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Higher mercury contamination is associated with shorter telomeres in a long-lived seabird – A direct effect or a consequence of among-individual variation in phenotypic quality?

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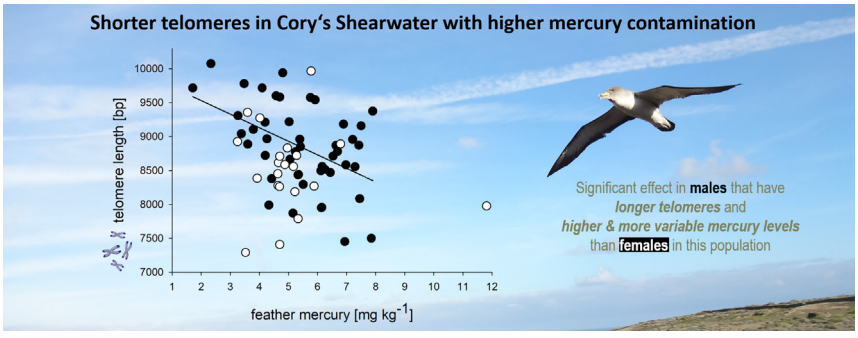
HIGHLIGHTS

- We investigated the relationship between mercury contamination and telomere length in the Cory's shearwater.
- Higher feather mercury concentration was associated with shorter telomeres, and this effect was stronger in males.
- Maleshad longer telomeres and higher, more variable mercury concentrations than females in this population.
- The telomere-mercury relationship could reflect a direct effect and/or have resulted from phenotypic quality differences.

GRAPHICAL ABSTRACT



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ABSTRACT

Mercury is a heavy metal, which is pervasive and persistent in the marine environment. It bioaccumulates within organisms and biomagnifies in the marine food chain. Due to its high toxicity, mercury contamination is a major concern for wildlife and human health. Telomere length is a biomarker of aging and health, because it predicts survival, making it a potential tool to investigate sublethal effects of mercury contamination. However, the relationship between telomeres and mercury contamination is unclear. We measured feather mercury concentration in Cory's Shearwaters *Calonectris borealis*, long-lived seabirds and top predators, between 9 and 35 years of age and related it to telomere length in erythrocytes. Cory's Shearwaters with higher mercury concentrations had shorter telomeres and the effect was sex-dependent, reaching significance in males only. This may be explained by the fact that males have longer telomeres and higher and more variable mercury concentrations than females in this population. The mercury effect on telomere length was stronger on longer telomeres in the genome within individuals. We discuss the hypotheses that the negative correlation could either be a direct effect of mercury on telomere shortening and/or a consequence of variation in phenotypic quality among individuals that results in a covariation between mercury contamination and telomere length.

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1. Introduction

Environmental pollution is a major threat to human and wildlife health (Harada, 1995; Dietz et al., 2019). Some chemical pollutants are accumulated via the food chain, bioaccumulating in organisms and biomagnifying with increasing trophic level (Driscoll et al., 2013; Dietz et al., 2019). Top predators such as pelagic seabirds and humans are therefore susceptible to high pollutant contamination due to their position in the marine food chain and their longevity. Among chemical pollutants, mercury is a heavy metal of high toxicity with long-lasting and globally widespread effects (Bjørklund et al., 2017; UN Environment, 2019). In the environment, mainly in reducing zones such as in freshwater, coastal environments, and the subsurface ocean, elemental mercury is transformed into methylmercury and enters the food chain mainly in this form (Driscoll et al., 2013). Mercury contamination in bird species has been widely studied (Burger and Gochfeld, 2004; Becker et al., 2016; Albert et al., 2021), but there is a surprising paucity of robust studies on its effects on health and population demography in the wild (Seewagen, 2010; Tartu et al., 2013; Fort et al., 2014; Goutte et al., 2014, 2015; Carravieri et al., 2018). Potential toxic effects of mercury contamination on health in wild animals are challenging to identify, since species, populations and individuals differ in exposure risk and sensitivity to detrimental effects (Dietz et al., 2013; UN Environment, 2019).

Telomere length and telomere dynamics (i.e. variation in length over time) are potential biomarkers of pollution effects on health. Telomeres are evolutionarily conserved nucleoprotein structures at the chromosome ends that function in genome integrity and chromosome stability (O'Sullivan and Karlseder, 2010). There is growing evidence across taxa that a shorter telomere length is associated with poorer health (Aviv and Shay, 2018) and lower survival probability (meta-analyses: wild vertebrates: Wilbourn et al., 2018, humans: Boonekamp et al., 2013). Telomere length generally shortens with age, but varies strongly between individuals of the same age (Sabharwal et al., 2018; Remot et al., 2021). Sources of this variation are inherited differences in telomere length (reviewed in Bauch et al., 2021) and variation in telomere shortening during cell replication, which can be enhanced by DNA- and protein-damaging factors or counteracted by maintenance mechanisms (Chan and Blackburn, 2004). When telomeres reach a critically short length, the cell undergoes replicative senescence or apoptosis (Chan and Blackburn, 2004). Longer telomeres, on the other hand, could be a larger target for damaging factors (Grasman et al., 2011). Therefore, it is not only the individual's average telomere length, but also the telomere length variability within the genome that is of relevance for a better understanding of telomere length as a biomarker and its role in senescence.

Mercury contamination may affect telomere dynamics directly, given that toxic mercury effects increase DNA damage and oxidative stress (Rice et al., 2014; Whitney and Cristol, 2017), which in turn has been shown to result in higher telomere shortening in vitro (von Zglinicki, 2003). In vivo, the relationship between mercury and oxidative stress (and ultimately telomere dynamics) may additionally be amplified by interactions with environmentally influenced physical condition, life stage or sex, affecting the susceptibility to toxic effects (Costantini et al., 2014; Bustnes et al., 2015). Thus, a short telomere length could be a direct consequence of high mercury exposure. However, when making inferences from mercury-telomere associations in observational data the possibility needs to be taken into account that there may be a third factor affecting both mercury levels and telomeres that explains the observed association and such a factor may be phenotypic quality.

Whether telomere length and telomere dynamics relate to mercury concentration has rarely been assessed and current evidence for such an association is weak at best. No association between blood mercury concentrations and relative telomere length was detectable in the Black guillemot *Cepphus grylle*, but this species accumulates low mercury concentrations (0.3 mg/kg; Eckbo et al., 2019). Similarly, in human children and their mothers, blood mercury concentrations were unrelated to relative telomere length and in children also unrelated to telomere shortening (Yeates et al., 2017). In nestlings of the Red Kite *Milvus milvus,* blood mercury concentrations did not directly relate to telomere length, but to higher concentrations of corticosterone (a metabolic hormone) in the feathers, which was at the same time negatively associated with relative telomere length, suggesting the possibility of an indirect effect of mercury on telomere length (Powolny et al., 2020).

We investigated the relationship between mercury contamination and telomere length in Cory's Shearwaters *Calonectris borealis*, long-lived, pelagic seabirds, which are top predators in the marine environment and thus, at risk of high mercury contamination. Telomere length was measured in erythrocytes using high precision telomere restriction fragment analysis (Nussey et al., 2014), which provides information on average telomere length and the intra-individual telomere length distribution within the genome (Bauch et al., 2014; Pineda-Pampliega et al., 2019). Mercury concentration was measured in secondary 8 flight feathers, which is an integrated measure of contamination accumulated over the period of feather growth (Gatt et al., 2021a). Specifically, our aims were to test (1) whether mercury concentration is related to telomere length; (2) whether the association between mercury concentration and telomere length depends on sex or age; (3) whether the relationship between mercury concentration and telomere length is intra-individually differentially detectable in short and long telomeres. We predicted the following: (1) A shorter telomere length in individuals with higher mercury contamination, if mercury negatively affects telomere length. (2a) A sex-specific relationship between telomere length and mercury, based on our findings that phenotypic quality, i.e. long-term reproductive success, was negatively associated with telomere length in males and positively associated with telomere length in females (Bauch et al., 2020), that males in this population display higher telomere shortening (Bauch et al., 2020) and have higher mercury contamination (Gatt et al., 2020). (2b) A negative age-specific effect of mercury concentration on telomere length, if mercury accumulates in the body with increasing age and leads to negative long-term effects. (3) Since longer telomeres could present a larger target for damaging effects (Grasman et al., 2011), we expect a stronger effect on the longest telomeres within individuals and a decreased variability in telomere lengths within the genome in individuals with higher mercury contamination.

2. Material & methods

2.1. Study species

The Cory's Shearwater *Calonectris borealis* is a long-lived, pelagic seabird species from the order Procellariiformes. Cory's Shearwaters are marine top predators and transequatorial migrants, except for ca. a fifth of males that remains predominantly resident year-round, with a wide winter distribution, including the Benguela and Agulhas currents, central South Atlantic, Brazilian current and northwest Atlantic (Dias et al., 2011). Our study individuals belong to a population breeding on Selvagem Grande (30°09′ N, 15°52′W), the main island within a nature reserve located ca. 300 km south of the Madeiran archipelago of Portugal. This population is the subject of a long-term study, where birds were ringed with numbered metal rings since 1978 (Campioni et al., 2016; Mougin et al., 2000). The dataset contains birds aged between 9 and 35 years in 2017 (average age ± SD: males: 18.0 ± 5.6 years, $n = 46$; females: 19.3 ± 4.6 years, $n = 21$). Thirty percent of the birds included in this study were ringed as chicks and hence their exact age was known (average age ± SD = 18.8 ± 8.7 years, $n = 18$ males and 2 females). The remainder of birds was ringed as adults and presumed to be first-time breeders when first captured, as breeding birds are highly philopatric (Mougin et al., 1999) and birds that occupy nests (successful and unsuccessful breeding attempts) have been identified systematically in our study area. Therefore, an age of 9 years was assigned to these birds at ringing, as 8.9 (±1.7) years is the average (±SD) age of recruitment in this colony for both sexes (Mougin et al., 2000). We previously found that telomere length declines significantly with age in males and remains relatively stable in females of this population (Bauch

et al., 2020). A detailed analysis confirmed that the above age assumption did not bias the age effects found for telomere length (Bauch et al., 2020). The sexes are dimorphic with males being on average larger in all available morphological characteristics (Granadeiro, 1993). Study birds were sexed with high accuracy (>99%) by a combination of three methods and their cross-validation: a discriminant function based on bill measurements (Granadeiro, 1993), vocalisations (Thibault et al., 1997) and a cross-validation of the sexes of breeding partners.

2.2. Feather collection & mercury analysis

In 2017, 2 cm of the tips of the secondary 8 flight feather from both wings were sampled. These specific feathers are postulated to moult or regrow while the birds are in the non-breeding area and after many other flight feathers have already moulted (Ramos et al., 2009), reflecting accumulated mercury birds are exposed to in the non-breeding area (Gatt et al., 2021a). Mercury concentration in homogenised feather samples was quantified by thermal decomposition atomic absorption spectrometry with gold amalgamation using an AMA-254 spectrophotometer (LECO, Czech Republic), as described by Costley et al. (2000). This procedure does not require sample pre-treatment or sample pre-concentration. Accuracy and precision were assured by regular analysis of certified reference material SRM2976, obtained from the National Research Council of Canada, throughout each day of analyses. The mercury recovery rates ranged between 80% and 100% and sample mercury concentrations were corrected for the daily recovery percentage of the reference material. The lower limit of detection was 0.2 mg/kg (dry weight). All samples were measured in duplicate, or until obtaining two readings with a coefficient of variation under 10%, and their average used in all statistical tests.

2.3. Blood sampling & telomere length measurement

Adult birds were blood sampled for telomere length analysis by puncturing the *vena brachialis*. Samples were collected between June and July 2017 during incubation. Telomere length in the blood has been shown to be an adequate surrogate for telomere length in the whole avian organism (Reichert et al., 2013). Samples were first stored in 2% EDTA buffer at 4–7 °C and then snap frozen in 40% glycerol buffer for permanent storage at −80 °C within 4 weeks of collection. We measured the terminally located telomere sequence length, using telomere restriction fragment analysis without DNA denaturation. First, we removed the glycerol buffer, washed the cells and isolated DNA from 5 μl of erythrocytes using CHEF Genomic DNA Plug kit for preparation of intact, chromosome-sized DNA (Bio-Rad, Hercules, CA, USA). Cells in the agarose plugs were digested overnight with Proteinase K at 50 °C. Isolated DNA (half of the plug per sample) was restricted overnight simultaneously with *Hind*III (60 U), *Hinf*I (30 U) and *Msp*I (60 U) in NEB2 buffer (New England Biolabs Inc., Beverly, MA, USA) at 37 °C. Subsequently, the restricted DNA was separated by pulsed-field gel electrophoresis in a 0.8% agarose gel (Pulsed Field Certified Agarose, Bio-Rad) at 14 °C for 24 h at 3.5 V/cm, initial switch time 0.5 s, final switch time 7.0 s. For size calibration ^{32}P-labelled size markers (1 kb DNA ladder, New England Biolabs Inc.; DNA Molecular Weight Marker XV, Roche Diagnostics, Basel, Switzerland) were added. Subsequently, gels were dried (gel dryer, Bio-Rad, model 538) at room temperature and hybridised overnight at 37 °C with ^{32}P-labelled oligonucleotides (5'-CCCT AA-3')$_4$ that bind to the single-strand overhang of telomeres of non-denatured DNA. Unbound oligonucleotides were removed by washing the gel for 30 min at 37 °C with 0.25x saline-sodium citrate buffer. The radioactive signal of the sample specific telomere length distribution was detected by a phosphor screen (MS, Perkin-Elmer Inc., Waltham, MA, USA), exposed for ~20 h, and visualised using a phosphor imager (Cyclone Storage Phosphor System, Perkin-Elmer Inc.). Telomere length was calculated using ImageJ (v. 1.38x). Every sample contains an individual-specific telomere length distribution as telomere length differs between chromosomes within cells and between cells of different age (Fig. S1). For each sample the limits including the entire telomere distribution was lane-specifically set at the point of the lowest signal (i.e. background intensity). We calculated the individual average of the telomere length distribution (referred to as 'telomere length' throughout the text, as this is the most commonly used measure in the literature). Additionally, since telomere shortening rates may differ between chromosomes with shorter or longer telomeres, which would consequently affect the telomere length distribution, we calculated the telomere length of every 10th percentile, i.e. sets of different telomere lengths within individuals (10th < 90th percentile; Fig. S2; Grasman et al., 2011; Bauch et al., 2014). We analysed telomere length for a larger dataset of individuals than mercury concentration. Therefore, samples were run on 14 gels. Sexes and ages were randomised over all gels. Also, individuals whereof feather mercury was measured were on all gels. Within-individual repeatability for telomere length of five individuals sampled repeatedly in 2018 (sampling interval between 21 and 38 days) and analysed on the same gel and together with samples from 2017 was 89.9% (calculated following Lessells and Boag, 1987; Bauch et al., 2020). The coefficient of variation of one control sample of one randomly chosen Cory's Shearwater run on all gels was 2.49%. Gel as a random effect was non-significant for the entire telomere length dataset and therefore not included in the final models presented here.

2.4. Statistics

For data exploration, we first ran ANOVAs to test for differences between the sexes in telomere length and mercury concentration. Telomere length and mercury concentrations were normally distributed, the latter after excluding one outlier (a female with particularly high feather mercury). As we have no reason to believe that the value was due to measurement error, we kept this datapoint in the following analyses. The outlier did not change the direction of the results in the following analyses. Residuals in all the following models fulfilled normality assumptions.

We ran a linear model to investigate the relationship between mercury concentration and telomere length, with telomere length as the dependent variable and mercury concentration as covariate. Age was also included as covariate, since telomere length shortens with age, as was the factor 'sex', since males have longer telomeres than females in this population (Bauch et al., 2020). We tested for an age-specific relationship between mercury concentration and telomere length by including the interaction between mercury concentration and age in the model. We tested whether the relationship between telomere length and mercury concentration is sex-specific by including the interaction mercury and sex. We consequently ran the model separately for the two sexes with telomere length as dependent variable and mercury concentration and age as covariates.

Telomere length varies within individuals due to variation in telomere length between chromosomes and erythrocytes of different ages. It is possible that the effect of mercury on telomeres depends on the length of the telomeres on the chromosomes (e.g. longer telomeres could be a stochastically larger target for damage (Grasman et al., 2011)). Therefore, in addition to testing the association between mercury and the average telomere length of each individual, we subdivided the intra-individual telomere length distribution into percentiles (10th < 90th, shortest to longest telomeres) and tested if the association differs depending on the telomere length within individuals. We treated the telomere length measure as the dependent variable and ran the model with percentile, age and mercury concentration as covariates, sex as factor and bird identity as random effect. We added the interactions between sex and mercury concentration and the interaction between percentile and mercury concentration to test if the telomere-mercury association is affected by telomere length. A three-way interaction between percentile*mercury concentration*sex was included in the model to test if a potential telomere length dependent effect of mercury concentration is sex-specific. To assess if the telomere length distribution relates to mercury concentration, we ran a model with telomere length range between percentiles 10 and 90 as dependent variable and mercury concentration and age as covariates and sex as factor.

Variables 'mercury concentration', 'sex' and 'percentile' were mean-centred in all models to improve the interpretability of regression

coefficients of main effects when interactions are included (Schielzeth, 2010). Statistical analyses were carried out on R (version 4.0.3. R Core Team, 2020) using the packages LME4 (Bates et al., 2015), LMERTEST (Kuznetsova et al., 2017) and OLSRR (Hebbali and Hebbali, 2017).

3. Results

3.1. Mercury concentration and telomere length compared between the sexes

Mercury concentrations averaged (±SD) 5.45 ± 1.48 mg/kg (n = 46) in males and 5.12 ± 1.75 mg/kg in females (n = 21) or 4.78 ± 0.86 (n = 20) after removal of one outlier with 11.8 mg/kg (Fig. 1a). Thus, males tended to have higher mercury concentrations than females (F = 3.57, p = 0.06, n = 66) and show higher variability in mercury concentrations (coefficient of variation: males: 0.272, females: 0.180, *Bartlett test*: F = 6.61, p = 0.01, n = 66). Telomere length was significantly longer in males (8841 ± 624 bp, n = 46) than in females (8511 ± 623 bp, n = 21; F = 4.04, p = 0.049, n = 67) with a similar coefficient of variation at 0.071 and 0.073, respectively. The within-individual telomere length distribution (from the shortest to the longest telomere length in a sample, Fig. S1) in males ranged from 2301 ± 227 bp to 21,195 ± 1909 bp (range: 18895 bp) and in females from 2169 ± 207 bp to 20,933 ± 2149 bp (range: 18,764 bp).

3.2. Mercury concentration in relation to telomere length

Individuals with higher mercury concentrations had a significantly shorter telomere length. However, this effect was sex-specific (Table 1a, Fig. 1a), and subsequent analyses showed the effect to be significant in males (Table 1b), but not in females (Table 1c). The interaction between age and mercury concentration added to the model in Table 1a, testing whether the effect of mercury is age-dependent on the population level, was non-significant (estimate ± SE = -0.5 ± 8.2 bp, t = −0.07, p = 0.95), independent of sex (males: estimate ± SE = 9.4 ± 10.8 bp, t = 0.87, p = 0.390; females: estimate ± SE = -13.9 ± 12.9 bp, t = −1.08, p = 0.296).

3.3. Mercury concentration in relation to telomere length within individuals

When we repeated the analysis using different percentiles of the individual telomere length distribution, longer telomeres within individuals (higher percentiles of the individual telomere length distribution) were more negatively related to mercury concentrations than shorter telomeres as reflected by a significant interaction between mercury concentration*percentile (estimate ± SE = -17.8 ± 8.7 bp, t = −2.06, p = 0.04; Table 2), independent of sex (mercury concentration*percentile*sex: estimate ± SE = 6.5 ± 14.0 bp t = 0.46, p = 0.64; Fig. 1b). In line with this finding, the range of the telomere distribution between percentiles 10 and 90 tended to be smaller in

Table 1
Linear model results on the relationship of mercury concentrations in feathers (mg/kg) and telomere length in the blood (bp) in adult Cory's Shearwaters. **a)** Testing for sex-differences in the relationship between mercury level and telomere length. The variables sex and mercury were mean centered for interpretability of main effects. (n = 67 individuals) **b)** Males (n = 46) **c)** Females (n = 21). See also Fig. 1a.

	Model terms	Estimate	Std. error	t	p
a)	*Intercept*	9299.8	270.4	34.40	<0.001
	Age	−24.3	14.2	−1.71	0.093
	Sex (females)	−318.4	153.7	−2.07	0.042
	Mercury	−204.9	57.6	−3.56	<0.001
	Mercury*sex	210.3	98.2	2.14	0.036
b)	*Intercept*	10,547.5	403.6	26.14	<0.001
	Age	−32.2	14.0	−2.30	0.027
	Mercury	−206.5	53.5	−3.86	<0.001
c)	*Intercept*	8387.7	618.8	13.56	<0.001
	Age	37.3	47.2	0.79	0.44
	Mercury	−116.9	124.5	−0.94	0.36

Table 2
Linear model result on the relationship of mercury concentrations (mg/kg) and different parts of the within-individual telomere length distribution (percentiles: 10th < 90th; bp) in adult Cory's Shearwaters (n = 67). The variables percentile, sex and mercury were mean centered for interpretability of main effects. See also Fig. 1b.

Model terms	Estimate	Std. error	t	p
Intercept	9051.8	264.4	34.24	<0.001
Age	−24.4	13.9	−1.75	0.085
Percentile	1150.2	12.7	90.3	<0.001
Sex (females)	−324.4	150.3	−2.16	0.035
Mercury	−207.9	56.3	−3.69	<0.001
Mercury*percentile	−17.8	8.7	−2.06	0.040
Mercury*sex	218.1	96.0	2.27	0.027
Percentile*sex	−3.3	22.9	−0.14	0.886
Mercury*percentile*sex	6.5	14.0	0.46	0.643

Variance explained by the random effect bird ID: 37.1%, residual variance: 62.9%.

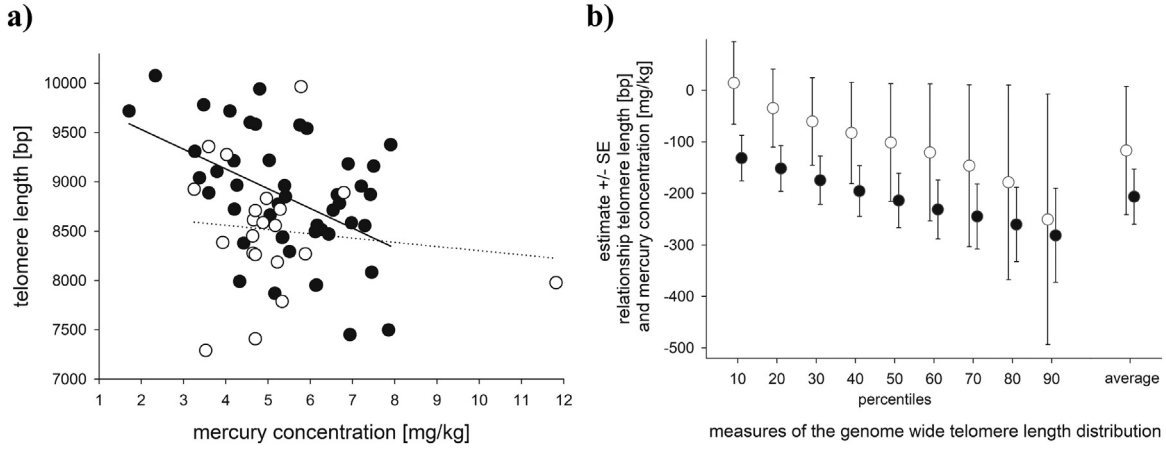

Fig. 1. a) Telomere length in relation to mercury concentration in males (black dots, continuous line) and females (white dots, dotted line, n.s.). b) The coefficient (±SE) of the relationship between mercury concentration and telomere length for different percentiles of the telomere length distribution of each sample. Also shown is the coefficient for the sample specific average telomere length – note these are the coefficients of the regression lines in panel a. For statistics see Tables 1 & 2.

individuals with higher mercury concentration (estimate ± SE = -134.2 ± 73.6 bp, $t = -1.82$, $p = 0.073$), independent of age (estimate ± SE = -11.6 ± 22.0 bp, $t = -0.53$, $p = 0.60$) or sex (estimate ± SE = -49.6 ± 249.4 bp, $t = -0.20$, $p = 0.84$).

4. Discussion

Our results expose a negative correlation between mercury contamination and telomere length in a seabird and marine top predator. The effect was sex-specific in our study population. Male Cory's Shearwaters with higher mercury concentrations had shorter telomere lengths, while there was a non-significant trend in females. Males in this population had longer telomere lengths on average and higher and more variable feather mercury concentrations than females, which likely explains the sex-specific pattern. Feather (S8) mercury concentrations reflect mercury exposure in the non-breeding areas, where feathers are moulted, and a higher variation in mercury exposure in males is in agreement with their greater diversity of non-breeding destinations as compared to females (Gatt et al., 2020). The higher mercury concentrations in males may be explained by their larger body size and associated higher bioaccumulation potential or higher trophic levels (De Felipe et al., 2019; Mills et al., 2022). We have shown previously, that in Cory's shearwater telomeres shortened more in males compared to females (Bauch et al., 2020). If longer telomeres are larger targets for DNA-damaging factors, as suggested by Grasman et al. (2011), and tend to shorten more than shorter telomeres, as shown within individual storks (*Ciconia ciconia*, Pineda-Pampliega et al., 2019), this would further contribute to the stronger effect in males. It is supported by our finding that longer telomeres within individuals (higher percentiles) declined more strongly in length with increasing mercury concentration than the lower percentiles. This could have led to the tendency for the range of telomere lengths to be smaller within individuals with higher mercury concentration.

We found no evidence of a long-term effect of mercury concentration on telomere length with increasing age in our study individuals, as reflected in the non-significant interaction between mercury concentration and age. It has also been shown in several bird species that the current mercury concentration detected in feathers is independent of age (Becker et al., 2002). The ability of birds to excrete a large part of the ingested mercury via their feathers (Furness et al., 1986) may protect them from (long-lasting) consequences on telomeres. Furthermore, in long-lived birds, such as Cory's Shearwaters, somatic maintenance is expected to be prioritized (Gatt et al., 2021b; Ricklefs and Wikelski, 2002) and accordingly, their telomere shortening is comparatively low (Sudyka et al., 2016; Bauch et al., 2020).

The relationship between (short) telomere length and (high) mercury concentration is not necessarily caused by an accelerating effect of mercury on telomere shortening. Instead, telomere length and telomere dynamics may be two different traits (Benetos et al., 2013; Martens et al., 2021; Bauch et al., 2021). The variation in telomere length among Cory's shearwater males is large (SD 624 bp) and individual differences in telomere length are highly consistent between years ($r = 0.90$; Bauch et al., 2020). We hypothesize that the relationship between telomere length and mercury concentration could also result from heterogeneity in phenotypic quality among males. Telomere length has been shown to relate to multiple components of phenotypic quality, specifically to foraging effort and reproductive success (Bauch et al., 2013, 2016; Le Vaillant et al., 2015; Young et al., 2015; Angelier et al., 2019). In our population males with higher long-term reproductive success had shorter telomeres (Bauch et al., 2020). On the other hand, mercury contamination was higher in individuals within populations that occupy a higher trophic level (Carravieri et al., 2018; Gatt et al., 2020) and dependent on migratory strategy (Gatt et al., 2020). Thus, telomere length and mercury contamination may covary if they are both determined by intrinsic factors that impact where individuals forage and their reproductive success. In this scenario, negative effects of mercury on telomere dynamics would be more difficult to detect, as they could be masked by heterogeneity in phenotypic quality. Additional studies are needed to gain a more comprehensive picture on what causes the relationship between mercury contamination and telomere length. Independent of whether the shorter telomere length in males is a consequence of higher telomere shortening or resulting from a covariance of phenotypic quality traits, the correlation between telomere length and mercury contamination is of interest and relevance for potential effects on population demographics, since telomere length has been shown to relate to survival probability (Wilbourn et al., 2018). Note also that this scenario may apply more generally to the many pollutants to which seabirds or top predators are exposed, or that an accumulation of different pollutants could amplify the effect. For mercury as for other environmental pollutants, telomeres are promising biomarkers for contamination effects (seabirds: Blévin et al., 2016; Blévin et al., 2017; this study; reviewed across taxa in Salmón and Burraco, 2022).

Since mercury is highly persistent in the environment and effects of climate change have been suggested to increase hazardous methylmercury levels, mercury pollution can be expected to remain of high concern in the future (Stern et al., 2012; Provencher et al., 2014; Schartup et al., 2019), particular in interaction with degrading environmental conditions, which could exacerbate toxic effects (Bustnes et al., 2015).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Credit authorship contribution statement

Conceptualization of this study by CB and of the long-term project by PC, JPG; Funding acquisition by PC, JPG; Project administration and resources by PC, JPG, SV; Field work by MCG; Telomere analysis by CB; Data analysis by CB; Writing original draft by CB, review & editing by all authors.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.156359.

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