Causes and consequences of variation in early-life telomere length in a bird metapopulation

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ABSTRACT

1. Environmental conditions during early-life development can have lasting effects on individual quality and fitness. Telomere length (TL) may correlate with early-life conditions and may be an important mediator or biomarker of individual quality or pace-of-life, as periods of increased energy demands can increase telomere attrition due to oxidative stress. Thus, knowledge of the mechanisms that generate variation in TL, and the relation between TL and fitness, is important in understanding the role of telomeres in ecology and life-history evolution.

2. Here, we investigate how environmental conditions and morphological traits are associated with early-life TL and if TL predicts natal dispersal probability or components of fitness in two populations of wild house sparrows (*Passer domesticus*).
3. We measured morphological traits and blood TL in 2746 nestlings from 20 cohorts (1994-2013) and retrieved data on weather conditions. We monitored population fluctuations, and individual survival and reproductive output using field observations and genetic pedigrees. We then used generalized linear mixed-effects models to test which factors affected TL in early-life, and if TL predicted dispersal propensity, or was associated with recruitment probability, mortality risk, or reproductive success.
4. We found a negative effect of population density on TL, but only in one of the populations. There was a curvilinear association between TL and the maximum daily North Atlantic Oscillation (NAO) index during incubation, suggesting that there are optimal weather conditions that result in the longest TL. Dispersers tended to have shorter telomeres than non-dispersers. TL did not predict survival, but we found a tendency for individuals with short telomeres to have higher annual reproductive success.
5. Our study showed how early-life TL is shaped by effects of growth, weather conditions and population density, supporting that environmental stressors negatively affect TL in wild populations. In addition, TL may be a mediator or biomarker of individual pace-of-life, with higher dispersal rates and annual reproduction tending to be associated with shorter early-life TL in this study. However, clear associations between early-life TL and individual fitness seems difficult to establish and may differ between different populations in the wild.

INTRODUCTION

Telomeres are short repetitive nucleotide sequences capping the ends of linear chromosomes (Blackburn & Szostak, 1984). Recent studies have shown that individual variation in telomere dynamics might play an important role shaping the life-history of many species, including wild birds (Eastwood et al., 2019; Spurgin et al., 2018; Vedder et al., 2021), reptiles (Olsson et al., 2018a), mammals (Foley et al., 2020; van Lieshout et al., 2019) and fish (McLennan et al., 2016). Telomeres shorten during growth due to cell divisions and oxidative damage (Jennings et al., 1999; von Zglinicki, 2002). Individual differences in telomere length (TL) are established early in life (Entringer et al., 2018; Martens et al., 2021) and may reflect cumulative effects of physiological stress incurred during early life (Chatelain et al., 2020; Nettle et al., 2017; Ridout et al., 2018).

From an eco-evolutionary perspective, individual telomere dynamics are interesting because they have been shown to be associated with survival and reproductive success in some free-living animal populations (Chatelain et al., 2020; Fairlie et al., 2016; Froy et al., 2021; Haussmann et al., 2005; Heidinger et al., 2021; Olsson et al., 2018b; Sudyka, 2019). Furthermore, TL has been shown to predict individual health, quality, or lifespan within several species (Asghar et al., 2015; Eastwood et al., 2019; Fairlie et al., 2016; Heidinger et al., 2012; van Lieshout et al., 2019; Wilbourn et al., 2018). Long telomeres are expected to infer better immune competency (Blackburn et al., 2015), resistance to oxidative damage and metabolic aging (Muñoz-Lorente et al., 2019) and hence higher survival probability (Wilbourn et al., 2018). Covariation between TL dynamics and fitness therefore suggests that TL could act as mediator of the life-history trade-offs between growth, survival, and reproduction (Heidinger et al., 2021; Monaghan, 2014; Monaghan & Haussmann, 2006). Alternatively, TL may be a transient, environmentally pliant trait reflecting experienced stress (i.e. a biomarker, Bateson & Poirier, 2019; Boonekamp et al., 2013), but with few direct fitness consequences.

Whether telomere dynamics underpin constraints in individual variation in life-history strategies remains debated (Monaghan, 2010; Vedder et al., 2017). Giraudeau et al. (2019a) speculated that TL could act as an important physiological mediator of the individual variation in suites of life-history traits (pace-of-life syndromes, e.g. Reale et al., 2010) within species. It has also been suggested that telomere dynamics may underlie behavioral patterns or individual animal personalities (Adriaenssens et al., 2016; Bateson & Nettle, 2018; Espigares et al., 2021). However, studies have yet to identify the mechanisms underlying TL dynamics in natural populations and the potential of using TL as a biomarker of physiological costs of individual experiences, or somatic redundancy, in the wild (Bateson & Poirier, 2019; Boonekamp et al., 2013; Pepke et al., 2021c). To understand the ecological and evolutionary significance of TL it is therefore important to identify causes and consequences of individual variation in TL.

Several environmental stressors may induce oxidative stress-mediated effects on TL, in particular harsh abiotic conditions, poor nutrition, or pathogen infection has been identified (Chatelain et al., 2020; Pepper et al., 2018). Harsh weather conditions are expected to negatively affect TL through an increased stress response elevating glucocorticoid hormone concentrations (Lemaître et al., 2021; Quirici et al., 2016) and metabolic rate resulting in increased production of reactive oxygen species (ROS, e.g. Casagrande et al., 2020; Metcalfe & Olsson, 2021). Weather conditions may thus have direct effects on TL, e.g. through thermoregulation and metabolic activity (Angelier et al., 2018), or indirect effects, e.g. changes in food availability (Criscuolo et al., 2020; Spurgin et al., 2018) or pathogen prevalence (Asghar et al., 2015; Giraudeau et al., 2019b). Depending on the species-specific optima and the range of weather conditions experienced there could be linear or non-linear associations between environmental conditions and TL (Axelsson et al., 2020).

Local demography such as population density may influence the competitive regimes experienced by parents during breeding (Dhondt, 2010). In populations of house sparrows

(*Passer domesticus*), density regulation affected recruit production, which generated variation in pace of life-history strategies across populations (Araya-Ajoy et al., 2021). However, physiological mechanisms mediating such demographic and evolutionary processes remain largely unknown (e.g. Edwards et al., 2021). Changes in TL dynamics may underpin physiological stress responses to changes in demography (Bergman et al., 2019; Gangoso et al., 2021). For instance, Spurgin et al. (2018) found weak evidence for a negative effect of population density on early-life TL and telomere attrition in an island population of Seychelles warblers (*Acrocephalus sechellensis*). They also found that TL was positively associated with abundance of insects, the main food resource for the warblers, indicating that increased food availability may have masked negative effects of increased density on TL (Brown et al., 2021).

Short telomeres may predispose individuals to opt for a faster pace-of-life (Giraudeau et al., 2019a), which could involve an increased probability of dispersal (Cote et al., 2010; Dingemanse et al., 2020). Alternatively, TL may act as a cue that tracks features of the surroundings, such as changes in the environment (e.g. weather conditions and food availability) or demographic changes (e.g. population density) that could influence dispersal. Thus, individuals with long telomeres may be less likely to disperse, if long telomeres are an internal state indicator of an overall benign habitat (mild weather conditions, abundant food resources, or low competition, Wilbourn et al., 2017), which may not induce emigration (Lin & Batzli, 2001). However, if dispersal is condition-dependent (Ims & Hjermann, 2001), and the telomere–survival relationship is causal (Wilbourn et al., 2018) even in early life (Monaghan & Ozanne, 2018), short telomeres may have physiological consequences that prevent dispersal, rendering individuals with long telomeres more likely to become successful dispersers. However, little is known about the physiological mechanisms that could mediate suites of traits associated with dispersal (Clobert et al., 2012). Investigating spatiotemporal variation in traits such as TL that may be involved in producing individual variation in life-history traits therefore seems to be fundamental to a proper understanding of population ecology and life-history evolution.

In this study, we investigate causes and consequences of spatiotemporal variation in early-life TL across two decades in two populations of wild house sparrows located within a large island metapopulation study system (see Fig. S1.1 in Appendix S1 in the Supporting Information). The two populations in our study occupy contrasting habitats: One farm-living population with access to shelter and food throughout the year, and one garden-living population that may be more exposed to weather conditions (Pärn et al., 2009). We have previously showed that there is a low heritability of early-life TL (h^2=0.04) in this metapopulation, and that individual variation in TL is mainly driven by environmental (among year) variance resulting in consistent cohort effects in early-life TL (Pepke et al., 2021a). This long-term study allows us to disentangle the effects of weather conditions during pre- and post-natal stages on variation in TL. First, we investigate functional relationships between early-life TL, fledgling body size and condition, local population density fluctuations, weather variables and habitat type. Second, we test if early-life TL is associated with natal dispersal within the metapopulation. We hypothesize that short TL may be associated with exploratory behavior (Adriaenssens et al., 2016) that increases the chance of dispersal (Dingemanse et al., 2003). Finally, we quantify consequences on recruitment probability, mortality risk, and reproductive success of variation in early-life TL and whether these differ between habitat types.

MATERIALS AND METHODS

Study system and field data collection

We monitored two insular house sparrow populations; one on Hestmannøy (66°33’N, 12°50‘E, 12.9 km^2) in the years 1994-2020, and one on Træna (i.e. Husøy island, 66°30’N, 12°05‘E, 1.5 km^2) from 2004-2020, both located in an archipelago in northern Norway (Fig.

S1.1). These islands are characterized by heathland, mountains, and sparse forest. On Hestmannøy ("farm island"), close to the mainland, cultivated grassland (silage production and grazing) dominates the landscape, and the sparrows live closely associated with humans on dairy farms, where they have access to food (grain) and shelter (barns) all year. Most nests are found in cavities inside sheltered or heated barns. In contrast, on Træna ("non-farm island"), ca. 34 km further out into the sea (Fig. S1.1), there are no farms, but a small village largely consisting of detached houses. Here, the sparrows live in gardens and urban spaces, and nest in artificial nest boxes on the outside walls of the houses. Nests were visited at least every 9th day during the breeding season (May-August) to record hatch day. Fledglings were ringed with a unique color combination at around 10 days old (5-14 days) and tarsometatarsus (tarsus) was measured using calipers to nearest 0.01 mm. Body mass was measured using a Pesola spring balance to nearest 0.1 g. Nestling body condition was then calculated as the residuals of a regression of $\log_{10}$-transformed mass against $\log_{10}$-transformed tarsus length (Schulte-Hostedde et al., 2005). Because tarsus length increases with nestling age, we used the residuals from a regression of tarsus length on age and age squared as a measure of age-corrected (age-standardized) tarsus length (Appendix S1). Birds were observed or captured using mist nets during summer and autumn (May-October). Blood samples (25 μL) were collected by venipuncture and stored in 96% ethanol at room temperature in the field and at -20°C in the laboratory until DNA extraction.

Molecular methods

Molecular sexing and microsatellite pedigree construction for this study was carried out as described in Jensen et al. (2003) and Rønning et al. (2016) and briefly summarized in Appendix S1. Genetic pedigrees were reconstructed for individuals born or captured from 1993-2013. The sampling of nestlings included 1314 males, 1348 females, and 84 individuals of unknown sex (total n=2746). Relative TLs of DNA extracted from whole blood (mainly erythrocytes) were measured on 70-90 % of the nestlings (5-14 days old) ringed each season on Hestmannøy in the years 1994-2013 (*n*=2110, 20 cohorts) and Træna from 2004-2013 (*n*=636, 10 cohorts, Table S1.1 in Appendix S1). Relative TLs (T/S ratios) were measured using the qPCR method as described in Pepke et al. (2021a; 2021b) and validated by Ringsby et al. (2015). Briefly, telomeric DNA was amplified using real-time qPCR and the telomere repeat copy number was estimated relative to an invariant control gene (GAPDH, Atema et al., 2013) and a reference sample (Appendix S1). Data was analyzed using the qBASE software (Hellemans et al., 2007) controlling for inter-run variation. Plate efficiencies were all within 100±10% (see Pepke et al., 2021a).

Factors affecting early-life telomere length

Previous studies have shown TL to be affected by body size or growth (Monaghan & Ozanne, 2018; Pepke et al., 2021b), age (Remot et al., 2021; Salomons et al., 2009), body condition (Barrett et al., 2013; Rollings et al., 2017b), hatch day (Beaulieu et al., 2017), and habitat quality (Angelier et al., 2013; McLennan et al., 2021; Spurgin et al., 2018; Watson et al., 2015; Wilbourn et al., 2017), or that there are sex-differences in TL (Barrett & Richardson, 2011; López-Arrabé et al., 2018). To examine factors that influence individual variation in TL in house sparrow nestlings (response variable, *n*=2456 excluding individuals with missing morphological measurements [*n*=224] and/or missing sex [*n*=84]), we constructed 27 candidate linear mixed effects models (LMMs) with a Gaussian error distribution fitted with maximum likelihood (ML) using the package *lme4* (Bates et al., 2015) in R v. 3.6.3 (R Core Team, 2020). The models were compared using Akaike's information criterion (Akaike, 1973) corrected for small sample sizes (AICc, Hurvich & Tsai, 1989) to identify the models best underpinned by the data. Sex and island identity (Hestmannøy or Træna) were included as fixed effects in all models, including combinations of age (number of days since hatching), age-corrected tarsus length, body condition, hatch day (mean centered ordinal day of the year), population density (spring pre-breeding census in the hatch year mean centered within populations), and an interaction term between population density and island identity. TL was $\log_{10}$-transformed for normalization of residuals. To account for the possible non-independence and temporal heterogeneity in broods and cohorts, random intercepts for brood identity (n=947, nested under hatch year) and hatch year (cohort identity, n=20) were included in all models. Models were validated visually using diagnostic plots and all model parameters are from models refitted with restricted maximum likelihood (REML).

Effects of weather on early-life telomere length

We compiled data on daily mean temperature (K), total daily amount of precipitation (mm) and mean daily atmospheric pressure (hPa) from the nearest weather station at the island of Myken (Fig. S1.1, around 30 km from both populations) from The Norwegian Meteorological Institute (2018). The daily North Atlantic Oscillation (NAO) index was retrieved from the National Oceanic and Atmospheric Administration (2019). The effects of weather conditions on TL were analyzed using a sliding window approach (van de Pol et al., 2016) to determine the best weather predictors within a range of time frames leading up to the TL measurement. TL was measured in nestlings at around 10 days after hatching, which had been preceded by a continuous incubation time of up to 14 days that often begins after laying of the penultimate egg (Anderson, 2006). The approximate time from conception to TL measurement is therefore around 30 days, which was used as the total relative timeframe (days before individual TL measurement date) for relevant weather factors affecting TL. We used the R package *climwin* and its dependencies (Bailey & van de Pol, 2016) to identify the optimal time frame during which TL is most sensitive to weather effect. This approach also allowed identifying the best descriptive weather metric (mean, maximum, minimum or sum across the time frame to reflect cumulative environmental effects on TL) and type of relationship (linear or quadratic) between TL and the weather variable (temperature, precipitation, pressure, and the NAO index). Analyses using minimum daily precipitation were not included since this variable would too often be zero within multiday timeframes, which prevented model convergence. All possible timeframes for each weather metric and relationship were then compared using AICc (van de Pol et al., 2016). As the baseline model (without climate effects) we used the best model of non-weather factors affecting early-life TL (n=2462) identified from the analyses described above. Weather variables are correlated across the study system (Ringsby et al., 2002), but the microclimate may differ between the two structurally different habitats (Hestmannøy and Træna). We therefore also tested models including an interaction term between island identity and the respective weather variable. In total, 60 models were compared using AICc (Table S2.1 in Appendix S2). Hatch year and nested brood identity were included as random intercepts in all models. We tested for over-fitting by randomizing data and re-running the analyses 100 times using the *randwin* and *pvalue* functions provided in *climwin* (Bailey & van de Pol, 2016).

A positive summer NAO is often associated with warmer and drier weather in northwestern Europe (Bladé et al., 2012; Folland et al., 2009). To understand the relationship between the NAO index and local weather conditions (Stenseth et al., 2003), we tested for intercorrelation among all four weather variables (Table S2.2) within the total time frame actually included in the analyses (effectively between April 4th, corresponding to 30 days before the earliest nestling sampling date until the last sampling date of August 19th, from 1994-2013). This showed that a high daily NAO index primarily reflects a high daily amount of precipitation (Pearson's r=0.13, p<0.0001) during spring and summer in this area of the Norwegian coast. However, high daily amounts of precipitation were also negatively correlated with mean daily temperature and atmospheric pressure (Table S2.2).

Does early-life telomere length predict natal dispersal?

House sparrows generally show strong site fidelity and dispersal occurs mainly among juveniles in the autumn (i.e. natal dispersal, Altwegg et al., 2000) and over short distances (Anderson, 2006; Tufto et al., 2005). All islands surrounding Hestmannøy and Træna and the inhabited areas on the mainland shores (Fig. S1.1) were visited regularly to identify dispersers (Ranke et al., 2021; Saatoglu et al., 2021). To reduce effects of any selective disappearance of certain phenotypes before registration of dispersal, only individuals that survived until the following spring (i.e. recruits), were included in the analyses. A total of 41 individuals (18 [6 males, 12 females] out of 342 from Hestmannøy and 23 [14 males, 9 females] out of 113 from Træna) were observed on islands different from their natal islands within their first year of life (out of *n*=455 recruits). We used logistic regression with a binomial error distribution (using the ‘bobyqa’ optimizer throughout to facilitate model convergence, Bates et al., 2014) to test if early-life TL predicts the probability of successful natal dispersal. Within this house sparrow metapopulation, dispersal is female-biased and dispersal rates depend on habitat type (Ranke et al., 2021; Saatoglu et al., 2021). We therefore included sex and island identity as covariates in explaining dispersal propensity in all models. Hatch year was included as random intercept. We also included two- and three-way interactions between TL, sex, and island identity to test for differing relationships between TL and dispersal across sexes and island types. With this approach, a total of nine candidate models were compared using AICc.

Fitness consequences of variation in early-life telomere length

We used three approaches to investigate the consequences of variation in early-life TL on fitness (survival and reproduction). First, we tested if TL predicts whether an individual survives its first year (*n*=445, excluding individuals with missing tarsus length measurements) or not (*n*=2017), i.e. recruitment probability, using a logistic regression with a binomial error distribution and a logit link function (*lme4* package). Explanatory variables were TL, tarsus length, non-linear effects of TL (TL^2) and tarsus length (tarsus length^2), and interaction terms between island identity and tarsus length and TL, respectively. Sex and island identity were included as fixed effects, and year and nested brood identity as random intercepts, in all models. A total of 14 candidate models were constructed.

Second, we used Cox proportional hazards regression to test whether TL predicted mortality risk over the lifespan using the *survival* package (Therneau, 2015). The last observation of an individual was used as an estimate of minimum lifespan (number of days since hatching). Birds were assumed to have died if they had not been observed during two subsequent field seasons. Only two individuals (out of *n*=2462) may still have been alive when observations ended (autumn 2020) and were therefore right-censored (Cox, 1972). We constructed the same 14 candidate models as in the first-year survival analyses above. Brood identity was included as a random effect (cluster) and model assumptions were tested using the Schoenfeld test. To meet model assumptions, data was stratified by island identity, allowing for different hazard functions within each population (strata). The *simPH* package was used to simulate and plot the effects of the predictor variables on the hazard ratios (Gandrud, 2015). Finally, we used the Kaplan-Meier method to construct cumulative survival curves (*survminer* package, Kassambara et al., 2020).

Third, we tested if TL predicts annual reproductive success (ARS; the number of recruits produced per year by an individual) among individuals that survived their first year and were thus able to breed (starting from year 1995). Genetic parenthood data was not available after 2013, so subsequent years were excluded from the analysis. We fitted generalized LMMs with a Poisson distribution using the package *glmmTMB* (Brooks et al., 2017) to test whether TL predicts ARS (*n*=709 annual reproductive events of *n*=396 individuals). Tarsus length and non-linear effects of TL and tarsus length were included in 14 candidate models (same as described above). All models included sex and island identity as fixed factors, and individual identity (*n*=396) and year (*n*=19) as random intercepts. Models were validated using the DHARMa package (Hartig, 2020). The 14 candidate models within each of the three approaches above were compared using AICc.

RESULTS

Factors affecting early-life telomere length

There was considerable variation in TL among cohorts with no obvious directional trend (Fig. S2.1). The best model of variation in TL included a negative effect of tarsus length (β_{tarsus}=-0.0038±0.0016, CI=[-0.0079, -0.0006], Tables 1 and 2) indicating that larger individuals had shorter telomeres. The model also included evidence for an interaction term between population density and island identity ($\beta_{island*density}$=0.0008±0.0004, CI=[0.4E-4, 0.0016], $\beta_{density}$=-0.0008±0.0004, CI=[-0.0015, -0.5E-4]), indicating that individuals born in years with higher population densities had shorter telomeres, but only in the Træna (non-farm) population (Fig. 1a). Thus, there was apparently no evidence for an effect of variation in population density on TL in the Hestmannøy population (Fig. 1b). The second-best model ($\Delta AICc$=0.4, Table 1) did not include the effects of population density. The third and fourth best models included very uncertain effects of hatch day and age, respectively (Table 1).

Effects of weather on early-life telomere length

The best model ($\Delta AICc$=-13.49 compared to a model without weather effects, Table S2.1 and Fig. S2.2) identified from the sliding window analysis of weather variables included a negative quadratic effect of the maximum NAO index during 26 to 12 days before TL sampling (Table 3 and Fig. 1c), which corresponds approximately to the timing of the incubation phase. This suggests that there is a set of (optimal) environmental conditions, reflected by intermediate values of the maximum NAO index during incubation, that results in the longest telomeres in fledglings. The model output was unlikely to be a result of overfitting (p=0.001, see Fig. S2.2). The second-best model, which differed by $\Delta AICc$=-12.82, included only a linear negative effect of maximum NAO during approximately the same time window (30 to 16 days before sampling, Table S2.1).

Does early-life telomere length predict natal dispersal?

Four of the six models with $\Delta AICc$<2 describing variation in successful natal dispersal probability included a tendency for a negative association between TL and dispersal probability (model ranked second with $\Delta AICc$=0.0; β_{TL}=-0.795±0.630, CI=[-2.248, 0.268],Table S2.3 and Fig. 3). The two highest ranked models (both $\Delta AICc$=0.0) included an interaction between island and sex, indicating a tendency for males from Træna to be more likely to disperse than males from Hestmannøy ($\beta_{island\ (Hestmannøy)*sex\ (female)}$=1.196±0.713, CI=[-0.189, 2.659], $\beta_{island\ (Hestmannøy)}$=-2.434±0.558, CI=[-3.526, -1.341], $\beta_{sex\ (female)}$=-0.496±0.497, CI [-1.512, 0.472]). The model ranked third ($\Delta AICc$=0.6) included a three-way interaction term between TL, island identity, and sex, suggesting that the negative association (tendency) between dispersal probability and TL was strongest in males from Hestmannøy ($\beta_{TL*island\ (Hestmannøy)*sex\ (male)}$=-3.049±1.765, CI=[-9.988, -0.862], see full model in Table S2.4 and the effect in Fig. 3).

Fitness consequences of early-life telomere length

There was no evidence of an effect of TL on first-year survival (Table S2.5 and Fig. 3b). There was however evidence for a positive association between tarsus length and first-year survival probability in all top models with $\Delta AICc$<2 (model ranked 1: β_{tarsus}=0.040±0.009, CI=[0.057, 0.023], Table S2.5). The best model also included a weak curvilinear effect of tarsus length ($\beta_{tarsus\wedge 2}$=-0.042±0.029, CI=[-0.101, 0.11]), indicating that survival probability increased less or even decreased with tarsus length in the largest individuals (Fig. 3a).

There was no evidence of an effect of TL on mortality risk (Table S2.6 and Fig. 4b). The Cox hazard regression analyses showed however that there was a strong negative association between tarsus length and mortality risk (model ranked 1: β_{tarsus}=-0.120±0.017, CI=[-0.157, -0.083], Table S2.6). The best model also included a weak curvilinear effect of tarsus length ($\beta_{tarsus^\wedge 2}$=0.011±0.006, CI=[-0.002, 0.024]), indicating that the decrease in the risk of mortality with increased tarsus length reached a plateau at large values (Fig. 4a).

We found weak evidence of an inverse relationship between TL and ARS (model ranked 1: β_{TL}=-0.446±0.275, CI=[-0.985, 0.092], *n*=709, Table S2.7 and Fig. 5b), indicating that individuals with long TL had lower ARS than individuals with short TL. The second ranked model ($\Delta AICc$=0.1) additionally included a weak positive effect of tarsus length on ARS (β_{tarsus}=0.106±0.075, CI=[-0.042, 0.253], Fig. 5a). It was thus difficult to separate models including a positive effect of tarsus length and/or a negative effect of TL on ARS (Table S2.7).

DISCUSSION

In this study, we have shown how individual variation in early-life telomere length is related to structural growth, weather conditions during incubation, and population density in a long-term study of two island populations of wild house sparrows. This suggests a mechanistic link between environmental change and physiological change mediated by TL dynamics in early-life (Chatelain et al., 2020; Giraudeau et al., 2019a). TL has been shown to be associated with important components of fitness in some wild species (Eastwood et al., 2019; Froy et al., 2021; van Lieshout et al., 2019; Wilbourn et al., 2018). However, we found little evidence that variation in TL in early life had any fitness consequences in terms of survival, but there was a tendency for a negative effect of TL on reproductive success (Tables S2.4-2.6). Instead, fitness was mainly determined by body size (Ringsby et al., 1998) with larger individuals having higher short-term survival (Fig. 3a), lower long-term mortality (Fig. 4a), and somewhat higher reproductive success (Fig. 5a). Larger individuals had shorter telomeres (Table 2), as documented previously in several species (Monaghan & Ozanne, 2018), including house sparrows (Pepke et al., 2021a; Pepke et al., 2021b; Ringsby et al., 2015), but little of the residual variation in fitness appeared to be explained by TL.

Recent studies have established early-life environmental conditions as important drivers of TL dynamics in free-living organisms (Angelier et al., 2018; Chatelain et al., 2020; Foley et al., 2020; Herborn et al., 2014; Nettle et al., 2015; Spurgin et al., 2018). Thermoregulatory and nutritional stress can increase production of ROS resulting in stress-induced changes in TL (Friesen et al., 2021; Reichert & Stier, 2017). Effects of weather conditions on telomere dynamics is known from other wild animal populations, including dark-eyed juncos (*Junco hyemalis*), in which females experienced greater telomere loss during breeding at colder temperatures, probably due to cold stress (Graham et al., 2019). In black-tailed gulls (*Larus crassirostris*), telomeres were even elongated during an El Niño year, in which weather was generally milder and sea surface temperatures lower, resulting in improved foraging conditions (Mizutani et al., 2013). Similarly, the change in TL in greater-eared bats (*Myotis myotis*, Foley et al., 2020) and early-life TL in European badgers (*Meles meles*, van Lieshout et al., 2021) was positively associated with generally good weather conditions (higher temperatures and favorable rainfall). Furthermore, in house sparrow nestlings, TL was positively associated with the NAO index averaged across approximately two weeks before and after hatching, which locally reflected higher temperatures, lower rainfall, and lower wind speed (Pepke et al., 2021b). Bird embryos are effectively ectothermic during incubation, justifying a comparison with studies on ectothermic species, in which temperature may be more directly affecting ROS production and cell division through increased metabolic activity and growth (Friesen et al., 2021; Olsson et al., 2018a). Accordingly, in brown trout (*Salmo trutta*, Debes et al., 2016) and Siberian sturgeon (*Acipenser baerii*, Simide et al., 2016), higher temperatures led to shorter telomeres, possibly caused by heat stress, but also increased growth. Similarly, TL decreased with higher temperatures experienced by common lizards (Dupoué et al., 2017), desert toad-headed agamas (*Phrynocephalus przewalskii*, Zhang et al., 2018), and dairy cattle (*Bos taurus*, Seeker et al., 2021), but not in Gouldian finches (*Chloebia gouldiae*, Fragueira et al., 2019). However, TL increased with higher temperature in Eastern mosquitofish (*Gambusia holbrooki*, Rollings et al., 2014), spotted snow skinks (*Niveoscincus ocellatus*, Fitzpatrick et al., 2019), and dark-eyed juncos (Graham et al., 2019) and there was no effect of temperature manipulation on TL in Atlantic salmon (*Salmo salar*, McLennan et al., 2018) or three-spined sticklebacks (*Gasterosteus aculeatus*, Kim et al., 2019). Axelsson et al. (2020) documented a thermal optimum associated with long telomers in sand lizards (*Lacerta agilis*). These idiosyncratic patterns demonstrate how environmental factors and degree of harshness may trigger a physiological stress response (Chatelain et al., 2020) with different consequences on TL dynamics depending on the deviation from species-specific environmental optima (Axelsson et al., 2020; McLennan et al., 2016). In our study, we observed a similar curvilinear association between fledgling TL and the maximum NAO index during the incubation phase, suggesting that this weather variable best reflects the effects of environmental conditions on TL, and that there are optimal environmental conditions that result in the longest TL. A two week period corresponds to the summer NAO life cycle (see Feldstein, 2007), and the maximum summer NAO may reflect extreme weather events such as drought or flooding (Drouard et al., 2019; Folland et al., 2009). At our study site, the daily NAO index was primarily positively correlated with the daily amount of precipitation (Table S2.2). Rainfall may have immediate effects on food availability and hence nest attendance (Bambini et al., 2019) and incubation temperature (Simmonds et al., 2017), which can elicit a stress response in the organism with effects on TL (Dupoué et al., 2020; Stier et al., 2020; Vedder et al., 2018). Prenatal exposure to environmental stressors can also have significant negative effects on embryonic TL (Entringer et al., 2011; Noguera & Velando, 2019). Variation in the NAO index locally captures complex associations between weather variables reflecting "harsh" or “benign” weather conditions (Folland et al., 2009; Stenseth et al., 2003), and it has been linked to morphological and demographic changes in several northern hemisphere species (Ottersen et al., 2001; Hallett et al., 2004; Stenseth et al., 2002; Stenseth et al., 2003). For instance, the NAO index may reflect insect abundance and phenology (Nott et al., 2002; Welti et al., 2020; Westgarth-Smith et al., 2012). The NAO can have considerable lagged effects on weather (Halkka et al., 2006), or there may be developmental time lags between weather conditions and the response in insect abundance (Visser et al., 2006). Thus, the effect of NAO during incubation may be acting on food availability during the important nestling growth stage. Food availability was positively associated with TL and TL lengthening in Seychelles warblers (Brown et al., 2021; Spurgin et al., 2018), but negatively associated with TL in American black bears (*Ursus americanus*, Kirby et al., 2017). In African striped mice (*Rhabdomys pumilio*), TL decreased during the dry season, when food availability was low, and increased during the wet season, when food availability was high (Criscuolo et al., 2020). Such associations may be complicated by the fact that some level of food restriction may reduce oxidative damage during growth (Noguera et al., 2011). Accordingly, the curvilinear effect of weather conditions on TL (Table 3) may therefore also reflect the growth conditions optimizing TL (Monaghan & Ozanne, 2018).

Habitat quality may be an important driver of differences in TL dynamics across populations (McLennan et al., 2021; Wilbourn et al., 2018). We found evidence for an interaction effect between habitat type (island) and population density (Table 2), suggesting that pre-breeding population density was negatively related to TL on the non-farm island (Træna), but not on the farm-island (Hestmannøy). On Hestmannøy, which holds a larger sparrow population than Træna (Fig. S2.1 and Table S1.1), the sparrows live and nest in a sheltered environment around farms, in contrast to Træna, where the sparrows nest in artificial nest boxes in a village environment. House sparrows are gregarious but exhibit territorial behavior by defending nest sites during the breeding season (Anderson, 2006). Thus, there may be more competition for nest sites on Træna compared to Hestmannøy at high population densities. Furthermore, as population density increases, competition increases, and poorer quality nest and foraging sites are increasingly occupied (Møller et al., 2018; Newton, 1998). The farms on Hestmannøy provide adults with a continuous supply of grain or food pellets and we speculate that the intensity of competition for resources may therefore be higher in the more unpredictable habitats on Træna, when population size is relatively larger (e.g. Dhondt, 2010). Again, malnutrition or exposure to suboptimal microclimatic conditions during early-life, may lead to elevated levels of oxidative stress and hence shorter telomeres in fledglings, consistent with our observations. Similar negative effects of population density on TL have been observed in griffon vultures (*Gyps fulvus*, Gangoso et al., 2021) and Atlantic salmon (*Salmo salar*, McLennan et al., 2021), and in crowding experiments with mice (*Mus musculus*, Kotrschal et al., 2007).

We found some evidence for successful dispersers to have shorter telomeres prior to dispersal than non-disperser, especially among males from the farm-island (Hestmannøy, with only 6 dispersers out of 167 males, Fig. 3). These analyses were limited by the relatively small number of dispersers. In the introduction we suggested that short telomeres may inform a dispersal syndrome (pace-of-life), where bolder and faster-lived individuals are more likely to disperse. Short telomeres have been correlated with bold, aggressive, pessimistic, or impulsive behavior in fish and birds (Adriaenssens et al., 2016; Bateson et al., 2015; Espigares et al., 2021). Increases in the level of glucocorticoids are linked to dispersal in birds (Belthoff & Dufty, 1998; Silverin, 1997), which indicate the relevance of oxidative stress and hence that TL may be associated with successful dispersal (Casagrande & Hau, 2019; Récapet et al., 2016). Although Pegan et al. (2019) found a small negative effect of corticosterone treatment on TL in wild tree swallows (*Tachycineta bicolor*), this did not affect the age of initial departure from the natal site. Boonekamp et al. (2014) compared telomere loss within the first month of life among philopatric and dispersing jackdaws (*Coloeus monedula*), but did not find any differences, however their study was limited by a small sample size (5 dispersers out of 30 recruits). House sparrows are short-distance dispersers (Tufto et al., 2005), and TL may not be a generally significant physiological indicator of dispersal probability at the scale of metapopulations. In contrast, metabolically demanding long-distance migration or dispersal increases oxidative stress (Costantini et al., 2007) and may thus have direct negative impacts on TL, as observed in migratory birds (Angelier et al., 2013; Bauer et al., 2016; Schultner et al., 2014).

In several species, longer TL is associated with higher survival (Bichet et al., 2020; Crocco et al., 2021; Eastwood et al., 2019; Froy et al., 2021; Heidinger et al., 2021; Ilska-Warner et al., 2019; van Lieshout et al., 2021; Wilbourn et al., 2018, but see Vedder et al., 2017). We found no evidence for an association between TL and first-year survival or mortality over the lifespan in house sparrows (Figs. 3b and 4b). Perhaps early-life TL is uncoupled from survival because of high extrinsic mortality of (primarily juvenile) house sparrows (Fig. S2.3) not related to early-life TL (e.g. Criscuolo et al., 2020; Eastwood et al., 2019; Wood & Young, 2019). Alternatively, house sparrows may be able to mitigate negative effects of short telomeres later in life through telomere maintenance (e.g. Vedder et al., 2017). Pepke et al. (2021b) also found no associations between TL and first-year survival in house sparrows from two populations that were part of a bidirectional artificial body size selection experiment. However, both short and long early-life TL tended to be weakly associated with the lowest mortality rates over the lifespan in that study (Pepke et al., 2021b), suggesting disruptive selection on TL. Furthermore, some studies have showed that early-life TL was a poor predictor of survival, which was instead predicted by changes in TL (Boonekamp et al., 2014; Seeker et al., 2021; Wood & Young, 2019), which we did not measure in this study.

We found a tendency for a negative association between ARS and TL even when accounting for the positive effect of body size on ARS, i.e. individuals with short TL tended to produce more recruits annually (Fig. 5b). Within species, individuals with short telomeres may exhibit a faster pace-of-life reflected in higher ARS, while individuals with longer telomeres allocate more resources into self-maintenance (Giraudeau et al., 2019a; Rollings et al., 2017a; Young, 2018). Perhaps individuals with short TL adopt a terminal investment strategy (Clutton-Brock, 1984). Interestingly, across bird species, the reciprocal relationship emerges, i.e. species with short telomeres are slow-lived (Pepke et al., 2021d). Heidinger et al. (2021) found no associations between early-life TL and annual reproductive performance (number of offspring) in wild American house sparrows. However, they found a positive relationship between early-life TL and lifespan in females, but a negative trend between TL and lifespan in males. They therefore suggested that TL reflected differences in quality or condition in females, but did not predict pace-of-life (Heidinger et al., 2021). It will be interesting to see if other studies find contrasting associations between TL and fitness across different populations within the same species in the wild.

There is some evidence that telomere loss rates are higher in longer telomeres (Atema et al., 2019; Atema et al., 2021; Verhulst et al., 2013; Victorelli & Passos, 2017) suggesting that early-life TL may not be a good linear predictor of later-life TL. Alternatively, individual TL changes in response to environmental variables through life (Brown et al., 2021; Chatelain et al., 2020) suggesting that TL must be measured closer to reproduction events (Marasco et al., 2021).

Our study suggests that environmental stressors negatively affected TL in young house sparrows, probably through the action of oxidative damage by ROS, but questions the common expectation of long-term fitness costs associated with shorter early-life TL in the wild. We also found some evidence that TL may be a biomarker of pace-of-life syndromes with fast-paced individuals with short telomeres tending to have higher dispersal rates and higher ARS. Thus, there may be few long-term physiological disadvantages associated with having short telomeres in early-life in wild populations, but TL may rather act as a biomarker of individual pace-of-life. However, associations between early-life TL, individual fitness, and complex environmental interactions seems difficult to establish and may vary between populations in the wild.

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AUTHOR CONTRIBUTIONS

MLP measured telomeres, analyzed the data, and wrote the manuscript with contributions from all authors. THR, B-ES, and HJ, initiated the study system. THR, HJ, TK, PSR, YGA-A, and MLP contributed to the fieldwork.

DATA AVAILABILITY

All data is available on request from the first author, and it will be made available on a public repository upon publication of the manuscript.

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TABLES AND FIGURES

Table 1: Linear mixed effects models with ΔAICc≤4 of variation in early-life telomere length in house sparrow nestlings from two island populations. All models included random intercepts for year and brood identity. Models are ranked by AICc, and number of degrees of freedom (df) and model weights (w) are shown.

Model		**ΔAICc**	**df**	**w**
1	**TL = sex + island + tarsus + density + island*density**	0.0	9	0.1405
2	TL = sex + island + tarsus	0.4	7	0.1138
3	TL = sex + island + tarsus + density + island*density + hatch day	1.0	10	0.0872
4	TL = sex + island + tarsus + density + island*density + condition	1.1	10	0.0814
5	TL = sex + island + tarsus + density + island*density + age	1.1	10	0.0793
6	TL = sex + island + tarsus + condition	1.5	8	0.0652
7	TL = sex + island + tarsus + age	1.6	8	0.0619
8	TL = sex + island + tarsus + density + island*density + age + hatch day	1.9	11	0.0535
9	TL = sex + island + tarsus + density	2.2	8	0.0460
10	TL = sex + island + tarsus + density + island*density + condition + age	2.2	11	0.0457
11	TL = sex + island + tarsus + density + island*density + condition + age + hatch day	3.0	12	0.0311
12	TL = sex + island + density + island*density	3.2	9	0.0284
13	TL = sex + island + tarsus + density + condition	3.4	9	0.0261
14	TL = sex + island + tarsus + density + age	3.5	9	0.0249
15	TL = sex + island + hatch day	3.5	7	0.0247
16	TL = sex + island	4.0	6	0.0191

Table 2: Estimates (*β*) with standard errors (SE) and lower and upper 95% confidence intervals (CI) from a linear mixed effects model of variation in telomere length (TL, *n*=2456). The model included random intercepts for brood identity and year. Italics indicate parameters with CIs not overlapping zero.

Response variable: TL	***β***	**SE**	**Lower CI**	**Upper CI**
intercept	-0.0205	0.0133	-0.0466	0.0053
sex (female)	-0.0041	0.0041	-0.0121	0.0039
island (Hestmannøy)	-0.0086	0.0093	-0.0269	0.0094
tarsus	*-0.0038*	*0.0016*	*-0.0070*	*-0.0006*
density	*-0.0008*	*0.0004*	*-0.0015*	*-0.5E-4*
*island (Hestmannøy)*density*	*0.0008*	*0.0004*	*0.4E-4*	*0.0016*
$\sigma^2_{\text{brood ID}}$ (n=947)	0.0036		0.0029	0.0043
σ^2_{year} (n=20)	0.0020		0.0010	0.0039

Marginal R^2 / Conditional R^2: 0.007 / 0.410

Table 3: Best model identified from sliding window analyses (Table S2.1) of the effect of weather variables on telomere length in house sparrow fledglings (n=2462). Italics indicate parameters with CIs not overlapping zero.

Response variable: TL	***β***	**SE**	**Lower CI**	**Upper CI**
intercept	-0.0049	0.0138	-0.0321	0.0220
sex (female)	-0.0052	0.0041	-0.0131	0.0028
island (Hestmannøy)	-0.0125	0.0092	-0.0305	0.0054
tarsus	-0.0042	0.0016	-0.0074	-0.0011
density	-0.0009	0.0004	-0.0016	-0.0002
island (Hestmannøy)*density	0.0009	0.0004	0.0002	0.0016
max. NAO$_{26\text{-}12\ \text{days}}$	0.0124	0.0084	-0.0040	0.0287
(max. NAO$_{26\text{-}12\ \text{days}}$)^2	*-0.0223*	*0.0052*	*-0.0325*	*-0.0121*
$\sigma^2_{\text{brood ID}}$ (n=948)	0.0033		0.0026	0.0040
σ^2_{year} (n=20)	0.0022		0.0011	0.0042

Marginal R^2 / Conditional R^2: 0.029 / 0.418

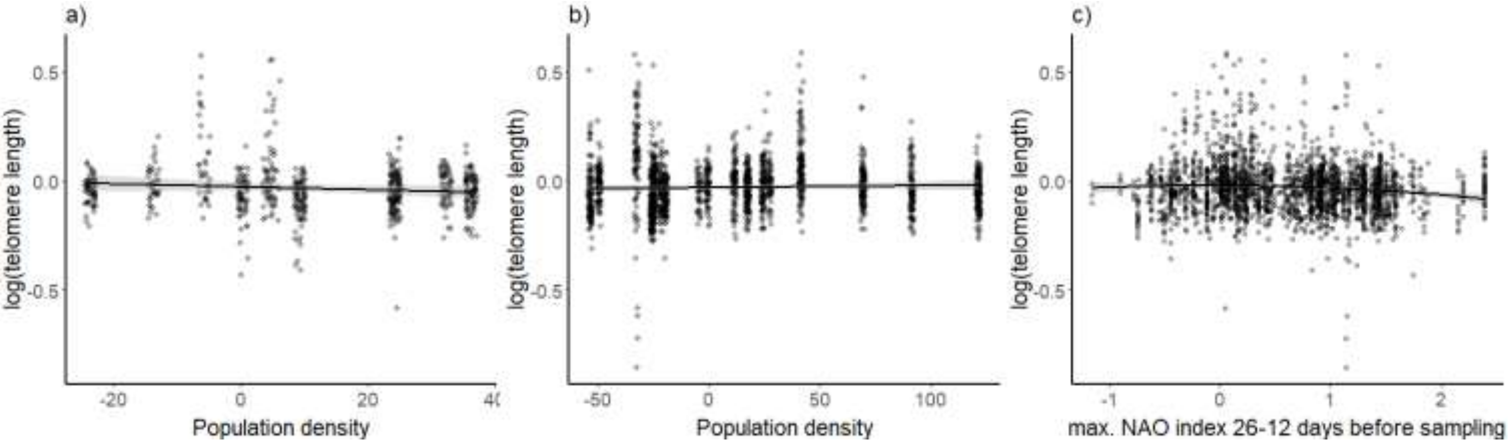

Fig. 1: The effect of population density (mean centered) on log$_{10}$-transformed early-life telomere length in a) the Træna population (negative association) and b) in the Hestmannøy population (no association), see Tables 1 and 2. c) The negative quadratic association between early-life TL and the best weather variable predictor (max. NAO index during incubation) from a sliding window analysis (Tables S2.1 and 3).

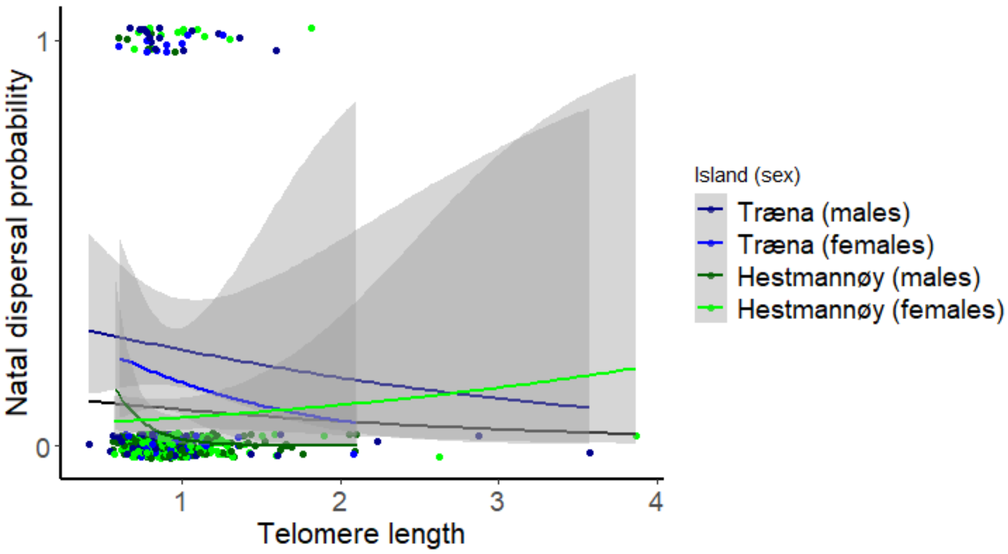

Fig. 2: Binomial logistic regression of successful natal dispersal probability predicted by early-life TL. The highest ranked models (Table S2.3) suggested a weak negative association between dispersal probability and TL (black regression line). One of these top models suggested that there was a stronger negative association between TL and dispersal probability among males born on Hestmannøy (*n*=167, dark green regression line with 95% confidence intervals in grey areas).

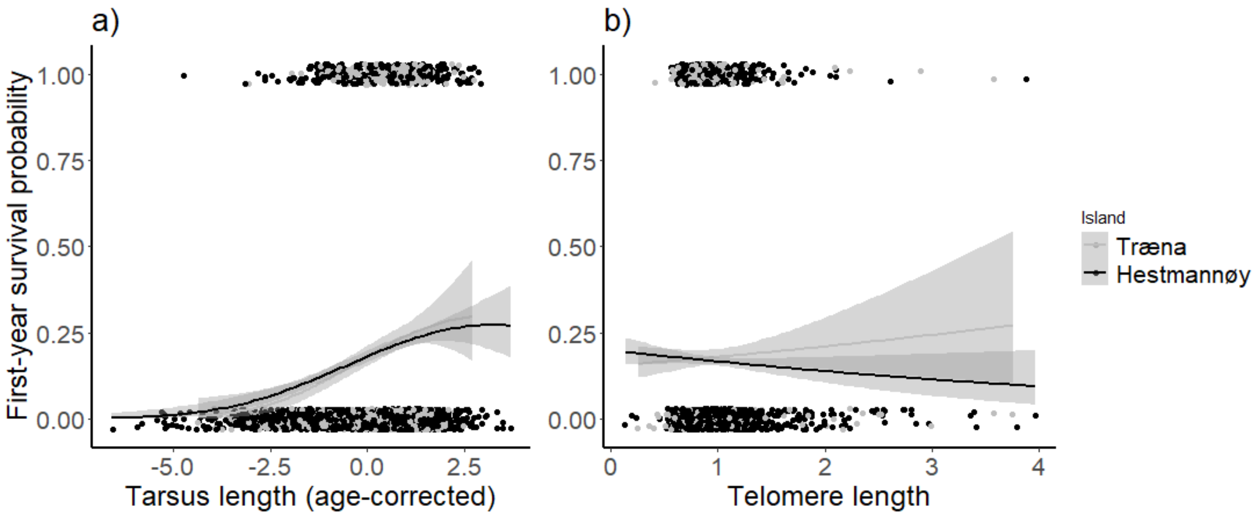

Fig. 3: Relationship between first-year survival (recruitment) probability in two populations of house sparrows (grey: Træna, black: Hestmannøy) and **a)** fledgling tarsus length (negative quadratic association) and **b)** fledgling TL (no evidence for any associations). The logistic regression lines are from the top models shown in Table S2.5 including tarsus length (model ranked 1) and telomere length (model ranked 4). There was no evidence for differences in first-year survival probability between the two populations.

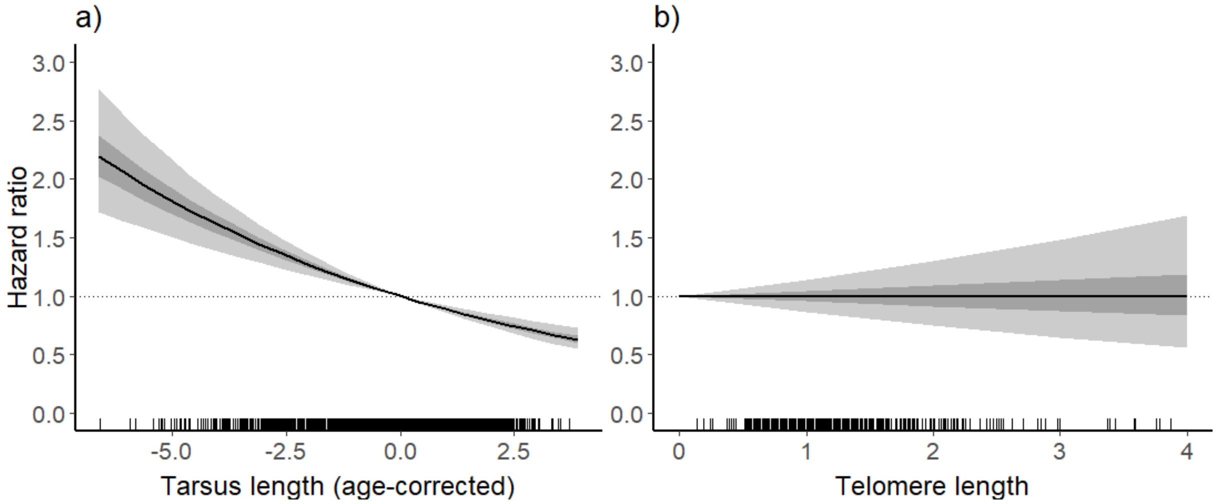

Fig. 4: Mortality risk measured as hazard ratio in two populations of house sparrows (grey: Træna, black: Hestmannøy) as a function of **a)** fledgling tarsus length (positive quadratic association) and **b)** fledgling telomere length (no evidence for any associations). The regression lines (black) show the modelled effect from the top models in Table S2.6 with 95% and 50% confidence intervals in light grey and dark grey respectively.

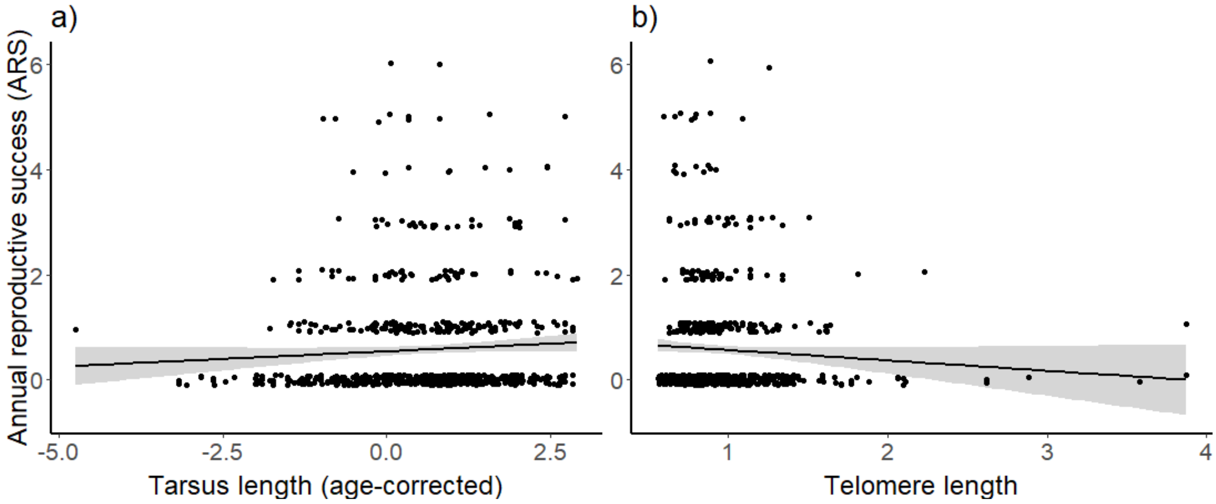

Fig. 5: The associations between annual recruit production (ARS: annual reproductive success) and **a)** fledgling tarsus length and **b)** fledgling telomere length. The regressions lines (black, with 95% confidence intervals in grey) show the uncertain tendencies (see the main text) predicted from the top models in Table S2.7.