



Effects of persistent organic pollutants on telomere dynamics are sex and age-specific in a wild long-lived bird

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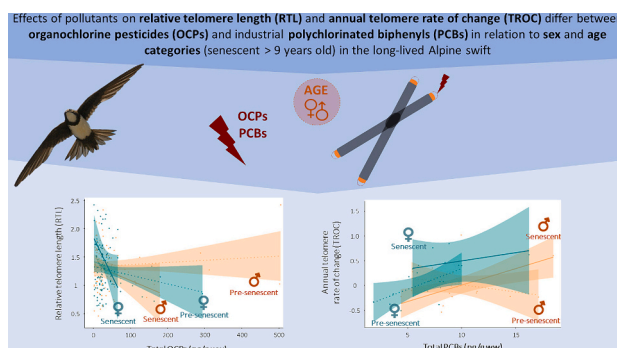
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HIGHLIGHTS

- POPs effects on Alpine swift telomeres accounting for senescence status and sex.
- Senescent females presented longer RTL and elongated telomeres over time.
- OCPs negatively associated with RTL, particularly in senescent females.
- PCBs led to slower rates of telomere shortening, especially in females.
- Life-history traits (sex & age) are required to disentangle POPs effects on wildlife.

GRAPHICAL ABSTRACT



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ABSTRACT

Chemical pollution is a major man-made environmental threat to ecosystems and natural animal populations. Of concern are persistent organic pollutants (POPs), which can persist in the environment for many years. While bioaccumulating throughout the lives of wild animals, POPs can affect their health, reproduction, and survival. However, measuring long-term effects of POPs in wild populations is challenging, and therefore appropriate biomarkers are required in wildlife ecotoxicology. One potential target is telomere length, since telomere preservation has been associated to survival and longevity, and stressors as chemical pollution can disrupt its maintenance. Here, we investigated the effects of different classes of POPs on relative telomere length (RTL) and its rate of change (TROC) in wild long-lived Alpine swifts (*Tachymarpis melba*). As both RTL and TROC are often reported to differ between sexes and with chronological age, we tested for sex- and age-specific (pre-senescent vs. senescent, ≥ 9 age of years, individuals) effects of POPs. Our results showed that senescent females presented longer RTL and elongated telomeres over time compared to pre-senescent females and males. These sex- and age-related differences in RTL and TROC were influenced by POPs, but differently depending on whether they were

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organochlorine pesticides (OCPs) or industrial polychlorinated biphenyls (PCBs). OCPs (particularly dioxins) were negatively associated with RTL, with the strongest negative effects being found in senescent females. Conversely, PCBs led to slower rates of telomere shortening, especially in females. Our study indicates diametrically opposed effects of OCPs on RTL and PCBs on TROC, and these effects were more pronounced in females and senescent individuals. The mechanisms behind these effects (e.g., increased oxidative stress by OCPs; upregulation of telomerase activity by PCBs) remain unknown. Our results highlight the importance in wildlife ecotoxicology to account for sex- and age-related effects when investigating the health effects of pollutants on biomarkers such as telomeres.

1. Introduction

Chemical pollution is one of the major environmental alterations imposed by humans on natural ecosystems (Bauerová et al., 2017; Goulson, 2013; Landrigan et al., 2018; Sigmund et al., 2023). A major threat comes from persistent organic pollutants (POPs), which branch off into organochlorine pesticides (OCPs) and industrial contaminants, such as polychlorinated biphenyls (PCBs) and poly- and perfluoroalkyl compounds (PFAS). POPs can persist from years to centuries after their release into the environment, earning them the nickname of ‘forever chemicals’, and pose risks to human and wildlife health. Because POPs are lipophilic, they can easily accumulate in organisms throughout their lives (i.e., bioaccumulation) and increase in concentration at each successive stage of the food chain (i.e., biomagnification). POPs can exert a wide range of consequences on metabolism, even at low concentrations, by interfering, for example, with endocrine, immune, and neural functioning (Acosta-Tlapalamatl et al., 2022; González-Mille et al., 2019; Hao et al., 2021; Letcher et al., 2010). POPs disrupt individuals’ homeostatic state and health, which can occur during critical life-history periods (e.g., growth, breeding, or wintering) and their associated performances (i.e., senescence onset and rate). Therefore, consequences on the reproductive success and survival of individuals and, ultimately, on population dynamics are expected (Annunziato and Cooper, 2018; Aulsebrook et al., 2020; Bursian et al., 2013; Bustnes et al., 2003; but see Lister et al., 2016 as an example of a compensatory mechanism, a resilient offspring). However, measuring the fitness consequences of POPs in wild populations is challenging, and there is a need in wildlife ecotoxicology to develop appropriate biomarkers. Good biomarkers should be easy, accurate, and reproducible, to measure and help predict fitness in the wild (Strimbu and Tavel, 2010). In this context, there is growing interest in using telomeres to study the consequences of POPs in natural populations (Blévin et al., 2017, 2016; Eckbo et al., 2019; Hansen et al., 2022; Louzon et al., 2019; Salmón and Burraco, 2022; Sebastiano et al., 2020; Sletten et al., 2016).

Telomeres are repeated non-coding DNA sequences that protect the end of eukaryotic chromosomes. Telomere preservation plays a key role in the maintenance of cell replication potential and organismal life-expectancy because they shorten with age during normal DNA replication in somatic cells or in response to stress (Kotrschal et al., 2007; Monaghan and Haussmann, 2006), and induce cell senescence when reaching a lower threshold of telomere length (Blackburn, 2000, 1991; Blasco, 2007). Thus, both telomere length per se (i.e., the shortest telomere length within a cell; Xu et al., 2013) or the telomere rate of erosion have been found to be associated with lifespan or survival in birds, both at the species or individual level (Bize et al., 2009; Boonekamp et al., 2014; Eastwood et al., 2019; Haussmann et al., 2005; Salmons et al., 2009; Sheldon et al., 2022; Tricola et al., 2018). As relationships between telomere length and fitness associated traits have been underlined previously (e.g., body size, offspring productivity, stress status), telomeres have been suggested as a marker of individual quality (Angelier et al., 2019; Viblanc et al., 2020). Senescence patterns and/or lifespan differ between sexes in some species, and telomeres have therefore been considered to have a mechanistic role behind such sex-biased longevity depending on the life-history of each species (Barrett and Richardson, 2011; Bauch et al., 2020; Dantzer and Garratt, 2017;

Domínguez-de-Barros et al., 2023; but see Remot et al., 2020). The measurement of telomeres is attractive for wildlife studies because of its accurate and reproducible outcome with minimally-invasive sampling at the organismal level (e.g., blood, buccal swabs, or feathers; Salmón and Burraco, 2022). Telomerase is the cellular enzyme that allows partial compensation for telomere shortening by adding new telomeric sequences onto the ends of chromosomes (Rubtsova et al., 2012). If telomerase may be transiently activated after a stressful event to elongate primarily the shortest telomere ends (Hemann et al., 2001), it may make telomeres a dynamic structure, shortening and elongating with time over the lifetime of individuals (Criscuolo et al., 2020; Fairlie et al., 2016; Hares et al., 2018; Haussmann et al., 2003; Pepke et al., 2023; Svenson et al., 2011; Tricola et al., 2018).

Telomeres are of particular interest to wildlife ecotoxicologists because, as well as varying with age and between sexes, they also respond to a wide range of stressors (Bauch et al., 2020; Chatelain et al., 2020; Lin and Epel, 2022). Among them, environmental pollution has been shown to disrupt telomere length (or relative telomere length, RTL; Cawthon, 2002) and the telomere rate of change (TROC) over time (Bauch et al., 2022; Louzon et al., 2019; Miri et al., 2019; Salmón and Burraco, 2022). There has been little research into the effects of contaminants on wildlife telomeres in recent decades when compared to other stressors, but interest has strongly increased in recent years (Salmón and Burraco, 2022). In this regard, birds are currently one of the best studied groups (Salmón and Burraco, 2022), with research focusing on both organic (Blévin et al., 2017, 2016; Eckbo et al., 2019; Hansen et al., 2022; Sebastiano et al., 2020; Sletten et al., 2016) and inorganic (Bauch et al., 2022; Eckbo et al., 2019; Grunst et al., 2020; Powolny et al., 2020; Sánchez-Virosta et al., 2020; Saulnier et al., 2020; Stauffer et al., 2017) pollutants. Regarding organic contaminants, ecotoxicologists have studied the impact of POPs on the telomeres of nestlings (Hansen et al., 2022; Sletten et al., 2016) and adults (Blévin et al., 2017, 2016; Eckbo et al., 2019; Sebastiano et al., 2020) of top bird predators. However, current knowledge remains limited, and the conclusions tend to be contradictory and inconclusive. For instance, in adults of black-legged kittiwake (*Rissa tridactyla*), oxychlordane is negatively associated with absolute telomere length in females but not in males (Blévin et al., 2016). Similar results were found for pesticides (including chlordanes) and additional POPs measured in Mandt’s Black guillemot (*Cephus grylle mandtii*) but with a limited sample size ($n = 11$) and low contaminant concentrations (Eckbo et al., 2019). A follow-up study in the same population of adults measured in Blévin et al. (2016) showed no association with absolute telomere length in PFAS (Blévin et al., 2017), yet the most highly exposed individuals showed the slowest rate of telomere shortening (or even elongated telomeres) regardless of sex (Blévin et al., 2017). Similar positive effects of PFAS on TROC were found in adults of a related species, the glaucous gull (*Larus hyperboreus*; Sebastiano et al., 2020). Other studies reported no relationship between, for instance, telomeres and POPs in nestlings of the white-tailed eagle (*Haliaeetus albicilla*; Sletten et al., 2016) even after studying large samples sizes ($n = 152$) over a period of 19 years (Hansen et al., 2022), and in adults of Mandt’s Black guillemots for specific POPs categories such as PCBs or PFAS (Eckbo et al., 2019). Although age is one of the most important factors that can contribute to the variation of RTL, we still lack a clear evaluation of how TROC varies with age, age-related

performances (senescence) and how pollutants may alter these relationships among age, senescence, RTL and TROC.

To better understand these differences between species and types of pollutant, we investigated the consequences of exposure to POPs on RTL and TROC in a long-term (>20 years) monitored population of a long-lived bird, the Alpine swift (*Tachymarptis melba*). Previous studies in this Swiss population of Alpine swifts have shown that RTL and TROC predict lifespan under natural conditions (Bize et al., 2009), and that lifespan is strongly positively correlated with lifetime reproductive fitness (Tettamanti et al., 2012). Alpine swifts can live up to 26 years (median lifespan of breeders is 7 years of age; Bize et al., 2009), and both males and females show signs of senescence from around 10 years, although the onset and rate of senescence can differ between traits and sexes (Moullec et al., 2023). As factors including exposure to POPs, RTL, and TROC, can vary between sexes (Barrett and Richardson, 2011; Bauch et al., 2020; Dantzer and Garratt, 2017; but see Remot et al., 2020), one aim was to test whether the effects of POPs on RTL and TROC were sex-specific, as suspected in previous studies (Blévin et al., 2016; Sebastiano et al., 2020). POPs, RTL, and TROC, can also vary with age (Remot et al., 2022; Tricola et al., 2018), and therefore we also tested for age-specific associations. When studying the effects of age, one likely important distinction between individuals in how they may cope with the effects of POPs on their health, is whether they are in the prime of life or have reached senescence. Hence, we tested whether the effects of POPs exposure on RTL and TROC differ between pre-senescent and senescent individuals using measures on adults ranging from 1 to 19 years of age. Finally, because the effects of POPs on RTL and TROC were found to differ between chemicals (e.g., OCPs as oxychlordane vs PFAS; Blévin et al., 2017, 2016; Sebastiano et al., 2020), we tested for class-specific effects of POPs, namely OCPs and PCBs, on RTL and TROC.

2. Material and methods

2.1. Study system and general methods

Fieldwork was conducted over a period of four years (2017–2020) in seven different urban colonies of Alpine swift located under the roofs of buildings in Swiss cities: Baden (8°18'39.46" E, 47°28'22.3" N), Biel (7°14'46.21" E, 47°8'29.8" N), Lausanne (6°37'59.84" E, 46°31'8.94" N), Lenzburg (8°10'42.68" E, 47°23'13.40" N), Luzern (8°18'50.08" E, 47°3'20.48" N), Seengen (8°12'6.91" E, 47°19'31.58" N), and Solothurn (7°32'1.21" E, 47°12'33.12" N). Alpine swifts are 90 g aerial insectivorous birds that spend almost all their life aloft, landing mainly during the breeding season to incubate eggs and provision nestlings (Liechti et al., 2013; Meier et al., 2018). They are migratory birds which, in our population, are present on their breeding ground between April and September and migrate to sub-Saharan Africa to spend the winter there (Meier et al., 2020). Alpine swifts are socially monogamous and breed in colonies of a few to several hundred pairs located in the holes of cliffs or tall buildings. A single clutch of one to four eggs (mean 2.6) is produced per year, and both parents incubate the clutch and feed the offspring up to fledging. Offspring are recruited as breeders, mostly locally, at two to four years of age (Tettamanti et al., 2012), and recruits return each year to breed in the same colony, often in the same nest (Bize et al., 2017). Throughout the long-term monitoring of these populations (>20 years), nestlings have been ringed each year with a unique ring-number. For example, the Alpine swift population in Solothurn, monitored since 1942, is the longest monitored population. Around 70 % of the adults of these populations have been ringed as nestlings and are of known age. The remaining 30 % were ringed as adults and assigned as one year of age, or two years, or older, based on their plumage characteristics. Newly ringed adults are usually ringed when visiting the colony for the first time as none-breeders, or when breeding for the first time. As Alpine swifts start breeding at three years of age, and there is no breeding dispersal in our population, we assigned birds 'two years of age' when visiting the colony for the first time as non-breeders or as 'three years of

age' if seen breeding for the first time.

For this project, adults were captured in their colonies by hand either during the day while breeding (May–July) or at night before (April) and after reproduction (August). While breeding, individuals are captured on their nest while incubating eggs or feeding nestlings. Outside reproduction, all the adults in a colony are captured on the same day, after dusk, using trap doors that are manually closed after they entered their colony (i.e. building) to roost for the night (Robinson et al., 2020). After doors are closed, all the birds are immediately captured by hand and sampled. Blood samples were then collected by venipuncture from the metatarsal vein of the birds, stored in heparin-lithium microvettes® (Starstedt), centrifuged to separate plasma and red blood cells (3000 pm for 10 min), and stored at −20 °C until laboratory analyses. Most birds possess a preen oil gland that produces a fatty solution used to preen and waterproof the plumage. Preen oil contains high concentrations of lipophilic compounds such as POPs (e.g., PCBs; Jaspers et al., 2008; Gray et al., in press). In fact, previous studies showed correlations of organic contaminants between preen oil and other biological matrices such as blood, showing higher POPs levels in the former than in other matrices (e.g., blood, feathers; Eulaers et al., 2011; Yamashita et al., 2007; see in Gray et al., in press for a meta-analytic approach) likely because of its high lipid content allowing accumulation of lipophilic POPs. Moreover, preen oil is a measure of ongoing POPs exposure as it is continuously replenished and well-vascularised (Acampora et al., 2017; Aslan et al., 2000). Therefore, measures from preen oil provide minimally-invasive POPs estimates of internal body contamination within a short period of time after exposure (weeks to months; see Pacyna-Kuchta, 2023 and references therein; Gray et al., in press). By gently squeezing the preen oil gland on the sides, preen oil samples were collected (30 mg) and conserved in gas chromatography–mass spectrometry (GC–MS) vials at −20 °C until laboratory analyses. All the individuals sampled as part of this project were adults of known age and, as males and females are sexually monomorphic, individuals were sexed using molecular markers (Griffiths et al., 1998). In total, we collected 224 blood samples and 224 preen oil samples from 169 adults. Disparity between number of samples and adults falls on 43 adults which were repeatedly captured at different times during the study period to assess TROC (see below).

2.2. Telomere measurements

Relative telomere length (RTL) was measured on DNA extracted from red blood cell samples by quantitative real-time amplification method (qPCR) adapted for birds (Crisuolo et al., 2009) and previously used in Alpine swifts (Bize et al., 2009; Crisuolo et al., 2017). DNA was extracted and purified using Nucleospin® Blood QuickPure kit (from Macherey-Nagel®) by following the manufacturer's protocol. DNA integrity was verified by gel electrophoresis for 38 samples. The quantity and purity of the extracted DNA were measured using a microvolume spectrometer, the Nanodrop 1000 (Thermo scientific®). Following Bize et al. (2009), the glyceraldehyde-3-phosphate dehydrogenase (GAPDH) gene was used as a single control gene. The primers used for this control gene were: GAPDH-F, 5'-AACCAGCCAAGTACGATGACAT-3' and GAPDH-R, 5'-CCATCAGCAGCAGCCTTCA-3' diluted 200 nM. The primers used for telomeres were: Tel1b, 5'-CGGTTTGTGGGTTGGGTTGGGTTGGGTTGGGTTGGGTT-3' and Tel2b, 5'-GGCTTGCCCTTACCCTTACCCTTACCCTTACCCTTACCCTTACCCT-3' diluted to 75 nM. The amplification cycle was performed with 2 ng of DNA per well using the GoTaq® qPCR mix (Promega, Madison, USA). Conditions for telomere amplification started with 15 min at 95 °C, next 2 cycles of 15 s at 94 °C, 15 s at 49 °C, and followed by 30 cycles 15 s at 94 °C and 30 s at 59 °C. For GAPDH, amplification started with 2 min at 95 °C followed by 40 cycles of 15 s at 95 °C, 30 s at 56 °C, and 30 s at 72 °C. Each plate included a serial dilution of referent individual's DNA (10 ng, 5 ng, 2.5 ng, 1.25 ng, 0.625 ng and 0.3125 ng). These are used as a standard curve to control the amplification efficiency, which was 93.7 % for GAPDH and 100 % for telomere. Both negative control (water) and melting

curves were run for each plate to check for non-specific amplification and primer-dimer artefacts. Each sample was run in duplicate. The RTL corresponds to the ratio (T/S) of telomere repeat copy number (T) to control gene copy number (S), following (Pfaffl, 2001). The sample corresponding to the referent individual was designated the 'golden sample' with a ratio (T/S) arbitrarily set to 1. Intra- and inter-individual repeatability of RTL, evaluated using the Intra Class Coefficient (Eastwood et al. 2018), were 0.872 and 0.864, respectively. All analyses were conducted in the Telomere laboratory at the Department of Ecology, Physiology and Ethology, at the Hubert Curien Pluridisciplinary Institute (DEPE, IPHC-CNRS).

2.3. POPs analyses

The QuEChERS (Quick, Easy, Cheap, Effective, Rugged and Safe) method based on AOAC 2007.01 or EN 15662 2007 standards was used for the extraction of preen oil samples using internal standards (IS, see below) and the following modifications (Anastassiades et al., 2003; Filigenzi et al., 2019; Sadowska-Rociek et al., 2013; Taliany-Chamudis et al., 2017). All samples were kept at -20°C until they were extracted. Exactly 30 mg of preen oil sample was taken and transferred to a 6 mL falcon tube containing 2 mL acetonitrile (ACN) (1.0 % acetic acid) and 10 μL triphenyl phosphate as an internal standard (IS). The samples were shaken at 100 rpm for 5 min with a multi-tube vortex block shaker. Then, NaCl mixture containing 2 g MgSO_4 and 0.5 g sodium acetate was added to each tube, and the mixture was shaken at 100 rpm and centrifuged at 3500 rpm for 5 min. All supernatant was taken into QuEChERS tubes containing 150 mg MgSO_4 , 100 mg PSA, 50 mg C18. The tubes were shaken with a multi-tube vortex block shaker at 100 rpm for 5 min and then centrifuged at 3500 rpm for 5 min. 1 mL of the supernatant formed after extraction was taken into a 1.5 mL glass auto-sampler vial and analysed in GC-MS (Lehner et al., 2015; Manz et al., 2021). Solvents were purchased from Merck (Darmstadt, Germany).

Forty POPs were analysed in preen oil samples of Alpine swifts in this study (22 OCPs and 18 PCBs). The OCPs investigated were the α -, β -, γ -, and δ -isomers of hexachlorocyclohexane (HCHs), dichlorodiphenyltrichloroethanes (DDTs; 2,4'-DDE, 2,4'-DDD, 2,4'-DDT, 4,4'-DDE, 4,4'-DDD, and 4,4'-DDT), hexachlorobenzene (HCB), chlordanes (CHLs; oxy-chlordane, trans-chlordane, and cis-chlordane), chlorothalonil, pesticides derived from hexachlorocyclopentadienes (HCCPDs) (Bergman et al., 2012; endosulfan, heptachlor, hexachlor exoepoxide, aldrin, endrin), and dicofols (dicofol and 2,4'-dicofol). The PCBs congeners targeted were (IUPAC numbers) 28, 52, 95, 99, 101, 105, 110, 118, 138, 146, 149, 151, 153, 170, 177, 180, 183, and 187. All standards were purchased from Dr. Ehrenstorfer Laboratories (Augsburg, Germany) at a concentration of 10 ng/ μL in iso-octane.

Chromatography was performed with a Shimadzu (Kyoto, Japan) GC-MS-QP2010 Ultra, equipped with a 30 m length, 0.25 mm inner diameter, 0.25 μm -thick film Restek (USA) capillary column. Three calibration curves of ten points (from 0.1 to 250 $\mu\text{g/L}$) were created for quantification by use of PCBs and OCPs solutions in iso-octanes; good linearity ($r^2 \geq 0.99$) was observed in the ranges tested (Arikan et al., 2018). The r^2 (0.99 ± 0.0004), percent recovery ($100 \pm 3.16\%$), relative standard deviation (3.83 ± 1.69), limit of detection (0.12 ± 0.02), and limit of quantitation (0.36 ± 0.06) values of the analytical methods were determined from the linear regression of the multi-level calibration. All analyses were conducted in the Pesticide Research and Reference Laboratory at Hacettepe University.

2.4. Statistical analyses

To analyse the effects of POPs on RTL and TROC, we grouped POPs into different categories based on the similarity of their chemical structure. For total OCPs, the following contaminants were summed: total HCHs (Σ of all HCH isomers: α -, β -, γ -, and δ -isomers), total DDTs (Σ of 2,4'-DDT, 4,4'-DDT and its metabolites 2,4'-DDE, 4,4'-DDE, 2,4'-DDD,

and 4,4'-DDD), chlorothalonil, total chlordanes (Σ of oxychlordane, cis-chlordane, trans-chlordane, and heptachlor), endosulfan, total drins (Σ of aldrin and endrin), total dicofols (Σ of dicofol and 2,4'-dicofol), HCB, and hexachlor exo-epoxide. For total PCBs, the following congeners were summed: 28, 52, 95, 99, 101, 105, 110, 118, 138, 146, 149, 151, 153, 170, 177, 180, 183, and 187. In addition for PCBs, we calculated indicator PCBs (Σ PCBs congeners 28, 52, 101, 138, 153, 180), and different groups of PCBs based on the number and position of the chlorine atoms on the biphenyl molecule (e.g., trichlorobiphenyls (three chlorines), tetrachlorobiphenyls (four chlorines), etc.): tri-CB (PCBs congener 28), tetra-CB (PCBs congener 52), penta-CBs (Σ PCBs congeners 95, 99, 101, 105, 110, 118), hexaCBs (Σ PCBs congeners 138, 146, 149, 151, 153), and hepta-CBs (Σ PCBs congeners 170, 177, 180, 183, 187). From all these POPs categories, only those with occurrences $>50\%$ in our samples were used for statistical analyses (see Table 1).

Age is one of the most important factors that can contribute to the variation of RTL (Remot et al., 2022; Tricola et al., 2018), and therefore one of our aims was to assess the importance of chronological age in shaping effects of POPs on RTL and TROC, particularly at older ages when birds are senescing. A previous study reported a weak quadratic relationship between RTL and chronological age in adult Alpine swifts (Bize et al., 2009). Therefore, we first performed preliminary analyses to establish how to best model age-related variation in RTL in our dataset. We compared a series of mixed effects models where age was fitted as a linear effect, as a quadratic effect, or as segments with a single breakpoint varying between 6 and 15 years of age (using threshold models as described in e.g., Berman et al., 2009; Moullec et al., 2023). All these models included sampling year and individual identity (ring ID) nested within the sampling colony as random factors to control for temporal heterogeneity and pseudo-replication within location. Models, fitted with maximum likelihood (ML) estimation, were compared using the Akaike Information Criterion (AIC; model selection with $\Delta\text{AIC} < 2$; Burnham and Anderson, 2002) to identify the best models. Results of these preliminary analyses showed that threshold models with breakpoints set at an age from 9 to 13 years old best described the age-related variation in RTL in our dataset (Table S1). Therefore, we chose 9 years old as the threshold because statistically, it is the minimum age at which RTL started to shorten with age, and therefore the onset of senescence (Table S1 and Fig. S1). In fact, RTLs showed little age-related variation before the breakpoint and declined in size at older ages (Fig. S1). Note that similar onsets of senescence were observed for biometric and reproductive traits in this population of Alpine swifts (Moullec et al., 2023). To study the combined effects of POPs, senescence and sex on RTL, individuals older than or equal to 9 years old when sampled were considered senescent, accounting for the negative association between RTL and age. Conversely, individuals younger than 9 years old at sampling were considered pre-senescent. To study these effects on TROC, we used the same categories as RTL, but since individuals were repeatedly sampled, the threshold ($<$ or ≥ 9 years) was applied to the last sampling age.

To test the association between RTL and POPs, we used linear mixed effects models including RTL as the response variable and the interaction between each POPs category, sex, and senescent status, as predictors. These models included ring ID nested within colony and year of sampling as random factors to control for pseudo-replication within location and temporal heterogeneity, respectively. In summary, 169 adults captured several times over a period of 4 years (2017–2020) were used in these models resulting in 224 observations. Both POPs and RTL were measured in each observation. Nevertheless, sample sizes varied across models since all measured POPs were not detected in all individuals (Table 1).

To test the effect of POPs exposure on TROC, we calculated the annual change in RTL over the first- and last-time recaptured individuals were sampled. This was considered as the response variable in linear mixed effects models. We also calculated the mean concentration of a given POPs category for each recaptured individual over the same

Table 1
Descriptive statistics (sample size, frequency of occurrence, mean, standard deviation, minimum and maximum) for POP concentrations measured in preen oil samples in adult Alpine swifts from Switzerland (ng/g ww). Frequencies of occurrences (FO) > 50 % present [†] and bold FOs are those used for statistical analyses.

	Telomere length (N = 224)						Telomere dynamics (N = 45)					
	n	FO (%)	Mean	Sd	Min	Max	n	FO (%)	Mean	Sd	Min	Max
Alpha HCH	32	14.29	3.895	1.078	3.308	9.071	4	9.30	4.309	0.886	3.510	5.560
Beta HCH	0	NA	NA	NA	NA	NA	0	0.00	NA	NA	NA	NA
Gama HCH	12	5.36	3.893	0.585	3.057	5.242	3	6.98	3.964	0.469	3.425	4.279
Delta HCH	14	6.25	5.142	0.304	4.944	5.949	4	9.30	5.042	0.056	4.957	5.074
Total HCHs	53	23.66	4.592	1.587	3.057	9.318	11	25.58	4.481	0.706	3.425	5.560
2,4-DDE	61	27.23	2.460	0.560	2.286	6.410	8	18.60	3.015	1.412	2.288	6.410
4,4-DDE	88	39.29	6.414	6.213	2.383	36.625	30	69.77 [†]	6.926	6.617	2.393	36.625
sum.DDE	128	57.14 [†]	5.582	6.129	2.286	43.035	33	76.74 [†]	7.027	7.625	2.288	43.035
2,4-DDD	94	41.96	5.144	0.480	4.841	7.444	8	18.60	5.026	0.147	4.861	5.236
4,4-DDD	50	22.32	10.836	23.923	3.901	168.102	11	25.58	24.669	48.076	3.923	168.102
sum.DDD	128	57.14 [†]	8.010	15.085	3.909	168.102	18	41.86	17.309	38.083	4.861	168.102
2,4-DDT	115	51.34 [†]	8.456	22.873	4.571	240.178	18	41.86	21.899	55.143	4.599	240.178
4,4-DDT	76	33.93	7.595	4.859	5.063	34.338	20	46.51	10.015	6.945	5.067	34.338
sum.DDT	148	66.07 [†]	10.471	23.327	4.571	274.516	26	60.47 [†]	22.865	52.198	4.599	274.516
Total DDTs	197	87.95 [†]	16.698	36.644	2.288	485.653	40	93.02 [†]	28.448	75.863	2.288	485.653
Chlorothalonil	31	13.84	7.947	0.039	7.895	8.035	9	20.93	7.955	0.050	7.895	8.035
Oxychlorodane	13	5.80	4.059	1.683	2.490	6.938	2	4.65	3.469	0.772	2.923	4.015
Cis_Chlorodane	35	15.63	7.406	0.292	7.135	8.443	5	11.63	7.590	0.373	7.252	8.209
Trans_Chlorodane	16	7.14	9.264	0.150	9.087	9.550	2	4.65	9.123	0.008	9.117	9.128
Heptachlor	37	16.52	5.253	2.598	1.718	10.337	8	18.60	5.731	2.168	1.718	7.180
Total Chlordanes	82	36.61	7.982	3.140	1.899	18.225	15	34.88	7.266	1.924	2.834	10.338
Endosulfan	9	4.02	9.331	0.435	8.781	9.968	1	2.33	9.968	NA	NA	NA
Aldrin	67	29.91	8.920	12.687	1.779	54.700	18	41.86	10.251	12.884	1.878	38.630
Endrin	56	25.00	55.847	80.041	1.382	429.746	6	13.95	80.346	49.620	11.418	132.382
Total Drins	108	48.21 [†]	34.491	65.051	1.382	468.954	22	51.16 [†]	30.300	41.461	1.878	132.382
Dicofol	7	3.13	4.981	0.245	4.717	5.345	0	0.00	NA	NA	NA	NA
2,4-Dicofol	7	3.13	3.404	0.263	3.064	3.864	1	2.33	3.864	NA	NA	NA
Total Dicofols	13	5.80	4.515	1.432	3.064	8.438	1	2.33	3.864	NA	NA	NA
HCB	59	26.34	6.122	0.514	5.789	8.795	14	32.56	6.284	0.405	5.789	7.067
Hexachlor-exo-epoxide	0	NA	NA	NA	NA	NA	0	0.00	NA	NA	NA	NA
Total OCPs	221	98.66 [†]	39.178	62.643	1.832	504.121	43	100.00 [†]	49.679	81.307	2.288	504.121
PCB 28	5	2.23	0.231	0.053	0.141	0.274	0	0.00	NA	NA	NA	NA
PCB 52	0	NA	NA	NA	NA	NA	0	0.00	NA	NA	NA	NA
PCB 95	13	5.80	0.313	0.028	0.288	0.380	2	4.65	0.323	0.024	0.306	0.340
PCB 99	35	15.63	0.844	0.312	0.695	2.302	6	13.95	0.934	0.221	0.705	1.223
PCB 101	39	17.41	1.270	0.317	1.085	2.638	8	18.60	1.293	0.189	1.095	1.596
PCB 105	27	12.05	0.736	0.228	0.616	1.564	3	6.98	0.690	0.076	0.631	0.775
PCB 110	14	6.25	0.972	0.009	0.959	0.993	2	4.65	0.969	0.002	0.967	0.970
PCB 118	76	33.93	1.208	0.030	1.170	1.306	12	27.91	1.214	0.034	1.174	1.297
PCB 138	123	54.91 [†]	2.117	0.744	1.801	8.620	22	51.16 [†]	2.326	0.633	1.801	4.025
PCB 146	184	82.14 [†]	2.413	0.926	1.618	6.838	37	86.05 [†]	2.679	0.968	1.634	6.096
PCB 149	186	83.04 [†]	2.715	1.865	1.706	20.882	38	88.37 [†]	3.250	1.527	1.706	8.339
PCB 151	97	43.30	2.259	0.094	2.080	2.656	14	32.56	2.284	0.109	2.181	2.492
PCB 153	55	24.55	2.231	0.930	1.593	7.339	15	34.88	2.178	0.480	1.613	2.992
PCB 170	43	19.20	1.901	0.469	1.191	2.899	13	30.23	2.102	0.418	1.386	2.850
PCB 177	55	24.55	1.603	0.487	1.066	2.570	19	44.19	1.771	0.449	1.103	2.570
PCB 180	8	3.57	0.643	0.363	0.443	1.496	2	4.65	0.636	0.226	0.476	0.796
PCB 183	34	15.18	0.962	1.185	0.181	6.399	11	25.58	1.078	0.833	0.211	2.704
PCB 187	17	7.59	1.203	1.117	0.429	5.098	5	11.63	1.145	0.473	0.751	1.832
Trichlorobiphenyl	5	2.23	0.231	0.053	0.141	0.274	0	NA	NA	NA	NA	NA
Tetrachlorobiphenyl	0	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
Pentachlorobiphenyl	132	58.93 [†]	1.579	0.892	0.288	4.940	21	48.84 [†]	1.675	0.939	0.306	3.917
Hexachlorobiphenyl	218	97.32 [†]	7.115	4.385	1.801	43.704	42	97.67 [†]	8.058	3.600	1.801	17.835
Heptachlorobiphenyl	93	41.52 [†]	2.454	2.521	0.181	17.110	26	60.47 [†]	3.070	2.353	0.211	9.603
Indicator PCBs	175	78.13 [†]	3.033	2.110	0.443	20.093	33	76.74 [†]	3.334	1.938	0.476	9.018
Total PCBs	222	99.11 [†]	8.959	6.413	0.248	65.754	43	100.00 [†]	10.544	5.957	1.174	28.152

period of time as an explanatory variable. Since all individuals were sampled from April to August while they were on their breeding ground in Switzerland, POPs measurements in preen oil provide relatively short-term exposure. The new explanatory variable (mean POPs category) represents the pollutant load birds encountered/bioaccumulated on their breeding grounds. Then, models were built with TROC as the response variable and the interaction between mean POPs category, sex, and senescent status, as predictors. These models included colony and year of sampling as random factors to control for sampling location and temporal heterogeneity. We used a total of 43 observations resulting from 43 recaptured adults sampled 98 times in total (31 birds twice, and 12 birds three times) over a minimum period of 257 days and a

maximum period of 1208 days between 2017 and 2020. Some previous studies on TROC have included the initial RTL measure as a covariate in the models because the rate of telomere shortening is often higher for birds with long telomeres at baseline. Other authors also corrected estimates of TROC for possible measurement errors known as regression to the mean using the equation suggested by Verhulst et al. (2013). However, Bateson et al. (2019) reported that (i) controlling statistically for baseline RTL by adding it to models as a covariate incorrectly inflates estimates of the difference in TROC, and the magnitude of this bias is positively related to the size of telomere measurement error; and (ii) correcting TROC estimates for possible measurement errors using regression to the mean does not solve the problem of biased parameter

estimates. Hence, following Bateson et al. (2019), we did not include the initial RTL as a covariate nor corrected for regression to the mean in our models on TROC.

Statistical analyses were performed using R 4.0.2 (R Core Team., 2016). We visually inspected the raw data and normality of residuals for each model as response variable to check for linear model assumptions and possible outliers. For all models, all independent variables were tested for collinearity using Variance Inflation Factors (VIF) according to the suggestions by (Zuur et al., 2010), and contaminants were scaled to a mean of 0 and a standard deviation of 1.

2.5. Ethics declarations

The study which complied with the standards of animal experimentation and animal welfare was approved by the Federal Food Safety and Veterinary Office (FSVO; permits 30,983). Capturing and ringing wild Alpine swifts was performed under the legal authorisation of the Swiss Federal Agency for Environment, Forests and Landscapes (annual ringing permits to P Bize and C Meier).

3. Results

Sample size, frequency of occurrence, mean, standard deviation, and minimum and maximum of each concentration measured are reported in Table 1. Hexachlor exo-epoxide, β -isomer of hexachlorocyclohexane and PCBs congener 52 were not detected. TROC was not analysed for dicofol and PCBs congener 28 due to unrepeatable intra-individual pollutant measures (Table 1). Regarding RTL measures, the least abundant compound was PCBs congener 28 (0.141 ng/g ww) and the most abundant was endrin (429.746 ng/g ww; Table 1). However, for repeated intra-individual measures used to study TROC, the least abundant compound was PCBs congener 183 (0.211 ng/g ww) and the most abundant was 2,4-DDT (240.178 ng/g ww; Table 1).

Total OCPs had significant effects on RTL interacting with sex as well as with senescent status (Table 2). RTL decreased with increasing levels of OCPs (Fig. 1). OCPs effects were stronger in senescent individuals and in females, and therefore the strongest in senescent females (Fig. 1). Follow-up models with total DDTs and total drins as the main OCPs suggest that the effects of OCPs on RTL were primarily driven by exposure to total drins which showed alike effects (Table 2; Fig. S2). Total PCBs did not influence RTL, either alone or in interaction with sex or senescent status (Table 2). The same results were found when the analysis was restricted to indicator PCBs (Table 2) or long-chain PCBs (penta-, hexa-, and hepta-CBs; Table S2). Our results also indicated a significant effect of senescent status in interaction with sex on RTL (Tables 2 and S2). While no significant difference was found in RTL between sexes at pre-senescent stage, senescent females showed longer RTL than senescent males (Fig. 2).

Analyses on a subsample of individuals with repeated measures of RTL allowed us to look at the association between telomere rate of change (TROC) and OCPs or PCBs. PCBs had significant effects on TROC, but not OCPs (Table 2). TROC was positively related to increased PCBs levels in senescent males and pre-senescent females and senescent females, but not in pre-senescent males (Figs. 3, and S3 and S4 for hexa- and hepta-CBs, respectively). This meant lower rates of telomere erosion when PCBs levels were higher, except for pre-senescent males. In senescent females, TROC were greater than zero, therefore suggesting telomere elongation with greater PCBs exposure (Fig. 3). Although DDTs showed a limited significant effect in interaction with sex and senescent stage on TROC (Fig. S5 and Table 2), none of the relationships between DDTs and TROC reached significance when tested individually (Table 2). TROC demonstrated individual variation between sexes and senescent status with elongated telomeres in senescent females compared to pre-senescent females and males (Table 2; Fig. 4).

Table 2

Results of mixed effect models testing for senescence- (2 levels: adults < 9 years old are pre-senescent, and adults $\geq$ 9 years old are senescent) and sex-specific effects of total organochlorine pesticides (OCPs), and its breakdown in DDTs and Drins, and of total polychlorinated biphenyls (PCBs) on relative telomere length (RTL) and annual rate of telomere dynamics (TROC, change in relative telomere length, ratio T/S, per year over the first- and last-time recaptured individuals were sampled) in adult Alpine swifts from Switzerland. Significant (p -value $\leq$ 0.05) results are highlighted in bold and *.

Effects	Relative telomere length (RTL)			Annual telomere rate of change (TROC)		
	Estimate	SE	p-Value	Estimate	SE	p-Value
<i>Organochlorine pesticides (OCPs)</i>						
Total OCPs	−0.274	0.087	0.002*	0.153	0.202	0.468
Senescence	0.018	0.038	0.631	−0.142	0.066	0.038*
Sex	−0.0008	0.038	0.984	0.138	0.066	0.045*
Total OCPs * senescence	0.246	0.086	0.005*	−0.243	0.208	0.251
Total OCPs * sex	−0.220	0.086	0.012*	0.179	0.210	0.402
Senescence * sex	−0.033	0.038	0.391	−0.155	0.066	0.024*
Total OCPs * senescence * sex	0.160	0.086	0.066	−0.211	0.209	0.325
Model information	N obs = 221, N indiv = 169, N years = 4, N colonies = 7 Var _{ID} = 0.050, Var _{year} = 0.003, Var _{colony} = 0.002, Var _{residuals} = 0.092			N obs = 43, N indiv = 43, N years = 3, N colonies = 6 Var _{year} = 0.002, Var _{colony} = 0.019, Var _{residuals} = 0.110		
Total DDTs	−0.069	0.164	0.672	0.329	0.440	0.460
Senescence	−0.007	0.041	0.863	0.015	0.096	0.878
Sex	−0.0004	0.041	0.992	0.133	0.095	0.171
Total DDTs * senescence	0.119	0.163	0.465	0.398	0.434	0.365
Total DDTs * sex	−0.067	0.163	0.680	−0.104	0.434	0.813
Senescence * sex	−0.024	0.040	0.562	0.004	0.097	0.969
Total DDTs * senescence * sex	0.036	0.163	0.825	0.885	0.436	0.050*
Model information	N obs = 197, N indiv = 155, N years = 4, N colonies = 7 Var _{ID} = 0.051, Var _{year} = 0.008, Var _{colony} = 0.004, Var _{residuals} = 0.084			N obs = 43, N indiv = 43, N years = 3, N colonies = 6 Var _{year} = 0.00, Var _{colony} = 0.013, Var _{residuals} = 0.10		
Total drins	−0.431	0.132	0.003*	0.105	0.600	0.863
Senescence	0.119	0.060	0.050*	−0.142	0.119	0.243
Sex	−0.002	0.059	0.969	0.136	0.119	0.264
Total drins * age	0.314	0.132	0.023*	0.008	0.599	0.990
Total drins * sex	−0.399	0.132	0.005*	0.015	0.599	0.980
Senescence * sex	0.052	0.059	0.384	−0.158	0.119	0.198
Total drins * senescence * sex	0.335	0.132	0.016*	−0.117	0.600	0.848
Model information	N obs = 108, N indiv = 92, N years = 4, N colonies = 7 Var _{ID} = 0.066, Var _{year} = 0.000, Var _{colony} = 0.008, Var _{residuals} = 0.069			N obs = 33, N indiv = 33, N years = 3, N colonies = 5 Var _{year} = 0.00, Var _{colony} = 0.010, Var _{residuals} = 0.118		
<i>Industrial polychlorinated biphenyls (PCBs)</i>						
Total PCBs	−0.007	0.0565	0.899	0.127	0.054	0.026*
Senescence	−0.021	0.034	0.548	−0.030	0.058	0.606
Sex	0.036	0.034	0.283	0.167	0.058	0.007*
Total PCBs * senescence	0.047	0.054	0.382	−0.039	0.054	0.476
Total PCBs * sex	−0.078	0.054	0.148	0.074	0.056	0.191

(continued on next page)

Table 2 (continued)

Effects	Relative telomere length (RTL)			Annual telomere rate of change (TROC)		
	Estimate	SE	p-Value	Estimate	SE	p-Value
Senescence *	-0.076	0.034	0.025*	-0.098	0.058	0.100
sex						
Total PCBs *	-0.035	0.054	0.521	0.114	0.055	0.045*
senescence *						
sex						
Model information	N obs = 222, N indiv = 168, N years = 4, N colonies = 7 Var _{ID} = 0.042, Var _{year} = 0.010, Var _{colony} = 0.003, Var _{residuals} = 0.098			N obs = 43, N indiv = 43, N years = 3, N colonies = 6 Var _{year} = 0.00, Var _{colony} = 0.008, Var _{residuals} = 0.091		
Indicator PCBs	0.042	0.048	0.376	0.074	0.057	0.205
Senescence	-0.014	0.038	0.717	-0.071	0.064	0.277
Sex	0.028	0.038	0.462	0.167	0.065	0.015*
Indicator PCBs *	0.003	0.045	0.954	-0.058	0.057	0.319
senescence						
Indicator PCBs * sex	-0.072	0.045	0.112	0.044	0.057	0.445
Senescence *	-0.060	0.037	0.112	-0.118	0.065	0.083
sex						
Indicator PCBs *	0.040	0.044	0.368	0.050	0.057	0.384
senescence *						
sex						
Model information	N obs = 175, N indiv = 140, N years = 4, N colonies = 7 Var _{ID} = 0.040, Var _{year} = 0.009, Var _{colony} = 0.002, Var _{residuals} = 0.107			N obs = 40, N indiv = 40, N years = 3, N colonies = 6 Var _{year} = 0.0004, Var _{colony} = 0.008, Var _{residuals} = 0.106		

4. Discussion

Our results strengthen the idea of class-specific effects of POPs (i.e., OCPs vs PCBs) on RTL and TROC as demonstrated in previous research (e.g., OCPs, such as oxychlordan, were reported to be negatively associated with RTL and PFAS were reported to be positively associated with TROC; Blévin et al., 2017, 2016; Sebastiano et al., 2020). Specifically, in the long-lived Alpine swift, OCPs (and drins in particular) were

negatively associated with RTLs, while PCBs were positively associated with TROC. Consistent with reports that telomere preservation and chemical bioaccumulation often differ between sexes (Barrett and Richardson, 2011; Bauch et al., 2020; Dantzer and Garratt, 2017; but see Remot et al., 2020) and chronological age (Remot et al., 2022; Tricola et al., 2018), our results also show that senescent females presented longer RTL and elongated telomeres over time compared to pre-senescent females and males. These sex- and age-related differences in RTL and TROC were affected by POPs, showing more pronounced effects of POPs in females and senescent individuals.

4.1. Telomeres and senescence

Previous studies have reported that the relationship between longevity and either RTL or TROC may differ between the sexes depending on the life-history of each species (Bauch et al., 2020; Domínguez-de-Barros et al., 2023; Young et al., 2013). Indeed, sex-specific differences in resource allocation between traits can lead to sex-specific differences in telomere dynamics, such as the trade-off between somatic maintenance and either growth rate (Foote et al., 2011) or reproduction (with high fitness gain increasing telomere loss; Sudyka et al., 2019). In addition, the original idea that telomeres erode continuously with age has been challenged by recent studies highlighting a large variation in telomere shortening among species (Crisuolo et al., 2020; Haussmann et al., 2003; Monaghan et al., 2018; Remot et al., 2022; Tricola et al., 2018) or within individuals. In the latter case, telomeres were found to erode in some individuals over time and elongate in others (Fairlie et al., 2016; Hares et al., 2018; Pepke et al., 2023; Svenson et al., 2011). Thus, not only can telomere dynamics vary dependent on sex and age, but it may also respond to environmental pollution as seen in our study. Indeed, our results indicate that females reaching senescence (i.e. aged over 9 years based on the effect of chronological age on RTL) showed elongated telomeres and, in turn, had longer RTLs compared to pre-senescent females and males. Interestingly, our results also indicate that the effects of POPs on telomeres were mainly observed in females and senescent individuals (see discussion below). A long-term study of biometric and reproductive traits on the studied population of Alpine swifts showed differences in aging patterns between the sexes, with stronger senescence in females, particularly for

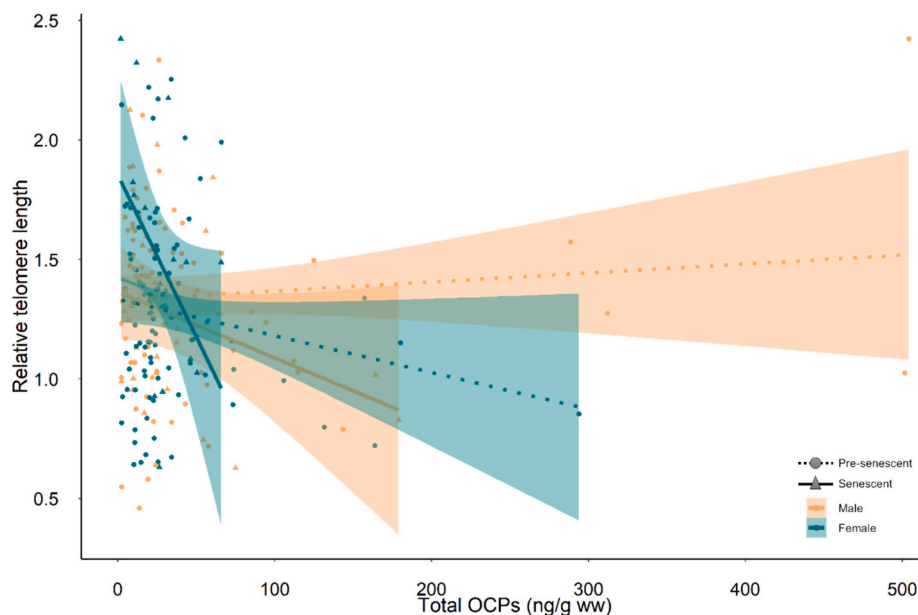


Fig. 1. Relationships between relative telomere length (RTL) measured in red blood cells and total organochlorine pesticides (OCPs) measured in preen oil samples in adult Alpine swifts from Switzerland. Males are reported in orange and females in turquoise. Circles and dashed lines refer to pre-senescent adults (<9yo), and triangles and solid lines refer to senescent adults (≥9yo). Lines represent trends, while their shadows represent 95 % confidence intervals.

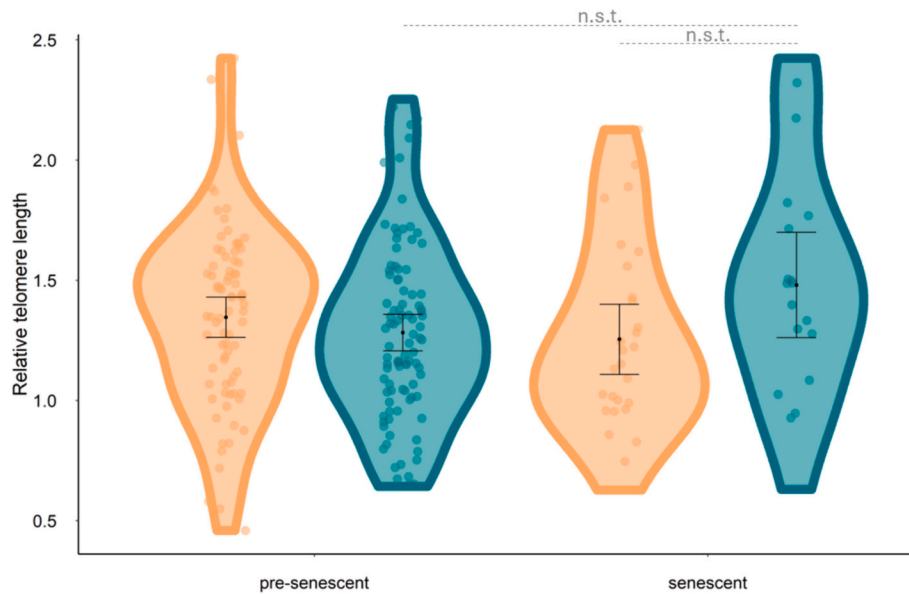


Fig. 2. Violin plot showing the relationship between relative telomere length (RTL) measured in red blood cells and the interaction of sex with senescent status (pre-senescent < 9yo, senescent $\geq$ 9yo) in adult Alpine swifts from Switzerland. Males are reported in orange and females in turquoise. Black dot indicates the mean, error bars show 95 % confident intervals, and *n.s.t.* indicates non-significant trends ($p = 0.06$).

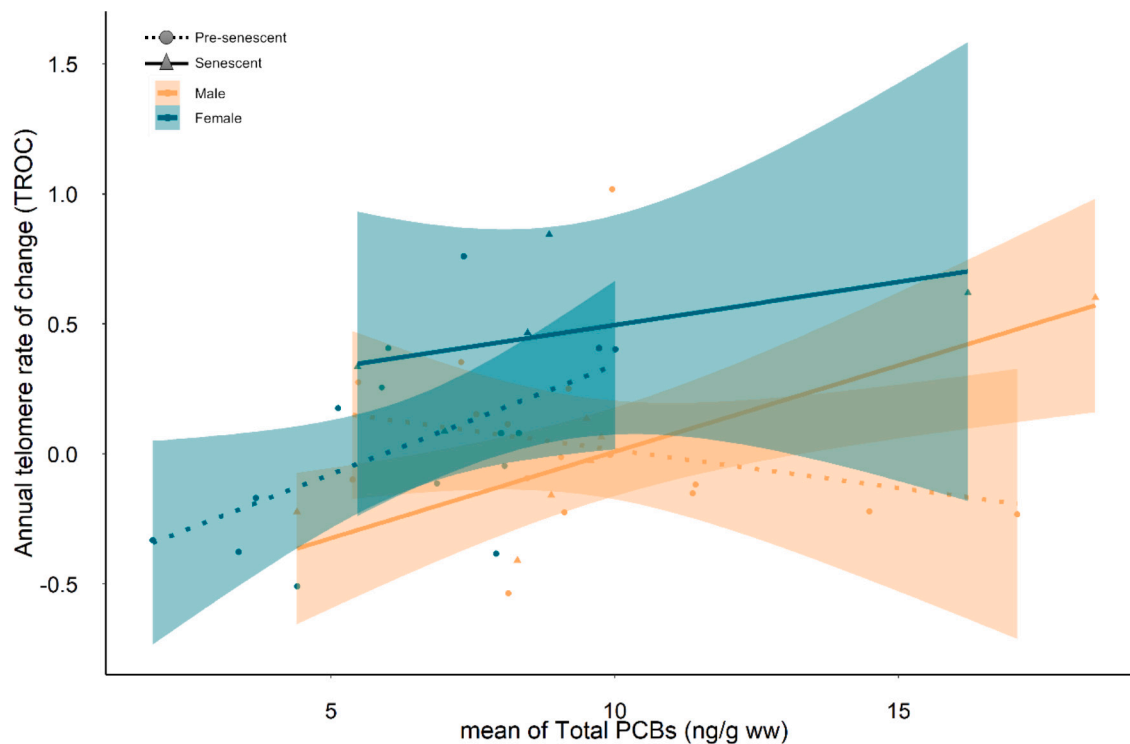


Fig. 3. Relationship between annual telomere rate of change (TROC; change in relative telomere length, T/S ratio, per year over the first- and last-time recaptured individuals were sampled) measured in red blood cells and the mean for the study period of total polychlorobiphenyls (PCBs) measured in preen oil samples in adult Alpine swifts from Switzerland. Males are reported in orange and females in turquoise. Circles and dashed lines refer to pre-senescent adults (<9yo), and triangles and solid lines refer to senescent adults ($\geq$ 9yo). Lines represent trends, while their shadows represent 95 % confidence intervals.

reproductive traits (Moullec et al., 2023). The onset of reproductive senescence in this latter study was similar to our onset of senescence for RTL based on the minimum age at which RTL started to shorten (9 years-old; see Table S1 & Fig. S1). This finding supports the hypothesis that sex-specific differences in resource allocation to reproduction may underlie sex differences in telomere attrition in free-living animals (Dantzer and Garratt, 2017; Watson et al., 2017). Telomere elongation in

senescent females may reflect a higher investment in cell maintenance, and thus be interpreted as an evolutionary strategy to mitigate the stronger effects of senescence seen in females in this species (Moullec et al., 2023). Telomere restoration in senescent females may involve telomerase activity (Blackburn, 2005; Rubtsova et al., 2012) or telomere rearrangement (i.e., alternative lengthening of telomeres, ALT; Cesare and Reddel, 2008), although further research is needed to identify the

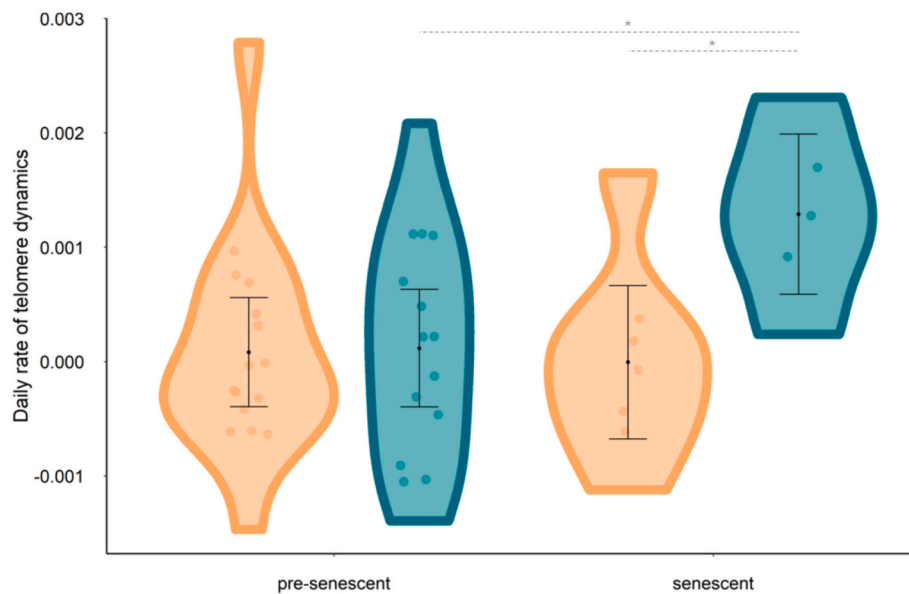


Fig. 4. Violin plot showing the relationship between annual telomere rate of change (TROC; change in relative telomere length, T/S ratio, per year over the first- and last-time recaptured individuals were sampled) measured in red blood cells and the interaction of sex with senescent status (pre-senescent < 9yo, senescent $\geq$ 9yo) in adult Alpine swifts from Switzerland. Males are reported in orange and females in turquoise. Black dot indicates the mean, error bars show 95 % confident intervals, and * indicates significant differences ($p < 0.05$).

mechanism(s) involved. Males and pre-senescent individuals showed high within-individual variation in RTL and TROC, with no clear pattern in the erosion and elongation of telomeres. This is consistent with other studies suggesting that there is a subsequent loss and gain of telomere ends within individuals over the course of life (Fairlie et al., 2016; Hares et al., 2018; Pepke et al., 2023; Svenson et al., 2011).

4.2. RTL and POPs

Higher levels of OCPs, but not PCBs, were associated with shorter RTL, dependent on sex and senescent status. Negative associations between OCPs and RTL were observed in females and senescent individuals (i.e., both sexes) but not in males and pre-senescent individuals. The most common OCPs in our dataset were drins and DDTs, and further analyses suggested that drins may be the OCP driving the relationship with RTL. In birds, drins have been associated with a reduction in fitness and increased mortality (Fleming et al., 1982; Muralidharan, 1993; Newton et al., 1992), but as far as we know there is little information on the underlying physiological pathways behind these relationships. Our results are in line with a marginally significant association found in humans, with aldrin exposure associated with shorter RTLs (Andreotti et al., 2015). Our results thus reinforce the hypothesis of genotoxic consequences (chromosomal aberrations, gene mutation, etc.) of an exposure to this group of contaminants. Drins trigger DNA breaks (Georgian, 1975; Latre et al., 2003; NTP, 2016) which is a well-known molecular pathway responsible for DNA sequences translocations that may result in aberrant telomere end-joining and shorter RTLs (Bosco and Haber, 1998; Latre et al., 2003).

We found a negative association between OCPs and RTL, which is in line with Eckbo et al. (2019) who reported similar results using 11 Mandt's Black guillemots, and with Blévin et al. (2016) who found a negative association between the OCP Oxychlordane and RTL in female but not male kittiwakes. In contrast, Blévin et al. (2017) and Sebastiano et al. (2020) did not characterize any significant associations between RTL and other classes of organic contaminants, such as PFAS, with the exception of perfluorodecanoate (PFDA). In adult glaucous gulls, there was a negative correlation RTL and PFDA in females and a positive correlation in males (Sebastiano et al., 2020). In other bird species, absence of relationships between POPs (including OCPs) and RTL were

also reported, such as in nestling eagles (Hansen et al., 2022; Sletten et al., 2016). In our study, senescent females seemed to be the most vulnerable to OCPs exposures, which is consistent with previous studies where black-legged kittiwake and glaucous gull females were more sensitive to OCPs regardless of age. Both species showed a negative association between OCPs concentration and telomere length (e.g., negative association between oxychlordane and RTL, Blévin et al., 2016) and survival rate (Erikstad et al., 2013; Goutte et al., 2015). Thus, the sensitivity of senescent female Alpine swifts to OCPs could affect their telomere length, indicating that shortened telomeres could be responsible for the lower survival rate reported in other long-lived bird species (Erikstad et al., 2013). Despite all these species share a similar lifespan (~ 20 y; Sletten et al., 2016; Blévin et al., 2017, 2016; Eckbo et al., 2019; Sebastiano et al., 2020; Hansen et al., 2022), such a general conclusion at the interspecific level needs further exploration, as confounding factors like life stages, dose-dependent consequences of environmental contaminants or ecological differences (e.g., swifts versus seabirds) have to be taken into account. For example, high levels of oxychlordane (4.019 ± 1.315 ng/g ww) in the blood were associated with shorter RTL in female kittiwakes during chick rearing (Blévin et al., 2016), whereas no relationship between plasma oxychlordane and RTL was observed in incubating guillemots (< 2 ng/g ww, Eckbo et al., 2019) or in nestling white-tailed eagles (blood and serum < 0.25 ng/mL ww, Hansen et al., 2022; plasma: 1.483 ± 0.197 ng/g ww, Sletten et al., 2016). The lack of results in guillemots and white-tailed eagles could be explained by the lower exposure to oxychlordane in these species. The choice of biological matrices to measure organic contaminants need also to be considered when evaluating exposure effects since contaminant loads can vary between tissues (Løseth et al., 2019; Gray et al., in press; Pacyna-Kuchta, 2023). Although telomere measurements were comparable across studies (RTLs by qPCR from genomic DNA extract from blood samples), POPs were measured in different tissues: blood (Blévin et al., 2016; Eckbo et al., 2019), plasma (particularly for PFAS; Blévin et al., 2017; Sebastiano et al., 2020) and preen oil (current study). POPs are lipophilic and have been found to be the second most concentrated element in preen oil gland (after the body fat; Gray et al., in press). Thus, preen oil sampling which is less invasive than blood collection, can contain significantly higher concentrations of POPs than blood and plasma (OCPs, Briels et al., 2019; PCBs, polybrominated diphenyl ethers

(PBDEs) and OCPs, Eulaers et al., 2011; PCBs and OCPs, Løseth et al., 2019; Pacyna-Kuchta, 2023; PCBs, Wang et al., 2015). Although POPs concentrations are found to correlate across matrices (Briels et al., 2019; Eulaers et al., 2011; Gray et al., in press; Løseth et al., 2019), the higher POPs concentrations in preen oil samples may help to strengthen inter-individual differences in contamination levels (e.g., higher detection frequencies and sample sizes), and therefore the probability to detect associations between POPs and RTL.

4.3. TROC and POPs

Stressors and cumulative stress situations, such as environmental pollution, can intensify telomere disruption over the lifetime of organisms (Bauch et al., 2022; Blévin et al., 2017; Chatelain et al., 2020; Salmón and Burraco, 2022; Sebastiano et al., 2020; Yuan et al., 2018; Ziegler et al., 2017). Accordingly, our results reported PCBs-specific effects on TROC depending on sex and senescent status, whereas no clear associations between OCPs and TROC were found. Higher concentrations of PCBs (also seen when data are restricted to hexa- and hepta-CBs) led to slower rates of telomere shortening, especially in senescent and non-senescent females and in senescent males. Our results partially agree with the very little data available in the literature reporting effects of POPs exposure on TROC in birds. Despite not controlling for age effects, which may have covered up further consequences of environmental contaminants on TROC (see conclusion below), both Blévin et al. (2017) and Sebastiano et al. (2020) reported that higher exposure to organic contaminants (i.e., PFAS) slowed down the rate of telomere shortening in long-lived top bird predators (black-legged kittiwakes and glaucous gulls). However, these relationships did not vary between sexes, in contrast to our results, which could be explained by the lack of sex-biased life-history strategies (e.g., senescence trajectories, foraging behaviour, diet) influencing TROC in their study species (Harris et al., 2020; but see Goutte et al., 2014). Interestingly, only swift senescent females were characterized by telomere elongation when exposed to higher levels of PCBs, which could be explained by an interaction of PCBs with corticosterone (CORT; the primary glucocorticoid in birds) as suggested by Sebastiano et al. (2020). CORT responds to stressors and can be modulated according to several factors such as environmental contaminants (Tartu et al., 2015a, 2015b) or age (Angelier et al., 2020). For instance, old snow petrels (*Pagodroma nivea*) downregulated their CORT stress response in comparison to younger individuals (Angelier et al., 2020), and organic contaminants such as PFAS were associated with lower baseline CORT in black-legged kittiwakes (Tartu et al., 2014). Other studies have also highlighted a potential role of CORT as a driver of telomere dynamics including a direct effect on the activity of the enzyme telomerase (Angelier et al., 2018 and references therein). Thus, since females present a faster rate of senescence in the Alpine swift (Moullec et al., 2023), an evolutionary mitigation strategy to reduce aging by elongating telomeres towards the end of life might occur via either PCBs-induced downregulation of CORT and/or upregulation of telomerase activity with age. Unfortunately, we did not measure CORT level or the enzymatic activity of telomerase to corroborate this hypothesis. Alternatively, senescent females during breeding may enhance an antioxidant shield in the presence of chemical pollutants to avoid genotoxic effects due to oxidative stress (Lan et al., 2022; Pérez et al., 2010; Wu et al., 2021). Such a hypothesis would fit well with the specificity of females' telomere lengthening as breeding females would avoid transmission of damaged molecules to the embryo (Blount et al., 2016). As another explanation, exposure to low concentrations of PCBs and DDTs have been associated with the elongation of telomere length in presumed healthy humans (Shin et al., 2010), although exposition to higher concentration of these contaminants also induced telomere shortening and subsequent aging-related diseases in humans (Lifang et al., 2013; Yuan et al., 2018; Ziegler et al., 2017). Further research is needed to unravel the mechanism(s) linking POPs exposure to telomere elongation in

senescent females. In contrast, pre-senescent male Alpine swifts were the most vulnerable to PCBs exposure, showing a faster rate of shortening telomeres with higher concentrations. This trend agrees with previous harmful consequences of these contaminants on bird physiology and reproduction (Bouwman et al., 2019; Dean et al., 2019; Halbrook and Arenal, 2003; Hao et al., 2021; Iwaniuk et al., 2006; Smits et al., 2002), and points out the lack of any coping mechanism of pre-senescent males with environmental contamination.

5. Conclusion

Despite birds being one of the most studied groups in wildlife ecotoxicology, with increasing interest in recent years, there is a lack of widespread knowledge on the long-term consequences of POPs exposure on biomarkers of health and fitness such as telomeres (Salmón and Burraco, 2022). Most critical is the usually overlooked life-history traits that can drive telomere dynamism such as sex and age in previous studies (Blévin et al., 2017, 2016; Eckbo et al., 2019; Sebastiano et al., 2020). Our study shows that sex and senescent status (based on the effect of chronological age on RTL) influence telomere responses to POPs exposure in birds. Our calculated senescent status (senescent adults ≥ 9 years old) concurs with the sex-biased aging patterns found in Alpine swifts, with stronger senescence in females, particularly for reproductive traits (Moullec et al., 2023). Thus, longer RTL and telomere elongation found in senescent females compared to pre-senescent females and males, might be an evolutionary strategy to mitigate stronger senescence effects (Moullec et al., 2023) via a higher investment in cell maintenance. These sex- and senescence-related differences in RTL and TROC were also POPs-specific. OCPs (mainly drins) negatively associated with RTLs, and PCBs led to slower TROC, both with more pronounced effects in females and senescent individuals. Therefore, senescent females seem to have a mitigation mechanism (elongation of telomeres) towards specific-POPs toxicity based on their life-history. Overall, our study paves the way for future research in wildlife ecotoxicology when using telomeres as biomarkers of anthropogenic pollution, highlighting how the consequences of environmental contaminants can be revealed by better considering the life-history of species. However, we are conscious that long-term monitoring of such traits is incredibly challenging in wildlife, especially for age.

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CRediT authorship contribution statement

Roger Colominas-Ciuró: Writing – original draft, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Francesca E. Gray:** Writing – review & editing, Methodology. **Kalender Arian:** Writing – review & editing, Methodology. **Sandrine Zahn:** Writing – review & editing, Methodology. **Christoph Meier:** Writing – review & editing, Methodology, Investigation, Data curation, Conceptualization. **François Criscuolo:** Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Pierre Bize:** Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) did not use any generative AI for scientific writing.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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References

- Acampora, H., White, P., Lyashevskaya, O., O'Connor, I., 2017. Presence of persistent organic pollutants in a breeding common tern (*Sterna hirundo*) population in Ireland. *Environ. Sci. Pollut. Res. Int.* 24, 13025–13035. <https://doi.org/10.1007/s11356-017-8931-7>.
- Acosta-Tlapalamatl, M., Romo-Gómez, C., Anaya-Hernández, A., Juárez-Santacruz, L., Gaytán-Oyarzún, J.C., Acevedo-Sandoval, O.A., García-Nieto, E., 2022. Metabolomics: a new approach in the evaluation of effects in human beings and wildlife associated with environmental exposition to POPs. *Toxics* 10. <https://doi.org/10.3390/toxics10070380>.
- Anastasiadis, M., Lehotay, S.J., Stajnbaher, D., Schenck, F.J., 2003. Fast and easy multiresidue method employing acetonitrile extraction/partitioning and "dispersive solid-phase extraction" for the determination of pesticide residues in produce. *J. AOAC Int.* 86, 412–431.
- Andreotti, G., Hoppin, J.A., Hou, L., Koutros, S., Gadalla, S.M., Savage, S.A., Lubin, J., Blair, A., Hoxha, M., Baccarelli, A., Sandler, D., Alavanja, M., Beane Freeman, L.E., 2015. Pesticide use and relative leukocyte telomere length in the agricultural health study. *PLoS One* 10, e0133382.
- Angelier, F., Costantini, D., Blévin, P., Chastel, O., 2018. Do glucocorticoids mediate the link between environmental conditions and telomere dynamics in wild vertebrates? A review. *Gen. Comp. Endocrinol.* <https://doi.org/10.1016/j.ygcen.2017.07.007>.
- Angelier, F., Weimerskirch, H., Barbraud, C., Chastel, O., 2019. Is telomere length a molecular marker of individual quality? Insights from a long-lived bird. *Funct. Ecol.* 33, 1076–1087. <https://doi.org/10.1111/1365-2435.13307>.
- Angelier, F., Chastel, O., Lendvai, A.Z., Parenteau, C., Weimerskirch, H., Wingfield, J.C., 2020. When do older birds better resist stress? A study of the corticosterone stress response in snow petrels. *Biol. Lett.* 16, 20190733 <https://doi.org/10.1098/rsbl.2019.0733>.
- Annunziato, K., Cooper, K.R., 2018. In: Burggren, W., Dubansky, B. (Eds.), *The Impact of Early Developmental Exposure to Stressors Related to Individual Fitness in Aquatic Organisms and the Subsequent Reproductive Success and Failure on Populations BT - Development and Environment*. Springer International Publishing, Cham, pp. 115–153. https://doi.org/10.1007/978-3-319-75935-7_6.
- Arikan, K., Arikan, Z.Y., Turan, S.L., 2018. Persistent organochlorine contaminant residues in tissues of hedgehogs from Turkey. *Bull. Environ. Contam. Toxicol.* 100, 361–368. <https://doi.org/10.1007/s00128-018-2272-1>.
- Aslan, K., Özcan, S., Kurtul, I., 2000. Arterial vascularization of the uropygial glands (Gl. uropygialis) in geese (*Anser anser*) and ducks (*Anas platyrhynchos*). *Anat. Histol. Embryol.* 29, 291–293. <https://doi.org/10.1046/j.1439-0264.2000.00274.x>.
- Aulsebrook, L.C., Bertram, M.G., Martin, J.M., Aulsebrook, A.E., Brodin, T., Evans, J.P., Hall, M.D., O'Bryan, M.K., Pask, A.J., Tyler, C.R., Wong, B.B.M., 2020. Reproduction in a polluted world: implications for wildlife. *Reproduction* 160, R13–R23. <https://doi.org/10.1530/REP-20-0154>.
- Barrett, E.L.B., Richardson, D.S., 2011. Sex differences in telomeres and lifespan. *Aging Cell.* <https://doi.org/10.1111/j.1474-9726.2011.00741.x>.
- Bateson, M., Eisenberg, D.T.A., Nettle, D., 2019. Controlling for baseline telomere length biases estimates of the rate of telomere attrition. *R. Soc. Open Sci.* 6 <https://doi.org/10.1098/rsos.190937>.
- Bauch, C., Gatt, M.C., Granadeiro, J.P., Verhulst, S., Catry, P., 2020. Sex-specific telomere length and dynamics in relation to age and reproductive success in Cory's shearwaters. *Mol. Ecol.* 29, 1344–1357. <https://doi.org/10.1111/mec.15399>.
- Bauch, C., Gatt, M.C., Verhulst, S., Granadeiro, J.P., Catry, P., 2022. 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? *Sci. Total Environ.* 839, 156359 <https://doi.org/10.1016/j.scitotenv.2022.156359>.
- Bauerová, P., Vinklerová, J., Hraníček, J., Čorba, V., Vojtek, L., Svobodová, J., Vinkler, M., 2017. Associations of urban environmental pollution with health-related physiological traits in a free-living bird species. *Sci. Total Environ.* 601–602, 1556–1565. <https://doi.org/10.1016/j.scitotenv.2017.05.276>.
- Bergman, Å., Rydén, A., Law, R.J., de Boer, J., Covaci, A., Alaa, M., Birnbaum, L., Petreas, M., Rose, M., Sakai, S., Van den Eede, N., van der Veen, I., 2012. A novel abbreviation standard for organobromine, organochlorine and organophosphorus flame retardants and some characteristics of the chemicals. *Environ. Int.* 49, 57–82. <https://doi.org/10.1016/j.envint.2012.08.003>.
- Berman, M., Gaillard, J.-M., Weimerskirch, H., 2009. Contrasted patterns of age-specific reproduction in long-lived seabirds. *Proc. Biol. Sci.* 276, 375–382. <https://doi.org/10.1098/rspb.2008.0925>.
- Bize, P., Criscuolo, F., Metcalfe, N.B., Nasir, L., Monaghan, P., 2009. Telomere dynamics rather than age predict life expectancy in the wild. *Proc. R. Soc. B Biol. Sci.* 276, 1679–1683. <https://doi.org/10.1098/rspb.2008.1817>.
- Bize, P., Daniel, G., Viblanc, V.A., Martin, J.G.A., Doligez, B., 2017. Negative phenotypic and genetic correlation between natal dispersal propensity and nest-defence behaviour in a wild bird. *Biol. Lett.* 13 <https://doi.org/10.1098/rsbl.2017.0236>.
- Blackburn, E.H., 1991. Structure and function of telomeres. *Nature* 350, 569–573. <https://doi.org/10.1038/350569A0>.
- Blackburn, E.H., 2000. Telomere states and cell fates. *Nature* 408, 53–56. <https://doi.org/10.1038/35040500>.
- Blackburn, E.H., 2005. Telomeres and telomerase: their mechanisms of action and the effects of altering their functions. *FEBS Lett.* 579, 859–862. <https://doi.org/10.1016/j.febslet.2004.11.036>.
- Blasco, M.A., 2007. Telomere length, stem cells and aging. *Nat. Chem. Biol.* 3, 640–649. <https://doi.org/10.1038/NCHEMBIO.2007.38>.
- Blévin, P., Angelier, F., Tartu, S., Ruault, S., Bustamante, P., Herzke, D., Moe, B., Bech, C., Gabrielsen, G.W., Bustnes, J.O., Chastel, O., 2016. Exposure to oxychlorane is associated with shorter telomeres in arctic breeding kittiwakes. *Sci. Total Environ.* 563–564, 125–130. <https://doi.org/10.1016/j.scitotenv.2016.04.096>.
- Blévin, P., Angelier, F., Tartu, S., Bustamante, P., Herzke, D., Moe, B., Bech, C., Gabrielsen, G.W., Bustnes, J.O., Chastel, O., 2017. Perfluorinated substances and telomeres in an Arctic seabird: cross-sectional and longitudinal approaches. *Environ. Pollut.* 230, 360–367. <https://doi.org/10.1016/j.envpol.2017.06.060>.
- Blount, J.D., Vitikainen, E.I.K., Stott, I., Cant, M.A., 2016. Oxidative shielding and the cost of reproduction. *Biol. Rev.* 91, 483–497. <https://doi.org/10.1111/brev.12179>.
- Boonekamp, J.J., Mulder, G.A., Salomons, H.M., Dijkstra, C., Verhulst, S., 2014. Nestling telomere shortening, but not telomere length, reflects developmental stress and predicts survival in wild birds. *Proc. R. Soc. B Biol. Sci.* 281, 20133287 <https://doi.org/10.1098/rspb.2013.3287>.
- Bosco, G., Haber, J.E., 1998. Chromosome break-induced DNA replication leads to nonreciprocal translocations and telomere capture. *Genetics* 150, 1037–1047. <https://doi.org/10.1093/genetics/150.3.1037>.
- Bouwman, H., Yohannes, Y.B., Nakayama, S.M.M., Motohira, K., Ishizuka, M., Humphries, M.S., van der Schyff, V., du Preez, M., Dinkelmann, A., Ikenaka, Y., 2019. Evidence of impacts from DDT in pelican, cormorant, stork, and egret eggs from KwaZulu-Natal, South Africa. *Chemosphere* 225, 647–658. <https://doi.org/10.1016/j.chemosphere.2019.03.043>.
- Briels, N., Torgersen, L.N., Castaño-Ortiz, J.M., Løseth, M.E., Herzke, D., Nygård, T., Bustnes, J.O., Ciesielski, T.M., Poma, G., Malarvannan, G., Covaci, A., Jaspers, V.L.B., 2019. Integrated exposure assessment of northern goshawk (*Accipiter gentilis*) nestlings to legacy and emerging organic pollutants using non-destructive samples. *Environ. Res.* 178, 108678 <https://doi.org/10.1016/j.envres.2019.108678>.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference*, 2nd ed. Springer, New York, USA. <https://doi.org/10.1007/b97636>.
- Bursian, S.J., Kern, J., Remington, R.E., Link, J.E., Fitzgerald, S.D., 2013. Dietary exposure of mink (*Mustela vison*) to fish from the upper Hudson River, New York, USA: effects on reproduction and offspring growth and mortality. *Environ. Toxicol. Chem.* 32, 780–793. <https://doi.org/10.1002/etc.2110>.
- Bustnes, J.O., Erikstad, K.E., Skaare, J.U., Bakken, V., Mehlum, F., 2003. Ecological effects of organochlorine pollutants in the Arctic: a study of the glaucousgull. *Ecol. Appl.* [https://doi.org/10.1890/1051-0761\(2003\)013\[0504:EEOOPI\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2003)013[0504:EEOOPI]2.0.CO;2).
- Cawthon, R.M., 2002. Telomere measurement by quantitative PCR. *Nucleic Acids Res.* 30, e47 <https://doi.org/10.1093/nar/30.10.e47>.
- Cesare, A.J., Reddel, R.R., 2008. Telomere uncapping and alternative lengthening of telomeres. *Mech. Ageing Dev.* 129, 99–108. <https://doi.org/10.1016/j.mad.2007.11.006>.
- Chatelain, M., Drobnik, S.M., Szulkin, M., 2020. The association between stressors and telomeres in non-human vertebrates: a meta-analysis. *Ecol. Lett.* 23, 381–398. <https://doi.org/10.1111/ele.13426>.
- Criscuolo, F., Bize, P., Nasir, L., Metcalfe, N.B., Foote, C.G., Griffiths, K., Gault, E.A., Monaghan, P., 2009. Real-time quantitative PCR assay for measurement of avian telomeres. *J. Avian Biol.* 40, 342–347. <https://doi.org/10.1111/j.1600-048X.2008.04623.x>.
- Criscuolo, F., Zahn, S., Bize, P., 2017. Offspring telomere length in the long lived Alpine swift is negatively related to the age of their biological father and foster mother. *Biol. Lett.* 13, 20170188 <https://doi.org/10.1098/rsbl.2017.0188>.
- Criscuolo, F., Pillay, N., Zahn, S., Schradin, C., 2020. Seasonal variation in telomere dynamics in African striped mice. *Oecologia* 194, 609–620. <https://doi.org/10.1007/s00442-020-04801-x>.

- Dantzer, B., Garratt, M., 2017. Sex differences in telomeres and lifespan in Soay sheep: from the beginning to the end. *Mol. Ecol.* <https://doi.org/10.1111/mec.14129>.
- Dean, K.M., Marcell, A.M., Baltos, L.D., Carro, T., Bohannon, M.E.B., Ottinger, M.A., 2019. Comparative lethality of in ovo exposure to PCB 126, PCB 77, and 2 environmentally relevant PCB mixtures in Japanese quail (*Coturnix japonica*). *Environ. Toxicol. Chem.* 38, 2637–2650. <https://doi.org/10.1002/etc.4578>.
- Dominguez-de-Barros, A., Sifaoui, I., Borecka, Z., Dorta-Guerra, R., Lorenzo-Morales, J., Castro-Fuentes, R., Córdoba-Lanús, E., 2023. An approach to the effects of longevity, sexual maturity, and reproduction on telomere length and oxidative stress in different Psittacidae species. *Front. Genet.* 14, 1156730 <https://doi.org/10.3389/fgene.2023.1156730>.
- Eastwood, J.R., Hall, M.L., Teunissen, N., Kingma, S.A., Hidalgo Aranzamendi, N., Fan, M., Roast, M., Verhulst, S., Peters, A., 2019. Early-life telomere length predicts lifespan and lifetime reproductive success in a wild bird. *Mol. Ecol.* 28, 1127–1137. <https://doi.org/10.1111/mec.15002>.
- Eckbo, N., Le Bohec, C., Planas-Bielsa, V., Warner, N.A., Schull, Q., Herzke, D., Zahn, S., Haarr, A., Gabrielsen, G.W., Borgå, K., 2019. Individual variability in contaminants and physiological status in a resident Arctic seabird species. *Environ. Pollut.* 249, 191–199. <https://doi.org/10.1016/j.envpol.2019.01.025>.
- Erikstad, K.E., Sandvik, H., Reierson, T.K., Bustnes, J.O., Strøm, H., 2013. Persistent organic pollution in a high-Arctic top predator: sex-dependent thresholds in adult survival. *Proc. R. Soc. B Biol. Sci.* 280 <https://doi.org/10.1098/rspb.2013.1483>.
- Eulaers, I., Covaci, A., Hofman, J., Nygård, T., Halley, D.J., Pinxten, R., Eens, M., Jaspers, V.L.B., 2011. A comparison of non-destructive sampling strategies to assess the exposure of white-tailed eagle nestlings (*Haliaeetus albicilla*) to persistent organic pollutants. *Sci. Total Environ.* 410–411, 258–265. <https://doi.org/10.1016/j.scitotenv.2011.09.070>.
- Fairlie, J., Holland, R., Pilkington, J.G., Pemberton, J.M., Harrington, L., Nussey, D.H., 2016. Lifelong leukocyte telomere dynamics and survival in a free-living mammal. *Aging Cell* 15, 140–148. <https://doi.org/10.1111/acel.12417>.
- Filigenzi, M.S., Graves, E.E., Tell, L.A., Jelks, K.A., Poppenga, R.H., 2019. Quantitation of neonicotinoid insecticides, plus qualitative screening for other xenobiotics, in small-mass avian tissue samples using UHPLC high-resolution mass spectrometry. *J. Vet. diagnostic Investig. Off. Publ. Am. Assoc. Vet. Lab. Diagnosticians*, Inc 31, 399–407. <https://doi.org/10.1177/1040638719834329>.
- Fleming, W.J., McLane, M.A.R., Cromartie, E., 1982. Endrin decreases screech owl productivity. *J. Wildl. Manag.* 46, 462–468. <https://doi.org/10.2307/3808658>.
- Foot, C.G., Daunt, F., González-Solís, J., Nasir, L., Phillips, R.A., Monaghan, P., 2011. Individual state and survival prospects: age, sex, and telomere length in a long-lived seabird. *Behav. Ecol.* 22, 156–161. <https://doi.org/10.1093/beheco/arq178>.
- Georgian, L., 1975. The comparative cytogenetic effects of aldrin and phosphamidon. *Mutat. Res.* 31, 103–108. [https://doi.org/10.1016/0165-1161\(75\)90072-2](https://doi.org/10.1016/0165-1161(75)90072-2).
- González-Mille, D.J., Ilizaliturri-Hernández, C.A., Espinosa-Reyes, G., Cruz-Santiago, O., Cuevas-Díaz, M.D.C., Martín Del Campo, C.C., Flores-Ramírez, R., 2019. DNA damage in different wildlife species exposed to persistent organic pollutants (POPs) from the delta of the Coatzacoalcas river. Mexico. *Ecotoxicol. Environ. Saf.* 180, 403–411. <https://doi.org/10.1016/j.ecoenv.2019.05.030>.
- Goulson, D., 2013. Review: an overview of the environmental risks posed by neonicotinoid insecticides. *J. Appl. Ecol.* 50, 977–987. <https://doi.org/10.1111/1365-2664.12111>.
- Goutte, A., Angelier, F., Bech, C., Clément-Chastel, C., Dell'Omo, G., Gabrielsen, G.W., Lendvai, A.Z., Moe, B., Noreen, E., Pinaud, D., Tartu, S., Chastel, O., 2014. Annual variation in the timing of breeding, pre-breeding foraging areas and corticosterone levels in an Arctic population of black-legged kittiwakes. *Mar. Ecol. Prog. Ser.* 496, 233–247. <https://doi.org/10.3354/meps10650>.
- Goutte, A., Barbraud, C., Herzke, D., Bustamante, P., Angelier, F., Tartu, S., Clément-Chastel, C., Moe, B., Bech, C., Gabrielsen, G.W., Bustnes, J.O., Chastel, O., 2015. Survival rate and breeding outputs in a high Arctic seabird exposed to legacy persistent organic pollutants and mercury. *Environ. Pollut.* 200, 1–9. <https://doi.org/10.1016/j.envpol.2015.01.033>.
- Gray, F., Derous, D., Bize, P., 2024. Is minimally-invasive sampling the future of persistent organic pollutant (POP) research in birds? A meta-analysis on tissue comparisons. *Chemosphere* (In press).
- Griffiths, R., Double, M.C., Orr, K., Dawson, R.J.G., 1998. A DNA test to sex most birds. *Mol. Ecol.* 7, 1071–1075. <https://doi.org/10.1046/j.1365-294x.1998.00389.x>.
- Grunst, A.S., Grunst, M.L., Bervoets, L., Pinxten, R., Eens, M., 2020. Proximity to roads, but not exposure to metal pollution, is associated with accelerated developmental telomere shortening in nestling great tits. *Environ. Pollut.* 256, 113373 <https://doi.org/10.1016/j.envpol.2019.113373>.
- Halbrook, R.S., Arenal, C.A., 2003. Field studies using European starlings to establish causality between PCB exposure and reproductive effects. *Hum. Ecol. Risk Assess.* 9, 121–136. <https://doi.org/10.1080/13690855>.
- Hansen, E., Skotnes, T., Bustnes, J.O., Helander, B., Eulaers, I., Sun, J., Covaci, A., Bårdsen, B.J., Zahn, S., Criscuolo, F., Bourgeon, S., 2022. Telomere length in relation to persistent organic pollutant exposure in white-tailed eagle (*Haliaeetus albicilla*) nestlings from Sweden sampled in 1995–2013. *Environ. Res.* 208 <https://doi.org/10.1016/j.envres.2022.112712>.
- Hao, Y., Zheng, S., Wang, P., Sun, H., Matsiko, J., Li, W., Li, Y., Zhang, Q., Jiang, G., 2021. Ecotoxicology of persistent organic pollutants in birds. *Environ. Sci. Process. Impacts*. <https://doi.org/10.1039/d0em00451k>.
- Hares, M.C., Vitikainen, E.L.K., Marshall, H.H., Thompson, F.J., Blount, J.D., Cant, M.A., 2018. Telomere dynamics in wild banded mongooses: evaluating longitudinal and quasi-longitudinal markers of senescence. *Exp. Gerontol.* 107, 67–73. <https://doi.org/10.1016/j.exger.2017.09.021>.
- Harris, S.M., Descamps, S., Sneddon, L.U., Bertrand, P., Chastel, O., Patrick, S.C., 2020. Personality predicts foraging site fidelity and trip repeatability in a marine predator. *J. Anim. Ecol.* 89, 68–79. <https://doi.org/10.1111/1365-2656.13106>.
- Hausmann, M.F., Winkler, D.W., O'Reilly, K.M., Huntington, C.E., Nisbet, I.C.T., Vleck, C.M., 2003. Telomeres shorten more slowly in long-lived birds and mammals than in short-lived ones. *Proc. R. Soc. B Biol. Sci.* 270, 1387–1392. <https://doi.org/10.1098/rspb.2003.2385>.
- Hausmann, M.F., Winkler, D.W., Vleck, C.M., 2005. Longer telomeres associated with higher survival in birds. *Biol. Lett.* 1, 212–214. <https://doi.org/10.1098/rsbl.2005.0301>.
- Hemann, M.T., Strong, M.A., Hao, L.Y., Greider, C.W., 2001. The shortest telomere, not average telomere length, is critical for cell viability and chromosome stability. *Cell* 107, 67–77. [https://doi.org/10.1016/S0092-8674\(01\)00504-9](https://doi.org/10.1016/S0092-8674(01)00504-9).
- Iwaniuk, A.N., Koperski, D.T., Cheng, K.M., Elliott, J.E., Smith, L.K., Wilson, L.K., Wylie, D.R.W., 2006. The effects of environmental exposure to DDT on the brain of a songbird: changes in structures associated with mating and song. *Behav. Brain Res.* 173, 1–10. <https://doi.org/10.1016/j.bbr.2006.05.026>.
- Jaspers, V.L.B., Covaci, A., Deleu, P., Neels, H., Eens, M., 2008. Preen oil as the main source of external contamination with organic pollutants onto feathers of the common magpie (*Pica pica*). *Environ. Int.* 34, 741–748. <https://doi.org/10.1016/j.envint.2007.12.002>.
- Kotschal, A., Ilmonen, P., Penn, D.J., 2007. Stress impacts telomere dynamics. *Biol. Lett.* 3, 128–130. <https://doi.org/10.1098/rsbl.2006.0594>.
- Lan, J., Tang, L., Wu, S., Huang, R., Zhong, G., Jiang, X., Tang, Z., Hu, L., 2022. Curcumin alleviates arsenic-induced injury in duck skeletal muscle via regulating the PINK1/Parkin pathway and protecting mitochondrial function. *Toxicol. Appl. Pharmacol.* 434, 115820 <https://doi.org/10.1016/j.taap.2021.115820>.
- Landrigan, P.J., Fuller, R., Acosta, N.J.R., Adeyi, O., Arnold, R., Basu, N., Baldé, A.B., Bertollini, R., Bose-O'Reilly, S., Boufford, J.L., Breyse, P.N., Chiles, T., Mahidol, C., Coll-Seck, A.M., Cropper, M.L., Fobil, J., Fuster, V., Greenstone, M., Haines, A., Hanrahan, D., Hunter, D., Khare, M., Krupnick, A., Lanphear, B., Lohani, B., Martin, K., Mathiasen, K.V., McTeer, M.A., Murray, C.J.L., Ndahimananjara, J.D., Perera, F., Potočnik, J., Preker, A.S., Ramesh, J., Rockström, J., Salinas, C., Samson, L.D., Sandilya, K., Sly, P.D., Smith, K.R., Steiner, A., Stewart, R.B., Suk, W. A., van Schayck, O.C.P., Yadama, G.N., Yumkella, K., Zhong, M., 2018. The Lancet Commission on pollution and health. *Lancet* 391, 462–512. [https://doi.org/10.1016/S0140-6736\(17\)32345-0](https://doi.org/10.1016/S0140-6736(17)32345-0).
- Latre, L., Tusell, L., Martin, M., Miró, R., Egozcue, J., Blasco, M.A., Genescà, A., 2003. Shortened telomeres join to DNA breaks interfering with their correct repair. *Exp. Cell Res.* 287, 282–288. [https://doi.org/10.1016/S0014-4827\(03\)00134-4](https://doi.org/10.1016/S0014-4827(03)00134-4).
- Lehner, A., Bokhart, M.T., Buchweitz, J., Johnson, M., 2015. Determination of organochlorine pesticides in wildlife liver and serum using gas chromatography tandem quadrupole mass spectrometry. *J. Chromatogr. Sep. Tech.* 06 <https://doi.org/10.4172/2157-7064.1000286>.
- Letcher, R.J., Bustnes, J.O., Dietz, R., Jenssen, B.M., Jørgensen, E.H., Sonne, C., Verreault, J., Vijayan, M.M., Gabrielsen, G.W., 2010. Exposure and effects assessment of persistent organohalogen contaminants in arctic wildlife and fish. *Sci. Total Environ.* 408, 2995–3043. <https://doi.org/10.1016/j.scitotenv.2009.10.038>.
- Liechti, F., Witvliet, W., Weber, R., Bächler, E., 2013. First evidence of a 200-day non-stop flight in a bird. *Nat. Commun.* 41 (4), 1–7. <https://doi.org/10.1038/ncomms3554>.
- Lifang, H., Gabriella, A., A. B.A., Sharon, S., A. H.J., P. S.D., Joseph, B., Zhong-Zheng, Z., Mirjam, H., Laura, D., Xiao, Z., Stella, K., Beane, F.L.E., Ca, A.M., 2013. Lifetime pesticide use and telomere shortening among male pesticide applicators in the agricultural health study. *Environ. Health Perspect.* 121, 919–924. <https://doi.org/10.1289/ehp.1206432>.
- Lin, J., Epel, E., 2022. Stress and telomere shortening: insights from cellular mechanisms. *Ageing Res. Rev.* 73, 101507 <https://doi.org/10.1016/j.arr.2021.101507>.
- Lister, K.N., Lamare, M.D., Burritt, D.J., 2016. Dietary pollutants induce oxidative stress, altering maternal antioxidant provisioning and reproductive output in the temperate sea urchin *Evechinus chloroticus*. *Aquat. Toxicol.* 177, 106–115. <https://doi.org/10.1016/j.aquatox.2016.05.013>.
- Løseth, M.E., Briels, N., Flo, J., Malarvannan, G., Poma, G., Covaci, A., Herzke, D., Nygård, T., Bustnes, J.O., Jenssen, B.M., Jaspers, V.L.B., 2019. White-tailed eagle (*Haliaeetus albicilla*) feathers from Norway are suitable for monitoring of legacy, but not emerging contaminants. *Sci. Total Environ.* 647, 525–533. <https://doi.org/10.1016/j.scitotenv.2018.07.333>.
- Louzon, M., Coeurdassier, M., Gimbert, F., Pauget, B., de Vaulleury, A., 2019. Telomere dynamic in humans and animals: review and perspectives in environmental toxicology. *Environ. Int.* 131, 105025 <https://doi.org/10.1016/j.envint.2019.105025>.
- Manz, K.E., Yamada, K., Scheidl, L., La Merrill, M.A., Lind, L., Pennell, K.D., 2021. Targeted and nontargeted detection and characterization of trace organic chemicals in human serum and plasma using QuEChERS extraction. *Toxicol. Sci.* 185, 77–88. <https://doi.org/10.1093/toxsci/kfab121>.
- Meier, C.M., Karaardic, H., Aymf, R., Peev, S.G., Bächler, E., Weber, R., Witvliet, W., Liechti, F., 2018. What makes Alpine swift ascend at twilight? Novel geolocators reveal year-round flight behaviour. *Behav. Ecol. Sociobiol.* 72, 45. <https://doi.org/10.1007/s00265-017-2438-6>.
- Meier, C.M., Karaardic, H., Aymf, R., Peev, S.G., Witvliet, W., Liechti, F., 2020. Population-specific adjustment of the annual cycle in a super-swift trans-Saharan migrant. *J. Avian Biol.* 51 <https://doi.org/10.1111/jav.02515>.
- Miri, M., Nazarzadeh, M., Alahabadi, A., Ehrampoush, M.H., Rad, A., Lotfi, M.H., Sheikhkh, M.H., Sakhradi, M.J.Z., Nawrot, T.S., Dadvand, P., 2019. Air pollution and telomere length in adults: a systematic review and meta-analysis of observational

- studies. *Environ. Pollut.* 244, 636–647. <https://doi.org/10.1016/j.envpol.2018.09.130>.
- Monaghan, P., Haussmann, M.F., 2006. Do telomere dynamics link lifestyle and lifespan? *Trends Ecol. Evol.* 21, 47–53. <https://doi.org/10.1016/j.tree.2005.11.007>.
- Monaghan, P., Eisenberg, D.T.A., Harrington, L., Nussey, D., 2018. Understanding diversity in telomere dynamics. *Philos. Trans. R. Soc. B Biol. Sci.* 373, 20160435 <https://doi.org/10.1098/rstb.2016.0435>.
- Moullec, H., Reichert, S., Bize, P., 2023. Aging trajectories are trait- and sex-specific in the long-lived Alpine swift. *Front. Ecol. Evol.* 11, 983266 <https://doi.org/10.3389/fevo.2023.983266>.
- Muralidharan, S., 1993. Aldrin poisoning of Sarus cranes (*Grus antigone*) and a few granivorous birds in Keoladeo National Park, Bharatpur, India. *Ecotoxicology* 2, 196–202. <https://doi.org/10.1007/BF00116424>.
- Newton, I., Wyllie, I., Asher, A., 1992. Mortality from the pesticides aldrin and dieldrin in British Sparrowhawks and Kestrels. *Ecotoxicology* 1, 31–44. <https://doi.org/10.1007/BF00702654>.
- NTP, 2016. Genetic Toxicity Evaluation of Aldrin in *Salmonella/E. coli* Mutagenicity Test or Ames Test Study 127997. National Toxicology Program, Research Triangle Park, NC.
- Pacyna-Kuchta, A.D., 2023. What should we know when choosing feather, blood, egg or preen oil as biological samples for contaminants detection? A non-lethal approach to bird sampling for PCBs, OCPs, PBDEs and PFASs, Critical Reviews in Environmental Science and Technology. <https://doi.org/10.1080/10643389.2022.2077077>.
- Pepke, M. Le, Kvalnes, T., Wright, J., Araya-Ajoy, Y.G., Ranke, P.S., Boner, W., Monaghan, P., Sæther, B.-E., Jensen, H., Ringsby, T.H., 2023. Longitudinal telomere dynamics within natural lifespans of a wild bird. *Sci. Rep.* 13, 4272. <https://doi.org/10.1038/s41598-023-31435-9>.
- Pérez, C., Lores, M., Velando, A., 2010. Oil pollution increases plasma antioxidants but reduces coloration in a seabird. *Oecologia* 163, 875–884. <https://doi.org/10.1007/s00442-010-1677-2>.
- Pfaffl, M.W., 2001. A new mathematical model for relative quantification in real-time RT-PCR. *Nucleic Acids Res.* 29, e45 <https://doi.org/10.1093/nar/29.9.e45>.
- Powolny, T., Bassin, N., Crini, N., Fourel, I., Morin, C., Pottinger, T.G., Massemin, S., Zahn, S., Coeurdassier, M., 2020. Corticosterone mediates telomere length in raptor chicks exposed to chemical mixture. *Sci. Total Environ.* 706, 135083 <https://doi.org/10.1016/j.scitotenv.2019.135083>.
- Remot, F., Ronget, V., Froy, H., Rey, B., Gaillard, J.-M., Nussey, D.H., Lemaître, J.-F., 2020. No sex differences in adult telomere length across vertebrates: a meta-analysis. *R. Soc. Open Sci.* 7, 200548 <https://doi.org/10.1098/rsos.200548>.
- Remot, F., Ronget, V., Froy, H., Rey, B., Gaillard, J.-M., Nussey, D.H., Lemaître, J.-F., 2022. Decline in telomere length with increasing age across nonhuman vertebrates: a meta-analysis. *Mol. Ecol.* 31, 5917–5932. <https://doi.org/10.1111/mec.16145>.
- Robinson, R.A., Meier, C.M., Witvliet, W., Kéry, M., Schaub, M., 2020. Survival varies seasonally in a migratory bird: linkages between breeding and non-breeding periods. *J. Anim. Ecol.* 89, 2111–2121. <https://doi.org/10.1111/1365-2656.13250>.
- Rubtsova, M.P., Vasilkova, D.P., Malaykova, A.N., Naraikina, Y.V., Zvereva, M.I., Dontsova, O.A., 2012. Telomere lengthening and other functions of telomerase. *Acta Nat.* 4, 44–61.
- Sadowska-Rociak, A., Surma, M., Cieślak, E., 2013. Application of QuEChERS method for simultaneous determination of pesticide residues and PAHs in fresh herbs. *Bull. Environ. Contam. Toxicol.* 90, 508–513. <https://doi.org/10.1007/s00128-012-0951-x>.
- Salmón, P., Burraco, P., 2022. Telomeres and anthropogenic disturbances in wildlife: a systematic review and meta-analysis. *Mol. Ecol.* 31, 6018–6039. <https://doi.org/10.1111/mec.16370>.
- Salomons, H.M., Mulder, G.A., van de Zande, L., Haussmann, M.F., Linskens, M.H.K., Verhulst, S., 2009. Telomere shortening and survival in free-living corvids. *Proc. R. Soc. B Biol. Sci.* 276, 3157–3165. <https://doi.org/10.1098/rspb.2009.0517>.
- Sánchez-Virostka, P., Espín, S., Ruiz, S., Panda, B., Ilmonen, P., Schultz, S.L., Karouna-Renier, N., García-Fernández, A.J., Eeva, T., 2020. Arsenic-related oxidative stress in experimentally-dosed wild great tit nestlings. *Environ. Pollut.* 259, 113813 <https://doi.org/10.1016/j.envpol.2019.113813>.
- Saulnier, A., Bleu, J., Boos, A., El Masoudi, I., Ronot, P., Zahn, S., Del Nero, M., Massemin, S., 2020. Consequences of trace metal cocktail exposure in zebra finch (*Taeniopygia guttata*) and effect of calcium supplementation. *Ecotoxicol. Environ. Saf.* 193 <https://doi.org/10.1016/j.ecoenv.2020.110357>.
- Sebastiano, M., Angelier, F., Blévin, P., Ribout, C., Sagerup, K., Descamps, S., Herzke, D., Moe, B., Barbraud, C., Bustnes, J.O., Gabrielsen, G.W., Chastel, O., 2020. Exposure to PFAS is associated with telomere length dynamics and demographic responses of an arctic top predator. *Environ. Sci. Technol.* 54, 10217–10226. <https://doi.org/10.1021/acs.est.0c03099>.
- Sheldon, E.L., Eastwood, J.R., Teunissen, N., Roast, M.J., Aranzamendi, N.H., Fan, M., Louise Hall, M., Kingma, S.A., Verhulst, S., Peters, A., 2022. Telomere dynamics in the first year of life, but not later in life, predict lifespan in a wild bird. *Mol. Ecol.* 31, 6008–6017. <https://doi.org/10.1111/mec.16296>.
- Shin, J.Y., Choi, Y.Y., Jeon, H.S., Hwang, J.H., Kim, S.A., Kang, J.H., Chang, Y.S., Jacobs, D.R., Park, J.Y., Lee, D.H., 2010. Low-dose persistent organic pollutants increased telomere length in peripheral leukocytes of healthy Koreans. *Mutagenesis* 25, 511–516. <https://doi.org/10.1093/mutage/geq035>.
- Sigmund, G., Ågerstrand, M., Antonelli, A., Backhaus, T., Brodin, T., Diamond, M.L., Erdelen, W.R., Evers, D.C., Hofmann, T., Hueffer, T., Lai, A., Torres, J.P.M., Mueller, L., Perrigo, A.L., Rillig, M.C., Schaeffer, A., Scherlinger, M., Schirmer, K., Thili, A., Soehl, A., Triebkorn, R., Vlahos, P., vom Berg, C., Wang, Z., Groh, K.J., 2023. Addressing chemical pollution in biodiversity research. *Glob. Chang. Biol.* 29, 3240–3255. <https://doi.org/10.1111/gcb.16689>.
- Sletten, S., Bourgeon, S., Bårdsen, B.J., Herzke, D., Criscuolo, F., Massemin, S., Zahn, S., Johnsen, T.V., Bustnes, J.O., 2016. Organohalogenated contaminants in white-tailed eagle (*Haliaeetus albicilla*) nestlings: an assessment of relationships to immunoglobulin levels, telomeres and oxidative stress. *Sci. Total Environ.* 539, 337–349. <https://doi.org/10.1016/j.scitotenv.2015.08.123>.
- Smits, J.E., Fennie, K.J., Bortolotti, G.R., Marchant, T.A., 2002. Thyroid hormone suppression and cell-mediated immunomodulation in American kestrels (*Falco sparverius*) exposed to PCBs. *Arch. Environ. Contam. Toxicol.* 43, 338–344. <https://doi.org/10.1007/s00244-002-1200-9>.
- Stauffer, J., Panda, B., Eeva, T., Rainio, M., Ilmonen, P., 2017. Telomere damage and redox status alterations in free-living passerines exposed to metals. *Sci. Total Environ.* 575, 841–848. <https://doi.org/10.1016/j.scitotenv.2016.09.131>.
- Strimbu, K., Tavel, J.A., 2010. What are biomarkers? *Curr. Opin. HIV AIDS* 5, 463–466. <https://doi.org/10.1097/COH.0b013e32833ed177>.
- Sudyka, J., Arct, A., Drobnik, S.M., Gustafsson, L., Cichoń, M., 2019. Birds with high lifetime reproductive success experience increased telomere loss. *Biol. Lett.* 15, 20180637 <https://doi.org/10.1098/rsbl.2018.0637>.
- Svenson, U., Nordfjäll, K., Baird, D., Roger, L., Osterman, P., Hellenius, M.-L., Roos, G., 2011. Blood cell telomere length is a dynamic feature. *PLoS One* 6, e21485. <https://doi.org/10.1371/journal.pone.0021485>.
- Taliansky-Chamudis, A., Gómez-Ramírez, P., León-Ortega, M., García-Fernández, A.J., 2017. Validation of a QuEChERS method for analysis of neonicotinoids in small volumes of blood and assessment of exposure in Eurasian eagle owl (*Bubo bubo*) nestlings. *Sci. Total Environ.* 595, 93–100. <https://doi.org/10.1016/j.scitotenv.2017.03.246>.
- Tartu, S., Gabrielsen, G.W., Blévin, P., Ellis, H., Bustnes, J.O., Herzke, D., Chastel, O., 2014. Endocrine and fitness correlates of long-chain perfluorinated carboxylates exposure in Arctic breeding black-legged kittiwakes. *Environ. Sci. Technol.* 48, 13504–13510. <https://doi.org/10.1021/es503297n>.
- Tartu, S., Angelier, F., Bustnes, J.O., Moe, B., Hanssen, S.A., Herzke, D., Gabrielsen, G.W., Verboven, N., Verreault, J., Labadie, P., Budzinski, H., Wingfield, J.C., Chastel, O., 2015a. Polychlorinated biphenyl exposure and corticosterone levels in seven polar seabird species. *Environ. Pollut.* 197, 173–180. <https://doi.org/10.1016/j.envpol.2014.12.007>.
- Tartu, S., Angelier, F., Wingfield, J.C., Bustamante, P., Labadie, P., Budzinski, H., Weimerskirch, H., Bustnes, J.O., Chastel, O., 2015b. Corticosterone, prolactin and egg neglect behavior in relation to mercury and legacy POPs in a long-lived Antarctic bird. *Sci. Total Environ.* 505, 180–188. <https://doi.org/10.1016/j.scitotenv.2014.10.008>.
- Tettamanti, F., Witvliet, W., Bize, P., 2012. Selection on age at first and at last reproduction in the long-lived Alpine Swift *Apus melba*. *Ibis (Lond. 1859)* 154, 338–344. <https://doi.org/10.1111/j.1474-919X.2012.01215.x>.
- Tricola, G.M., Simons, M.J.P., Atema, E., Boughton, R.K., Brown, J.L., Dearborn, D.C., Divoky, G., Eimes, J.A., Huntington, C.E., Kitaysky, A.S., Juola, F.A., Lank, D.B., Litwa, H.P., Mulder, E.G.A., Nisbet, I.C.T., Okanoya, K., Safran, R.J., Schoech, S.J., Schreiber, E.A., Thompson, P.M., Verhulst, S., Wheelwright, N.T., Winkler, D.W., Young, R., Vleck, C.M., Haussmann, M.F., 2018. The rate of telomere loss is related to maximum lifespan in birds. *Philos. Trans. R. Soc. B Biol. Sci.* 373, 20160445 <https://doi.org/10.1098/rstb.2016.0445>.
- Verhulst, S., Aviv, A., Benetos, A., Berenson, G.S., Kark, J.D., 2013. Do leukocyte telomere length dynamics depend on baseline telomere length? An analysis that corrects for “regression to the mean.” *Eur. J. Epidemiol.* 28, 859–866. <https://doi.org/10.1007/s10654-013-9845-4>.
- Viblan, V.A., Schull, Q., Stier, A., Durand, L., Lefol, E., Robin, J.-P., Zahn, S., Bize, P., Criscuolo, F., 2020. Foster rather than biological parental telomere length predicts offspring survival and telomere length in king penguins. *Mol. Ecol.* 29, 3154–3166. <https://doi.org/10.1111/mec.15485>.
- Wang, J., Caccamise, S.A.L., Woodward, L.A., Li, Q.X., 2015. Polychlorinated biphenyls in the plasma and preen oil of black-footed albatross (*Diomedea nigripes*) chicks and adults on Midway Atoll, North Pacific Ocean. *PLoS One* 10, e0123041.
- Watson, R.L., Bird, E.J., Underwood, S., Wilbourn, R.V., Fairlie, J., Watt, K., Salvo-Chirnside, E., Pilkington, J.G., Pemberton, J.M., McNeilly, T.N., Froy, H., Nussey, D. H., 2017. Sex differences in leukocyte telomere length in a free-living mammal. *Mol. Ecol.* 26, 3230–3240. <https://doi.org/10.1111/mec.13992>.
- Wu, S., Yu, W., Jiang, X., Huang, R., Zhang, X., Lan, J., Zhong, G., Wan, F., Tang, Z., Hu, L., 2021. Protective effects of curcumin on ATO-induced nephrotoxicity in ducks in relation to suppressed autophagy, apoptosis and dyslipidemia by regulating oxidative stress. *Ecotoxicol. Environ. Saf.* 219, 112350 <https://doi.org/10.1016/j.ecoenv.2021.112350>.
- Xu, Z., Duc, K.D., Holman, D., Teixeira, M.T., 2013. The length of the shortest telomere as the major determinant of the onset of replicative senescence. *Genetics* 194, 847–857. <https://doi.org/10.1534/genetics.113.152322>.
- Yamashita, R., Takada, H., Murakami, M., Fukuwaka, M.-A., Watanuki, Y., 2007. Evaluation of noninvasive approach for monitoring PCB pollution of seabirds using preen gland oil. *Environ. Sci. Technol.* 41, 4901–4906. <https://doi.org/10.1021/es0701863>.
- Young, R.C., Kitaysky, A.S., Haussmann, M.F., Descamps, S., Orben, R.A., Elliott, K.H., Gaston, A.J., 2013. Age, sex, and telomere dynamics in a long-lived seabird with male-biased parental care. *PLoS One* 8, e74931. <https://doi.org/10.1371/journal.pone.0074931>.
- Yuan, J., Liu, Y., Wang, J., Zhao, Y., Li, K., Jing, Y., Zhang, X., Liu, Q., Geng, X., Li, G., Wang, F., 2018. Long-term persistent organic pollutants exposure induced telomere

- dysfunction and senescence-associated secretory phenotype. *Journals Gerontol. Ser. A* 73, 1027–1035. <https://doi.org/10.1093/gerona/gly002>.
- Ziegler, S., Schettgen, T., Beier, F., Wilop, S., Quinete, N., Esser, A., Masouleh, B.K., Ferreira, M.S.V., Vankann, L., Uciechowski, P., Rink, L., Kraus, T., Brümmendorf, T. H., Ziegler, P., 2017. Accelerated telomere shortening in peripheral blood lymphocytes after occupational polychlorinated biphenyls exposure. *Arch. Toxicol.* 91, 289–300. <https://doi.org/10.1007/s00204-016-1725-8>.
- Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* 1, 3–14. <https://doi.org/10.1111/j.2041-210X.2009.00001.x>.