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Telomere length is a strong predictor of foraging behavior in a long-lived seabird

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Abstract. Telomeres are an increasingly studied component of physiological ecology. However, in long-lived birds a large telomere loss with chronological age is not the norm. Telomeres are now regarded less as a chronological aging tool and more as an indicator of individual quality, residual lifespan, or biological age. If telomeres indicate biological aging processes, then they should also be associated with other variables that change with age, especially foraging and reproductive behaviors. This study compared telomere length to a suite of foraging parameters in Thick-billed Murres breeding on three colonies in the Bering Sea. Telomere length, environmental conditions at colonies, and sex played pivotal roles in determining foraging habitat selection. Spatial habitat use, foraging efficiency, and prey selection variables all changed with telomere length. The behavioral evidence indicates that despite losing telomeres, birds with short telomere length retain their ability to use the environment efficiently. This indicates that aging birds remain behaviorally flexible, despite paying physiological costs. Changes in spatial use were largely sex-dependent: females and males differed in their use of the environment as telomere lengths declined. Prey selection was related to telomere length and colony; changes in murre trophic level depended on telomere length, but their direction also depended on habitat quality. We found much support for the continued able functioning of birds with shorter telomeres, indicating that physiological aging does not carry only costs. Murres appear to modify their behavior depending on environmental conditions as their physiological reserves decline.

Key words: Brunnich's Guillemot; data logger; diving behavior; foraging ecology; Pribilof Islands; seabird; telomeres; temperature-depth recorder; Thick-billed Murre; *Uria lomvia*.

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INTRODUCTION

Telomeres are an increasingly studied component of physiological ecology. These non-coding DNA repeats cap eukaryotic chromosomes and function to identify chromosome ends and protect coding DNA from damage (Monaghan 2010). Telomere degradation occurs when cells divide, and loss rates are accelerated by DNA damage, especially oxidative damage (von Zglinicki 2002, Monaghan 2014). Traditionally, telomeres are associated with the biology of aging (Holmes and Martin 2009, Dunshea et al. 2011) and have been shown to shorten with age in many species (Haussmann and Vleck 2002, Haussmann et al. 2003, Pauli et al. 2011, Müezzinler et al. 2013), but see (Francis et al. 2006). However, in long-lived birds a large telomere loss with chronological age is not the norm (Hall et al. 2004, Foote et al. 2011). Instead, most telomeres are lost from chick to adult and loss rates are much slower in adults (reviewed in Barrett and Richardson 2011).

Because telomere length is also highly variable within age groups, it is now regarded less as a chronological aging tool and more as an indicator of individual quality, residual lifespan, or biological age (Benetos et al. 2001, Monaghan and Haussmann 2006, Monaghan 2010). Ecologically, telomere length and dynamics have been tied to habitat use (Angelier et al. 2013), individual quality, reproductive success (Bauch et al. 2012), exposure to stress hormones, and migration patterns (Schultner et al. 2014). If telomeres truly cause or result from aging processes, then they should also be associated with other variables that change with aging, especially foraging and reproductive behaviors.

This study compared telomere length (TL) to a suite of foraging parameters in Thick-billed Murres (*Uria lomvia*, hereafter murres) breeding on three colonies in the Bering Sea. Murres, like most long-lived seabirds, show higher TL in chicks than adults (chicks: 3564 ± 82 bp; adults: 3441 ± 27 bp) and slow variable rates of change in adult birds, where loss rate in a cross-sectional sample of adults was 5.2 ± 10 bp per year (Young et al. 2013). Longitudinal changes in TL in murres indicate that colony-specific environmental conditions may play a mediating role in whether birds gain, lose, or maintain TL (Young et al. 2013; Young et al., *unpublished manuscript*). Habitat choice (high or low quality) can affect TL losses (Angelier et al. 2013), and exposure to stress, simulating the decreased food availability of poor environmental conditions, also exacerbates TL loss (Schultner et al. 2014). We also included sex in our analyses as it is a common driver of foraging behaviors in many taxa (Aho et al. 1997, Codding et al. 2011) including seabirds (e.g., Weimerskirch et al. 1997, Welcker et al. 2009). Adult male murres have longer telomeres than females (Young et al. 2013), which follows the pattern seen in other bird species (Horn et al. 2011). In murres, diving patterns differ by sex (Jones et al. 2002), and in the Common Murre (*Uria aalge*), females provide more food to the chick, perhaps because males invest in themselves during the nestling phase, saving chick investment for the extended weeks of post-fledging care provided only by the male (Thaxter et al. 2009).

We examined foraging behaviors along three axes: spatial use of habitat, temporal use of habitat, and prey selection. Since shortened telomeres indicate a deteriorated state or advancing age, we predict that birds with shorter telomeres will forage closer to the colony (Pelletier et al. 2014), at shallower depths, and spend less time diving at night. However, in some species, foraging distance from the colony increases when poor conditions decrease food availability (Huettman and Diamond 2001, Buren et al. 2012, Ponchon et al. 2014), therefore colony conditions may also drive foraging distance, and poor quality birds may forage further from the colony. In addition, we predict birds with deteriorated telomeres will spend less time underwater, indicating decreased foraging efficiency. Foraging efficiency declines with age in several seabird species (Oro et al. 2014) and may be a driver of aging patterns overall (Lecomte et al. 2010), although in some species foraging efficiency or success increased with age (Desrochers 1992, Rutz et al. 2006, Le Vaillant et al. 2013). Lastly, we predict that the stable isotope signatures of birds with short telomeres will indicate more inshore prey (if they forage closer to the colony) and lower trophic levels, since they cannot specialize on high quality, high trophic-level prey.

METHODS

Study sites and sampling

Adult Thick-billed Murres were sampled in five colony-years (e.g., St. George 2008, Bogoslof 2009). The Pribilof Islands (St. Paul and St. George) were sampled in 2008 and 2009, while Bogoslof Island was only sampled in 2009. Both years of our study had similar conditions (Harding et al. 2013). Year differences were minimal and are not considered here, as more sample years would be needed to detect differences due to interannual trends. The three colonies are part of a single genetic population (Friesen et al. 1992) and form a north-south gradient in the Bering Sea (Fig. 1). This study takes advantage of a gradient of colony-specific environmental conditions and habitat qualities (Byrd et al. 2008, Harding et al. 2013; Young et al., *unpublished manuscript*). Previous work has characterized the study system during our study years (2008 and 2009) as a "food-rich colony," Bogoslof; a "food-poor colony," St. Paul; and one which presents intermediately, St. George; hereafter "good," "poor," and "middling" (Harding et al. 2013; Young et al., *unpublished manuscript*). These colony differences are also reflected in Thick-billed Murre population trends and stress hormone patterns; Bogoslof is an increasing colony with low stress levels, St. Paul is declining or stabilizing after a crash and has high stress levels, and St. George is stable after recovery from a crash with middling stress levels (Byrd et al. 2008, Dragoo et al. 2012). However, longitudinal changes in murre telomeres on the three colonies were comparable (Young et al. 2013).

Chick-rearing murres were captured at their nests using noose poles, and were targeted when the chick was 7–10 days old. Diving and telomere data were available from 101 birds: St. George 2008: 19; St. George 2009: 20, St. Paul 2008: 11, St. Paul 2009: 25, and Bogoslof 2009: 26. Each bird took an average of 4.7 ± 0.37 trips. Trips were comprised of 7.2 ± 0.35 diving bouts (for a total of 34 ± 1.6 bouts per bird) and bouts contained 15 ± 0.53 dives (for a total of 510 ± 43 dives per bird). However, not all data were available for each bird for each analysis (e.g., return flight times for each trip or sea-surface temperature for each bout), specific sample sizes can be found in Appendix A. Blood was sampled from the brachial vein for TL assays and genetic sexing, with some red blood cells set aside for stable isotope analysis. Blood for TL analysis was preserved in a 2% EDTA buffer, transferred to a glycerol storage buffer, and frozen for shipment to the laboratory. Temperature-depth recorders (TDRs, Cefas G5, Cefas Technologies) were attached to the keel feathers with Tesa tape (Tesa, Charlotte, NC; Ito et al. 2010). Weight of deployment package was ~1.5 g. This mass is less than one percent of bird body mass, well below masses demonstrated to affect behaviour (Vandenabeele et al. 2012). TDRs recorded time, pressure, and temperature every two seconds. Birds were recaptured after an average of three days: deployment length = 73.1 ± 3.7 h, and skeletal measurements for body condition were taken.

Diving parameters and variables of interest

TDR data were used in conjunction with stable isotope analysis to generate foraging parameters along three axes: spatial use of habitat, temporal use of habitat, and prey selection. Variable names are given in parentheses. Spatially, we recorded how far birds foraged from the colony, using return flight times as recorded by loggers (return time); waters chosen for foraging, described by sea-surface temperature (SST); depth of foraging (foraging depth); and the maximum foraging depth for each bird (maximum depth). Return time was calculated as the time of return to the colony minus the time of leaving the sea from the last foraging bout of a trip. Average return time was 27 ± 1.9 minutes. Work in a closely related species has shown that when finished foraging, birds return directly to the nest (Evans et al. 2013). This measure was not available for all trips (186 of 475 trips), as temperature and pressure profiles did not always show a clear change between foraging and flying. SST was defined by a stable post-diving temperature at the sea surface after a diving bout. SST can indicate water mass selection as cooler waters are less stratified than warmer ones (Stabeno et al. 1999). Foraging depth described the average bottom depth of each dive recorded to a bird and indicated prey depth or ocean depth, if murres were foraging on shallow ocean floor. Maximum depth was the deepest dive depth recorded for each bird; it represented a combination of the maximum depth available for foraging and the physiological capacity of the birds themselves. Foraging depth averaged 20 ± 0.098 m and maximum depth averaged 90 ± 2.3 m.

Temporally, dives were recorded as being in daylight or at night (night diving). Light status of a dive was determined by colony specific sunrise and sunset times (day = 0, night = 1), and then averaged for each trip, so that each trip's light status is read as the proportion

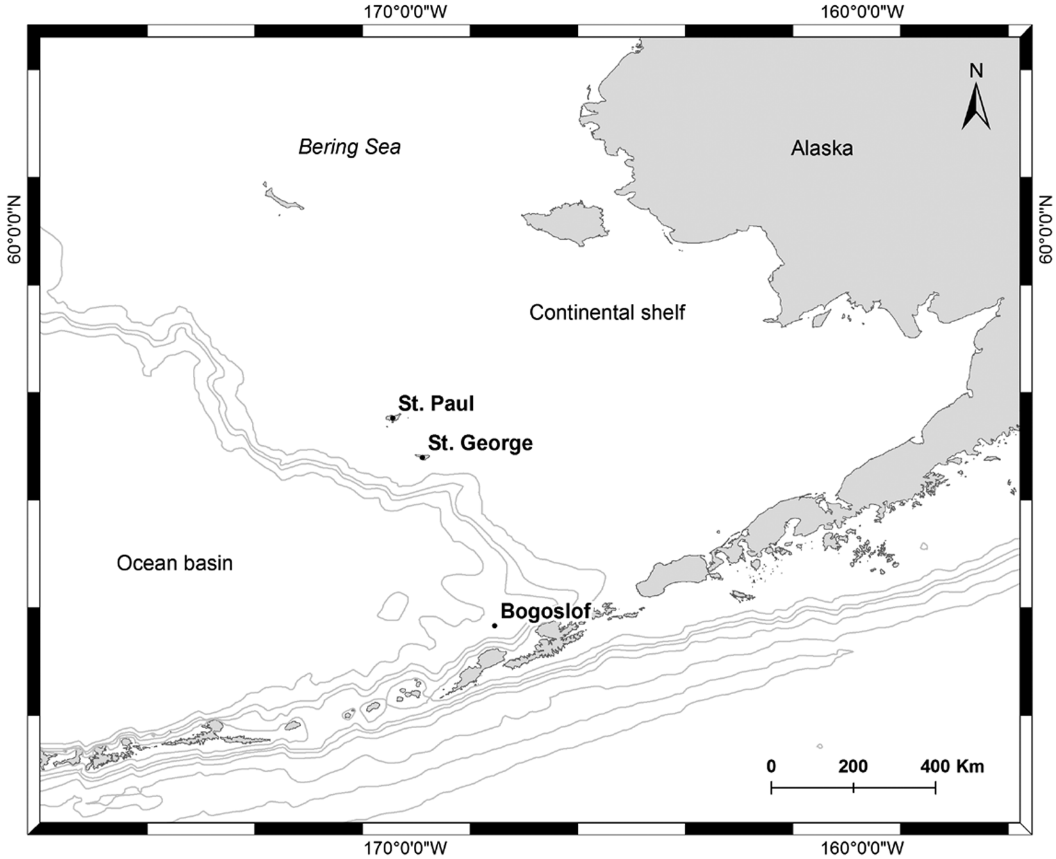

Fig. 1. Study area in the Bering Sea. The continental shelf and ocean basin are indicated and topographic lines show the shelf edge, near St. George.

occurring at night. We also used the time spent underwater as an index of foraging effort and time budgeting (foraging efficiency). Foraging efficiency was the time underwater, including descent, bottom time, and ascent, measured in hours per day. Lastly, prey selection was determined by stable isotope signatures of red blood cells; we measured both δ^{13}C, as an indicator of pelagic vs. inshore food webs, and δ^{15}N, as an indicator of trophic level.

TDR data were analyzed following Ito et al. (2010) using IGOR Pro (WaveMetrics 2008). The macros and extraction software identified dives and generated maximum dive depth and sea-surface temperature data from raw records. Presence at the colony, in the air, or on the sea were determined by temperature changes via visual examination of temperature and depth (pressure) records.

Laboratory techniques

Telomere restriction fragment assay.—Telomeres were measured using the telomere restriction fragment (TRF) assay, according to Young et al. (2013) and Haussmann and Mauck (2007). Briefly, whole blood, stored frozen in a glycerol buffer, was extracted into agarose plugs using the Chef Genomic DNA Plug Kit (Bio-Rad, Hercules, CA) and digested with a mixture of 3 U HinfI, 15 U HaeIII, and 40 U RsaI (Roche Applied Science, Indianapolis, IN). DNA was separated using pulsed field gel electrophoresis (PFGE) on a 0.8% agarose gel. Run parameters were 21 hours at 3 V/cm and 0.5–7s switch times. Buffer (0.5× TBE) was circulated and kept at 14°C. Hybridization was at 37°C with 3,000,000 cpm of the telomere-specific radio-labeled oligo $(CCCTAA)_4$. After hybridization, rinsing and visualization followed Haussmann and Mauck (2007). Samples were analyzed in random order on four gels with two control samples per gel to determine inter- (10.9%) and intra-assay variability (1.42%). TRF values were calculated from gel images following Salomons et al. (2009) and using ImageJ (Schneider et al. 2012). The shortest telomeres in a cell are the drivers of cellular senescence (Hemann et al. 2001, Zou et al. 2004), and it is believed they are more sensitive to aging in whole organisms as well (Haussmann and Mauck 2007, Smith et al. 2011). Following Haussmann and Mauck's (2007) identification of the optimal analysis window, we have analyzed the TRF smear from 5 kb to the bottom of the gel. In murres this area of the gel has shown to be the most related to chronological ageing (Young et al. 2013), and was more related to our foraging parameters than average TRF (data not shown).

Stable isotope analysis and genetic sexing.—Prey choice was described by two stable isotope signatures, $\delta^{13}C$ and $\delta^{15}N$. In our study system, carbon signatures indicated whether prey were sourced through inshore food webs or off-shore marine systems: lower carbon signatures were indicative of a more pelagic food web, while higher ones indicated inshore food sources. Trophic level of prey was indicated with nitrogen signature; ^{15}N enrichment indicated foraging on prey of a higher trophic level. Sub-samples of red blood cells were freeze-dried and analyzed with continuous flow isotope ratio mass spectrometry (CF-IRMS) using a Costech Elemental Analyzer (Model ECS 4010, Valencia, CA), a Thermo Finnigan MAT ConFlo III interface (San Jose, CA), and a Delta Plus IRMS (Asheville, NC) at the Alaska Stable Isotope Facilities of the University of Alaska Fairbanks (Williams et al. 2007). Isotope results are presented in δ notation according to:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}} - 1)]‰$$

where X is ^{13}C or ^{15}N and R is the ratio of heavy to light isotope ($N(^{13}C)/N(^{12}C)$ or $N(^{15}N)/N(^{14}N)$). The standard for carbon was PDB belemnite; and for nitrogen, atmospheric N_2. Measurement precision (SD) was ±0.13‰ for $\delta^{13}C$ and ±0.16‰ for $\delta^{15}N$. Sexing was done using PCR amplification of two CHD genes, following Griffiths et al. (1998).

Statistical analyses

Analyses were performed in the program R (R Development Core Team 2011, v. 2.12.2), using package nlme. Response parameters, used to characterize habitat selection, were the eight variables which comprise the three foraging axes: spatial variables (return time, SST, foraging depth, and maximum depth), temporal variables (night diving and foraging efficiency), and prey selection variables ($\delta^{13}C$ and $\delta^{15}N$). Explanatory variables were TL, sex, colony of origin, and in some analyses whether the dive was in daylight or darkness (see Appendix A). In order to make effect sizes more comparable, telomere length was standardized. The night diving variable was highly correlated with some of the other response variables, e.g., depth (Dias et al. 2012), and is expected to drive some foraging patterns, so it was included in relevant analyses. Each parameter was analyzed with generalized linear mixed models. The GLM approach was used to control heterogeneity in the dataset, and the random term in the mixed model controlled for repeated sampling. For example, in some cases variables were analyzed at the level of the dive, diving bout, or trip, thus birds were represented by more than one observation. Most response variables were correlated with Julian date at the level of the colony × year, and were therefore detrended (i.e., residuals on Julian date were used); details can be found in Appendix A. For most variables, the full model for each response was TL, colony of origin, sex, and all two-way interactions. For SST, foraging depth, and maximum depth, the full model additionally included the night diving variable and two-way interactions (indicated by joining variables with a colon), except terms which included colony and night diving, as the relationship with night diving was not predicted to differ on different colonies. Model selection was carried out using AIC_c for small sample sizes. Statistics are reported for the best model (defined as that with the lowest AIC_c) and as mean ± SE, unless otherwise noted. Model averaging was done on all models up to 90% of model weight. More details on model building and model selection can be found in Appendix A.

RESULTS

The lower window of the TRF smear which we used is less variable than the full smear. Our birds had an average lower window TRF of 3380 ± 45 bp, ranging from 1884 bp to 4020 bp.

Spatial variables

The best model for return time, indicating foraging distance, included colony and sex (Table 1). Females foraged farther from the colony than males (females: 37.5 ± 4.0 min; males: 20.4 ± 1.7 min), and foraging distances were higher in the Pribilofs than on Bogoslof (St. Paul: 29.4 ± 2.5 min; St. George: 44.2 ± 6.1 min; Bogoslof: 18.5 ± 1.8 min). TL did not strongly affect foraging distance.

The best model for SST included TL, colony, sex, night diving, TL:sex, and sex:night diving (Table 1). Warmer waters were preferred by individuals at the two colonies with access to oceanic water masses, Bogoslof and St. George, as compared to St. Paul in the north (St. Paul: 7.88° ± 0.034°C; St. George: 8.58° ± 0.030°C; Bogoslof: 8.36° ± 0.031°C). Males with longer TL preferred warmer waters, while females had no preference by TL. Although all birds foraged in slightly warmer waters during darkness, this relationship was stronger in males.

Results for foraging depth were similar to those of SST, the best model included TL, colony, sex, night diving, TL:night diving, and sex:night diving (Table 1). Dives in the Pribilofs were deeper than dives on Bogoslof, where birds usually foraged over shallow near-shore features (St. Paul: 20.2 ± 0.17 m; St. George: 20.3 ± 0.15 m; Bogoslof: 18.4 ± 0.20 m). Dive depths were deeper for birds with shorter TL, indicating that deteriorated TL does not impair the ability to reach deep depths (Table 1). In addition, males dove more deeply than females (males: 21.8 ± 0.17 m; females: 18.5 ± 0.12 m). Although male murres in this sample were heavier than females (body mass: males: 1104 ± 14 g, females: 1050 ± 10 g, mass difference: $t = 3.14$, $df = 89.9$, $p = 0.0023$), mass was negatively related to diving depth, indicating that larger birds dove more shallowly ($t = -2.24$, $df = 84$, $p = 0.028$, $\beta = -0.036 \pm 0.016$).

The model selection for maximum depth told a comparable story to average depth; the best model included TL, colony, and night diving (Table 1). As with foraging depth, older birds dove deeper, but Bogoslof had birds with deeper maximum depth records than those on St. Paul, in contrast to foraging depth results (see Appendix B). Despite nighttime diving being on average shallower, birds who dove more at night, were also more likely to have deeper maximum depth records.

Temporal variables

Diving occurred at night on each colony. Major drivers of night timing were colony and sex (Table 1). Predictably, more night diving occurred on colonies at lower latitude, where there are more hours of darkness during the midsummer breeding season, and on all colonies, females spent more time than males diving in darkness.

The best model for foraging efficiency included the terms TL, colony, sex, and the interaction of colony and sex (Table 1). Birds with shorter TL spent less time underwater, indicating higher efficiency ($t = 2.087$, $p = 0.040$; Fig. 2). Male efficiency did not vary by colony (Bogoslof = 2.65 ± 0.22 h/day; St. George = 2.53 ± 0.41 h/day; St. Paul = 2.70 ± 0.24 h/day), but female efficiency was negatively associated with colony quality, i.e., female murres had higher efficiency (spent less time underwater) at poor colonies (Bogoslof = 3.55 ± 0.28 h/day; St. George = 3.20 ± 0.18 h/day; St. Paul = 2.04 ± 0.22 h/day).

Prey selection variables

In our analysis, carbon signature was strongly driven by colony and TL, although sex also contributed (Table 1). Carbon signatures enriched (became more inshore) as TL shortened. As predicted, carbon signatures were highest on St. Paul, the most inshore colony (St. Paul males: −19.0‰ ± 0.083‰, St. Paul females: −19.0‰ ± 0.076‰). Other carbon signatures were similar, with the lowest carbon signatures in St. George males (St. George males: −19.6‰ ± 0.063‰), who foraged more oceanically than Bogoslof murres (Bogoslof males: −19.3‰ ± 0.029‰; Bogoslof females: −19.3‰ ± 0.053‰) or St. George females (St. George females: −19.4‰ ± 0.079‰).

The best model of nitrogen signature included colony and sex (Table 1). Nitrogen signature was positively related to TL on Bogoslof, had no relationship on St. George, and was negatively

Table 1. Weighted term estimates and the percentage of the intercept for each response parameter in each model. Estimates are based on all models up to a combined weight of 90%. Percent change indicates the percent change in the intercept value for factors and for 1% changes in continuous terms. ND = night diving.

	Model output	
Variable and model term	Weighted value	Percentage of intercept
Return time: Intercept	23.7	100
TL	0.0304	0.128
Colony-St.George	19.1	80.8
Colony-St.Paul	8.89	37.6
Sex-M	−9.53	40.3
TL:colony-St.George	−1.55	6.57
TL:colony-St.Paul	0.222	0.936
TL:sex-M	0.233	0.986
Colony-St.George:sex-M	−0.155	0.656
Colony-St.Paul:sex-M	0.389	1.64
SST: Intercept	7.72	100
TL	−0.00351	0.0454
Colony-St.George	−0.169	2.19
Colony-St.Paul	−0.585	7.54
Sex-M	−0.247	3.20
ND	0.176	2.27
TL:colony-St.George	−0.0168	0.217
TL:colony-St.Paul	−0.00687	0.0890
TL:sex-M	−0.224	2.90
TL:ND	0.00665	0.0861
Colony-St.George:sex-M	−0.0176	0.228
Colony-St.Paul:sex-M	−0.000584	0.00756
Sex-M:ND	0.0572	0.740
Foraging depth: Intercept	38.9	100
TL	−4.12	10.6
Colony-St.George	−1.81	4.66
Colony-St.Paul	−9.60	24.7
Sex-M	3.12	8.02
ND	−10.6	27.1
TL:colony-St.George	0.945	2.43
TL:colony-St.Paul	1.65	4.24
TL:sex-M	−0.997	2.56
TL:ND	1.04	2.68
Colony-St.George:sex-M	−0.326	0.837
Colony-St.Paul:sex-M	−1.93	4.96
Sex-M:ND	2.99	7.69
Maximum depth: Intercept	77.0	100
TL	−3.78	4.91
Colony-St.George	6.71	8.71
Colony-St.Paul	−10.1	13.1
Sex-M	2.95	3.83
ND	9.77	12.7
TL:colony-St.George	0.500	0.649
TL:colony-St.Paul	0.470	0.610
TL:sex-M	0.474	0.615
TL:ND	−1.54	1.99
Colony-St.George:sex-M	−3.54	4.60
Colony-St.Paul:sex-M	−2.52	3.27
Sex:ND	−0.205	0.266
Night diving: Intercept	0.309	100
TL	0.00242	0.782
Colony-St.George	0.0148	4.79
Colony-St.Paul	−0.152	49.2
Sex-M	−0.0781	25.3
TL:colony-St.George	−0.00313	1.01
TL:colony-St.Paul	−0.00193	0.624
TL:sex-M	0.000332	0.107
Colony-St.George:sex-M	0.00270	0.871
Colony-St.Paul:sex-M	0.00408	1.32
Foraging efficiency: Intercept	3.28	100
TL	0.153	4.66
Colony-St.George	−0.251	7.65
Colony-St.Paul	−1.42	43.4
Sex-M	−0.871	26.5
TL:colony-St.George	0.00169	0.0516
TL:colony-St.Paul	0.0169	0.514
TL:sex-M	0.00840	0.256
Colony-St.George:sex-M	0.158	4.80
Colony-St.Paul:sex-M	1.51	46.1
δ^{13}C: Intercept	−17.6	100
TL	−0.0322	0.183
Colony-St.George	−0.130	0.741
Colony-St.Paul	0.278	1.58
Sex-M	0.00208	0.0118
TL:colony-St.George	0.00221	0.0126
TL:colony-St.Paul	−0.00284	0.0162
TL:sex-M	−0.00629	0.0358
Colony-St.George:sex-M	−0.0318	0.181
Colony-St.Paul:sex-M	0.0139	0.0790
δ^{15}N: Intercept	10.8	100
TL	0.0450	0.415
Colony-St.George	0.872	8.03
Colony-St.Paul	2.26	20.8
Sex-M	0.180	1.65
TL:colony-St.George	−0.0215	0.198
TL:colony-St.Paul	−0.122	1.13
TL:sex-M	−0.00170	0.0157
Colony-St.George:sex-M	−0.165	1.52
Colony-St.Paul:sex-M	−0.147	1.35

related on St. Paul (Fig. 3). Nitrogen signature was also negatively related to habitat quality, increasing from Bogoslof to St. Paul. The interaction of colony and sex, which was retained in the top model, meant that the sex which foraged at a higher trophic level differs by colony: males were more ^{15}N enriched on Bogoslof, while females were more enriched on St. Paul.

DISCUSSION

We found telomere length to have a widespread predictive value for determining foraging behavior of individuals. We found that telomere length compared to sex and colony in explaining key parameters of foraging ecology. TL was retained in the top models for SST, foraging depth, maximum depth, foraging efficiency, and carbon signature (Table 1). Predictive ability for SST and also for carbon signatures indicate that foraging habitat selection may change with

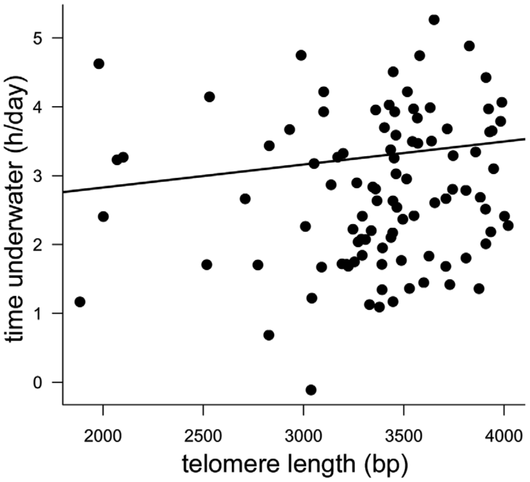

Fig. 2. Foraging efficiency: time underwater in relation to telomere length. Birds with longer telomeres spend more time underwater.

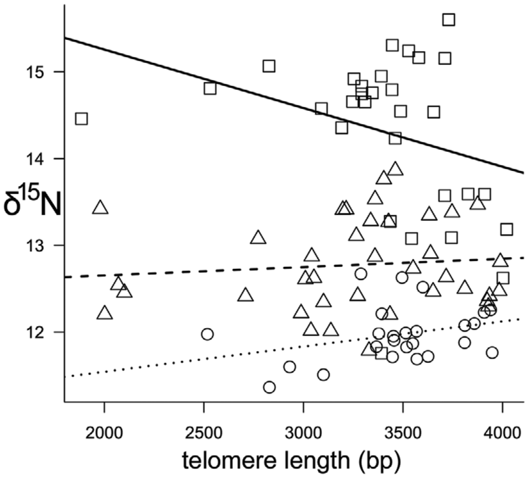

Fig. 3. Nitrogen isotope signatures. St. Paul: squares and solid line, St. George: triangles and dashed line, and Bogoslof: circles and dotted line. Trophic changes with telomere length are colony dependent.

physiological changes due to age. Foraging efficiency was also well predicted by telomere length (Fig. 2). The association between foraging efficiency and TL is similar to the pattern of increasing efficiency with chronological age found in goshawks (Rutz et al. 2006). Murres become more efficient foragers as their telomeres are deteriorated. This discussion focuses on our results as they pertain to telomere length; discussion of other results is found in Appendix B.

Telomere length and spatial habitat choice

Previous work with murres has shown that they make physiological trade-offs rather than compromise parental and foraging behaviors as they age chronologically or through telomere degradation (Elliott et al. 2014; Young et al., *unpublished manuscript*). Elliott et al. (2014) found that thyroid hormones, hematocrit, and metabolic rate all declined with age while diving and flying patterns remained the same. In our previous work (Young et al., *unpublished manuscript*) we found that under good conditions stress levels increased with telomere degradation, but attendance at the nest and rate of chick-provisioning trips did not. Consistent with these results, we did not find that TL explained how far from the colony birds foraged or whether they foraged during daylight or nighttime. Aging in the wandering albatross produces different patterns by sex (Lecomte et al. 2010). Similarly, we found that TL interacted with sex to determine spatial habitat selection: males with shorter telomeres foraged in warmer waters than males with long telomeres, but females showed no preference associated with TL. This difference may indicate that males with deteriorated telomeres prefer to forage in more stratified waters, as opposed to cooler mixed waters (Stabeno et al. 1999). Use of stratified or mixed waters indicates differences of foraging strategy in murres (Takahashi et al. 2008).

Telomere length, diving depth, and foraging efficiency

Both measures of diving depth (foraging depth and maximum depth) became deeper as TL became shorter, indicating that birds with deteriorated telomeres were not compromised in their ability to dive deeply. Lowered metabolic rates in older birds (Elliott et al. 2014) might have inhibited diving ability. The ability to maintain diving depth while expressing a physiologically deteriorated phenotype is yet more evidence that behavior is maintained while physiology declines in murres (Elliott et al. 2014). At the same time, birds with longer telomeres dove less efficiently than those with short telomeres. This is somewhat counterintuitive, considering that short telomere birds consistently dove to greater depths. Deeper dives take longer, not only in the longer ascent and descent times needed to reach and return from depth, but also the amount of time spent foraging at the bottom of the dive is higher for deeper dives ($t = 64.4$, $df = 48351$, $p < 0.0001$, $\beta = 0.17$ s). Shallower dives, yet more time underwater, could be the result of birds with long telomeres lingering to find high quality prey for the chick, yet it may also indicate that birds with long telomeres, which may be younger, were less efficient or experienced divers. These birds may have poorer foraging abilities, be unable to locate high quality prey patches, or have a physiological inability to dive to the depths achievable by the birds with short telomeres; despite diving to deeper depths, short telomere birds did not need to stay there long to achieve their goals.

Telomere length and stable isotopes

Diet, as indicated by stable isotopes, may indicate self-maintenance tactics in murres with short telomeres. Reproductive trade-offs between current and future reproduction are common and complex (Cotter et al. 2010). Older individuals or those in poor condition may invest more heavily, as their residual lifespan is low (Velando et al. 2006), or may become more "prudent," hoarding their limited resources until ideal conditions (Drent and Daan 1980). ^{15}N signatures became less enriched with increasing TL on St. Paul, enriched with TL on Bogoslof, and showed no pattern with TL on St. George. Birds with deteriorated telomeres relied on higher trophic sources of prey on St. Paul, the food-poor colony, while on Bogoslof, the food-rich colony, murres with short telomeres switched to lower trophic levels. Squid and euphausiids are common prey items on Bogoslof, and murres choose between them and higher trophic level prey items like pollock (Benoit-Bird et al. 2011, Harding et al. 2013) which dominate in the more northerly waters surrounding the Pribilof Islands. Searching for high-trophic level prey for adult foraging takes time away from foraging for the chick (St. Paul) while loafing near the colony foraging on easy-access prey (Bogoslof) could also indicate self-maintenance strategies. Nitrogen patterns supported a previous finding that under good conditions, birds with deteriorated telomere signatures showed evidence of higher stress, while under poor conditions, when food was scarce and population stress levels higher, they had relatively lower stress levels than birds with longer telomeres (Young et al., *unpublished manuscript*). Work in ptarmigan has shown that aged birds (or here, birds with deteriorated telomeres) demonstrate senescence in reproductive output, but under poor conditions, offset this by increasing fledging success due to the benefits of a lifetime of experience (Wiebe and Martin 1998). Murre signatures of ^{13}C declined with TL, potentially indicating that those with shorter telomeres reduce reliance on pelagic food webs, but the effects were small, so they may be due to trophic level increases, as carbon signatures are positively correlated with nitrogen signatures. It is also possible that the differences in stable isotope signatures indicated that birds differing in telomere length may also differ in isotopic turnover rates. Declines in isotopic turnover may be age-related, as older murres have a lower metabolic rate (Elliott et al. 2014) or could be making seasonal shifts in diet later or more slowly than younger birds. Diet composition shifts as birds move from incubation to chick-rearing (Williams et al. 2008), and although the process of turnover is not important to this study, it is a potential explanation of the differences in stable isotope signatures.

Previous work has shown that murre behavior is relatively constant throughout the lifespan, while physiological parameters change with age (Elliott et al. 2014). Some behavioral parameters did not change with telomere length in our study, yet others were strongly related to this telomeric parameter of physiological aging. Prior studies addressed endocrine and metabolic physiology (Elliott et al. 2014; Young et al., *unpublished manuscript*), and it is possible that those parameters change with age in order to support physiological diving capabilities that result in more effective foraging of older individuals. Subtle changes in diet composition with telomere length may be a form of biological age-related change. A more detailed study of the energy content and qualities of various food sources would be needed to address the full ramifications of these age-related changes in diet. Patterns of behavior and physiology in the Thick-billed Murre are in accordance with life history theory predictions for long-lived species. Younger birds do not perform at the same level as adults in some parameters, evidence of "constraint" (Wiebe and Martin 1998) but reproductive output is comparable for the many years of adulthood. Murres appear to be "prudent parents" (Drent and Daan 1980) because they do not compromise their physiology until future reproductive attempts are few.

Conclusion

Telomere length, environmental conditions at colonies, and sex all play pivotal roles in determining foraging habitat selection. The behavioral evidence indicates that despite losing telomeres, birds with short TL retain or improve their ability to use the environment efficiently, which is consistent with previous findings in this species that older birds remain behaviorally flexible, despite paying physiological costs (Elliott et al. 2014; Young et al., *unpublished manuscript*). Spatial habitat use, foraging efficiency, and prey selection variables all changed with telomere length. Changes in spatial use were largely sex-dependent: females and males changed their spatial use of the environment differently as telomere lengths decline. Prey selection was related to TL and colony; changes in murre trophic level depended on TL, but their direction also depended on habitat quality. We found much support for the increased ability of birds with shorter telomeres, indicating that evidence of physiological aging does not carry only costs. Several mechanisms appear to be working simultaneously, perhaps the loss of function of senescence combined with the increased efficiency of experience. Organisms modify their behavior depending on environmental conditions as their physiological reserves decline. Experience associated with longevity is an important factor that might enhance resilience of long-lived seabirds and ameliorate the effects of climate change on their populations.

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LITERATURE CITED

Aho, T., M. Kuitunen, J. Suhonen, T. Hakkari, and A. Jantti. 1997. Effects of male removal on female foraging behavior in the Eurasian Treecreeper. Behavioral Ecology and Sociobiology 41(1):49–53.

Angelier, F., C. M. Vleck, R. L. Holberton, and P. P. Marra. 2013. Telomere length, non-breeding habitat and return rate in male American redstarts. Functional Ecology 27(2):342–350.

Barrett, E. L. B., and D. S. Richardson. 2011. Sex differences in telomeres and lifespan. Aging Cell 10:913–921.

Bauch, C., P. H. Becker, and S. Verhulst. 2012. Telomere length reflects phenotypic quality and costs of reproduction in a long-lived seabird. Proceedings of the Royal Society B 280(1752):1–8.

Benetos, A., K. Okuda, M. Lajemi, M. Kimura, F. Thomas, J. Skurnick, C. Labat, K. Bean, and A. Aviv. 2001. Telomere length as an indicator of biological aging. The gender effect and relation with pulse pressure and pulse wave velocity. Hypertension 37:381–385.

Benoit-Bird, K., K. Kuletz, S. Heppell, N. Jones, and B. Hoover. 2011. Active acoustic examination of the diving behavior of murres foraging on patchy prey. Marine Ecology Progress Series 443:217–235.

Buren, A. D., M. Koen-Alonso, and W. A. Montevecchi. 2012. Linking predator diet and prey availability: common murres and capelin in the Northwest Atlantic. Marine Ecology Progress Series 445:25–35.

Byrd, G. V., J. A. Schmutz, and H. M. Renner. 2008. Contrasting population trends of piscivorous seabirds in the Pribilof Islands: A 30-year perspective. Deep Sea Research II 55(16-17):1846–1855.

Codding, B. F., R. Bliege Bird, and D. W. Bird. 2011.

Provisioning offspring and others: risk-energy trade-offs and gender differences in hunter-gatherer foraging strategies. Proceedings of the Royal Society B 278:2502–2509.

Cotter, S. C., R. J. S. Ward, and R. M. Kilner. 2010. Age-specific reproductive investment in female burying beetles: independent effects of state and risk of death. Functional Ecology 25:652–660.

Desrochers, A. 1992. Age and foraging success in European blackbirds: variation within and between individuals. Animal Behavior 43:885–894.

Dias, M. P., J. P. Granadeiro, and P. Catry. 2012. Working the day or the night shift? Foraging schedules of Cory's shearwaters vary according to marine habitat. Marine Ecology Progress Series 467:245–252.

Dragoo, D. E., H. M. Renner, and D. B. Irons. 2012. Breeding status, population trends, and diets of seabirds in Alaska, 2009. Report AMNWR 2012/01. US Fish and Wildlife Service, Homer, Alaska, USA.

Drent, R. H., and S. Daan. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68:225–252.

Dunshea, G., D. Duffield, N. Gales, M. Hindell, R. S. Wells, and S. N. Jarman. 2011. Telomeres as age markers in vertebrate molecular ecology. Molecular Ecology Resources 11:225–235.

Elliott, K. H., J. F. Hare, A. J. Gaston, Y. Ropert-Coudert, and W. G. Anderson. 2014. Ageing gracefully: physiology but not behaviour declines with age in diving birds. Functional Ecology. doi: 10.1111/1365-2435.12316

Evans, T. J., M. Kadin, O. Olsson, and S. Åkesson. 2013. Foraging behavior of common murres in the Baltic Sea, recorded by simultaneous attachment of GPS and time-depth recorder devices. Marine Ecology Progress Series 475:277–289.

Foote, C. G., F. Daunt, J. Gonzalez-Solis, L. Nasir, R. A. Phillips, and P. Monaghan. 2011. Individual state and survival prospects: age, sex, and telomere length in a long-lived seabird. Behavioral Ecology 22(1):156–161.

Francis, N., T. Gregg, R. Owen, T. Ebert, and A. Bodnar. 2006. Lack of age-associated telomere shortening in long- and short-lived species of sea urchins. FEBS Letters 580:4713–4717.

Friesen, V. L., W. A. Montevecchi, A. J. Gaston, and W. S. Davidson. 1992. Genetic structure of Thick-billed Murre (*Uria lomvia*) populations examined using direct sequence analysis of amplified DNA. Evolution 46(1):267–272.

Gaston, A. J., and I. L. Jones. 1998. Bird families of the world: the Auks (Alcidae). Oxford University Pres, Oxford, UK.

Griffiths, R., M. C. Double, K. Orr, and R. J. G. Dawson. 1998. A DNA test to sex most birds. Molecular Ecology 7:1071–1075.

Hall, M. E., L. Nasir, F. Daunt, E. A. Gault, J. P. Croxall, S. Wanless, and P. Monaghan. 2004. Telomere loss in relation to age and early environment in long-lived birds. Proceedings: Biological Sciences 271(1548):1571–1576.

Harding, A. M. A., R. Paredes, R. Suryan, D. Roby, D. B. Irons, R. Orben, H. M. Renner, R. C. Young, C. P. Barger, I. Dorresteijn, and A. S. Kitaysky. 2013. Does location really matter? An inter-colony comparison of seabirds breeding at varying distances from productive oceanographic features in the Bering Sea. Deep Sea Research II 94:178–191.

Harris, M. P., and S. Wanless. 1990. Breeding status and sex of common murres (*Uria aalge*) at a colony in autumn. Auk 107:603–605.

Haussmann, M. F., and R. A. Mauck. 2007. New strategies for telomere-based age estimation. Molecular Ecology Resources 8:264–274.

Haussmann, M. F., and C. M. Vleck. 2002. Telomere length provides a new technique for aging animals. Oecologia 130:325–328.

Haussmann, M. F., D. W. Winkler, K. M. O'Reilly, C. E. Huntington, I. C. T. Nisbet, and C. M. Vleck. 2003. Telomeres shorten more slowly in long-lived birds and mammals than in short-lived ones. Proceedings: Biological Sciences 270(1522):1387–1392.

Hemann, M. T., M. A. Strong, L.-Y. Hao, and C. W. Greider. 2001. The shortest telomere, not average telomere length, is critical for cell viability and chromosome stability. Cell 107:67–77.

Holmes, D. J., and K. Martin. 2009. A bird's-eye view of aging: what's in it for ornithologists? Auk 126(1):1–23.

Horn, T., B. C. Robertson, M. Will, D. K. Eason, G. P. Elliott, and N. J. Gemmell. 2011. Inheritance of telomere length in a bird. PLoS ONE 6(2):e17199.

Huettman, F., and A. W. Diamond. 2001. Seabird colony locations and environmental determination of seabird distribution: a spatially explicit breeding seabird model for the Northwest Atlantic. Ecological Modelling 141:261–298.

Ito, M., A. Takahashi, N. Kokubun, and A. S. Kitaysky. 2010. Foraging behavior of incubating and chick-rearing thick-billed murres *Uria lomvia*. Aquatic Biology 8:279–287.

Jones, I. L., S. Rowe, S. M. Carr, G. Fraser, and P. Taylor. 2002. Different patterns of parental effort during chick-rearing by female and male thick-billed murres (*Uria lomvia*) at a low-Arctic colony. Auk 119(4):1064–1074.

Lecomte, V. J., G. Sorci, S. Cornet, A. Jaeger, B. Faivre, E. Arnoux, M. Gaillard, C. Trouve, D. Besson, O. Chastel, and H. Weimerskirch. 2010. Patterns of aging in the long-lived wandering albatross. Proceedings of the National Academy of Sciences USA 107(14):6370–6375.

Le Vaillant, M., C. Le Bohec, O. Prud'homme, B.

Wienecke, Y. Le Maho, A. Kato, and Y. Ropert-Coudert. 2013. How age and sex drive the foraging behavior in the king penguin. Marine Biology 160:1147–1156.

Monaghan, P. 2010. Telomeres and life histories: the long and the short of it. Annals of the New York Academy of Sciences 1206:130–142.

Monaghan, P. 2014. Organismal stress, telomeres and life histories. Journal of Experimental Biology 217:57–66.

Monaghan, P., and M. F. Haussmann. 2006. Do telomere dynamics link lifestyle and lifespan? Trends in Ecology and Evolution 21(1):47–53.

Müezzinler, A., A. K. Zeineddine, and H. Brenner. 2013. A systematic review of leukocyte telomere length and age in adults. Ageing Research Reviews 12:509–519.

Oro, D., N. Hernández, L. Jover, and M. Genovart. 2014. From recruitment to senescence: food shapes the age-dependent pattern of breeding performance in a long-lived bird. Ecology 95(2):446–457.

Paredes, R., I. L. Jones, D. J. Boness, Y. Tremblay, and M. Renner. 2008. Sex-specific differences in diving behaviour of two sympatric Alcini species: thick-billed murres and razorbills. Canadian Journal of Zoology 86:610–622.

Pauli, J. N., J. R. Whiteman, B. G. Marcot, T. M. McClean, and M. Ben-David. 2011. DNA-based approach to aging martens (*Martes americana* and *M. caurina*). Journal of Mammology 92(3):500–510.

Pelletier, L., A. Chiaradia, A. Kato, and Y. Ropert-Coudert. 2014. Fine-scale spatial age segregation in the limited foraging area of an inshore seabird species, the little penguin. Oecologia 176:399–408.

Ponchon, A., D. Grémillet, S. Christensen-Dalsgaard, K. E. Erikstad, R. T. Barrett, T. K. Reiertsen, K. D. McCoy, T. Tveraa, and T. Boulinier. 2014. When things go wrong: intra-season dynamics of breeding failure in a seabird. Ecosphere 5(1):4.

R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Regular, P. M., G. K. Davoren, A. Hedd, and W. A. Montevecchi. 2010. Crepuscular foraging by a pursuit-diving seabird: tactics of common murres in response to the diel vertical migration of capelin. Marine Ecology Progress Series 415:295–304.

Rutz, C., M. J. Whittingham, and I. Newton. 2006. Age-dependent diet choice in an avian top predator. Proceedings of the Royal Society B 273:579–586.

Salomons, H. M., G. A. Mulder, L. van de Zande, M. F. Haussmann, M. H. K. Linskens, and S. Verhulst. 2009. Telomere shortening and survival in free-living corvids. Proceedings of the Royal Society B 276(1670):3157–3165.

Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. Nature Methods 9(7):671–675.

Schultner, J., B. Moe, O. Chastel, C. Bech, and A. S. Kitaysky. 2014. Migration and stress during reproduction govern telomere dynamics in a seabird. Biology Letters 10(1). doi: 10.1098/rsbl.2013.0889

Smith, D. L., J. A. Mattison, R. A. Desmond, J. P. Gardner, M. Kimura, G. S. Roth, D. K. Ingram, D. B. Allison, and A. Aviv. 2011. Telomere dynamics in rhesus monkeys: no apparent effect of caloric restriction. Journal of Gerontology 66A(11):1163–1168.

Stabeno, P. J., J. D. Schumacher, S. Salo, G. L. Hunt, and M. V. Flint. 1999. Physical environment around the Pribilof Islands. Pages 193–215 *in* T. R. Loughlin and K. Ohtani, editors. Dynamics of the Bering Sea. University of Alaska Sea Grant, Fairbanks, Alaska, USA.

Stevenson, D. E., and R. R. Lauth. 2012. Latitudinal trends and temporal shifts in the catch composition of bottom trawls conducted on the eastern Bering Sea shelf. Deep Sea Research II 65-70:251–259.

Takahashi, A., K. Matsumoto, G. L. Hunt, M. T. Shultz, A. S. Kitaysky, K. Sato, K. Iida, and Y. Watanuki. 2008. Thick-billed murres use different diving behaviors in mixed and stratified waters. Deep Sea Research II 55:1837–1845.

Thaxter, C. B., F. Daunt, K. C. Hamer, Y. Watanuki, M. P. Harris, D. Grémillet, G. Peters, and S. Wanless. 2009. Sex-specific food provisioning in a monomorphic seabird, the common guillemot *Uria aalge*: nest defence, foraging efficiency or parental effort? Journal of Avian Biology 40:75–84.

Vandenabeele, S. P., E. L. C. Shepard, A. Grogan, and R. P. Wilson. 2012. When three per cent may not be three per cent; device-equipped seabirds experience variable flight constraints. Marine Biology 159:1–14.

Velando, A., H. Drummond, and R. Torres. 2006. Senescent birds redouble reproductive effort when ill: confirmation of the terminal investment hypothesis. Proceedings of the Royal Society B 273:1443–1448.

von Zglinicki, T. 2002. Oxidative stress shortens telomeres. Trends in Biochemical Sciences 27(7):339–344.

WaveMetrics. 2008. IGOR Pro 6.0.3.1. WaveMetrics, Portland, Oregon, USA.

Weimerskirch, H., Y. Cherel, F. Cuenot-Chaillet, and V. Ridoux. 1997. Alternative foraging strategies and resource allocation by male and female wandering albatrosses. Ecology 78(7):2051–2063.

Welcker, J., H. Steen, A. M. A. Harding, and G. W. Gabrielsen. 2009. Sex-specific provisioning behavior in a monomorphic seabird with a bimodal foraging strategy. Ibis 151:502–513.

Wiebe, K. L., and K. Martin. 1998. Age-specific patterns of reproduction in White-tailed and

Willow Ptarmigan *Lagopus leucurus* and *L. lagopus*. Ibis 140:14–24.

Williams, C. T., C. L. Buck, J. Sears, and A. S. Kitaysky. 2007. Effects of nutritional restriction on nitrogen and carbon stable isotopes in growing seabirds. Oecologia 153:11–18.

Williams, C. T., S. J. Iverson, and C. L. Buck. 2008. Stable isotopes and fatty acid signatures reveal age- and stage-dependent foraging niches in tufted puffins. Marine Ecology Progress Series 363:287–298.

Young, R. C., A. S. Kitaysky, M. F. Haussmann, S. Descamps, R. Orben, K. H. Elliott, and A. J. Gaston. 2013. Age, sex, and telomere dynamics in a long-lived seabird with male-biased parental care. PLoS ONE 8(9):e74931.

Zou, Y., A. Sfeir, S. M. Gryaznov, J. W. Shay, and W. E. Wright. 2004. Does a sentinel or a subset of short telomeres determine replicative senescence? Molecular Biology of the Cell 15:3709–3718.

SUPPLEMENTAL MATERIAL

APPENDIX A

Variables and model building

Table A1. Each variable is listed with its observation level (i.e., a stable isotope signature for each bird, but a depth for each dive) and the sample sizes. The "observation level" and "nested pattern" columns describes level of analysis, and thus any repeated measures in the data which were addressed in the model. Detrending was done if the data were correlated with Julian date at the colony × year level. The GLS approach was also used to control for heterogeneity in the dataset, and this column indicates the variables that produced heterogeneity. The last column indicates the full model: all two-way interactions were included except for colony × dark. TL is telomere length.

Response	Observation level	Sample size and levels	Nested pattern	Detrended for Julian date	Heterogeneity	Full model variables
Return flight time	Trip	186 trips, 79 birds	Bird	No	Colony and sex	TL, colony, sex
SST	Bout	3122 bouts, 425 trips, 93 birds	Bird/trip	Colony × year	Colony and sex	TL, colony, sex, dark
Foraging depth	Dive	51785 dives, 3432 bouts, 475 trips, 101 birds	Bird/trip/bout	Colony × year	Colony and sex	TL, colony, sex, dark
Max depth	Bird	99 birds	n/a	Colony × year	Colony and sex	TL, colony, sex, dark
Night diving	Trip	475 trips, 101 birds	Bird	Colony × year	Colony, sex, TL	TL, colony, sex
Foraging efficiency	Bird	99 birds	n/a	Colony × year	None	TL, colony, sex
$\delta^{13}C$	Bird	93 birds	n/a	Colony × year	Colony, sex, TL	TL, colony, sex
$\delta^{15}N$	Bird	93 birds	n/a	Colony × year	Colony	TL, colony, sex

Table A2. Model output for foraging variables. Each variable is grouped within one of the three foraging axes and described by which niche characteristics it captures. The best model (lowest AIC_c) is listed, along with the number of models with $\Delta AIC_c < 2$. TL is telomere length.

Response	Foraging axis	Niche characteristics	Best model	Models: $\Delta AIC_c < 2$
Return flight time	Spatial	Distance from colony	Colony + sex	1
SST	Spatial	Water mass	TL + colony + sex + dark + TL:sex + sex:dark	4
Foraging depth	Spatial	Water column (vertical)	TL + colony + sex + dark + TL:dark + sex:dark	4
Max depth	Spatial	Physiological capability	TL + colony + dark	4
Night diving	Temporal	Timing of diving	Colony + sex	1
Foraging efficiency	Temporal	Foraging effort	TL + colony + sex + colony:sex	1
$\delta^{13}C$	Prey selection	Prey selection (on-/off-shore)	TL + colony	1
$\delta^{15}N$	Prey selection	Prey selection (trophic level)	colony + sex + colony:sex	8

Table A3. Models of return flight time.

Model	Terms
fli0.mod	null
fli1.mod	TL
fli2.mod	colony
fli3.mod	sex
fli4.mod	TL + colony
fli5.mod	TL + sex
fli6.mod	colony + sex
fli7.mod	TL + colony + sex
fli8.mod	TL + colony + TL:colony
fli9.mod	TL + colony + sex + TL:colony
fli10.mod	TL + sex + TL:sex
fli11.mod	TL + colony + sex + TL:sex
fli12.mod	colony + sex + colony:sex
fli13.mod	TL + colony + sex + colony:sex
fli15.mod	TL + colony + sex + TL:colony + TL:sex
fli16.mod	TL + colony + sex + TL:sex + colony:sex
fli17.mod	TL + colony + sex + TL:colony + colony:sex
fli18.mod	TL + colony + sex + TL:colony + TL:colony:sex
fli19.mod	TL + colony + sex + TL:sex + TL:colony:sex
fli21.mod	TL + colony + sex + TL:colony + TL:sex + colony:sex

Table A4. AIC results for return flight time. All results with ΔAICc < 2 are in boldface. The null model is in italics. The sum of weights is shown for all models up to a total weight of 0.9. These models (up to weight = 0.9) are used to generate model averaged parameters.

Model	df	AICc	ΔAICc	wi	Sum wi
fli6.mod	**9**	**1648.05105**	**0**	**0.439411335**	**0.43941**
fli7.mod	10	1650.1093	2.058245	0.157010603	0.59642
fli9.mod	12	1650.47539	2.424339	0.130747322	0.72717
fli11.mod	11	1651.62223	3.571173	0.073688693	0.80086
fli12.mod	11	1651.76423	3.713173	0.068638209	0.8695
fli15.mod	13	1652.82042	4.769365	0.040477792	0.90997
fli13.mod	12	1653.74139	5.690339	0.02554053	
fli17.mod	14	1654.295	6.243947	0.019364902	
fli2.mod	8	1654.931	6.879947	0.014089957	
fli16.mod	13	1655.58942	7.538365	0.010137622	
fli8.mod	11	1655.78423	7.733173	0.009196743	
fli21.mod	15	1656.65391	8.602857	0.005953666	
fli4.mod	9	1657.00905	8.958	0.004985013	
fli3.mod	7	1661.57271	13.52166	0.000508956	
fli5.mod	8	1663.684	15.63295	0.000177101	
fli10.mod	9	1665.58605	17.535	6.84218E-05	
fli0.mod	*6*	*1672.37382*	*24.32276*	*2.29747E-06*	
fli1.mod	7	1674.39471	26.34366	8.36409E-07	

Table A5. Models for sea-surface temperature (dark = night diving).

Model	Terms
SST0.mod	null
SST1.mod	TL
SST2.mod	colony
SST3.mod	sex
SST4.mod	dark
SST5.mod	TL + colony
SST6.mod	TL + sex
SST7.mod	TL + dark
SST8.mod	colony + sex
SST9.mod	colony + dark
SST10.mod	sex + dark
SST11.mod	TL + colony + sex
SST12.mod	TL + colony + dark
SST13.mod	TL + sex + dark
SST14.mod	colony + sex + dark
SST15.mod	TL + colony + sex + dark
SST16.mod	TL + colony + TL:colony
SST17.mod	TL + colony + sex + TL:colony
SST18.mod	TL + colony + dark + TL:colony
SST19.mod	TL + colony + sex + dark + TL:colony
SST20.mod	TL + sex + TL:sex
SST21.mod	TL + colony + sex + TL:sex
SST22.mod	TL + sex + dark + TL:sex
SST23.mod	TL + colony + sex + dark + TL:sex
SST24.mod	TL + colony + sex + TL:colony + TL:sex
SST25.mod	TL + colony + sex + dark + TL:colony + TL:sex
SST26.mod	TL + dark + TL:dark
SST27.mod	TL + colony + dark + TL:dark
SST28.mod	TL + sex + dark + TL:dark
SST29.mod	TL + colony + sex + dark + TL:dark
SST30.mod	TL + colony + dark + TL:colony + TL:dark
SST31.mod	TL + colony + sex + dark + TL:colony + TL:dark
SST32.mod	TL + sex + dark + TL:sex + TL:dark
SST33.mod	TL + colony + sex + dark + TL:sex + TL:dark
SST34.mod	TL + colony + sex + dark + TL:colony + TL:sex + TL:dark
SST35.mod	colony + sex + colony:sex
SST36.mod	TL + colony + sex + colony:sex
SST37.mod	colony + sex + dark + colony:sex
SST38.mod	TL + colony + sex + dark + colony:sex
SST39.mod	TL + colony + sex + TL:colony + colony:sex
SST40.mod	TL + colony + sex + dark + TL:colony + colony:sex
SST41.mod	TL + colony + sex + TL:sex + colony:sex
SST42.mod	TL + colony + sex + dark + TL:sex + colony:sex
SST43.mod	TL + colony + sex + TL:colony + TL:sex + colony:sex
SST44.mod	TL + colony + sex + dark + TL:colony + TL:sex + colony:sex
SST45.mod	TL + colony + sex + dark + TL:dark + colony:sex
SST46.mod	TL + colony + sex + dark + TL:colony + TL:dark + colony:sex
SST47.mod	TL + colony + sex + dark + TL:sex + TL:dark + colony:sex
SST48.mod	TL + colony + sex + dark + TL:colony + TL:sex + TL:dark + colony:sex
SST72.mod	sex + dark + sex:dark
SST73.mod	TL + sex + dark + sex:dark
SST74.mod	colony + sex + dark + sex:dark
SST75.mod	TL + colony + sex + dark + sex:dark
SST76.mod	TL + colony + sex + dark + TL:colony + sex:dark
SST77.mod	TL + sex + dark + TL:sex + sex:dark
SST78.mod	TL + colony + sex + dark + TL:sex + sex:dark
SST79.mod	TL + colony + sex + dark + TL:colony + TL:sex + sex:dark
SST80.mod	TL + sex + dark + TL:dark + sex:dark
SST81.mod	TL + colony + sex + dark + TL:dark + sex:dark
SST82.mod	TL + colony + sex + dark + TL:colony + TL:dark + sex:dark
SST83.mod	TL + sex + dark + TL:sex + TL:dark + sex:dark
SST84.mod	TL + colony + sex + dark + TL:sex + TL:dark + sex:dark
SST85.mod	TL + colony + sex + dark + TL:colony + TL:sex + TL:dark + sex:dark
SST86.mod	colony + sex + dark + colony:sex + sex:dark
SST87.mod	TL + colony + sex + dark + colony:sex + sex:dark
SST88.mod	TL + colony + sex + dark + TL:colony + colony:sex + sex:dark
SST89.mod	TL + colony + sex + dark + TL:sex + colony:sex + sex:dark
SST90.mod	TL + colony + sex + dark + TL:colony + TL:sex + colony:sex + sex:dark
SST91.mod	TL + colony + sex + dark + TL:dark + colony:sex + sex:dark
SST92.mod	TL + colony + sex + dark + TL:colony + TL:dark + colony:sex + sex:dark
SST93.mod	TL + colony + sex + dark + TL:sex + TL:dark + colony:sex + sex:dark
SST94.mod	TL + colony + sex + dark + TL:colony + TL:sex + TL:dark + colony:sex + sex:dark

Table A6. AIC results for SST. All results with ΔAICc < 2 are in boldface. The null model is in italics. The sum of weights is shown for all models up to a total weight of 0.9. These models (up to weight = 0.9) are used to generate model averaged parameters.

Model	df	AICc	ΔAICc	wi	Sum wi
SST78.mod	**13**	**7308.496**	**0**	**0.166063**	**0.166063**
SST23.mod	**12**	**7308.979**	**0.482974**	**0.130436**	**0.296499**
SST33.mod	**13**	**7310.23**	**1.734**	**0.069782**	**0.366281**
SST74.mod	**11**	**7310.242**	**1.745808**	**0.069371**	**0.435652**
SST84.mod	14	7310.542	2.045582	0.059715	0.495366
SST75.mod	12	7310.681	2.184974	0.055695	0.551061
SST14.mod	10	7310.762	2.26588	0.053487	0.604548
SST15.mod	11	7311.182	2.685808	0.043357	0.647904
SST12.mod	10	7312.245	3.74888	0.025481	0.673385
SST29.mod	12	7312.246	3.749974	0.025467	0.698852
SST79.mod	15	7312.505	4.008493	0.022379	0.721231
SST9.mod	9	7312.587	4.090635	0.021478	0.74271
SST81.mod	13	7312.587	4.091	0.021475	0.764184
SST89.mod	15	7312.859	4.362493	0.018749	0.782933
SST25.mod	14	7312.866	4.369582	0.018682	0.801615
SST42.mod	14	7313.247	4.750582	0.015442	0.817057
SST27.mod	11	7313.273	4.776808	0.015241	0.832298
SST72.mod	9	7314.001	5.504635	0.010592	0.842889
SST86.mod	13	7314.093	5.597	0.010113	0.853003
SST34.mod	15	7314.216	5.719493	0.009513	0.862515
SST73.mod	10	7314.275	5.77888	0.009234	0.87175
SST76.mod	14	7314.483	5.986582	0.008323	0.880073
SST37.mod	12	7314.552	6.055974	0.00804	0.888113
SST47.mod	15	7314.603	6.106493	0.007839	0.895952
SST85.mod	16	7314.655	6.158582	0.007638	0.90359
SST77.mod	11	7314.667	6.170808	0.007591	
SST10.mod	8	7314.713	6.216582	0.007419	
SST19.mod	13	7314.856	6.36	0.006906	
SST13.mod	9	7314.977	6.480635	0.006502	
SST93.mod	16	7315.015	6.518582	0.006379	
SST87.mod	14	7315.022	6.525582	0.006357	
SST22.mod	10	7315.351	6.85488	0.005392	
SST38.mod	13	7315.437	6.941	0.005165	
SST28.mod	10	7315.921	7.42488	0.004055	
SST80.mod	11	7316.078	7.581808	0.003749	
SST31.mod	14	7316.098	7.601582	0.003712	
SST32.mod	11	7316.424	7.927808	0.003153	
SST18.mod	12	7316.506	8.009974	0.003026	
SST82.mod	15	7316.539	8.042493	0.002978	
SST7.mod	8	7316.56	8.063582	0.002946	
SST83.mod	12	7316.573	8.076974	0.002927	
SST45.mod	14	7316.602	8.105582	0.002885	
SST91.mod	15	7317.034	8.537493	0.002325	
SST90.mod	17	7317.319	8.822789	0.002016	
SST26.mod	9	7317.482	8.985635	0.001858	
SST4.mod	7	7317.483	8.986294	0.001857	
SST44.mod	16	7317.59	9.093582	0.00176	
SST30.mod	13	7317.673	9.177	0.001689	
SST88.mod	16	7319.028	10.53158	0.000858	
SST48.mod	17	7319.051	10.55479	0.000848	
SST40.mod	15	7319.32	10.82349	0.000741	
SST94.mod	18	7319.588	11.09114	0.000648	
SST46.mod	16	7320.669	12.17258	0.000378	
SST92.mod	17	7321.199	12.70279	0.00029	
SST21.mod	11	7344.34	35.84381	2.73E-09	
SST8.mod	9	7345.996	37.49964	1.19E-09	
SST11.mod	10	7346.421	37.92488	9.66E-10	
SST5.mod	9	7347.84	39.34364	4.75E-10	
SST24.mod	13	7348.07	39.574	4.24E-10	
SST2.mod	8	7348.196	39.69958	3.98E-10	
SST41.mod	13	7348.483	39.987	3.45E-10	
SST35.mod	11	7349.659	41.16281	1.91E-10	
SST17.mod	12	7349.952	41.45597	1.65E-10	
SST36.mod	12	7350.551	42.05497	1.23E-10	
SST3.mod	7	7350.578	42.08129	1.21E-10	
SST6.mod	8	7350.848	42.35158	1.06E-10	
SST20.mod	9	7351.344	42.84764	8.24E-11	
SST16.mod	11	7352.021	43.52481	5.87E-11	
SST43.mod	15	7352.671	44.17449	4.25E-11	
SST1.mod	7	7352.819	44.32229	3.94E-11	
SST0.mod	*6*	*7353.766*	*45.2694*	*2.46E-11*	
SST39.mod	14	7354.295	45.79858	1.88E-11	

Table A7. Models for foraging depth (dark = night diving).

Model	Terms
dep0.mod	null
dep1.mod	TL
dep2.mod	colony
dep3.mod	sex
dep4.mod	dark
dep5.mod	TL + colony
dep6.mod	TL + sex
dep7.mod	TL + dark
dep8.mod	colony + sex
dep9.mod	colony + dark
dep10.mod	sex + dark
dep11.mod	TL + colony + sex
dep12.mod	TL + colony + dark
dep13.mod	TL + sex + dark
dep14.mod	colony + sex + dark
dep15.mod	TL + colony + sex + dark
dep16.mod	TL + colony + TL:colony
dep17.mod	TL + colony + sex + TL:colony
dep18.mod	TL + colony + dark + TL:colony
dep19.mod	TL + colony + sex + dark + TL:colony
dep20.mod	TL + sex + TL:sex
dep21.mod	TL + colony + sex + TL:sex
dep22.mod	TL + sex + dark + TL:sex
dep23.mod	TL + colony + sex + dark + TL:sex
dep24.mod	TL + colony + sex + TL:colony + TL:sex
dep25.mod	TL + colony + sex + dark + TL:colony + TL:sex
dep26.mod	TL + dark + TL:dark
dep27.mod	TL + colony + dark + TL:dark
dep28.mod	TL + sex + dark + TL:dark
dep29.mod	TL + colony + sex + dark + TL:dark
dep30.mod	TL + colony + dark + TL:colony + TL:dark
dep31.mod	TL + colony + sex + dark + TL:colony + TL:dark
dep32.mod	TL + sex + dark + TL:sex + TL:dark
dep33.mod	TL + colony + sex + dark + TL:sex + TL:dark
dep34.mod	TL + colony + sex + dark + TL:colony + TL:sex + TL:dark
dep35.mod	colony + sex + colony:sex
dep36.mod	TL + colony + sex + colony:sex
dep37.mod	colony + sex + dark + colony:sex
dep38.mod	TL + colony + sex + dark + colony:sex
dep39.mod	TL + colony + sex + TL:colony + colony:sex
dep40.mod	TL + colony + sex + dark + TL:colony + colony:sex
dep41.mod	TL + colony + sex + TL:sex + colony:sex
dep42.mod	TL + colony + sex + dark + TL:sex + colony:sex
dep43.mod	TL + colony + sex + TL:colony + TL:sex + colony:sex
dep44.mod	TL + colony + sex + dark + TL:colony + TL:sex + colony:sex
dep45.mod	TL + colony + sex + dark + TL:dark + colony:sex
dep46.mod	TL + colony + sex + dark + TL:colony + TL:dark + colony:sex
dep47.mod	TL + colony + sex + dark + TL:sex + TL:dark + colony:sex
dep48.mod	TL + colony + sex + dark + TL:colony + TL:sex + TL:dark + colony:sex
dep72.mod	sex + dark + sex:dark
dep73.mod	TL + sex + dark + sex:dark
dep74.mod	colony + sex + dark + sex:dark
dep75.mod	TL + colony + sex + dark + sex:dark
dep76.mod	TL + colony + sex + dark + TL:colony + sex:dark
dep77.mod	TL + sex + dark + TL:sex + sex:dark
dep78.mod	TL + colony + sex + dark + TL:sex + sex:dark
dep79.mod	TL + colony + sex + dark + TL:colony + TL:sex + sex:dark
dep80.mod	TL + sex + dark + TL:dark + sex:dark
dep81.mod	TL + colony + sex + dark + TL:dark + sex:dark
dep82.mod	TL + colony + sex + dark + TL:colony + TL:dark + sex:dark
dep83.mod	TL + sex + dark + TL:sex + TL:dark + sex:dark
dep84.mod	TL + colony + sex + dark + TL:sex + TL:dark + sex:dark
dep85.mod	TL + colony + sex + dark + TL:colony + TL:sex + TL:dark + sex:dark
dep86.mod	colony + sex + dark + colony:sex + sex:dark
dep87.mod	TL + colony + sex + dark + colony:sex + sex:dark
dep88.mod	TL + colony + sex + dark + TL:colony + colony:sex + sex:dark
dep89.mod	TL + colony + sex + dark + TL:sex + colony:sex + sex:dark
dep90.mod	TL + colony + sex + dark + TL:colony + TL:sex + colony:sex + sex:dark
dep91.mod	TL + colony + sex + dark + TL:dark + colony:sex + sex:dark
dep92.mod	TL + colony + sex + dark + TL:colony + TL:dark + colony:sex + sex:dark
dep93.mod	TL + colony + sex + dark + TL:sex + TL:dark + colony:sex + sex:dark
dep94.mod	TL + colony + sex + dark + TL:colony + TL:sex + TL:dark + colony:sex + sex:dark

Table A8. AIC results for foraging depth. All results with ΔAICc < 2 are in boldface. The null model is in italics. The sum of weights is shown for all models up to a total weight of 0.9. These models (up to weight = 0.9) are used to generate model averaged parameters.

Model	df	AICc	ΔAICc	wi	Sum wi
maxd81.mod	**15**	**378254.3**	**0**	**0.348244**	**0.348244**
maxd84.mod	**16**	**378255.8**	**1.517582**	**0.163059**	**0.511303**
maxd82.mod	**17**	**378256.3**	**1.989493**	**0.128787**	**0.64009**
maxd91.mod	**17**	**378256.3**	**1.989493**	**0.128787**	**0.768877**
maxd85.mod	18	378257.1	2.817582	0.085124	0.854001
maxd93.mod	18	378257.8	3.517582	0.059986	0.913987
maxd92.mod	19	378258.2	3.903789	0.049452	
maxd94.mod	20	378259	4.750141	0.032389	
maxd80.mod	13	378263.7	9.420808	0.003135	
maxd83.mod	14	378265.9	11.63497	0.001036	
maxd75.mod	14	378283.8	29.53497	1.34E-07	
maxd78.mod	15	378285.1	30.8	7.14E-08	
maxd87.mod	16	378285.7	31.41758	5.24E-08	
maxd76.mod	16	378285.8	31.51758	4.99E-08	
maxd79.mod	17	378286.4	32.08949	3.75E-08	
maxd89.mod	17	378287	32.68949	2.78E-08	
maxd88.mod	18	378287.6	33.31758	2.03E-08	
maxd90.mod	19	378288.3	34.00379	1.44E-08	
maxd74.mod	13	378288.6	34.32081	1.23E-08	
maxd86.mod	15	378291.8	37.5	2.51E-09	
maxd73.mod	12	378293.2	38.95588	1.21E-09	
maxd77.mod	13	378295.4	41.12081	4.1E-10	
maxd72.mod	11	378298.3	44.03864	9.53E-11	
maxd27.mod	13	378301.5	47.22081	1.94E-11	
maxd29.mod	14	378302.9	48.63497	9.57E-12	
maxd30.mod	15	378303.8	49.5	6.21E-12	
maxd33.mod	15	378304.4	50.1	4.6E-12	
maxd45.mod	16	378304.5	50.21758	4.34E-12	
maxd31.mod	16	378304.8	50.51758	3.73E-12	
maxd34.mod	17	378305.6	51.28949	2.54E-12	
maxd47.mod	17	378306	51.68949	2.08E-12	
maxd46.mod	18	378306.2	51.91758	1.85E-12	
maxd48.mod	19	378307.1	52.80379	1.19E-12	
maxd26.mod	11	378311.1	56.83864	1.58E-13	
maxd28.mod	12	378312.5	58.25588	7.79E-14	
maxd32.mod	13	378314.8	60.52081	2.51E-14	
maxd12.mod	12	378355.1	100.8559	4.38E-23	
maxd15.mod	13	378356.4	102.1208	2.33E-23	
maxd18.mod	14	378357.4	103.135	1.4E-23	
maxd23.mod	14	378357.7	103.435	1.21E-23	
maxd38.mod	15	378358	103.7	1.06E-23	
maxd19.mod	15	378358.4	104.1	8.65E-24	
maxd25.mod	16	378359	104.7176	6.35E-24	
maxd42.mod	16	378359.2	104.9176	5.75E-24	
maxd9.mod	11	378359.5	105.2386	4.89E-24	
maxd40.mod	17	378359.8	105.4895	4.32E-24	
maxd44.mod	18	378360.4	106.1176	3.15E-24	
maxd14.mod	12	378361.2	106.9559	2.07E-24	
maxd37.mod	14	378364.1	109.835	4.91E-25	
maxd7.mod	10	378365	110.6676	3.24E-25	
maxd13.mod	11	378366.3	112.0386	1.63E-25	
maxd22.mod	12	378368.4	114.1559	5.67E-26	
maxd4.mod	9	378369.4	115.1413	3.46E-26	
maxd10.mod	10	378371.4	117.0676	1.32E-26	
maxd5.mod	11	380669.3	2415.039	0	
maxd11.mod	12	380669.8	2415.556	0	
maxd16.mod	13	380670.9	2416.621	0	
maxd21.mod	13	380671.1	2416.821	0	
maxd17.mod	14	380671.1	2416.835	0	
maxd36.mod	14	380671.1	2416.835	0	
maxd24.mod	15	380671.8	2417.5	0	
maxd39.mod	16	380672.1	2417.818	0	
maxd41.mod	15	380672.3	2418	0	
maxd43.mod	17	380672.9	2418.589	0	
maxd2.mod	10	380673.8	2419.468	0	
maxd8.mod	11	380675	2420.739	0	
maxd1.mod	9	380675.3	2421.041	0	
maxd6.mod	10	380675.9	2421.568	0	
maxd35.mod	13	380677.7	2423.421	0	
maxd20.mod	11	380677.9	2423.639	0	
maxd0.mod	*8*	*380679.9*	*2425.658*	*0*	
maxd3.mod	9	380681.3	2427.041	0	

Table A9. Models for maximum depth (dark = night diving).

Model	Terms
deep0.mod	null
deep1.mod	TL
deep2.mod	colony
deep3.mod	sex
deep4.mod	dark
deep5.mod	TL + colony
deep6.mod	TL + sex
deep7.mod	TL + dark
deep8.mod	colony + sex
deep9.mod	colony + dark
deep10.mod	sex + dark
deep11.mod	TL + colony + sex
deep12.mod	TL + colony + dark
deep13.mod	TL + sex + dark
deep14.mod	colony + sex + dark
deep15.mod	TL + colony + sex + dark
deep16.mod	TL + colony + TL:colony
deep17.mod	TL + colony + sex + TL:colony
deep18.mod	TL + colony + dark + TL:colony
deep19.mod	TL + colony + sex + dark + TL:colony
deep20.mod	TL + sex + TL:sex
deep21.mod	TL + colony + sex + TL:sex
deep22.mod	TL + sex + dark + TL:sex
deep23.mod	TL + colony + sex + dark + TL:sex
deep24.mod	TL + colony + sex + TL:colony + TL:sex
deep25.mod	TL + colony + sex + dark + TL:colony + TL:sex
deep26.mod	TL + dark + TL:dark
deep27.mod	TL + colony + dark + TL:dark
deep28.mod	TL + sex + dark + TL:dark
deep29.mod	TL + colony + sex + dark + TL:dark
deep30.mod	TL + colony + dark + TL:colony + TL:dark
deep31.mod	TL + colony + sex + dark + TL:colony + TL:dark
deep32.mod	TL + sex + dark + TL:sex + TL:dark
deep33.mod	TL + colony + sex + dark + TL:sex + TL:dark
deep34.mod	TL + colony + sex + dark + TL:colony + TL:sex + TL:dark
deep35.mod	colony + sex + colony:sex
deep36.mod	TL + colony + sex + colony:sex
deep37.mod	colony + sex + dark + colony:sex
deep38.mod	TL + colony + sex + dark + colony:sex
deep39.mod	TL + colony + sex + TL:colony + colony:sex
deep40.mod	TL + colony + sex + dark + TL:colony + colony:sex
deep41.mod	TL + colony + sex + TL:sex + colony:sex
deep42.mod	TL + colony + sex + dark + TL:sex + colony:sex
deep43.mod	TL + colony + sex + TL:colony + TL:sex + colony:sex
deep44.mod	TL + colony + sex + dark + TL:colony + TL:sex + colony:sex
deep45.mod	TL + colony + sex + dark + TL:dark + colony:sex
deep46.mod	TL + colony + sex + dark + TL:colony + TL:dark + colony:sex
deep47.mod	TL + colony + sex + dark + TL:sex + TL:dark + colony:sex
deep48.mod	TL + colony + sex + dark + TL:colony + TL:sex + TL:dark + colony:sex
deep72.mod	sex + dark + sex:dark
deep73.mod	TL + sex + dark + sex:dark
deep74.mod	colony + sex + dark + sex:dark
deep75.mod	TL + colony + sex + dark + sex:dark
deep76.mod	TL + colony + sex + dark + TL:colony + sex:dark
deep77.mod	TL + sex + dark + TL:sex + sex:dark
deep78.mod	TL + colony + sex + dark + TL:sex + sex:dark
deep79.mod	TL + colony + sex + dark + TL:colony + TL:sex + sex:dark
deep80.mod	TL + sex + dark + TL:dark + sex:dark
deep81.mod	TL + colony + sex + dark + TL:dark + sex:dark
deep82.mod	TL + colony + sex + dark + TL:colony + TL:dark + sex:dark
deep83.mod	TL + sex + dark + TL:sex + TL:dark + sex:dark
deep84.mod	TL + colony + sex + dark + TL:sex + TL:dark + sex:dark
deep85.mod	TL + colony + sex + dark + TL:colony + TL:sex + TL:dark + sex:dark
deep86.mod	colony + sex + dark + colony:sex + sex:dark
deep87.mod	TL + colony + sex + dark + colony:sex + sex:dark
deep88.mod	TL + colony + sex + dark + TL:colony + colony:sex + sex:dark
deep89.mod	TL + colony + sex + dark + TL:sex + colony:sex + sex:dark
deep90.mod	TL + colony + sex + dark + TL:colony + TL:sex + colony:sex + sex:dark
deep91.mod	TL + colony + sex + dark + TL:dark + colony:sex + sex:dark
deep92.mod	TL + colony + sex + dark + TL:colony + TL:dark + colony:sex + sex:dark
deep93.mod	TL + colony + sex + dark + TL:sex + TL:dark + colony:sex + sex:dark
deep94.mod	TL + colony + sex + dark + TL:colony + TL:sex + TL:dark + colony:sex + sex:dark

Table A10. AIC results for maximum depth. All results with ΔAICc < 2 are in boldface. The null model is in italics. The sum of weights is shown for all models up to a total weight of 0.9. These models (up to weight = 0.9) are used to generate model averaged parameters.

Model	df	AICc	ΔAICc	wi	Sum wi
deep12.mod	**9**	**866.7211**	**0**	**0.135555**	**0.135555**
deep5.mod	**8**	**867.1116**	**0.390455**	**0.111514**	**0.247069**
deep27.mod	**10**	**867.9501**	**1.229028**	**0.073322**	**0.320391**
deep15.mod	**10**	**868.2076**	**1.486528**	**0.064464**	**0.384856**
deep38.mod	12	868.9533	2.23222	0.044401	0.429257
deep29.mod	11	869.2019	2.480793	0.039212	0.468469
deep11.mod	9	869.2247	2.5036	0.038767	0.507236
deep23.mod	11	869.6602	2.939093	0.031182	0.538418
deep45.mod	13	869.6693	2.948202	0.03104	0.569458
deep2.mod	7	869.8508	3.129702	0.028347	0.597805
deep21.mod	10	870.1683	3.447228	0.024186	0.621991
deep9.mod	8	870.2091	3.487955	0.023698	0.645689
deep18.mod	11	870.3362	3.615093	0.022239	0.667927
deep75.mod	11	870.3804	3.659293	0.021753	0.68968
deep36.mod	11	870.4785	3.757393	0.020711	0.710391
deep42.mod	13	870.7234	4.002302	0.018324	0.728716
deep87.mod	13	870.7486	4.027502	0.018095	0.74681
deep16.mod	10	871.1573	4.436228	0.01475	0.761561
deep19.mod	12	871.3706	4.64952	0.013258	0.774819
deep81.mod	12	871.4037	4.68262	0.013041	0.78786
deep33.mod	12	871.4093	4.68822	0.013004	0.800864
deep91.mod	14	871.4547	4.733612	0.012712	0.813576
deep40.mod	14	871.4986	4.777512	0.012436	0.826012
deep41.mod	12	871.7394	5.01832	0.011026	0.837038
deep30.mod	12	871.9085	5.18742	0.010132	0.84717
deep78.mod	12	871.9438	5.22272	0.009954	0.857124
deep8.mod	8	871.9999	5.278755	0.009679	0.866803
deep14.mod	9	872.0661	5.345	0.009364	0.876167
deep25.mod	13	872.0678	5.346702	0.009356	0.885524
deep47.mod	14	872.118	5.396912	0.009124	0.894648
deep44.mod	15	872.15	5.428902	0.008979	0.903627
deep89.mod	14	872.3947	5.673612	0.007945	
deep46.mod	15	872.7202	5.999102	0.006752	
deep37.mod	11	873.0095	6.288393	0.005843	
deep31.mod	13	873.0352	6.314102	0.005768	
deep17.mod	11	873.2705	6.549393	0.005128	
deep35.mod	10	873.3011	6.580028	0.00505	
deep76.mod	13	873.4462	6.725102	0.004697	
deep24.mod	12	873.5222	6.80112	0.004521	
deep88.mod	15	873.6749	6.953802	0.004189	
deep84.mod	13	873.7017	6.980602	0.004133	
deep93.mod	15	873.9139	7.192802	0.003717	
deep90.mod	16	874.1113	7.390209	0.003368	
deep79.mod	14	874.3079	7.586812	0.003053	
deep74.mod	10	874.331	7.609928	0.003017	
deep48.mod	16	874.3572	7.636109	0.002978	
deep34.mod	14	874.4227	7.701612	0.002882	
deep39.mod	13	874.4324	7.711302	0.002868	
deep86.mod	12	874.4924	7.77132	0.002784	
deep43.mod	14	874.5779	7.856812	0.002667	
deep92.mod	16	874.7863	8.065209	0.002403	
deep7.mod	7	874.8925	8.171402	0.002279	
deep82.mod	14	875.1883	8.467212	0.001966	
deep26.mod	8	875.8125	9.091355	0.001439	
deep13.mod	8	876.1437	9.422555	0.001219	
deep94.mod	17	876.3148	9.59366	0.001119	
deep22.mod	9	876.5957	9.8746	0.000972	
deep28.mod	9	876.636	9.9149	0.000953	
deep85.mod	15	876.7181	9.997002	0.000915	
deep73.mod	9	878.2548	11.5337	0.000424	
deep32.mod	10	878.3597	11.63863	0.000403	
deep80.mod	10	878.7854	12.06433	0.000325	
deep77.mod	10	878.8261	12.10503	0.000319	
deep83.mod	11	880.6164	13.89529	0.00013	
deep4.mod	6	881.3647	14.64361	8.96E-05	
deep10.mod	7	883.1547	16.4336	3.66E-05	
deep72.mod	8	885.3039	18.58275	1.25E-05	
deep20.mod	8	887.967	21.24585	3.3E-06	
deep1.mod	6	887.9989	21.27781	3.25E-06	
deep6.mod	7	890.0306	23.3095	1.18E-06	
deep0.mod	*5*	*892.3587*	*25.63762*	*3.67E-07*	
deep3.mod	6	894.4363	27.71521	1.3E-07	

Table A11. Models for night diving.

Model	Terms
dark0.mod	null
dark1.mod	TL
dark2.mod	colony
dark3.mod	sex
dark5.mod	TL + colony
dark6.mod	TL + sex
dark8.mod	colony + sex
dark11.mod	TL + colony + sex
dark16.mod	TL + colony + TL:colony
dark17.mod	TL + colony + sex + TL:colony
dark20.mod	TL + sex + TL:sex
dark21.mod	TL + colony + sex + TL:sex
dark24.mod	TL + colony + sex + TL:colony + TL:sex
dark35.mod	colony + sex + colony:sex
dark36.mod	TL + colony + sex + colony:sex
dark39.mod	TL + colony + sex + TL:colony + colony:sex
dark41.mod	TL + colony + sex + TL:sex + colony:sex
dark117.mod	TL + colony + sex + TL:sex + TL:colony:sex

Table A12. AIC results for night diving. All results with ΔAICc < 2 are in boldface. The null model is in italics. The sum of weights is shown for all models up to a total weight of 0.9. These models (up to weight = 0.9) are used to generate model averaged parameters.

Model	df	AICc	ΔAICc	wi	Sum wi
dark6.mod	**9**	**212.2918**	**0**	**0.522878**	**0.522878**
dark7.mod	10	214.5066	2.214845	0.172764	0.695642
dark12.mod	11	216.4391	4.147373	0.065737	0.761379
dark11.mod	11	216.7363	4.444573	0.05666	0.818039
dark2.mod	8	216.7746	4.482847	0.055586	0.873624
dark9.mod	12	217.2709	4.979139	0.04337	0.916995
dark13.mod	12	218.734	6.442239	0.020868	
dark15.mod	13	218.8202	6.528465	0.019988	
dark4.mod	9	218.8734	6.5816	0.019464	
dark8.mod	11	220.6148	8.323073	0.008148	
dark16.mod	13	221.0693	8.777565	0.006492	
dark17.mod	14	221.4163	9.124547	0.005458	
dark21.mod	15	222.9123	10.62056	0.002583	
dark3.mod	7	237.0508	24.75906	2.2E-06	
dark10.mod	9	238.9664	26.6746	8.43E-07	
dark5.mod	8	238.9929	26.70115	8.32E-07	
dark0.mod	*6*	*245.9877*	*33.69596*	*2.52E-08*	
dark1.mod	7	247.1661	34.87436	1.4E-08	

Table A13. Models for foraging efficiency.

Model	Terms
under0.mod	null
under1.mod	TL
under2.mod	colony
under3.mod	sex
under4.mod	TL + colony
under5.mod	TL + sex
under6.mod	colony + sex
under7.mod	TL + colony + sex
under8.mod	TL + colony + TL:colony
under9.mod	TL + colony + sex + TL:colony
under10.mod	TL + sex + TL:sex
under11.mod	TL + colony + sex + TL:sex
under12.mod	colony + sex + colony:sex
under13.mod	TL + colony + sex + colony:sex
under15.mod	TL + colony + sex + TL:colony + TL:sex
under16.mod	TL + colony + sex + TL:sex + colony:sex
under17.mod	TL + colony + sex + TL:colony + colony:sex
under21.mod	TL + colony + sex + TL:colony + TL:sex + colony:sex

Table A14. AIC results for foraging efficiency. All results with ΔAICc < 2 are in boldface. The null model is in italics. The sum of weights is shown for all models up to a total weight of 0.9. These models (up to weight = 0.9) are used to generate model averaged parameters.

Model	df	AICc	ΔAICc	wi	Sum wi
under13.mod	**8**	**286.6082**	**0**	**0.519596**	**0.519596**
under12.mod	7	288.8728	2.264635	0.167458	0.687054
under16.mod	9	288.9084	2.300226	0.164504	0.851558
under17.mod	10	290.4629	3.854709	0.075618	0.927176
under21.mod	11	292.8592	6.251019	0.022818	
under2.mod	4	294.0392	7.431009	0.012649	
under4.mod	5	294.2007	7.592461	0.011668	
under7.mod	6	295.3729	8.764707	0.006493	
under6.mod	5	295.4129	8.804661	0.006364	
under0.mod	*2*	*297.3178*	*10.70963*	*0.002455*	
under11.mod	7	297.5537	10.94553	0.002182	
under8.mod	7	297.711	11.10283	0.002017	
under3.mod	3	298.1647	11.55652	0.001608	
under1.mod	3	298.2201	11.61192	0.001564	
under5.mod	4	298.7129	12.10471	0.001222	
under9.mod	8	299.2343	12.6261	0.000942	
under10.mod	5	300.3031	13.69486	0.000552	
under15.mod	9	301.5853	14.97713	0.000291	

Table A15. Models for carbon stable isotope signatures.

Model	Terms
SIC0.mod	null
SIC1.mod	TL
SIC2.mod	colony
SIC3.mod	sex
SIC4.mod	TL + colony
SIC5.mod	TL + sex
SIC6.mod	colony + sex
SIC7.mod	TL + colony + sex
SIC8.mod	TL + colony + TL:colony
SIC9.mod	TL + colony + sex + TL:colony
SIC10.mod	TL + sex + TL:sex
SIC11.mod	TL + colony + sex + TL:sex
SIC12.mod	colony + sex + colony:sex
SIC13.mod	TL + colony + sex + colony:sex
SIC15.mod	TL + colony + sex + TL:colony + TL:sex
SIC16.mod	TL + colony + sex + TL:sex + colony:sex
SIC17.mod	TL + colony + sex + TL:colony + colony:sex
SIC21.mod	TL + colony + sex + TL:colony + TL:sex + colony:sex

Table A16. AIC results for carbon stable isotope signatures. All results with ΔAICc < 2 are in boldface. The null model is in italics. The sum of weights is shown for all models up to a total weight of 0.9. These models (up to weight = 0.9) are used to generate model averaged parameters.

Model	df	AICc	ΔAICc	wi	Sum wi
SIC4.mod	**8**	**19.8963226**	**0**	**0.383320166**	**0.383320166**
SIC7.mod	9	22.1135679	2.217245	0.126500715	0.509820881
SIC2.mod	7	22.44565	2.549327	0.107147554	0.616968435
SIC8.mod	10	23.2243558	3.328033	0.072591947	0.689560382
SIC11.mod	10	23.3893958	3.493073	0.066842158	0.756402541
SIC13.mod	11	23.4030113	3.506689	0.066388659	0.8227912
SIC16.mod	12	23.9963576	4.100035	0.049345822	0.872137022
SIC12.mod	10	24.5598058	4.663483	0.037230525	0.909367547
SIC6.mod	8	24.5778326	4.68151	0.036896459	
SIC9.mod	11	25.5142413	5.617919	0.023101816	
SIC17.mod	13	26.18274	6.286417	0.016538019	
SIC15.mod	12	27.5638976	7.667575	0.008290275	
SIC21.mod	14	28.2775501	8.381227	0.005802314	
SIC0.mod	*5*	*45.5141363*	*25.61781*	*1.04888E-06*	
SIC1.mod	6	45.6328713	25.73655	9.88419E-07	
SIC10.mod	8	46.0481026	26.15178	8.0311E-07	
SIC3.mod	6	47.5930913	27.69677	3.70924E-07	
SIC5.mod	7	47.66194	27.76562	3.58372E-07	

Table A17. Models for nitrogen stable isotope signatures.

Model	Terms
SIN0.mod	null
SIN1.mod	TL
SIN2.mod	colony
SIN3.mod	sex
SIN4.mod	TL + colony
SIN5.mod	TL + sex
SIN6.mod	colony + sex
SIN7.mod	TL + colony + sex
SIN8.mod	TL + colony + TL:colony
SIN9.mod	TL + colony + sex + TL:colony
SIN10.mod	TL + sex + TL:sex
SIN11.mod	TL + colony + sex + TL:sex
SIN12.mod	colony + sex + colony:sex
SIN13.mod	TL + colony + sex + colony:sex
SIN15.mod	TL + colony + sex + TL:colony + TL:sex
SIN16.mod	TL + colony + sex + TL:sex + colony:sex
SIN17.mod	TL + colony + sex + TL:colony + colony:sex
SIN21.mod	TL + colony + sex + TL:colony + TL:sex + colony:sex

Table A18. AIC results for nitrogen stable isotope signatures. All results with ΔAICc < 2 are in boldface. The null model is in italics. The sum of weights is shown for all models up to a total weight of 0.9. These models (up to weight = 0.9) are used to generate model averaged parameters.

Model	df	AICc	ΔAICc	wi	Sum wi
SIN12.mod	**9**	**162.078626**	**0**	**0.161**	**0.1610867**
SIN6.mod	**7**	**162.086853**	**0.008227**	**0.16**	**0.3215121**
SIN2.mod	**6**	**163.0066**	**0.927974**	**0.101**	**0.4227988**
SIN17.mod	**12**	**163.191**	**1.112374**	**0.092**	**0.5151644**
SIN13.mod	**10**	**163.388591**	**1.309965**	**0.084**	**0.5988411**
SIN9.mod	**10**	**163.419191**	**1.340565**	**0.082**	**0.6812472**
SIN8.mod	**9**	**163.525926**	**1.4473**	**0.078**	**0.7593708**
SIN7.mod	**8**	**163.587698**	**1.509072**	**0.076**	**0.8351184**
SIN4.mod	7	164.311753	2.233127	0.053	0.8878586
SIN21.mod	13	165.46441	3.385784	0.03	0.9174964
SIN16.mod	11	165.477118	3.398492	0.029	
SIN15.mod	11	165.600518	3.521892	0.028	
SIN11.mod	9	165.775726	3.6971	0.025	
SIN0.mod	*4*	*248.546216*	*86.46759*	*3E-20*	
SIN3.mod	5	248.891411	86.81279	2E-20	
SIN1.mod	5	250.629111	88.55049	1E-20	
SIN5.mod	6	250.9411	88.86247	8E-21	
SIN10.mod	7	253.109953	91.03133	3E-21	

APPENDIX B

DISCUSSION OF MURRE FORAGING BEHAVIOR IN RELATION TO HABITAT QUALITY (COLONY) AND SEX

Habitat quality (colony) and foraging behavior

All parameters were heavily colony-dependent. Colony-level differences usually reflect the large-scale ways in which habitat differs between the three colonies. For example, days are shorter at lower latitudes in the summer, and at lower latitude colonies we found birds allocating more of their time to diving after sunset. Night diving takes advantage of the diel migration of zooplankton (Regular et al. 2010). Night diving may also have been higher on colonies where a night spent at sea provided access to productive prey sources. St. George murres overnighted away from the colony on 50% of their trips, compared to 25% and 33% overnight trips on St. Paul and Bogoslof, respectively. The high percentage of overnight trips indicated that St. George murres were spending more time at the shelf edge, which is near the limit of foraging distance and thus more profitable for an overnight trip than a short day trip (Harding et al. 2013).

This is corroborated by the return flight time data. The average return time on St. George was nearly twice that on Bogoslof and 1.5× that on St. Paul, indicating long commuting trips to the shelf-edge on St. George. Bogoslof birds could access abundant prey close to their colony, indicated by their short return times as well as by their shallow dive depths, indicating near-colony foraging, while their maximum dive records were high, indicating access to oceanic habitat. St. Paul birds had fewer local food resources available, but were too far from the shelf-edge to make traveling there profitable (Harding et al. 2013). As a result, St. Paul birds stayed close to the colony, and foraged in the cooler waters of the Bering Sea cold pool (Stevenson and Lauth 2012).

Prey selection also differed by colony. Both stable isotopes (δ^{13}C and δ^{15}N) enriched with latitude, indicating more reliance on shelf sources of carbon in the north, as expected, but also higher trophic levels. Bogoslof murres' nitrogen signatures were almost an entire trophic level lower than St. Paul (Fig. 3). Although nitrogen signatures indicated that St. Paul murres ate the most fish, it is likely quantities were lower or that more energy was required to catch these prey, as their stress levels indicated lower food availability (Harding et al. 2013; Young et al., *unpublished manuscript*).

Sex and foraging behavior

Sex differences in behavior may be driven by the differing parental roles in the Thick-billed Murre: males care for the chick for 4–8 weeks post-fledging, while females pay the up-front costs of reproduction, i.e., egg production (Gaston and Jones 1998). In addition, females linger at the colonies, securing the nesting site for future years (Harris and Wanless 1990), and may feed the chick more while males invest in themselves in anticipation of their heavy post-fledging parental care (Thaxter et al. 2009). Unlike Thaxter et al. (2009) and Paredes et al. (2008), we found that females foraged farther from the colony and in warmer waters than males. At our colonies these distances likely indicated females searching the distant shelf-edge for high quality prey for the chick (at St. George) or searching farther abroad for fish instead of squid (at Bogoslof). Females' long return flight times indicated long trips, and were associated with more overnights away from the colony. Indeed, 43% of females' trips included a night away from the colony, while males only were away overnight on 26% of trips, thus females did more night diving than males (Fig. B1). Male murres attend the colony more at night so as to be available to accompany the chick to sea at fledging, which occurs at dusk. Night diving is usually shallower (Regular et al. 2010), and females dove more shallowly in our study, yet this difference was not driven by body size. Despite their longer commutes and more nights away from the colony, females did not perform fewer trips than males (Young et al., *unpublished manuscript*), so their parental investment is quite high. This corroborates previous findings that female murres may senesce more quickly than males (Young et al. 2013), which could be due to higher investment. A comparison of energy expenditures between males and females is warranted.

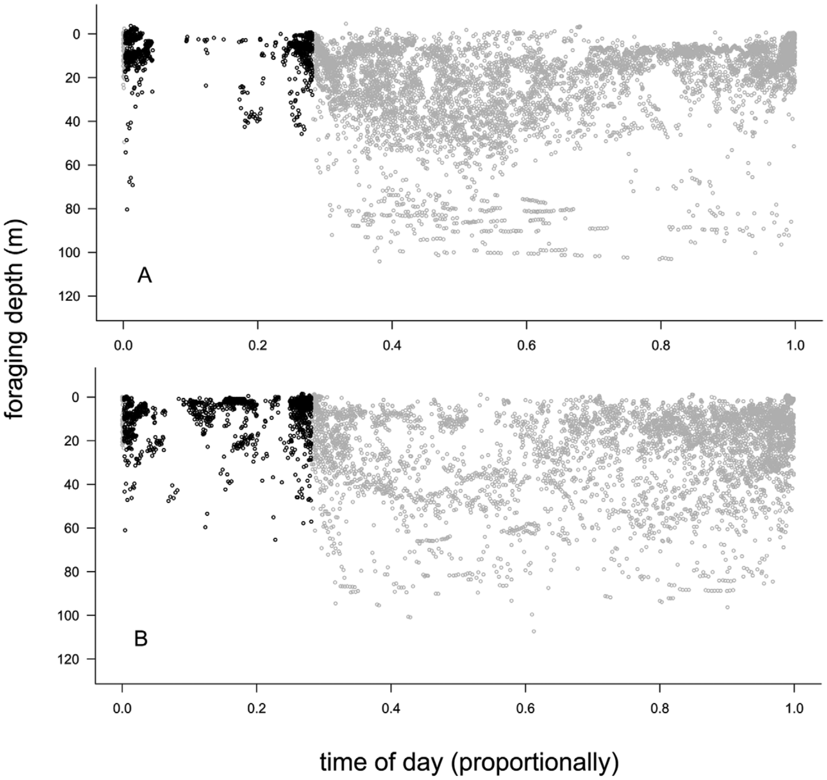

Fig. B1. Night diving on St. Paul. Hours of darkness were determined individually for St. Paul's latitude and for each day. Daylight diving is deeper and females (B) have more dives in darkness than males (A). Benthic diving can be seen on St. Paul where horizontal bars of dives at comparable depths indicate the ocean floor; this pattern is not seen on St. George and Bogoslof.

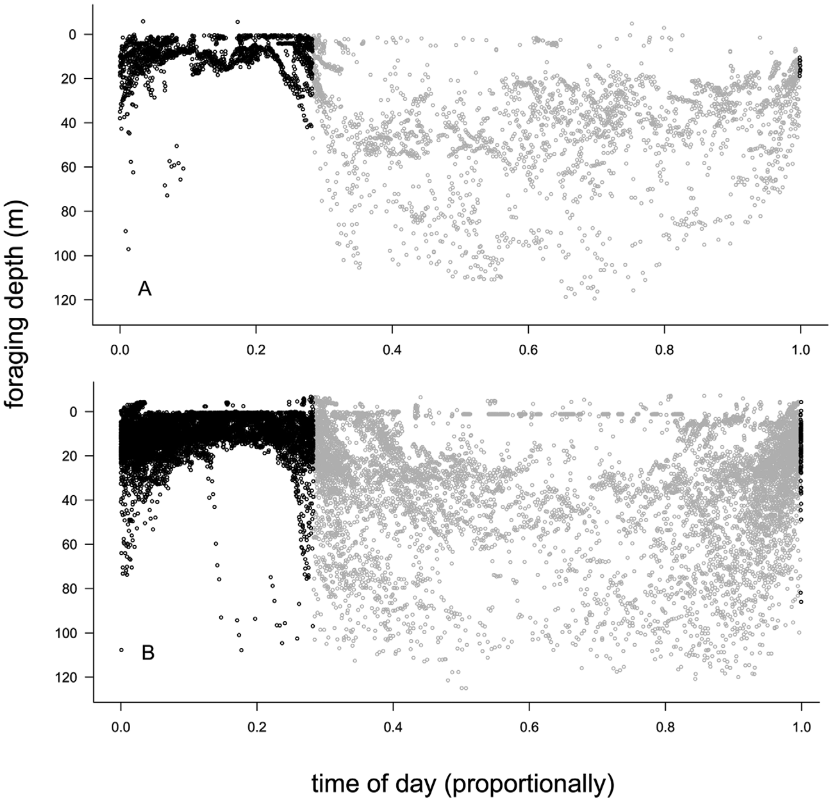

Fig. B2. Night diving on St. George. Hours of darkness were determined individually for St. George's latitude and for each day. Daylight diving is deeper and females (B) have more dives in darkness than males (A).

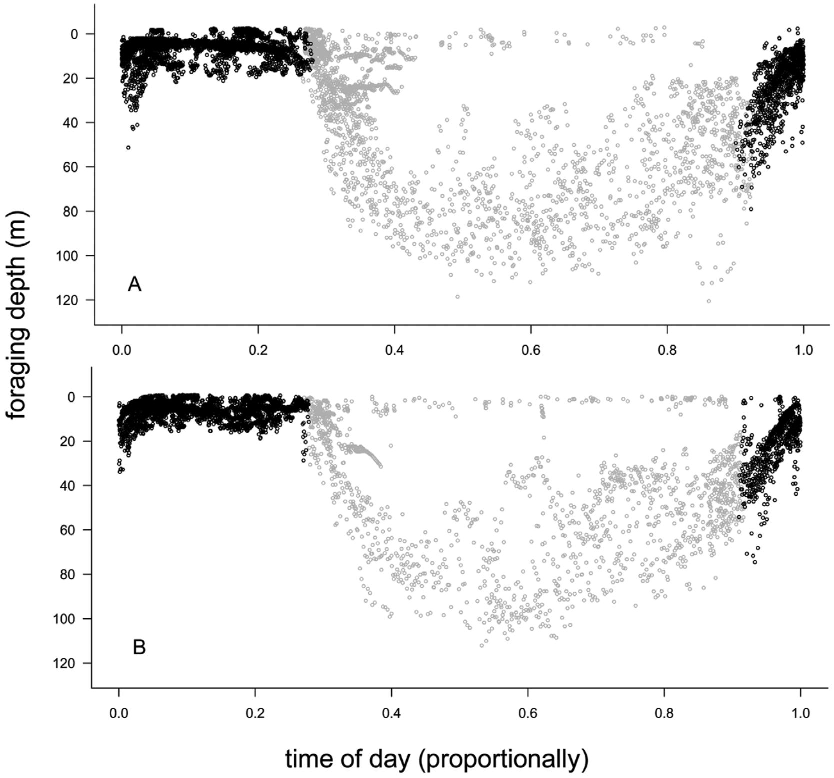

Fig. B3. Night diving on Bogoslof. Hours of darkness were determined individually for Bogoslof's latitude and for each day. Daylight diving is deeper and females (B) have more dives in darkness than males (A). Night diving is shallowest on Bogoslof, where night is longest. Benthic diving can be seen on St. Paul where horizontal bars of dives at comparable depths indicate the ocean floor; this pattern is not seen on St. George and Bogoslof.

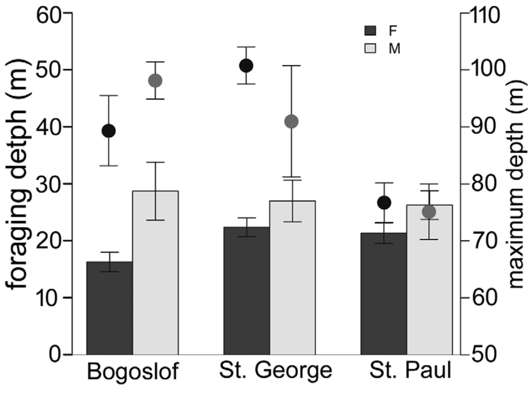

Fig. B4. Maximum depth and foraging depth by sex and colony. Dark points are maximum depth, and use the right-hand axis; bars are average depth and use the left-hand axis.