of early-life conditions and early-life TL on individual survival (approximated as the return to the natal colony). Kittiwakes typically lay one or two eggs (rarely three eggs; Moe et al. 2009), and enlarged brood size was previously found to negatively affect their early-life TL (Young et al. 2017). In Svalbard, kittiwakes feed on a variety of small fish and crustaceans of Arctic or Atlantic origins, including polar cods (*Boreogadus saida*), capelin (*Mallotus villosus*), herring (*Clupea harengus*), krill (*Thysanoessa inermis*), and amphipods (*Themisto libellula*), leading to large interindividual and between-year variation in trophic levels (Vihtakari et al. 2018; Tartu et al. 2022). Such variation in trophic levels provides an opportunity to study the effect of trophic level using the $^{15}N/^{14}N$ stable isotopic value ($\delta^{15}N$), where a higher value indicates a diet composed of higher-trophic-level prey (Post 2002; Tartu et al. 2022).

Based on previous empirical and theoretical studies, we expected that brood size (i.e., competition intensity) would have a negative effect on TL and body size (e.g., Mizutani et al. 2016;

Young et al. 2017; prediction 1) while $\delta^{15}N$ would have a positive effect on them (i.e., high-trophic-level prey is more nutritious; Vihtakari et al. 2018; prediction 2). This would lead to a positive relationship between TL and body size, as previously reported (Caprioli et al. 2013; Angelier et al. 2015, 2019; prediction 3a). However, according to the growth-TL trade-off hypothesis (Monaghan and Ozanne 2018), we also expected that TL could be negatively associated with body size (e.g., Ringsby et al. 2015; Pepke et al. 2022*b*; prediction 3b), especially when developmental conditions are too constraining to support both growth and telomere maintenance (i.e., in a large brood with increased sibling competition). Finally and according to previous studies (e.g., Wilbourn et al. 2018; Eastwood et al. 2023), we predicted that kittiwakes with longer early-life TL would be more likely to survive to the age of return to their natal colony (prediction 4). In addition, we tested whether early-life TL is a better predictor of return probability than other proxies of early-life conditions (brood size, $\delta^{15}N$, and body size).

## Methods

### Study Population and Sampling

The fieldwork took place in a colony of kittiwakes in Blomstrandhalvøya, Kongsfjorden, on the west coast of Spitsbergen, Svalbard, Norway (78°59′3″N, 12°7′46″E). In Svalbard, kittiwakes show a high annual survival rate (82%–88%) and relatively low fecundity (one fledgling per nest; Moe et al. 2009; Goutte et al. 2015). The study plot contained about 150 breeding pairs of kittiwakes on cliff ledges at heights of 5–10 m. The nests in the study plot were monitored to determine the hatching date and the number of hatched chicks (hereafter, brood size). No historical information was available for the parents, and we were therefore unable to know their age. Between August 5 and 7, 2010, 46 kittiwake chicks from the monitored nests were captured by hand from their nest. We were able to collect information on both age and brood size for 33 of the 46 captured individuals. The chicks were approximately 30 d old (ranging from 25 to 34 d). At this age, they reached a suitable body size to be ringed. Each captured chick was fitted with a metal ring and a white PVC plastic band with a unique three-letter code on its tarsus for identification from a distance. To minimize disturbances to the chicks, we did morphological and blood sampling during the same capture (i.e., ~30 d old). The body mass was measured using a scale ($\pm 5$ g). Their skull and tarsus lengths were measured with a caliper ($\pm 0.1$ mm), and their wing length was measured with a ruler ($\pm 1$ mm; $n = 46$). About 1 mL of blood was drawn from the brachial vein using a 1-mL heparinized syringe and a G25 needle for TL, $\delta^{15}N$ measurement, and sex determination ($n = 46$). The blood was centrifuged, and the red blood cells and blood plasma were transferred to and stored in separate tubes at −20°C until laboratory analyses.

From 2011 to 2016, the colony was scanned every breeding season to monitor the return of these 46 chicks. In general, among the kittiwake fledglings that return to their natal colony, over 90% of them return at an age between 2 and 5 yr (Cam et al. 2003; Coulson 2011). Therefore, the return rate up to 2016, when the sampled individuals reached 6 yr old, is likely to be representative of the final return rate of our study cohort. We resighted 24 birds in the colony (six in 2012, 13 in 2013, four in 2014, and one in 2015; no sampled individuals were resighted in 2016), and we were able to recapture 16 of them to take blood samples and morphological measurements. Because TL-age relationships can be nonlinear and vary among individuals, especially during early life (Marasco et al. 2022; Pepke 2024), the telomeres of the recaptured individuals were not directly comparable because of their different ages (age = 2–5 yr old). Given the small sample size of recaptured individuals and the relatively high number of covariates (e.g., age, sex), these telomere data could not be used for robust statistical analyses. We acknowledge that this return rate represents apparent survival, which is affected by both true mortality and permanent emigration out of the natal colony, and the results will be interpreted accordingly.

### Telomere Length Measurement and Molecular Sexing

TL was measured from red blood cell samples ($n = 46$) by Southern blot using the TeloTAGGG telomere length assay (Roche) at the Centre d'Etudes Biologiques de Chizé following a protocol by Blévin et al. (2016) that was modified from Foote et al. (2011) and Kimura et al. (2010). Briefly, after cell lysis by proteinase K, DNA was extracted from the samples using the DNeasy blood and tissue kit (Qiagen). DNA quality was checked using gel electrophoresis and optical density spectrophotometry. Then 0.7 $\mu$g of DNA from each sample was digested with the restriction enzymes Hinfl and Rsal for 16 h at 37°C. The telomere restriction fragments were separated using pulse-field gel electrophoresis (Bio-Rad) on 0.8% agarose gel at 3.0 V/cm with an initial switch time of 0.5 s and a final switch time of 7 s for 14 h. Each sample was run in four gels to which it was randomly assigned. After depurination, denaturation, and neutralization of the gel, the DNA fragments were transferred from the gel to a nitrocellulose membrane by Southern blot (Hybond N+, Amersham Life Science). Telomere smear densities on the membrane were extracted via ImageJ to determine TL (for further details, see Blévin et al. 2016). Using the DNA extracts, we determined the sex of the chicks by molecular sexing (polymerase chain reaction), as described in Blévin et al. (2016).

### Nitrogen Stable Isotopic Value Measurement

$\delta^{15}N$ was measured from freeze-dried red blood cell samples at the Littoral Environnement et Sociétés in La Rochelle, France. For each sample, about 0.3 mg of dry mass was analyzed with a continuous-flow mass spectrometer (Delta V Advantage, Thermo Scientific) coupled to an elemental analyzer (Flash EA 1112, Thermo Scientific). Results are shown as standard delta ($\delta$) notation in parts per thousand (‰) deviation relative to atmospheric $N_2$. Accuracy was checked using internal laboratory standards USGS-61 (caffeine) and USGS-62 (caffeine). Measurement errors were within 0.15‰.

### *Statistical Analyses*

All analyses were performed in R (ver. 4.4.1; R Core Team 2024). To derive a comprehensive measurement for body size, we performed a principal component analysis using the R package FactoMineR (Lê et al. 2008) on the body mass, skull length, wing length, and tarsus length of the kittiwake chicks and extracted the first principal component (PC1). PC1 explained the majority (56%) of the measured morphological variance (Kennedy et al. 2019, 2020) and was significantly correlated with all the morphometric variables (Pearson's correlation, all $P < 0.001$). As PC1 was positively correlated with chick age (linear regression, $t = 3.919$, $P < 0.001$, $r^2 = 0.303$), we calculated age-corrected PC1 (hereafter, body size index; $n = 33$) as a proxy of overall body size by taking the residual PC1 values from the PC1-age linear model. TL and $\delta^{15}$N were not age associated according to the linear models (all $P > 0.500$, all $r^2 < 0.010$).

We investigated the effects of brood size (prediction 1) and $\delta^{15}$N (prediction 2) on TL and body size index, separately, using linear regression models ($n = 33$) with chick sex as a covariate. We also included the pairwise interactions between brood size, $\delta^{15}$N, and chick sex as the explanatory variables of these two models. To test the relationship between TL and body size (predictions 3a and 3b), we fitted another linear model on TL with body size index, brood size, chick sex, and the interactions between body size index and the latter two as the explanatory variables. To test the relationship between return probability and chick TL (prediction 4), we fitted a binomial-family generalized linear model (GLM) on the binary return outcome of the chicks with TL, chick sex, and their interaction as the explanatory variables using the glm() function ($n = 46$). Finally, we fitted four GLMs on the return outcome with TL, body size index, brood size, or $\delta^{15}$N as the main predictor, respectively ($n = 33$), to compare the explanatory power of these four variables for return probability. Chick sex and interactions between sex and the main predictor were also included as the explanatory variables in these four GLMs. Given our limited sample size ($n = 33$), a single GLM including all four explanatory variables could not be fitted.

We performed model selection using the information-theoretic approach based on the corrected Akaike information criterion (AICc) values (Burnham and Anderson 2002) computed by the R package MuMIn (Bartoń 2024). When a model had a lower AICc value by more than two units than all other candidate models, we considered this model the best model in the candidate model set to describe the data. When there were alternative models with $\Delta\text{AICc} < 2$, where $\Delta\text{AICc} = \text{AICc}_{\text{alternative}} - \text{AICc}_{\text{lowest}}$, we considered that there was no support for a single best model. Instead, all models with $\Delta\text{AICc} < 2$ were composed of a top candidate model set. In this case, we reported and discussed the models in this set depending on their model weight and the level of improvement in their log likelihood compared to the model with the lowest AICc value (Anderson and Burnham 2002; Arnold 2010). The model weight represents the relative likelihood of a model being the best model in the candidate model set. The log likelihood represents how well a model describes the data. If an alternative model has $\Delta\text{AICc} < 2$ and a very similar or considerably higher log likelihood or model weight compared to the model with the lowest AICc value, we considered that this model received sufficient support to be reported and discussed.

The effect sizes and significance of the variables and interactions were reported using ANOVA. All the continuous response and explanatory variables were standardized to have a mean of 0 and a standard deviation of 1 to compare the slopes. Unless specifically stated, all the slopes of the variables were reported using full-model averaging of all the candidate models to take model uncertainty into account. The significance of the model average slope was represented by whether the 95% confidence interval (CI) excludes zero (Burnham and Anderson 2002). The explanatory variables of all the models had no collinearity (generalized variance inflation factor <3; Graham 2003).

## Results

### *Relationship of Telomere Length with Brood Size, Nitrogen Stable Isotopic Value, and Sex*

TL varied from 7.85 to 13.16 kbp among the 46 chicks (mean ± SD = 10.60 ± 1.20). Model selection suggested a top candidate model set consisting of five models (M1.1–M1.5), including the null model (table 1). This suggested that the other four top candidate models had similar abilities to describe the data as the null model. The model with the lowest AICc and highest model weight (M1.1) included $\delta^{15}$N, brood size, and their interaction as the explanatory variables (table 1). The $\delta^{15}$N × brood size interaction in model M1.1 was significant (M1.1: $F_{1,29} = 4.214$, $P = 0.049$) and considerably improved the log likelihood compared to the null model (M1.2) and the model including only $\delta^{15}$N and brood size (M5.1; table 1), suggesting that the effect of $\delta^{15}$N on TL varied with brood sizes. In broods of one chick, TL did not significantly change with $\delta^{15}$N (M1.1: $\beta \pm \text{SE} = 0.072 \pm 0.272$, $t = 0.265$, $P = 0.793$; fig. 1; table A1; tables A1–A5 are available online). In broods of two, chicks with higher $\delta^{15}$N had shorter TL (M1.1: $\beta \pm \text{SE} = -0.694 \pm 0.256$, $t = -2.713$, $P = 0.011$; fig. 1), but this relationship was nonsignificant after full-model averaging (averaged $\beta \pm \text{SE} = -0.243 \pm 0.328$, 95% CI = $-1.077$ to 0.229). The $\delta^{15}$N × brood size (two chicks) interaction remained negative after full-model averaging, although the slope of the 95% CI marginally included zero (averaged $\beta \pm \text{SE} = -0.187 \pm 0.381$, 95% CI = $-1.537$ to 0.043). The main effects of $\delta^{15}$N, brood size, and chick sex were included in some of the top candidate models, but they were not significant in those models (all $P > 0.05$) or after full-model averaging (table A1).

### *Relationship of Body Size with Brood Size, Nitrogen Stable Isotopic Value, and Sex*

The best model to describe the effect of brood size and $\delta^{15}$N on body size index (M2.1) included $\delta^{15}$N, chick sex, and their interaction as the explanatory variables (table 2). There was a significant sex difference in the body size index (M2.1: $F_{1,29} = 8.700$,

Table 1: Model selection results to investigate the effects of brood size, nitrogen stable isotopic value ($\delta^{15}$N), sex, and their interactions on the telomere length of black-legged kittiwake chicks ($n = 33$)

| Model | Explanatory variable(s) | df | logLik | AICc | ΔAICc | Weight | $r^2$ |
|---|---|---|---|---|---|---|---|
| M1.1 | $\delta^{15}$N + brood size + $\delta^{15}$N × brood size | 5 | −42.31 | 96.85 | .00 | .18 | .23 |
| M1.2 | Null model | 2 | −46.32 | 97.03 | .18 | .16 | .00 |
| M1.3 | Sex | 3 | −45.40 | 97.63 | .78 | .12 | .06 |
| M1.4 | $\delta^{15}$N | 3 | −45.61 | 98.06 | 1.21 | .10 | .04 |
| M1.5 | $\delta^{15}$N + brood size | 4 | −44.55 | 98.54 | 1.69 | .08 | .11 |
| M1.6 | $\delta^{15}$N + sex | 4 | −44.76 | 98.95 | 2.10 | .06 | .10 |
| M1.7 | Brood size | 3 | −46.08 | 98.99 | 2.14 | .06 | .02 |
| M1.8 | Brood size + sex + brood size × sex | 5 | −43.60 | 99.42 | 2.57 | .05 | .16 |
| M1.9 | $\delta^{15}$N + brood size + sex + $\delta^{15}$N × brood size | 6 | −42.25 | 99.74 | 2.89 | .04 | .23 |
| M1.10 | Brood size + sex | 4 | −45.31 | 100.05 | 3.20 | .04 | .06 |
| M1.11 | $\delta^{15}$N + brood size + sex | 5 | −44.10 | 100.41 | 3.56 | .03 | .13 |
| M1.12 | $\delta^{15}$N + brood size + sex + brood size × sex | 6 | −42.97 | 101.18 | 4.33 | .02 | .20 |
| M1.13 | $\delta^{15}$N + sex + $\delta^{15}$N × sex | 5 | −44.54 | 101.30 | 4.45 | .02 | .11 |
| M1.14 | $\delta^{15}$N + brood size + sex + $\delta^{15}$N × brood size + brood size × sex | 7 | −41.43 | 101.35 | 4.50 | .02 | .27 |
| M1.15 | $\delta^{15}$N + brood size + sex + $\delta^{15}$N × sex + brood size × sex | 7 | −42.03 | 102.54 | 5.69 | .01 | .24 |
| M1.16 | $\delta^{15}$N + brood size + sex + $\delta^{15}$N × brood size + $\delta^{15}$N × sex | 7 | −42.23 | 102.95 | 6.10 | .01 | .23 |
| M1.17 | $\delta^{15}$N + brood size + sex + $\delta^{15}$N × sex | 6 | −43.97 | 103.18 | 6.33 | .01 | .14 |
| M1.18 | $\delta^{15}$N + brood size + sex + $\delta^{15}$N × brood size + $\delta^{15}$N × sex + brood size × sex | 8 | −41.24 | 104.48 | 7.63 | .00 | .28 |

Note. Telomere length and $\delta^{15}$N were mean centered. The models are ranked by corrected Akaike information criterion (AICc) values. ΔAICc is the difference between the AICc values of the model and the lowest AICc among all the candidate models. Weight represents the relative likelihood that the corresponding model is the best model among all the candidate models. $r^2$ is the adjusted $r^2$ indicating the goodness of fit of the models. A single best model could not be determined. The null model includes only the intercept. logLik = maximum log likelihood.

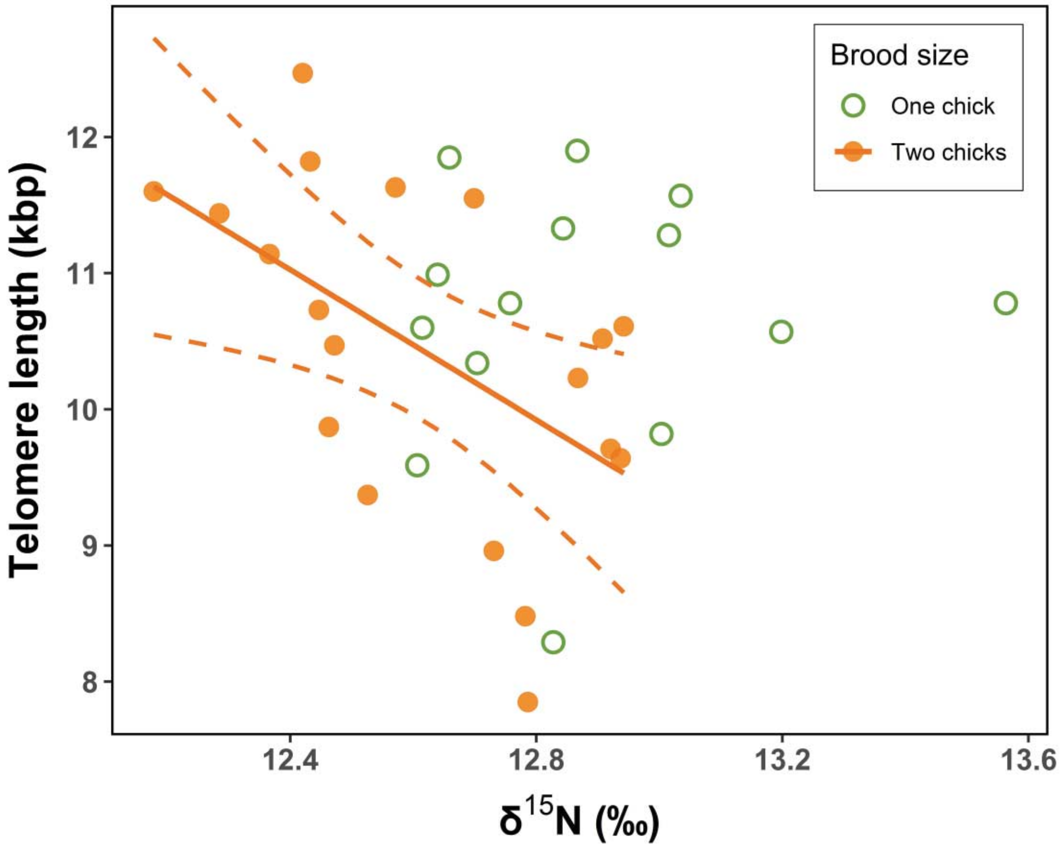

Figure 1. Telomere length of black-legged kittiwake chicks ($n = 33$) in relation to their nitrogen stable isotopic value ($\delta^{15}$N) by brood size. A regression line is shown when the slope is significant ($P < 0.05$). The dashed lines delimit the 95% confidence interval of the regression line.

Table 2: Model selection results to investigate the effects of brood size, nitrogen stable isotopic value ($\delta^{15}$N), sex, and their interactions on the body size index of black-legged kittiwake chicks ($n = 33$)

| Model | Explanatory variable(s) | df | logLik | AICc | ΔAICc | Weight | $r^2$ |
|---|---|---|---|---|---|---|---|
| **M2.1** | **$\delta^{15}$N + sex + $\delta^{15}$N × sex** | **5** | **−35.27** | **82.76** | **.00** | **.58** | **.52** |
| M2.2 | $\delta^{15}$N + brood size + sex + $\delta^{15}$N × brood size + $\delta^{15}$N × sex | 7 | −33.35 | 85.19 | 2.43 | .17 | .58 |
| M2.3 | $\delta^{15}$N + brood size + sex + $\delta^{15}$N × sex | 6 | −35.20 | 85.63 | 2.87 | .14 | .52 |
| M2.4 | $\delta^{15}$N + brood size + sex + $\delta^{15}$N × sex + brood size × sex | 7 | −34.42 | 87.32 | 4.56 | .06 | .55 |
| M2.5 | $\delta^{15}$N + brood size + sex + $\delta^{15}$N × brood + $\delta^{15}$N × sex + brood size × sex | 8 | −33.18 | 88.36 | 5.60 | .04 | .58 |
| M2.6 | Sex | 3 | −43.35 | 93.53 | 10.77 | .00 | .18 |
| M2.7 | $\delta^{15}$N + brood size + sex + brood size × sex | 6 | −39.24 | 93.71 | 10.95 | .00 | .37 |
| M2.8 | $\delta^{15}$N + sex | 4 | −42.58 | 94.58 | 11.82 | .00 | .22 |
| M2.9 | Brood size + sex + brood size × sex | 5 | −41.28 | 94.79 | 12.03 | .00 | .28 |
| M2.10 | Brood size + sex | 4 | −43.28 | 95.98 | 13.22 | .00 | .18 |
| M2.11 | $\delta^{15}$N + brood size + sex + $\delta^{15}$N × brood size + brood size × sex | 7 | −39.21 | 96.90 | 14.14 | .00 | .37 |
| M2.12 | Null model | 2 | −46.32 | 97.03 | 14.27 | .00 | .00 |
| M2.13 | $\delta^{15}$N + brood size + sex | 5 | −42.54 | 97.30 | 14.54 | .00 | .22 |
| M2.14 | $\delta^{15}$N | 3 | −45.48 | 97.79 | 15.03 | .00 | .05 |
| M2.15 | Brood size | 3 | −46.30 | 99.43 | 16.67 | .00 | .00 |
| M2.16 | $\delta^{15}$N + brood size | 4 | −45.08 | 99.60 | 16.84 | .00 | .08 |
| M2.17 | $\delta^{15}$N + brood size + sex + $\delta^{15}$N × brood size | 6 | −42.53 | 100.29 | 17.53 | .00 | .22 |
| M2.18 | $\delta^{15}$N + brood size + $\delta^{15}$N × brood size | 5 | −44.94 | 102.10 | 19.34 | .00 | .09 |

Note. Body size index is represented by the age-corrected first principal component value of morphological metrics (body mass, tarsus length, wing length, and skull length). Body size index and $\delta^{15}$N were mean centered. The models are ranked by corrected Akaike information criterion (AICc) values. ΔAICc is the difference between the AICc values of the model and the lowest AICc among all the candidate models. Weight represents the relative likelihood that the corresponding model is the best model among all the candidate models. $r^2$ is the adjusted $r^2$ indicating the goodness of fit of the models. The null model includes only the intercept. The best model is shown in bold. logLik = maximum log likelihood.

$P = 0.006$), with the male chicks (mean ± SD = 0.53 ± 1.44) being larger (averaged $\beta \pm$ SE = 0.828 ± 0.339, 95% CI = 0.166 to 1.491) than the female chicks (mean ± SD = −0.54 ± 1.02). Body size index was not directly affected by $\delta^{15}$N (M2.1: $F_{1,29} = 2.171$, $P = 0.151$), but its relationship with $\delta^{15}$N differed significantly between male and female chicks ($\delta^{15}$N × chick sex interaction in M2.1: $F_{1,29} = 16.155$, $P < 0.001$; $\delta^{15}$N × chick sex [male] interaction: averaged $\beta \pm$ SE = 1.161 ± 0.342, 95% CI = 0.545 to 1.802). Specifically, body size index was positively related to $\delta^{15}$N in male chicks (averaged $\beta \pm$ SE = 1.029 ± 0.329, 95% CI = 0.406 to 1.664) but not in female chicks (averaged $\beta \pm$ SE = −0.132 ± 0.212, 95% CI = −0.549 to 0.284; fig. 2).

### *Relationship between Telomere Length and Body Size*

Model selection suggested three top candidate models (M3.1–M3.3), all of which included body size index, brood size, and their interaction as the explanatory variables (table 3). The relationships between TL and body size index significantly differed with brood sizes in all the top candidate models (body size index × brood size interaction: all $F \geq 8.340$, all $P \leq 0.007$) and after full-model averaging (body size index × brood size [two chicks] interaction: averaged $\beta \pm$ SE = −0.783 ± 0.515, 95% CI = −1.673 to −0.342). In the most parsimonious top candidate model, chick TL significantly decreased with body size index in two-chick broods (M3.2: $\beta \pm$ SE = −0.676 ± 0.211, $t = -3.028$, $P = 0.003$; fig. 3), but this relationship was marginally nonsignificant after model averaging (averaged $\beta \pm$ SE = −0.471 ± 0.331, 95% CI = −1.125 to 0.060). In single-chick broods, chick TL did not vary with body size index (M3.2: $\beta \pm$ SE = 0.233 ± 0.234, $t = 0.995$, $P = 0.328$; fig. 3; table A2). Although the main effects of body size index, brood size, chick sex, and the body size index × chick sex interaction were included in the top candidate models (table 3), they were not significant in these models (all $P > 0.05$) or after full-model averaging (table A2).

### *Relationship between Telomere Length and Return Probability*

The return rate of the chicks was 0.52 ($n = 46$). The best model to describe the relationship between TL and the return probability of the 46 chicks (M4.1) included TL as the only explanatory variable (table 4). The return probability was significantly related to early-life TL (M4.1: $F_{1,44} = 18.855$, $P < 0.001$), and kittiwakes with shorter early-life TL were more likely to return to the natal colony (averaged $\beta \pm$ SE = −1.903 ± 0.631, 95% CI = −3.173 to −0.633; fig. 4*A*).

### *Predictability of Return Probability by Telomere Length, Body Size, and Early-Life Conditions*

When run on the subset of 33 chicks with brood size information, the best model to describe the relationship between

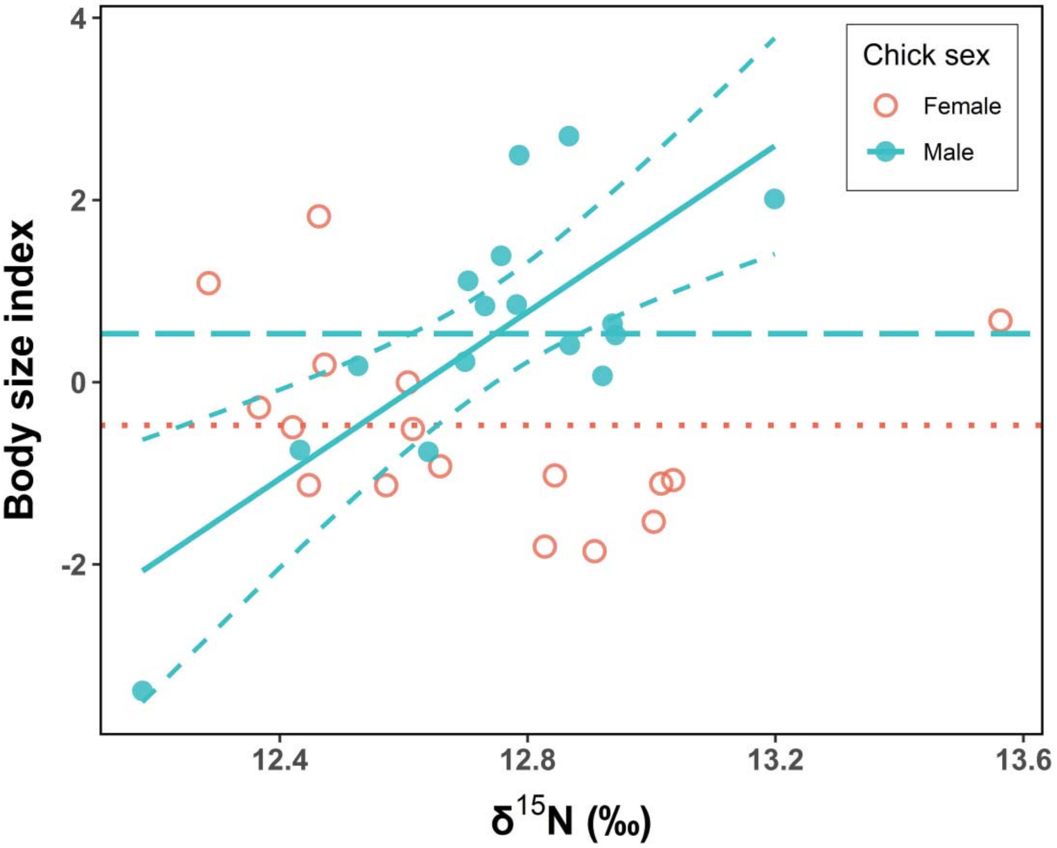

Figure 2. Body size index (age-corrected first principal component of morphological metrics) of black-legged kittiwake chicks ($n = 33$) in relation to their nitrogen stable isotopic value ($\delta^{15}N$) by sex. The long-dashed and dotted horizontal lines represent the mean body size index for male and female chicks, respectively. A regression line is shown when the slope is significant ($P < 0.05$). The dashed lines delimit the 95% confidence interval of the regression line. The morphometric measurements include body mass, tarsus length, wing length, and skull length. Removing the extreme data point (body size index $< -2$) did not change the model selection result, the significance, or the direction of the relationship between body size index and $\delta^{15}N$ in male chicks.

Table 3: Model selection results to investigate the relationship of telomere length with the body size index (BSI) of black-legged kittiwake chicks ($n = 33$) in different brood sizes and sexes

| Model | Explanatory variable(s) | df | logLik | AICc | ΔAICc | Weight | $r^2$ |
|---|---|---|---|---|---|---|---|
| M3.1 | BSI + brood size + BSI × brood size + sex | 6 | −39.04 | 93.30 | .00 | .32 | .38 |
| M3.2 | BSI + brood size + BSI × brood size | 5 | −40.66 | 93.54 | .24 | .28 | .31 |
| M3.3 | BSI + brood size + sex + BSI × brood size + BSI × sex | 7 | −38.02 | 94.52 | 1.22 | .17 | .42 |
| M3.4 | BSI | 3 | −45.05 | 96.93 | 3.63 | .05 | .08 |
| M3.5 | Null model | 2 | −46.32 | 97.03 | 3.73 | .05 | .00 |
| M3.6 | Sex | 3 | −45.40 | 97.63 | 4.33 | .04 | .06 |
| M3.7 | BSI + sex | 4 | −44.73 | 98.89 | 5.59 | .02 | .10 |
| M3.8 | Brood size | 3 | −46.08 | 98.99 | 5.69 | .02 | .02 |
| M3.9 | Brood size + BSI | 4 | −44.83 | 99.09 | 5.79 | .02 | .09 |
| M3.10 | Brood size + sex | 4 | −45.31 | 100.05 | 6.75 | .01 | .06 |
| M3.11 | BSI + sex + BSI × sex | 5 | −44.13 | 100.48 | 7.18 | .01 | .13 |
| M3.12 | Brood size + BSI + sex | 5 | −44.60 | 101.43 | 8.13 | .01 | .11 |
| M3.13 | BSI + brood size + sex + BSI × sex | 6 | −43.70 | 102.63 | 9.33 | .00 | .16 |

Note. BSI is represented by the age-corrected first principal component value of morphological metrics (body mass, tarsus length, wing length, and skull length). Telomere length and body size index were mean centered. The models are ranked by corrected Akaike information criterion (AICc) values. ΔAICc is the difference between the AICc values of the model and the lowest AICc among all the candidate models. Weight represents the relative likelihood that the corresponding model is the best model among all the candidate models. $r^2$ is the adjusted $r^2$ indicating the goodness of fit of the models. The null model includes only the intercept. A single best model could not be determined. logLik = maximum log likelihood.

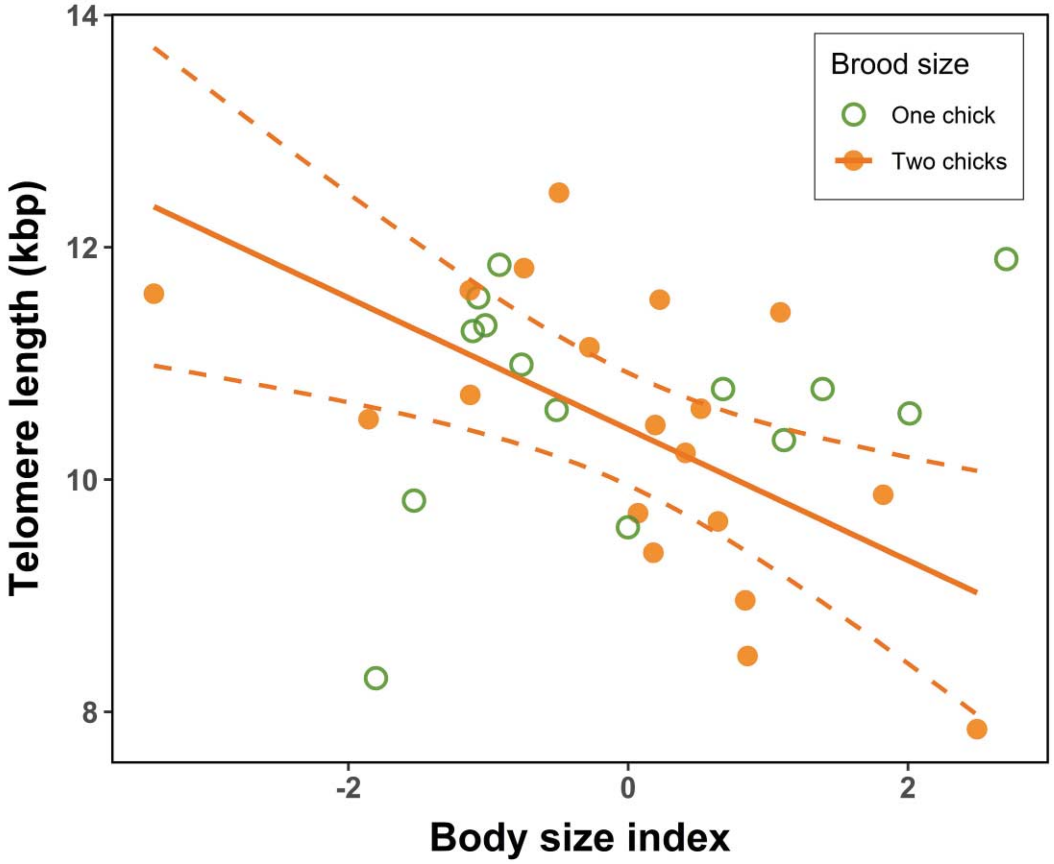

Figure 3. Telomere length of black-legged kittiwake chicks ($n = 33$) in relation to their body size index (age-corrected first principal component of morphological metrics) by brood size. A regression line is shown when the slope is significant ($P < 0.05$). The dashed lines delimit the 95% confidence interval of the regression line. The morphometric measurements include body mass, tarsus length, wing length, and skull length.

TL and return probability (M5.1) still included only TL as the explanatory variable (table 5), showing a similar negative relationship between early-life TL and return probability (M5.1: $F_{1,31} = 10.784$, $P = 0.001$; averaged $\beta \pm \mathrm{SE} = -1.560 \pm 0.663$, 95% CI = −2.890 to −0.273).

The best model to describe the effect of $\delta^{15}N$ on return probability (M7.1) included $\delta^{15}N$ as the only explanatory variable (table 5), which had a significant positive effect on return probability (M7.1: $F_{1,31} = 11.540$, $P < 0.001$; averaged $\beta \pm \mathrm{SE} = 1.653 \pm 0.657$, 95% CI = 0.364 to 2.974; fig. 4*B*). $\delta^{15}N$ and TL had similar abilities to predict the return probability of the kittiwakes ($\Delta\mathrm{AICc} < 2$; table 5). When fitted in the same GLM (return probability ~ TL + $\delta^{15}N$), $\delta^{15}N$ and TL were included in the best model (table A3) and had similar importance in predicting the return probability (evidence ratio of $\delta^{15}N$ to TL = 1.02).

When testing whether body size index or brood size predicted return probability, model selection suggested three top candidate models, including the null model, for both cases (M6.1–M6.3 and M8.1–M8.3; table 5). This suggested that these models with body size index (M6.1 and M6.2) or brood size (M8.2) as the explanatory

Table 4: Model selection results to investigate the effects of telomere length (TL), sex, and their interaction on the postfledging return probability to the natal colony of black-legged kittiwake chicks ($n = 46$)

| Model | Explanatory variable(s) | df | logLik | AICc | ΔAICc | Weight | $r^2$ |
|---|---|---|---|---|---|---|---|
| **M4.1** | **TL** | **2** | **−22.41** | **49.11** | **.00** | **.70** | **.45** |
| M4.2 | TL + sex | 3 | −22.40 | 51.38 | 2.27 | .23 | .45 |
| M4.3 | TL + sex + TL × sex | 4 | −22.39 | 53.76 | 4.65 | .07 | .45 |
| M4.4 | Null model | 1 | −31.84 | 65.77 | 16.66 | .00 | .00 |
| M4.5 | Sex | 2 | −31.44 | 67.15 | 18.04 | .00 | .02 |

Note. TL was mean centered. The models are ranked by corrected Akaike information criterion (AICc) values. ΔAICc is the difference between the AICc values of the model and the lowest AICc among all the candidate models. Weight represents the relative likelihood that the corresponding model is the best model among all the candidate models. $r^2$ is the adjusted $r^2$ indicating the goodness of fit of the models. The null model includes only the intercept. The best model is shown in bold. logLik = maximum log likelihood.

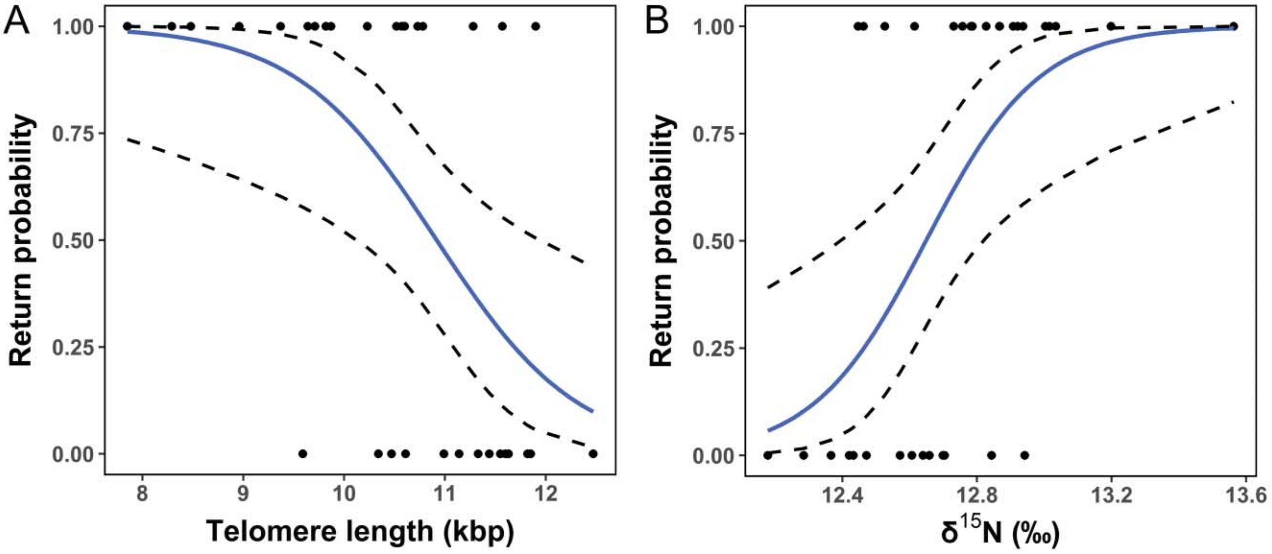

Figure 4. Relationship of the postfledging return outcomes to the natal colony of black-legged kittiwake chicks ($n = 33$) with their telomere length (*A*) and nitrogen stable isotopic value ($\delta^{15}$N; *B*). Regression lines are shown when the slope is significant ($P < 0.05$). The dashed lines delimit the 95% confidence interval of the regression lines.

variable had similar abilities to predict return probability as the null models (M6.2 and M8.1; table 5). The main effects of body size index, brood size, chick sex, and the body size index × chick sex interaction were not significant in the top candidate models (all $P > 0.05$) or after full-model averaging (tables A4, A5).

## Discussion

### *Effects of Early-Life Conditions on Telomere Length and Body Size*

We found that brood size did not directly affect the TL or body size of black-legged kittiwake chicks, even though the negative impacts of brood size on TL (Boonekamp et al. 2014; Costanzo et al. 2017; Young et al. 2017; Gil et al. 2020; Voirin et al. 2023) and body size (Arct et al. 2022; Hadad et al. 2024) have been relatively well established in many bird species. One possible explanation for our counterintuitive results is that parents may be able to adjust their clutch and brood sizes according to the environmental conditions encountered (i.e., food availability; Xu et al. 2023), minimizing the detrimental effect of sibling competition on offspring. Supporting this interpretation, some studies did not find strong evidence for a negative effect of natural brood size on TL (e.g., Herborn et al. 2014; Bauch et al. 2022; Marciau et al. 2025) and body size (e.g., Minias et al. 2012; O'Dea et al. 2015; Gilliland et al. 2016), whereas brood size manipulation studies (i.e., artificially increasing sibling competition) that created a mismatch between the brood size and the environmental conditions found such an effect (e.g., Costanzo et al. 2017; Belmaker et al. 2019; Badás et al. 2023), notably in kittiwakes (Young et al. 2017). In addition, several studies showed that the intensity of the brood size effect can change depending on other factors, such as the competitiveness of the brood siblings (Nettle et al. 2013), the nutritional value of food (Cram et al. 2017), and the habitat resource availability (Nicolaus et al. 2009). This indicates that the negative impact of brood size on TL and body size may become apparent only if the environmental conditions cannot provide sufficient resources to sustain the energetic requirements of such a brood size. Since the kittiwakes in our study area had a relatively small average clutch size and high breeding success in 2010 (Vihtakari et al. 2018), the environmental conditions during the year of our study may have been sufficient to sustain the energetic needs of two chicks, therefore masking the negative impact of brood size on TL and body size.

$\delta^{15}$N is commonly used in wild seabirds to evaluate the overall trophic level of their prey (Hobson et al. 1994; Post 2002; Cherel et al. 2005). This has been shown as a robust tool to evaluate interindividual differences in nutritional conditions among seabird chicks, including kittiwakes (Williams et al. 2007; Sears et al. 2009; González-Medina et al. 2017). Accordingly, we found that higher values of $\delta^{15}$N were associated with larger body size in male kittiwake chicks, probably because higher $\delta^{15}$N is associated with the higher nutritional benefits of eating high-trophic-level prey (i.e., fish) for kittiwakes (Renner et al. 2014; Charrier et al. 2024). Supporting this interpretation, a positive relationship between body condition and $\delta^{15}$N has been reported in adult black-legged kittiwakes (Charrier et al. 2024), and poorer nutritional conditions have also been associated with lower $\delta^{15}$N in growing seabird chicks (Williams et al. 2007; Sears et al. 2009). Although small crustaceans like krill can be more abundant and easier to catch than fish prey in the high Arctic (Hovinen et al. 2019), they have a lower energy value than fish in general (Hop and Gjøsæter 2013; Renkawitz et al. 2015; Vihtakari et al. 2018) and require more

Table 5: Model selection results to investigate the effects of telomere length (TL), body size index (BSI), nitrogen stable isotopic value ($\delta^{15}N$), and brood size, separately, on the postfledging return probability to the natal colony of black-legged kittiwake chicks ($n = 33$)

| Model | Explanatory variable(s) | df | logLik | AICc | ΔAICc | Weight | $r^2$ |
|---|---|---|---|---|---|---|---|
| | Main variable of interest = TL | | | | | | |
| **M5.1** | **TL** | **2** | **−17.10** | **38.60** | **.00** | **.71** | **.37** |
| M5.2 | TL + sex | 3 | −17.09 | 41.01 | 2.41 | .21 | .38 |
| M5.3 | TL + sex + TL × sex | 4 | −17.01 | 43.45 | 4.85 | .06 | .38 |
| M5.4 | Null model | 1 | −22.49 | 47.12 | 8.52 | .01 | .00 |
| M5.5 | Sex | 2 | −22.34 | 49.08 | 10.48 | .00 | .01 |
| | Main variable of interest = BSI | | | | | | |
| M6.1 | BSI + sex + BSI × sex | 4 | −18.43 | 46.28 | .00 | .37 | .29 |
| M6.2 | Null model | 1 | −22.49 | 47.12 | .84 | .24 | .00 |
| M6.3 | BSI | 2 | −21.42 | 47.25 | .97 | .23 | .08 |
| M6.4 | Sex | 2 | −22.34 | 49.08 | 2.80 | .09 | .01 |
| M6.5 | BSI + sex | 3 | −21.42 | 49.67 | 3.39 | .07 | .08 |
| | Main variable of interest = $\delta^{15}N$ | | | | | | |
| **M7.1** | **$\delta^{15}N$** | **2** | **−16.72** | **37.85** | **.00** | **.72** | **.40** |
| M7.2 | $\delta^{15}N$ + sex | 3 | −16.72 | 40.27 | 2.42 | .21 | .40 |
| M7.3 | $\delta^{15}N$ + sex + $\delta^{15}N$ × sex | 4 | −16.71 | 42.84 | 4.99 | .06 | .40 |
| M7.4 | Null model | 1 | −22.49 | 47.12 | 9.27 | .01 | .00 |
| M7.5 | Sex | 2 | −22.34 | 49.08 | 11.23 | .00 | .01 |
| | Main variable of interest = brood size | | | | | | |
| M8.1 | Null model | 1 | −22.49 | 47.12 | .00 | .50 | .00 |
| M8.2 | Brood size | 2 | −22.27 | 48.94 | 1.82 | .20 | .02 |
| M8.3 | Sex | 2 | −22.34 | 49.08 | 1.96 | .19 | .01 |
| M8.4 | Brood size + sex | 3 | −22.00 | 50.83 | 3.71 | .08 | .04 |
| M8.5 | Brood size + sex + brood size × sex | 4 | −21.60 | 52.62 | 5.50 | .03 | .07 |

Note. BSI is represented by the age-corrected first principal component value of morphological metrics (body mass, tarsus length, wing length, and skull length). The interactions of the predictor variable with chick sex are also included in each set of models. TL, BSI, and $\delta^{15}N$ were mean centered. The models are ranked by corrected Akaike information criterion (AICc) values. ΔAICc is the difference between the AICc values of the model and the lowest AICc among all the candidate models. Weight represents the relative likelihood that the corresponding model is the best model among all the candidate models. $r^2$ is the adjusted $r^2$ indicating the goodness of fit of the models. The null model includes only the intercept. The best models are shown in bold when they can be determined. logLik = maximum log likelihood.

energy to digest the exoskeletons (Wilson et al. 1985; Jackson et al. 1987, 1992). Thus, kittiwake chicks fed with a lower-trophic-level diet might have acquired less energy available for growth (Romano et al. 2006).

Intriguingly, we did not find any evidence for a link between female chick body size and $\delta^{15}N$. This sex difference could result from the sex-dependent energy requirement of growth in kittiwakes. Since male kittiwakes usually reach a slightly larger body size than the females (e.g., Welcker et al. 2010; Young et al. 2017; this study), they have higher energetic demands during the growth period (Merkling et al. 2015; Gil et al. 2020). This may explain why the body size of male chicks is more dependent on nutritional conditions, and thus on $\delta^{15}N$, than that of female chicks. Accordingly, several seabird studies have shown that male chicks require more energy during their development than female chicks (e.g., Weimerskirch et al. 2000; Merkling et al. 2012) and that male chicks are often more sensitive to nutritional constraints than females (e.g., Merkling et al. 2012; Svagelj et al. 2021).

Finally, we found some evidence for a brood size–dependent relationship between $\delta^{15}N$ and TL in kittiwake chicks. Specifically, chicks with higher $\delta^{15}N$ had shorter telomeres in two-chick broods, whereas this relationship was absent in single-chick broods. Although this finding contradicts our prediction 2, it aligns with the negative relationship between body size and TL in two-chick broods in this study, supporting our prediction 3b and the growth-TL trade-off hypothesis (Monaghan and Ozanne 2018). Nevertheless, this brood size–dependent relationship with $\delta^{15}N$ did not explain chick TL variation significantly better than the null model and is not robust across the model set.

Previous studies have convincingly shown that chick TL is linked to not only environmental factors (e.g., Gómez et al. 2021; Westneat et al. 2023) but also parental factors (e.g., heritability [Bauch et al. 2022; Chik et al. 2022, 2025; Marciau et al.

2025], parental age [Bouwhuis et al. 2018; Dupont et al. 2018; Marasco et al. 2025], parental stress [Haussmann and Heidinger 2015; Marasco et al. 2019], egg composition [Criscuolo et al. 2020; Noguera et al. 2022]). Therefore, it suggests that the developmental conditions during the year of our study may not have been constraining enough to drive the interindividual variation in TL and that most of the TL variation in this study may be driven by parental factors. However, this explanation may be unlikely because we found some relationships between body size and TL. Alternatively, the influence of $\delta^{15}$N on chick TL may not be consistently detected because of our small sample size ($n = 33$) and low statistical power (0.40). At least 74 chicks would be required to raise the power to 0.8. In addition, the relationship between $\delta^{15}$N and chick TL may be weakened by the confounding effects of nutritional constraints and growth rate on both $\delta^{15}$N and TL in seabird chicks (Williams et al. 2007; Sears et al. 2009; Mizutani et al. 2016; Noguera and Velando 2020). Since our study is, to our knowledge, the first one to test the relationship between $\delta^{15}$N and early-life TL in wild vertebrates, we call for more studies that incorporate potential confounding factors, such as parental TL, age, and provisioning behaviors, to assess whether $\delta^{15}$N can reliably reflect the influences of developmental conditions on TL.

### *Body Size–Telomere Length Trade-Off*

We did not find a positive relationship between body size and TL in kittiwake chicks. This is not necessarily surprising because this positive relationship was supposed to result from the simultaneous negative impacts of brood size on both body size and TL (prediction 1), and such effects were not found in our study. Instead, we found a negative relationship between body size and TL (supporting prediction 3b). However, this relationship was found only in broods of two chicks, thus supporting the idea of a growth-TL trade-off under constraining conditions (Monaghan and Ozanne 2018). Previous studies also reported such a negative relationship between TL and body size in developing animals (e.g., McLennan et al. 2016; Bae et al. 2022; Badás et al. 2023; Zhang et al. 2023); similarly, these relationships seem to appear mainly under constraining conditions (e.g., Geiger et al. 2012; Stier et al. 2014; Spießberger et al. 2022). Sibling competition can impose nutritional constraints (Benhaiem et al. 2012; Wojczulanis-Jakubas et al. 2023; Oelze et al. 2024), increase energy expenditure through competition for access to food (e.g., begging [Kilner 2001], aggression [Gonzalez-Voyer et al. 2007]), and activate stress responses (Benhaiem et al. 2013; Braasch et al. 2014) that entail energetic costs (Kitaysky et al. 2003; Schoech et al. 2011). As a result, the kittiwake chicks facing sibling competition in two-chick broods may not have sufficient resources to maintain both growth and TL, revealing the growth-TL trade-off (Monaghan and Ozanne 2018). However, this brood size–dependent relationship between body size and TL was supported only in the three top candidate models because it became nonsignificant after full-model averaging. This suggests that our sample size ($n = 33$) may not provide sufficient statistical power to consistently detect this relationship (power = 0.65). At least 43 chicks would be required to reach a power of 0.8.

In many species, including seabirds, a larger body size can drastically improve survival from early life to adulthood (Sagar and Horning 1998; Morrison et al. 2009; Ronget et al. 2018). Relatively, telomere maintenance may be of less importance than growth in early life because telomeres can potentially be lengthened by telomerase (Brown et al. 2022; Smith et al. 2022) and the costs of short telomeres might be paid only later in life (Eastwood et al. 2022; Tissier et al. 2022). In contrast, body size is determined during the developmental period and remains relatively stable in adulthood (Noordwijk et al. 1988). To maximize survival probability, developing animals might prioritize limited resources for growth rather than telomere maintenance. As this negative relationship between TL and body size was not detected in singleton chicks (no sibling competition), our result is also in line with previous evidence showing that the growth-TL trade-off can be masked by good external conditions that allow for sufficient resources to invest in both TL maintenance and growth (e.g., Spießberger et al. 2022; Wolf and Rosvall 2022). For instance, in great tits (*Parus major*), the last-hatched nestlings showed a significant and negative relationship between growth and TL, but this relationship was not apparent in first-hatched nestlings (Stier et al. 2015), which are likely to receive more food than their last-hatched siblings (Bakaloudis et al. 2020).

Some other studies found different body size–TL relationships than our result (e.g., Vedder et al. 2017; Boonekamp et al. 2022). For example, Parolini et al. (2015) showed a positive association between the body size and TL of barn swallow (*Hirundo rustica*) nestlings, and Nettle et al. (2016) showed a negative body size–TL association in European starling (*Sturnus vulgaris*) nestlings in smaller broods rather than in larger broods. However, these findings can still be explained, to some extent, by resource-modulated trade-offs. Parolini et al. (2015) stated that nestlings with longer telomeres and larger sizes might be in better nutritional conditions, which allowed for both telomere maintenance and rapid growth. Nettle et al. (2016) similarly proposed that larger nestlings in large broods may have a competitive advantage over their siblings in receiving more resources to reduce telomere shortening. This mutual rationale behind body size–TL relationships in different scenarios signifies the importance of accounting for resource availability differences when studying telomeres.

### *Telomere Length and Return Probability*

Surprisingly, we found that kittiwakes with shorter early-life telomeres were more likely to return to the natal colony within 6 yr after fledging, which signifies their survival to adulthood. This finding contradicts our prediction 4 and many previous studies showing TL as a positive indicator of survival probability (e.g., Fairlie et al. 2016; Wilbourn et al. 2018; van Lieshout et al. 2019; Noguera and Velando 2020). However, this positive relationship between TL and survival is not consistent among studies, most of which did not find any relationship between TL and survival (reviewed in Eastwood et al. 2023). A few studies found similar negative associations to ours between early-life TL and survival in other vertebrate species (McLennan et al. 2017), including birds (Wood and Young 2019). These mixed results suggest that the link between TL and survival can be context dependent (Eastwood et al. 2023).

Such a negative association between TL and return probability can again be explained by the resource-allocation trade-off between telomere maintenance and other physiological processes (e.g., growth in this study) in preparation for challenges in later life (Monaghan and Ozanne 2018). In Atlantic salmon (*Salmo salar*), TL before outward migration to the sea negatively predicted the survival probability during the first few years of their life in the sea and their return migration to the natal habitat, possibly due to the prioritization of physiological preparation for life at sea at a telomeric cost (McLennan et al. 2017). Similarly, we found that telomeres were shorter when individuals grew larger in broods of two chicks (i.e., facing sibling competition). Therefore, shorter telomeres may be associated with a larger body size (McLennan et al. 2016) and hence with better survival abilities (e.g., foraging abilities; Young et al. 2015) during the first few years of life at sea, explaining this counterintuitive relationship between TL and return probability. This plausible explanation is, however, not fully supported by our results because we did not find strong evidence for a link between body size and return probability. One possibility is that the negative association between TL and return probability may be attributed to the trade-offs with not only body size but also other developmental processes (Criscuolo et al. 2018), such as the development of the brain, muscles, immune system, and thermoregulation, that can also positively influence individual performance in general and survival in particular (Møller and Saino 2004; Dayananda and Webb 2017; Favilla and Costa 2020; Roast et al. 2020; Soravia et al. 2021).

Another possible explanation for the negative association between TL and return probability is hormesis, which refers to opposite physiological responses to low and high doses of stressors (Calabrese et al. 2007; Costantini et al. 2010; Costantini 2012; Monaghan 2014). As opposed to the detrimental impacts of strong stressors, mild stressors may not only moderately shorten telomeres but also activate various cellular pathways (e.g., Karatsoreos and McEwen 2013; Fontana and Partridge 2015) that enhance resilience and individual performance (Marasco et al. 2017, 2021; Young et al. 2022; see Costantini et al. 2010). Given that the developmental constraints during our study period may have been too mild to inflict strong negative impacts on TL, these mild constraints may have resulted in the negative link between TL and return probability via hormesis. However, this explanation contradicts the positive relationship between $\delta^{15}$N and return probability in this study. A more plausible explanation is the telomere hormesis hypothesis (see Jacome Burbano and Gilson 2021), where moderately shortened telomeres may act as a signal that directly triggers beneficial cellular responses (e.g., Pryde and Louis 1999; Ai et al. 2002; Ye et al. 2014; Bárcena et al. 2018) and potentially performance (e.g., survival).

We would expect that this negative link between TL and return probability was apparent only when kittiwake chicks had to prioritize growth at the expense of TL (i.e., in broods of two chicks) and not when the developmental conditions allowed the chicks to reach a large body size while maintaining long telomeres (i.e., in broods of one chick). Unfortunately, the power analysis showed that our sample size ($n = 33$) was too small to include the TL × brood size interaction in the return probability ~ TL model (for an effect size of 0.15, power $= 0.45$). A sample size of 76 individuals would be required to reach a power of 0.8 for an effect size of 0.15.

We found that TL is a much better predictor of return probability than body size or brood size in our study of kittiwakes, although the direction of the relationship was unexpected. These results support the idea that early-life TL can be a relatively comprehensive measurement of performance later in life and possibly a robust proxy of developmental conditions. Surprisingly, we found that $\delta^{15}$N and TL had similar importance in predicting kittiwake return probability, even though we found only weak evidence for a brood size–dependent relationship between $\delta^{15}$N and chick TL. This suggests that $\delta^{15}$N and TL may affect survival through different aspects. $\delta^{15}$N may encompass the effects of developmental conditions related to diet, such as parental foraging strategy or capability (Tarroux et al. 2020) and prey availability in the foraging ground (Pollock et al. 2017), while TL may integrate the effects of overall physiological development on the future performance of chicks.

Although we cannot fully exclude the possibility that some birds have dispersed or survived without being seen, this is quite unlikely as the 52% return rate of our study cohort is close to or higher than the maximum estimated survival rate of kittiwake subadults (i.e., 2–5 yr old) in other studies (Coulson and White 1959; Coulson 2011; Desprez et al. 2011). In addition, the extensive long-term seabird monitoring in Svalbard, which covers the most likely dispersal range for kittiwake subadults from our study colony (Coulson and Nève 1992), did not record any kittiwakes from our study cohort in other monitored colonies. Finally, missing some survivors would have more likely masked a potential relationship between TL and return probability than resulted in the reported relationship between these two variables.

### *Conclusion*

In conclusion, our study adds support to the idea of early-life TL as a predictor of later-life performance. However, it also highlights the context dependency of the relationship between TL and individual performance because we found that, contrary to several studies, shorter telomeres were related to better individual performance, represented by higher return probability. Therefore, whether it is long or short telomeres that associate with better individual performance needs to be further confirmed by accounting for the trade-offs between telomere maintenance and other developmental processes, such as growth (Monaghan and Ozanne 2018), and testing under different resource constraint intensities. When individuals are in environmental conditions or intrinsic biological states that impose mild resource constraints, they might prioritize the limited resources to physiological processes that promote immediate or short-term survival rather than telomere maintenance, which is more likely to reflect long-term performance. In addition, moderately shortened telomeres caused by mild constraints may also activate cellular mechanisms that enhance resilience and long-term performance (Costantini et al. 2010; Jacome Burbano and Gilson 2021). As these condition dependencies can complicate the feasibility of using TL as a fitness proxy, they should be considered in future studies to investigate the pattern in the relationship between early-life TL and individual performance.

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