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Original Article

Individual state and survival prospects: age, sex, and telomere length in a long-lived seabird

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Identifying markers that are indicative of individual state, related to fitness, and which could be used to study life-history trade-offs in wild populations is extremely difficult. Recently, it has been suggested that telomeres, the ends of eukaryote chromosomes, might be useful in this context. However, little is known of the link between telomere length and fitness in natural populations and whether it is a useful indicator of biological state. We measured average telomere length in red blood cell samples taken from a wide age range of individuals of a very long-lived and highly sexually dimorphic seabird, the southern giant petrel (*Macronectes giganteus*). We examined the relationship with age, sex, and subsequent survival over an 8-year period. Telomere length was longer in chicks than adults. Within the adult group, which ranged in age from 12 to 40 years, telomere length was not related to age. For the first time in birds, there was some evidence of a sex difference. Male giant petrels, which are substantially larger than females, had significantly shorter telomere lengths than females. This difference was evident from an early stage in life and is likely to relate to differences in growth trajectories. Those adults that died during the 8-year time window following the telomere length measurement had significantly shorter telomere lengths than those that survived this period, irrespective of age or sex, neither of which were significant predictors of survival. These results show that relatively short telomere length is related to future life expectancy at any adult age, demonstrating its usefulness as a state variable. *Key words:* giant petrel, life span, sex differences, survival, telomere dynamics. *[Behav Ecol 22:156–161 (2011)]*

Within the same species, individuals of the same age vary in their biological state as a consequence of differences in their genetic inheritance, their lifestyle, and the environment they inhabit. Recognition that this is so and that it limits the utility of age-based approaches to understanding life-history strategies led to the development of state-dependent life-history models (McNamara and Houston 1996). Identifying markers that are indicative of individual state, related to fitness, and could be used to study life-history trade-offs in wild populations is extremely difficult. Recently, it has been suggested that telomeres, the ends of eukaryotic chromosomes, might be useful in this context (Monaghan and Haussmann 2006; Monaghan 2010). Telomeres, specialized DNA and protein complexes that cap the ends of eukaryotic chromosomes, shorten at each cell division. Once a critical telomere length is reached, cells either enter a state of replicative senescence or die. Declines in average telomere lengths in cell populations are indicative of increasing numbers of cells in tissues approaching, reaching, and passing this critical stage without replenishment. Changes in telomere length are thus linked to impaired tissue function and organismal deterioration (Blackburn 1991; Blasco 2007; Campisi and d'Adda di Fagagna 2007; Aubert and Lansdorp 2008). Average telomere length has been shown in various target cell populations to be shorter in older individuals in a number of vertebrate species (e.g., rats *Rattus norvegicus*, Cherif et al. 2003; tree swallows *Tachycineta bicolor*, common terns *Sterna hirundo*, Haussmann et al. 2003; humans, Baird 2006; frigate birds *Fregata minor*, Juola et al. 2006), and the rate of loss is generally fastest early in postnatal life (Baird 2006). Sex differences in telomere length have been found in some mammal species (e.g., rats, Cherif et al. 2003; humans, Nawrot et al. 2004), possibly due to sexual dimorphism in growth and size and/or energy expenditure and behavior. However, such sex differences have not previously been reported in birds.

Initial cell telomere length is partly determined by genetic and developmental factors and decreases with the number of cell divisions (Njajou et al. 2007). Evidence from in vitro and in vivo studies suggests that environmental factors, particularly exposure to oxidative stress, also have a substantial effect on the rate of telomere attrition (von Zglinicki 2002; Richter and von Zglinicki 2007; Cattan et al. 2008; Houben et al. 2008; Ilmonen et al. 2008; Epel 2009). Substantial variation in telomere length generally exists among same-age individuals (e.g., Haussmann et al. 2003; Hall et al. 2004), presumably as a consequence of variation in both inherited and environmental factors. Differences in telomere dynamics might therefore depend on differences in life history or behavior that give rise to differences in exposure to oxidative stress.

There is therefore good reason to think that relatively short telomere length is an indicator of biological state, as a consequence of deterioration that progresses at a different pace in some individuals than in others. However, studies of variation in telomere length in natural populations are still in their

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infancy, and we lack data that allow us to evaluate the link between variation in telomere length and fitness parameters such as survival. In order to understand the extent to which comparisons of average telomere length in cell samples from individuals of the same species do provide a useful indicator of biological state, it is important to link telomere length to survival or performance (Monaghan and Haussmann 2006; Vleck et al. 2007; Monaghan 2010). Evidence is accumulating that telomere length is indicative of survival prospects in the wild (tree swallow *T. bicolor*, Haussmann et al. 2005; sand martins *Riparia riparia*, Pauliny et al. 2006; jackdaws *Corvus monedula*, Salomons et al. 2009; Alpine swifts *Alpus melba*, Bize et al. 2009). Studies in humans, generally based on elderly individuals (>70 years) have also found that those with relatively long telomeres have a greater chance of surviving (e.g., Cawthon et al. 2003; Bakaysa et al. 2007), though others have not found this to be the case (e.g., Martin-Ruiz et al. 2005; Bischoff et al. 2006). This variability in results is perhaps because those who survive to very old age are a biased subset of the human population (Monaghan 2010). To evaluate whether telomere length is a useful indicator of survival probability across ages and cohorts and to assess whether relatively short telomere length at any age is indicative of reduced survival prospects, we need to examine telomere length and survival across a wide range of species with different life histories and taxonomic backgrounds, include as wide an age range of individuals as possible and track survival over an appropriate period. For very long-lived species, where decline in tissue function may be particularly important in influencing survival patterns, data with which to do this in natural animal populations are extremely limited because the true age of a wide age range of individuals is often not known and survival data in the wild can be very difficult to obtain over the long time scales required.

In this paper, we provide data from a very long lived and highly sexually dimorphic bird, the southern giant petrel (*Macronectes giganteus*). We examine how average telomere length in red blood cells varies across a very wide age range of male and female individuals (ranging from chicks to 40-year-old adults) and examine whether telomere length varies in relation to adult survival over a period of 8 years.

MATERIALS AND METHODS

Study site and sampling

All individuals were blood sampled in the austral summer 1999/2000 at a breeding colony on Bird Island, South Georgia (54°00′ N, 38°03′ S). These birds are part of a long-term study of seabirds on the island by the British Antarctic Survey. Forty-seven adults whose ages were known from ringing data were sampled (age range: 12–40 years; maximum life span of giant petrels is unknown, but few live into the fifth decade; oldest known bird ca. 47 years, British Antarctic Survey, unpublished data). Although the range of ages of adult males and females was similar within our sample (12–40 years), the average age of the sampled birds differed significantly between the sexes; the majority of the very old birds in the sample were male (only 1 of the five 40-year-old birds was female; mean age of males 26.8 ± 1.5 years, mean age of females 20.45 ± 1.8 years, $t_{45} = 2.7$, $P = 0.01$). We also sampled 16 giant petrel chicks. Giant petrels lay one egg each breeding season, so all chicks came from different nests; the exact age of the chicks at the time of sampling was not known, but they were all still nestlings. The species is highly sexually dimorphic (Copello et al. 2006), with males being up to 40% larger than females in mass and structural size, and size differences between the sexes are evident as early as 8 weeks posthatching (Hunter 1984; González-Solis et al. 2000b). Blood was taken by superficial venipuncture of the brachial vein and stored in 90% ethanol at −20 °C until DNA extraction. Sex of adult individuals can be determined reliably in the field based on bill dimensions (Hunter 1984). Chicks were sexed using a polymerase chain reaction–based method (Griffiths et al. 1998).

The study colony of southern giant petrels was thoroughly checked for the presence of all color-ringed individuals in the 2007/2008 and 2008/2009 breeding seasons. Resighting of the individuals sampled in 1999/2000 up to and including the 2008/2009 breeding season was used to examine the link between telomere length and survival. Although southern giant petrels are faithful to their breeding site, approximately 20–30% of individuals can skip breeding each year (Hunter 1984; British Antarctic Survey, unpublished data). Accordingly, we need at least 2 years of recorded absence from the colony before individuals can be considered dead. We therefore compared the telomere length, measured at the time of sampling in 1999/2000, of those individuals assumed to have died by 2008/2009 compared with those that were still alive (i.e., were seen in the breeding colony at least until the 2007/2008 breeding season). Fledged chicks do not return to breed until they are 11–12 years old, so we were unable to gather any data on chick survival. However, the chick samples enabled us to compare telomere length in chicks and adults and also to examine whether any sex differences were detectable at an early stage.

Measurement of telomere restriction fragments

DNA was extracted from red blood cells, which are nucleated in birds. Samples were digested with proteinase K before DNA extraction by a standard phenol–chloroform–ethanol precipitation method. DNA was checked for degradation by 1% agarose gel electrophoresis. Telomere restriction fragment (TRF) lengths were measured by Southern blot analysis using the TeloTAGG Telomere Length Assay (Roche Diagnostics GmbH, Roche Applied Science, Mannheim, Germany) following the suppliers recommended protocol. Briefly, approximately 1 μg of DNA from each sample was digested with the restriction enzymes *Hinf*I and *Rsa*I for 16 h at 37 °C. Digested DNA samples were separated on a 0.8% agarose gel at 150 V for 3 h. Two marker lanes (23.1–2.0 kb) were run on each gel. The gel was then subjected to depurination, denaturation in an alkaline solution followed by neutralization. The DNA was transferred onto a nitrocellulose membrane (Hybond N+, Amersham Life Science, Amersham, UK) by Southern blotting and was UV crosslinked for 5 min. The blotted DNA was hybridized with a digoxigenin-labeled probe specific for telomeric sequences and incubated with antidigoxigenin-specific antibody coupled with alkaline phosphatase and incubated with alkaline phosphatase highly sensitive chemiluminescent substrate followed by exposure to autoradiography film. Interstitial repeats of the telomeric sequences have been found in the chromosomes all of the major classes of vertebrates, but there is substantial variation among orders and species (Meyne et al. 1990). Some birds, particularly ratites, have been found to have significant levels of such repeats of the telomeric sequence, whereas other groups, such as some birds of prey, appear to have none (Delany et al. 2000; Nanda et al. 2002). The situation for giant petrels is unknown. Because we used the standard TRF protocol, the DNA in our samples was denatured when blotted. It is therefore possible that such interstitial telomeric sequences, if they occur in giant petrels, were included in the TRF smear (Haussmann and Mauck 2008a). However, a clean DNA smear was observed in the majority (>95%) of samples, suggesting that interstitial banding was not a significant problem (see Figure 1). Autoradiography films were scanned, and intensity of TRF smears at different molecular sizes was

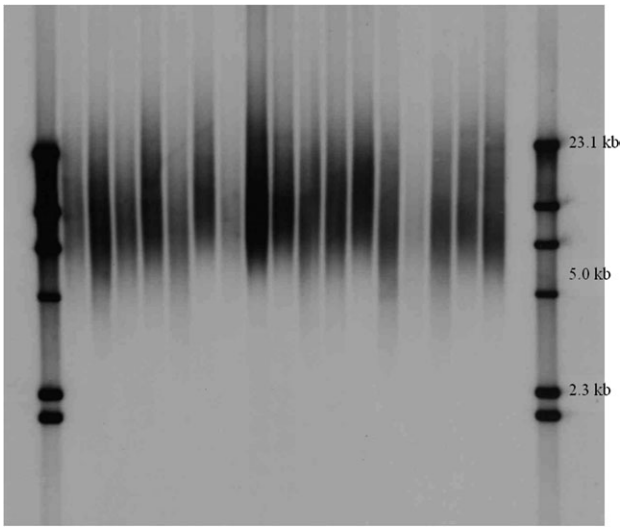

Figure 1
Representative TRF gel for southern giant petrels. Lanes 1 and 20 contain a size marker, lanes 2–18 contain a mixture of giant petrel adults and chicks (lane 19 is blank).

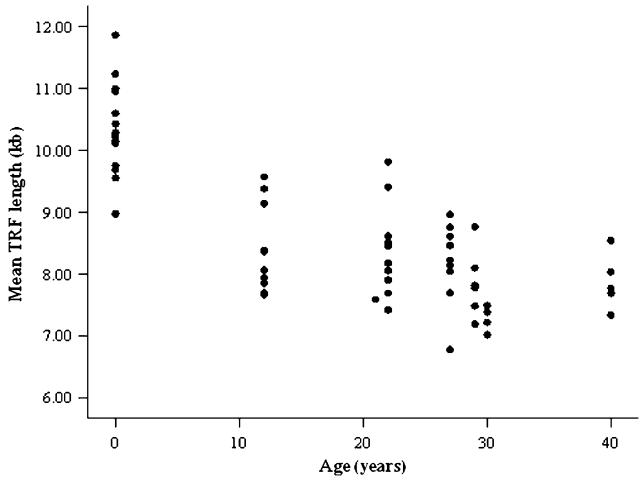

Figure 2
Southern giant petrel age in relation to individual mean TRF lengths ($n = 63$). There was no significant change in telomere length with age within the adult males or females (12–40 years old); see text for statistics.

calculated using TotalLab software (Photoretix). Briefly, each sample lane was overlaid with a grid ranging from 23 to 2.3 kb. The upper size limit was set to 23 kb because the agrose gel electrophoresis that we used does not resolve fragments greater than 23 kb. The lower size limit was set to 2.3 kb as no sample produced a smear containing telomere fragments shorter than this. For background subtraction, grid squares in each lane where no telomere-specific signal was detectable were used and subtracted from the grid squares containing telomere DNA; comparisons are lane specific. Several exposures of differing duration were produced for each blot, so if the signal in certain lanes was too weak in one exposure (as in lane 15 in Figure 1) a film from a longer exposure could be used for the analysis.

The mean TRF length was calculated using the formula: mean TRF length $= \sum(\mathrm{OD}_i)/\sum \mathrm{OD}_i/L_i$, where $\mathrm{OD_i}$ is signal intensity and L_i is DNA size (kb) at position i. The background intensity was subtracted from signal intensity before each calculation. All analyses were carried out blind with respect to age and sex.

Intragel repeatability is generally very high (e.g., see Criscuolo et al. 2009). However, given the number of samples, it was not possible to run them all on the same gel. The majority (50 of the 63) samples were each run on 2 different gels to control for intergel variability (we did not possess enough DNA to run the remaining 13 samples on 2 gels). The average of these 2 values was used in our analysis. Measurements of mean TRF length were highly repeatable between gels (mean difference = 0.33 ± 0.04 kb, equivalent of 3.82% of the average mean TRF length; repeatability analysis (as in Lessells and Boag 1987): $r = 0.945$, $F_{49,50} = 35.747$, $P < 0.001$).

Statistical analysis

Mean telomere length data were normally distributed. The relationship between mean telomere length, age, and sex was examined using general linear models (GLMs). The hatching date, and therefore age to the nearest day of chicks, was not known so they were all classified as being 0 years old. Because of the male bias in the oldest (age 40) of the sampled birds, we also compared the telomere length between the sexes across the age range within which there was a good sample of males and females (age 12–30 years). The relationship between telomere length and survival was examined in a binary logistic regression with backward elimination starting with the least significant variable to the minimum adequate model, with age, sex, and mean telomere length as independent variables and survival (i.e., if an individual was known to be alive or dead in the 2008/2009 breeding season) as the dependent variable. All means are quoted ±1 standard error. SPSS version 15.0 (IBM) was used for statistical analysis.

RESULTS

Southern giant petrels showed a substantial amount of interindividual variation in telomere length in both adults and chicks (Figures 2 and 3). Overall, adults had significantly shorter average telomere lengths than chicks, and males had shorter telomere lengths than females in both age classes (GLM with mean TRF as dependent variable, with age category [adult or chick] and sex as fixed factors: age effect, $F_{1,59} = 77.40$, $P < 0.0001$; sex effect, $F_{1,59} = 11.50$, $P = 0.001$; no significant interaction; Figure 3).

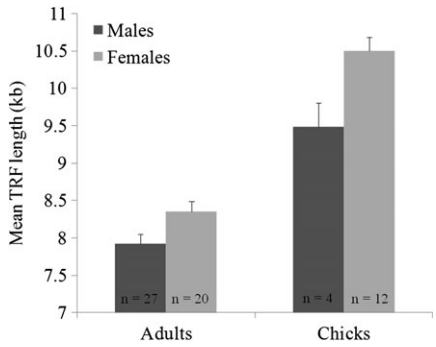

Figure 3
Telomere length in southern giant petrels, in terms of mean TRF length, separated by age (adult or chicks) and sex. Adults have significantly shorter mean TRF lengths than chicks, while for both age groups males have shorter mean TRF lengths than females. Error bars represent the standard error of the mean. See text for statistical comparisons.

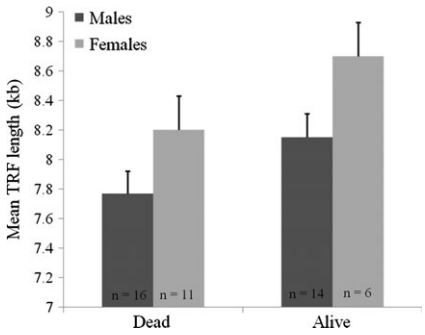

Figure 4
Average telomere length of male and female adult southern giant petrels sampled in 1999/2000 that were either alive or dead in the 2008/2009 breeding season. Error bars represent the standard error of the mean. See text for statistical comparisons.

We could not examine changes in telomere length with age within the chicks because their exact age at sampling was not known. Within the adult group, age in years was known for all individuals, allowing us to examine the extent to which telomere length changed with chronological age in adults. There was no relationship between age and telomere length in males or females (correlations between mean TRF and age: males $r = -0.16$, $P = 0.44$, $n = 27$; $r = -0.29$, $P = 0.22$, $n = 20$). Thus, the difference between the sexes does not appear to be a consequence of age differences in the sampled birds or a difference in the pattern of change with age in males and females. When age was included as a covariate in a GLM with sex as a fixed factor, it was not significant either when all adults were included ($P = 0.16$) or only those up to 30 years old (to avoid the male bias among the oldest birds $P = 0.20$) and was removed from the model; the sex difference was significant for both analytical groups ($P = 0.03$ in both cases).

Of the original 47 adults sampled, 30 (64%) had died by 2008/2009 (i.e., were absent in at least both the 2007/2008 and 2008/2009 breeding seasons); 70% of the females died over the period compared with 59% of the males; this was not a statistically significant difference. Figure 4 shows the average mean TRF length for individuals that were alive or dead by 2008/2009, separated by sex. Logistic regression showed that survival was linked to telomere length, with those that died during the 8-year period after sampling having significantly shorter telomere lengths on average at the time of measurement. Age was not related to survival and was eliminated from the model (Wald statistic 1.06, $P = 0.303$; no further variable removal caused any significant change in the model; final model telomere effect Wald statistic 4.33, $P = 0.037$, sex Wald statistic 1.92, $P = 0.165$; interactions not significant).

DISCUSSION

Adult southern giant petrels had shorter telomeres than chicks, but there was no detectable decline in telomere length with age among adults. However, it would be interesting to have samples from more older birds, particularly females given that we had only one female who was over 30 years old since the pattern of change in the very old birds could differ between the sexes. The absence of such a decline in telomere length with age among adults in this cross-sectional comparison is similar to the pattern found in other long-lived seabirds (e.g., wandering albatross *Diomedea exulans* and the European shag *Phalacrocorax aristotelis* Hall et al. 2004), although this pattern is not universal in birds, and declines with adult age in some species have been reported even in cross-sectional data (Haussmann et al. 2003; Juola et al. 2006). Our results do support the idea that most telomere loss occurs in young individuals, although we cannot say how much of this occurs prior to fledging and how much during the years after fledging before an individual returns to the breeding grounds. Note also that in a cross-sectional study such as this one, a lack of detectable telomere loss with age does not mean no such telomere loss is occurring. Small decreases in telomere lengths with age in adults could easily be obscured by the substantial amount of variation in telomere length between same age individuals. This is particularly true if individuals with longer telomeres have a better chance of surviving to older ages, as suggested in Leach's storm petrel (*Oceanodroma leucorhoa*; Haussmann and Mauck 2008b). Ideally, data on telomere loss should be collected longitudinally, enabling the telomere length of an individual to be followed throughout its life. In very long-lived species like the southern giant petrel, where individuals can probably live over 50 years, such data are very difficult to collect for obvious reasons.

In both adults and chicks, males had on average shorter telomeres than females. This is true in the adults even when we excluded the 40-year-old birds, which were male biased in our sample. To our knowledge, this is the first time such a sex difference has been seen in birds; however, males do have shorter telomeres than females in adult humans (Nawrot et al. 2004), rats (Cherif et al. 2003), pythons (Ujvari and Madsen 2009), and ants (Jemielity et al. 2007). Although there was a difference in the age of males and females in our sampled adults, the absence of any age-related changes in either sex suggest that the sex difference observed in chicks is consistent in adulthood. Sex differences could be related to sexual dimorphism in the pattern of growth between the sexes and/or to differences in circumstances in later life. Giant petrels show a considerable size difference between the sexes; indeed, they have been described as the "most sexually dimorphic of seabirds" (Croxall 1982; Hunter 1987). It is possible that this larger body size and the concomitantly faster chick growth rates could result in male giant petrels having shorter telomeres than females. However, European shags and wandering albatrosses also show a significant sexual size dimorphism, yet there appears to be no difference in telomere length between the sexes in these species (Hall et al. 2004). It is therefore possible that other differences in the lifestyles and energy expenditure of male and female giant petrels generate differences in exposure to oxidative stress and contribute to these differences. Males and females do differ in their foraging behavior during the breeding season; males forage more on land by scavenging, whereas females usually forage offshore (González-Solis et al. 2000a, 2002, 2007). Which of the 2 strategies might generate more oxidative stress is unknown, and little is known about their foraging behavior outside of the breeding season. However, that the sex difference was evident even in chicks suggests that it is more likely to be related to very early sex differences in growth or that initial telomere lengths differ between the sexes, but more data are needed because our sample of male chicks was small. Further studies of sex differences in telomere dynamics are clearly required, particularly in relation to growth patterns and to any sex differences in metabolism, senescence rates and life histories.

Irrespective of age, individuals with longer telomere lengths were more likely to have survived in the 8 years after sampling than individuals with shorter telomere lengths. Sex was not a significant predictor of survival in this sample. However, our sample size is not sufficient to examine sex differences in mortality rates in such a long-lived species. Telomere loss rate has also been found to be linked to survival prospects in alpine swifts and jackdaws (Bize et al. 2009; Salomons et al. 2009). However, estimating loss rate requires resampling of marked individuals over a significant time period. Its

usefulness is therefore restricted to species where resampling can take place over a time interval when changes would be expected to occur, which could be many years in long-lived species. We do not have data on telomere loss rates because our birds were sampled only once.

CONCLUSION

Evidence is accumulating that relative telomere length measured from red blood cell samples in birds can provide a useful indicator of future life expectancy in the wild, short telomere length presumably being indicative of generally poorer tissue and organ function. Our data on a wide age range of southern giant petrels also support the idea that telomere length is indicative of the biological state of individuals and that short telomere length is indicative of reduced survival prospects irrespective of chronological age. Our data also show that differences in average telomere length between the sexes can occur even from an early age, and more detailed studies are needed to find out what underlies this difference and how it links to growth and life-history strategies. Our study shows that, even in the absence of data on telomere loss rates, comparisons of telomere length within species can provide very useful information on biological state.

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