

Telomere length and environmental conditions predict stress levels but not parental investment in a long-lived seabird

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ABSTRACT: Telomeres are increasingly regarded as viable biomarkers of individual quality, and thus may be associated with other proximate markers of quality. We compared telomere length to such quality markers in a long-lived seabird, the thick-billed murre *Uria lomvia*, breeding under varying environmental conditions on 3 colonies in the Bering Sea. Individual quality was assessed using behaviors associated with parental investment (trip rate and nest attendance, determined by bird-borne data loggers), body condition, and physiological stress (baseline corticosterone). Telomere length was related to physiological stress and body condition, while parental investment in reproduction was not. This implies that maintenance of consistent levels of parental care was prioritized and that individual quality changes were expressed physiologically (changes in telomere length) rather than behaviorally. Under poor environmental conditions, short telomeres were associated with lower levels of physiological stress. However, under good environmental conditions, they were associated with higher levels of stress. These findings confirm that telomere length variation is related to patterns in stress hormones and support previous findings that environmental conditions are an important mediator of telomere dynamics.

KEY WORDS: Individual quality · Brünnich's guillemot · Corticosterone · Parental investment · Temperature–depth recorder · Telomeres · Thick-billed murre · *Uria lomvia*

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INTRODUCTION

Telomere length is increasingly being used as a signal of individual quality in ecological systems (Hall et al. 2004, Bize et al. 2009, Thaxter et al. 2009). Telomere length or loss rate has been linked to survival (Olsson et al. 2011, Barrett et al. 2013) and lifespan (Heidinger et al. 2012) as well as reproductive success (Le Vaillant et al. 2015). In most species studied, telomeres shorten throughout life (Haussmann et

al. 2003, Hatakeyama et al. 2008, Muezzinler et al. 2013, Aydinonat et al. 2014, Beirne et al. 2014), although this pattern is not universally observed (Haussmann & Mauck 2008b, Gruber et al. 2014, Le Vaillant et al. 2015). The large inter-individual variation that prevents telomeres from being a strictly accurate measure of chronological age allows for their utility as a measure of individual quality or biological age (Monaghan & Haussmann 2006, Shalev 2012, Barrett et al. 2013). Therefore, telomere length may

act as a quality indicator that integrates genetic differences, age, experience, and individual history (Monaghan & Hausmann 2006). Ecological studies often relate fitness outcomes to proximate measures of individual quality, such as body condition or mass, which change both within and between seasons and are not necessarily informative of past states (Schultner et al. 2013). If telomere length acts as an integrated quality measure, then it may be related to commonly used proximate quality indicators.

In this study, we examined telomere length in relation to several proximate measures of quality in a long-lived seabird, the thick-billed murre *Uria lomvia*. Thick-billed murre telomeres decline with age, but much inter-individual variation is unexplained, which may indicate quality (Young et al. 2013). Telomere length has also been shown to be related to foraging behaviors in murres (Young et al. 2015), and its loss may be correlated with environmental conditions (Young et al. 2013). These patterns increase the likelihood that telomere length will be related to proximate quality indicators which are strongly driven by environmental conditions and food availability. Stress levels, body condition, and behavioral investment in offspring are all used as proximate measures of quality in animals, including murres (Gaston & Hipfner 2006, Benowitz-Fredericks et al. 2008). Typically, a high-quality individual will show low levels of glucocorticoid stress hormones (CORT), high body condition, and high levels of parental investment.

Telomeres are known to indicate chronological age, so if relationships exist between age and other measures of individual quality, correlations with telomere length may merely reflect chronological age and not individual quality. However, in murres there is no significant relationship between baseline CORT levels and age, although maximum CORT response to a standardized acute stress of capture and handling shows a quadratic relationship with age (Elliott et al. 2014). Body condition has not, to our knowledge, been explicitly analyzed in relation to age in this species, but in the sister species *U. aalge*, body condition was uncorrelated with age in known-age adults (R. C. Young unpubl. data). Flying and diving behaviors also do not

change with age in murres (Elliott et al. 2015). Murres are behaviorally flexible and adjust their time budgets in order to provide consistent levels of parental investment as environmental conditions change (Bryant et al. 1999) and as they age (Elliott et al. 2015). As none of these proximate quality measures changes with age, relationships with telomere length would indicate a common pattern among quality indicators, and not age as an underlying driver. Therefore, we predict that longer telomere length will be associated with low baseline CORT, high body condition, and high parental investment (a large proportion of time attending the nest and a high rate of foraging trips). We also predict that these relationships will be stronger under poor environmental conditions, where individual quality plays a larger role in determining resource acquisition.

MATERIALS AND METHODS

Study sites and colony conditions

Chick-rearing adult murres were sampled on 3 colonies. The Pribilof Islands: St. Paul Island (57° 08' N, 170° 18' W) and St. George Island (56° 36' N, 169° 39' W), are located in the central Bering Sea along the shelf-edge, and were sampled in 2008 and 2009 (Table 1), but no birds were equipped with devices in both years. Bogoslof Island (53° 56' N, 168° 02' W) is located in oceanic waters in the eastern Aleutian Archipelago and due to the logistical challenges of its remote location was only sampled in 2009. Genetic structure indicates that these colonies

Table 1. Sample sizes and dates of logger deployment and recaptures of thick-billed murres *Uria lomvia* breeding on 3 colonies in the Bering Sea in 2 years

Colony	Males	Females	Deployment dates (days of year)	Recapture dates (days of year)
2008				
St. Paul Island	6	5	28 July – 11 August (210–224)	31 July – 14 August (213–227)
St. George Island	7	12	26 July – 16 August (208–229)	29 July – 18 August (211–231)
2009				
St. Paul Island	13	12	1 August – 16 August (213–228)	4 August – 20 August (216–232)
St. George Island	4	16	30 July – 17 August (211–229)	1 August – 22 August (213–234)
Bogoslof Island	18	8	25 July – 16 August (206–228)	27 July – 18 August (208–230)

are 1 population of thick-billed murre, so differences between colonies are not driven by genetic divergence (Tigano et al. 2015). However, these colonies display different environmental conditions, which drive overall murre population trends; both St. Paul and St. George saw dramatic population crashes during an oceanic regime change in the 1970s (Hare & Mantua 2000). Currently, St. Paul continues to decline, although St. George is seeing moderate recovery (Byrd et al. 2008), and the population of Bogoslof continues to increase. The post-1970s patterns of resource distribution and population trends indicate that these islands currently experience consistent environmental variation and can be characterized as follows. The Pribilofs are on the variably productive continental shelf, yet St. George remains within commuting distance of the extremely productive Bering Sea Green Belt, associated with the shelf break which marks a change from relatively shallow continental shelf waters to deeper oceanic ones (Dorresteijn et al. 2012, Harding et al. 2013). Bogoslof, located in the consistently productive oceanic basin waters near Aleutian passes, experiences good environmental conditions. Thus, Bogoslof has ready access to nearby food sources, St. George has access to more distant but reliable food, and St. Paul has access to nearby food sources unreliable in availability and nutritional content. Furthermore, both in long-term studies (Hare & Mantua 2000) and in birds sampled in our study years (Harding et al. 2013, Young et al. 2015), comparisons of nutritional stress and stable isotopes confirmed poor environmental conditions on St. Paul, good environmental conditions on Bogoslof, and intermediate environmental conditions on St. George. Murres breeding on each island relied on distinct food webs and prey sources (Young et al. 2015).

Chick-rearing murres were captured at their nests using noose poles when chicks were 7 to 10 d old (Table 1). At first capture, birds were weighed to the nearest 5 g, and banded for individual identification. Blood sampling was completed within 3 min of first capture for hormone analysis and genetic sexing. This time interval has been deemed suitable for sampling baseline stress levels in birds (Romero & Reed 2005), including the thick-billed murre (Benowitz-Fredericks et al. 2008). Plasma and red blood cells were separated by centrifugation and stored frozen. Since murres are monomorphic, sexing was done molecularly using primers and protocols described by Griffiths et al. (1998). Blood samples for telomere analysis were preserved in a 2% EDTA buffer, shipped to the laboratory where they were trans-

ferred to a glycerol storage buffer, and frozen at -80°C . Behavioral variables were measured with temperature–depth recorders (loggers, Cefas G5, Cefas Technologies) attached to the keel feathers with Tesa tape (Ito et al. 2010). The total deployment package (i.e. logger and tape) mass was 1.5 g, less than 1% of bird body mass. Loggers recorded time, pressure, and temperature every 2 s. Birds were recaptured after 3 d, with an average (\pm SE) deployment length of 73.1 ± 3.7 h (22–220 h). Skeletal measurements for body size (lengths of head and bill, tarsus, and wing) were also taken at second capture. In total, 101 birds were sampled (Table 1), but for 1 bird, a CORT sample could not be obtained. For a different bird, logger malfunction meant that attendance and trips per day could not be calculated. An additional observation was excluded in the trip rate analysis, as it was anomalously high and consistently drove patterns in model residuals. Scaled body condition was calculated as per Peig & Green (2009), using headbill as the length measurement. Four birds did not have sufficient measurements to calculate body condition. Accordingly, our analysis was done for 97 of 101 individuals.

Laboratory techniques

Corticosterone assay

Total baseline CORT (free and bound fractions) was measured according to established protocols (Benowitz-Fredericks et al. 2008) at the University of Alaska Fairbanks. Briefly, for each sample, 20 μl of plasma was equilibrated with 2000 cpm of tritiated CORT and then extracted with 4 ml of re-distilled dichloromethane. After extraction, recoveries (percent tritiated hormone recovered from each individual sample) were used to correct final values. Samples were reconstituted in PBSG buffer and combined with antibody and radiolabel in a radioimmunoassay (Wingfield & Farner 1975, Wingfield et al. 1991). Dextran-coated charcoal was used to separate antibody-bound hormone from unbound hormone. Inter- and intra-assay CV (standard deviation / square root of mean) were less than 4% and 2%, respectively.

Telomere restriction fragment assay

Telomeres were measured at the University of Alaska Fairbanks using the telomere restriction fragment (TRF) assay, according to Haussmann & Mauck

(2008a) and Young et al. (2015). Five microliters of red blood cells, previously stored at -80°C in a glycerol buffer, were extracted into agarose plugs using the Chef Genomic DNA Plug Kit (Bio-Rad) and digested with a mixture of 3 U *HinfI*, 15 U *HaeIII*, and 40 U *RsaI* (Roche Applied Science). DNA was separated using pulsed field gel electrophoresis (PFGE) on a 0.8% agarose gel. Run parameters were 21 h at 3 V cm^{-1} and 0.5 to 7 s switch times. Circulated buffer ($0.5\times\text{ TBE}$) was kept at 14°C . Hybridization was at overnight at 37°C with 3 million cpm of the telomere-specific radio-labeled oligo: $(\text{CCCTAA})_4$. After hybridization, rinsing and visualization followed Haussmann & Mauck (2008a).

Telomere samples were analyzed on 4 gels with 2 control samples per gel to determine inter- and intra-assay variability ($\text{CV} = \text{range}/\text{mean}$; inter-assay: 27.0%; intra-assay: 2.01%). Samples from each colony were evenly distributed between gels. To control for inter-assay variability, telomere lengths were standardized to the in-gel common standard, resulting in residual telomere length values, which were then added to the average value of the standard. Telomere length values were calculated from gel images following Salomons et al. (2009). The shortest telomeres in a cell appear to be the cause, or at least an indicator of, cellular senescence (Hemann et al. 2001, Zou et al. 2004), and it is believed they are also more sensitive to ageing in whole organisms (Haussmann & Mauck 2008a, Smith et al. 2011). Following Haussmann & Mauck's (2008a) technique for identification of the optimal analysis window, we analyzed the TRF smear from 5 kb to the bottom of the gel, a window which has shown a stronger relationship with age in this species (Young et al. 2013). Whole-smear values ranged from 1.98 to 9.87 kb, and the lower window values ranged from 1.88 to 4.02 kb. A comparison of results from analyses run on the whole smear vs. the lower window show qualitatively similar results, so we have presented data from the more age-driven measure: the lower window TRF, which we call telomere length (TL).

Parental behavior

Extraction of data from raw data logger output was performed according to Ito et al. (2010). Nest attendance was calculated as the proportion of total deployment time which the bird spent at the colony. Time at the colony brooding was determined by temperature readings which were higher than air or sea temperature, indicating incubation. Trip rate, the

number of trips per day, was calculated as the number of complete foraging trips performed during deployment divided by the total deployment time in days. This measure estimates the maximum provisioning rate, as murre parents bring back 1 fish per foraging trip. Temperature changes from incubation temperatures to cooler air (flying) or sea (diving, resting) temperatures indicated the beginning and end of trips.

Statistics

We assessed 2 physiological measures of individual quality, viz. baseline CORT and body condition at first capture, and 2 measures of reproductive investment, viz. trip rate and nest attendance. Each response variable (physiological: CORT and body condition; parental: trip rate and attendance) was analyzed using linear models in the R statistical environment (R Development Core Team 2011, v. 2.12.2). For each parameter, the same base family of models was tested (Table 2). Models were compared using Akaike's information criterion corrected for small sample size (AIC_c), and assumptions of linearity were verified by examination of residual plots and q-q plots of residuals (Boldina & Beninger 2016); examination of residuals plotted sequentially revealed no autocorrelation. Averaged parameter estimates and parameter variances were calculated using models making up 95% of AIC weight (Symonds & Moussalli 2011). A parameter was considered a good predictor if the averaged estimate bounded by its averaged standard deviation did not overlap zero. TL is a measure of the bird's history, age, and innate genetic quality, and may therefore affect our parameters of interest, making it appropriate as a predictor, but not as a response variable. In the analysis of body condi-

Table 2. Model family for testing 4 response variables for thick-billed murres *Uria lomvia*: baseline corticosterone, body condition, trip rate, and attendance

Model	Terms
0	Null
1	Telomere length (TL)
2	Colony
3	Sex
4	Year
5	Day of year
6	TL + colony + TL:colony
7	TL + sex + TL:sex
8	Colony + sex + colony:sex

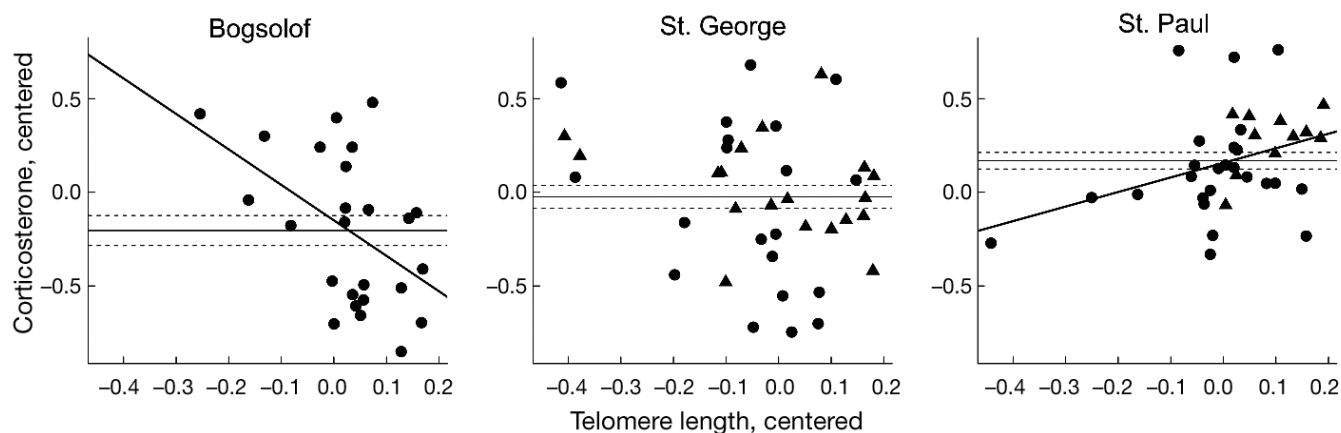


Fig. 1. Baseline corticosterone (CORT, $\text{ng } \mu\text{l}^{-1}$) of thick-billed murres *Uria lomvia* predicted by colony and telomere length. CORT was \log_{10} -transformed for normality and centered to standardize effect sizes. 2008 is indicated by circles, 2009 by triangles; note that Bogoslof Is. was sampled in 2009 only. Trend lines indicate relationships with non-zero effect sizes in the averaged model. Solid horizontal lines indicate colony CORT means, while dashed lines indicate \pm standard error of the mean

tion, 2 additional models were run: one with CORT as a predictor and the other testing the interaction of CORT and colony. CORT and body condition values were log-transformed to increase normality of error distributions. In order to standardize effect sizes, CORT, body condition, trip rate, TL, and day of year were centered: the residuals on the mean were divided by the mean. Attendance varied between 0 and 1; so for this variable, residuals were used but were not divided by the mean. Values are reported as mean \pm SE, unless otherwise noted.

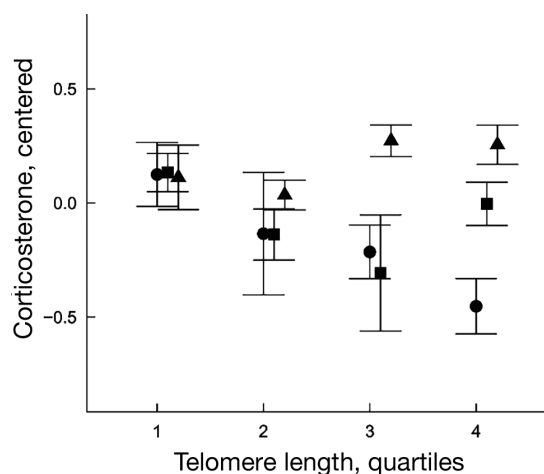


Fig. 2. Baseline corticosterone (CORT, $\text{ng } \mu\text{l}^{-1}$) of thick-billed murres *Uria lomvia* predicted by colony and telomere length. CORT was \log_{10} -transformed for normality and centered to standardize effect sizes. Bogoslof is indicated by circles, St. George by squares, and St. Paul by triangles. Bars indicate standard error. Birds with the shortest quartile of telomere length have similar stress levels on all colonies, but differences appear for birds with long telomeres, in the third and fourth quartiles

RESULTS

Physiological quality measures

CORT results from previous studies on these colonies in these years indicate that the colonies varied in their physiological stress exposure (Harding et al. 2013, Young et al. 2015). Colony-wide patterns were the same as the patterns in the subset of birds bearing our data loggers. Physiological stress was best predicted by the interaction of TL and colony (Figs. 1 & 2). Birds with shorter TL had higher physiological stress on Bogoslof and lower physiological stress on St. Paul, but there was no relationship with TL on St. George. Body condition was best predicted by the interaction of TL and sex (Table 3). Females had higher body condition than males, but male condition was positively related to TL, while female condition was not.

Reproductive investment

Colony was the only predictor for trip rate where the estimated parameter differed from zero, yet effect sizes remained small (Table 4). St. Paul birds performed the most trips per day, and St. George birds the fewest (St. Paul: 1.9 ± 0.2 ; St. George: 1.2 ± 0.1 ; Bogoslof: 1.6 ± 0.2 trips d^{-1}). Attendance was best predicted by the interaction of colony with sex. Males attended the colony a significantly higher percentage of the time than females on Bogoslof and St. George, while on St. Paul the sexes did not differ (Fig. 3).

Table 3. Best models for each response variable for thick-billed murres *Uria lomvia*. Models are presented up to 95% of Akaike's information criterion (AIC) weight. AIC_c: AIC corrected for small sample size, TL: telomere length

Response variable	Best model(s)	AIC _c weight	Sum AIC _c weight
Corticosterone (CORT)	TL + colony + TL:colony	0.972	0.972
Body condition	Sex + colony + sex:colony	0.516	0.516
	Sex	0.392	0.908
	TL + sex + TL:sex	0.0703	0.979
Trip rate	Colony	0.639	0.639
	TL + colony + TL:colony	0.139	0.777
	Day of year	0.079	0.857
	Null	0.042	0.899
	Sex + colony + sex:colony	0.030	0.928
	Year	0.026	0.955
Attendance	Sex + colony + sex:colony	0.917	0.917
	Sex	0.052	0.969

Table 4. Model averaged parameter estimates for thick-billed murres *Uria lomvia* and averaged parameter variances. SD: standard deviation, based on averaged variances, TL: telomere length. Colonies are abbreviated: STG: St. George; STP: St. Paul. Parameters with an SD that does not include zero are in **bold**

Response	Term	Model averaged parameter estimate	Model averaged variance	SD
Corticosterone (CORT)	Intercept	-0.150	0.00472	0.0687
	TL	-1.89	0.429	0.655
	Colony – STG	0.107	0.00763	0.0873
	Colony – STP	0.307	0.00779	0.0883
	TL:STG	1.32	0.542	0.736
	TL:STP	2.67	0.640	0.800
Body condition	Intercept	0.0871	0.00146	0.0381
	TL	-0.00448	0.00355	0.0596
	Colony – STG	-0.0226	0.00675	0.0821
	Colony – STP	-0.0495	0.0117	0.108
	Sex – male	-0.146	0.0248	0.157
	TL:sex	0.0634	0.00401	0.0634
	TL:STG	0.0297	0.00317	0.0563
	TL:STP	0.0214	0.00321	0.0566
Trip rate	Intercept	-0.0437	0.0151	0.123
	TL	-0.329	3.43	1.85
	Colony – STG	-0.225	0.0285	0.169
	Colony – STP	0.195	0.0283	0.168
	Sex – male	0.00436	0.0160	0.126
	Year – 2009	0.00470	0.0215	0.147
	Day of year	0.377	14.3	3.78
	TL:STG	0.396	4.92	2.22
	TL:STP	0.399	5.05	2.25
	STG:male	-0.00652	0.0351	0.187
	STP:male	-0.00121	0.00185	0.0430
	Attendance	Intercept	-0.110	0.0023
Colony – STG		0.0537	0.00292	0.0540
Colony – STP		0.114	0.00373	0.0611
Sex – male		0.215	0.00378	0.0615
STG:male		-0.0675	0.00558	0.0747
STP:male		-0.238	0.00692	0.0832

DISCUSSION

TL, CORT, and body condition

This study tested the relationships between TL and proximate measures of individual quality in thick-billed murres breeding at 3 colonies with varying environmental conditions. We predicted that birds with shorter telomeres would have higher stress levels and lower body condition and that these relationships would be stronger in a colony with poor environmental conditions. Males demonstrated a positive correlation between body condition and TL, but females did not. Males also had lower body condition than females, so perhaps as predicted, the relationship between TL and a quality indicator is stronger when condition is poorer.

The relationship between TL and stress was more complicated, and an interaction between colony and TL was the best predictor of CORT levels. The relatively strong effect sizes associated with CORT (Table 4) are not unexpected, as an increasing body of literature indicates that stress hormone dynamics may be directly related to causes of telomere shortening (Hausmann & Marchetto 2010, Herborn et al. 2014, Schultner et al. 2014). CORT levels indicated that food availability differed at each colony and supported the previous finding that the 3 colonies tested fall in a range from poor (St. Paul), to moderate (St. George), to good (Bogoslof) conditions during the study period (Harding et al. 2013). Varying environmental conditions affect food availability to murres (Kitaysky et al. 2010, Dorresteijn et al. 2012, Riechert et al. 2014, Barrett et al. 2015), thus CORT levels likely drove the significant effect of colony and TL on CORT. However, the direction of colony effects was unexpected. Under good conditions (Fig. 1, Bogoslof), we observed the predicted pattern, i.e. CORT was higher for birds with short telomeres, indicating that these birds may be of lower quality. But the pattern was reversed, instead of strengthened, under poor conditions (Fig. 1, St. Paul). This may be explained by the relative

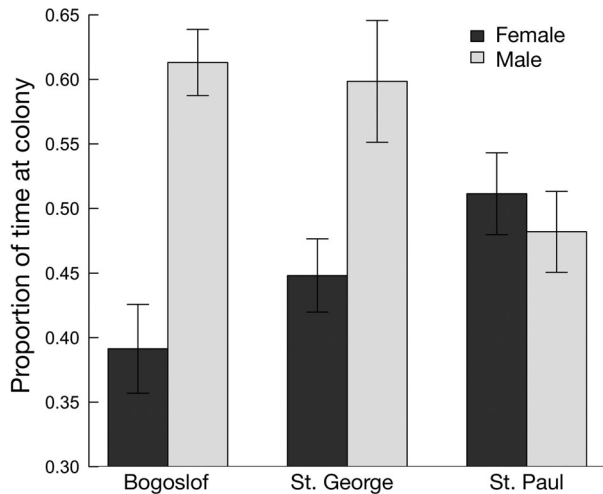


Fig. 3. Colony attendance of thick-billed murres *Uria lomvia* by colony and sex. Sex-dependent attendance patterns differed by colony: males on Bogoslof (food-rich colony) and St. George (middling foraging conditions) have higher attendance than birds on St. Paul (food-poor colony); the opposite pattern was observed for females. Reported means indicate the proportion of time attending the nest site, vertical bars indicate standard errors

CORT levels at each colony. In the colony with good conditions, stress levels ranged from low to medium, while in the colony with poor conditions, the levels ranged from medium to high. This pattern is clearly seen in Fig. 2, which shows that birds with the shortest quartile of TL had similar stress levels in all colonies, but differences appear for birds with long telomeres, in the third and fourth quartiles. Birds with short telomeres, and presumably low quality, had elevated stress under all conditions. The question is what drives the elevated stress in birds with long telomeres under poor conditions.

Perhaps these birds are of high quality, but lack experience foraging and raising a chick simultaneously under conditions of low food availability. This is especially likely if they are young birds or lack breeding experience. A similar pattern has been noted in other birds, where the benefits of experience (increased fledging success) offset senescence (reduced clutch size) (ptarmigan; Wiebe & Martin 1998). When a process that underlies changes in individual quality, like ageing of biological systems, carries both benefits and costs, an external environmental factor, such as foraging conditions, may tip the scales to display higher costs or higher benefits (Laaksonen et al. 2002). Aging processes are commonly associated with trade-offs between the benefits of increased experience and the costs of senescence (de Forest & Gaston 1996, Lewis et al. 2006,

Reed et al. 2008). It should be noted that analysis of 3 colonies allowed a more complete understanding of these dynamics as driven by environmental differences at the focal colonies than an analysis of only 1 colony would have. As found with albatross molt schedules (Catry et al. 2013), patterns found at 1 colony may not always be generalizable. Indeed, although murre colonies varied from good (Bogoslof) to poor (St. Paul) during our study years, these conditions may not be stable over longer timespans (Barger & Kitaysky 2012, Satterthwaite et al. 2012). This relationship between colony, TL, and stress levels is supported by evidence that the link between TL and foraging variables is mediated by current colony conditions (Young et al. 2015), strengthening the idea that TL is a measure of individual quality which incorporates responses to environmental conditions (Buxton et al. 2012, Mizutani et al. 2013).

Parental investment

In contrast to our predictions, TL was not a significant predictor of parental behaviors. However, this finding is consistent with previous studies which found that physiological measures changed with age, while parental behaviors were maintained (Elliott et al. 2015). Studies on thick-billed (Kitaysky et al. 2000) and common murres (Burger & Piatt 1990) have found that parents adjust time budgets and foraging behavior to provide constant levels of parental effort under all but the most extreme environmental conditions, and such extreme conditions fall outside of our study years and colonies. This adjustment of time budgets likely explains why the effect sizes were small for trip rate, but effects were stronger on attendance patterns: trip rates were maintained, but attendance suffered. Previous work on these colonies has shown that murre optimal foraging strategies do differ depending on distance to food sources (Harding et al. 2013), which likely explains the good explanatory power of colony in the trip rate analysis, and also may contribute to the interaction of sex and colony in explaining attendance patterns (Fig. 3).

CONCLUSION

This study addressed the relationship of an integrated lifetime measure of individual quality, TL, with proximate physiological and reproductive quality measures in thick-billed murres. In this long-lived species, TL was a good predictor of stress levels

(CORT), but the relationship was mediated by environmental conditions at the colonies. Birds with short telomeres always had elevated stress levels. Under good environmental conditions, birds with long telomeres had lower stress levels, as expected, whereas under poor environmental conditions, long telomeres were associated with high stress levels. This may imply that under stressful conditions, young or inexperienced birds have very high stress levels, even if their quality is high. However, more aged birds are able to maintain stress levels at more moderate levels. This study demonstrated that glucocorticoid stress levels and telomere dynamics are related and that environmental conditions are an important mediator of that relationship.

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