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Telomere length covaries with personality in wild brown trout

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Keywords: animal personality, telomere dynamics, behavioural syndromes, state dependent behaviour, life-history

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Abstract

The prevalence of consistent among-individual differences in behaviour, or personality, makes adaptive sense if individuals differ in stable state variables that shift the balance between the costs and benefits of their behavioural decisions. These differences may give rise to both individual differences in, and covariance amongst, behaviours that influence an individual's exposure to risks. We here study the link between behaviour and a candidate state variable previously overlooked in the study of state-dependent personality variation: telomere length. Telomeres are the protective endcaps of chromosomes and their erosion with age is thought to play a crucial role in regulating organismal senescence and intrinsic lifespan. Following evidence that shorter telomeres may reduce the lifespan of animals in a wide range of taxa, we predict individuals with shorter telomeres to behave more boldly and aggressively. In order to test this, we measured telomere length and behaviour in wild juvenile brown trout (*Salmo trutta*). We found individuals with shorter fin telomeres to behave consistently more boldly and aggressively under controlled conditions in the laboratory. No such relationship was found with muscle telomere length 3-4 months after the behavioural assays. We suggest that telomere dynamics are an important factor integrating personality traits with other state variables thought to be important in the regulation of behaviour, such as metabolism, disease resistance and growth.

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Introduction

The cause of consistent behaviour in most animals despite the absence of obvious constraints on flexible behaviour continues to be an evolutionary puzzle [1-3]. State-dependent models have taken a central role in our efforts to understand the adaptive nature of these so-called personality differences and suggest that individual behavioural differences result from underlying differences in stable state variables that affect optimal strategies in the face of life-history tradeoffs. In this, an individual's state is defined by all those features that are strategically relevant, i.e. features that it should take into consideration in behavioural decisions in order to increase fitness [4]. Some state variables proposed to be important for personality variation are differences in metabolism [5-7], immune response [8, 9], HPA stress reactivity , oxidative stress management [10, 11] and intrinsic growth rates [12]. Many of these mechanisms are likely interlinked, and the Pace-of-Life Syndrome hypothesis (POLS) was further adopted to join several of these state variables into a larger integrative model [13]. In brief, the extended POLS hypothesis poses that bold and aggressive behaviour is reflective of a fast life style (fast growth, early reproduction and short lifespan), underpinned by specific physiological trait values(e.g. high metabolism, low immune response, low HPA reactivity).

One state variable currently largely overlooked in this context is telomere length. Telomeres are protective endcaps of the eukaryotic chromosome composed of repetitive nucleotide sequences and proteins. Individual differences in telomere length tend to have a heritable component and are often maintained for extended periods of an individual's life [14-16] but see [17]. Telomeric DNA is subject to erosion throughout an individual's lifetime by incomplete replication during each cell division and incomplete repair through the action of a protein called telomerase. Telomeres are highly vulnerable to oxidative damage, and stress experienced in the current and parental lineage accelerates telomere attrition by suppressing oxidative damage protection and repair [18]. Furthermore, repair is not similarly effective in all tissues, causing most somatic cell lines to show a steady decrease of telomere length

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with age [19]. This decrease in telomere length is generally linked to impaired tissue function and symptoms of senescence. Overall, the close association between telomere dynamics, processes of growth, stress biology and aging makes telomeres promising candidates as key state variables in future studies of animal personality.

Despite the increased interest in links between life-history and telomere dynamics in evolutionary ecology, it remains unclear how telomere dynamics relate to personality traits. To our knowledge only one study tested the relationship between telomere length and behaviour [20]. Using captive starlings (*Sturnus vulgaris*) this study shows that, after manipulation of juvenile telomere length through brood size manipulations, individuals with shorter juvenile telomeres made more impulsive foraging decisions when adult, valuing smaller and sooner food rewards more highly than birds with longer telomeres. Indirect evidence from growth-hormone transgenes in salmonid fish further shows that accelerated growth results in fish that are more bold but are also subject to greater oxidative stress and faster telomere attrition [21-24]. However, it remains unclear how these results extend to natural telomere variation, since gene expression profiles of key mechanisms underlying telomere dynamics and behaviour often differ strongly between captive and wild animals [25, 26]. Therefore it is important to expand the existing knowledge by studies in the wild. Here, we investigated the association between telomere length and personality traits in juveniles of a wild sea-migrating population of brown trout (*Salmo trutta*). Yearlings were caught in a natural stream and scored repeatedly for exploration and aggressive behaviour in the lab before they were sampled for fin tissues and released back into nature. We also collected (terminal) muscle tissues for further telomere assays 3-4 months later. We then assessed the relationship between tissue telomere scores and consistent patterns of behaviour, predicting negative relationships between telomere length and behavioural types associated with a fast pace of life (e.g. bold and aggressive).

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Material and methods

Fish sampling and behavioural observations

Brown trout yearlings were caught during spring by electrofishing in river Stenunge on the Swedish west coast (58° 4' 48'' N, 11° 52' 3'' E). In total we caught three batches of 24 fish at three separate fishing events (24 April, 8 May and 22 May 2006) and in three separate, but adjacent, stream sections. Batches were kept four weeks in the animal department of the zoology house, University of Gothenburg for observations until release. Batches were kept and released separately on 22 May, 5 June, and 19 June 2006, respectively. Holding tanks (120 litres, 40 × 48 × 64 cm) were continuously provided with fresh, filtered, water (12-14 ºC) with a flow rate of 2 litres/minute and aerated with an airstone. The photoperiod was adjusted weekly to coincide with the current outdoor light cycle. Fish were daily fed 1 live maggot per individual (pinkies, length 8–10 mm, Fibe AB, O¨ verkalix, Sweden) and 2 g frozen bloodworms (Chironomidae spp., commercial fish food supplier) per 24 individuals and all fish readily consumed this food after initial acclimation (2-3 days). Each individual was moved to an individual tank after either 13 (N=12 / batch) or 17 (N=12 / batch) days of acclimation to be scored four times for exploratory behaviour and twice for aggression. This time period was deemed sufficient for fish to recover stress levels after capture and laboratory acclimation [27] and no differences were observed between fish undergoing these experimental procedures after either 13 or 17 days [28]. The morning of the second day after we measured each fish over a series of 6 consecutive trials (2/day for 3 consecutive days) whilst provided with a cryptic prey item after lifting an opaque PVC divider separating the tank in a covered start compartment and an open foraging area. Latency to activity, total active time and prey search time during the first four trials were collapsed with principal component analysis (PCA) to calculate an individual's exploration behaviour (four repeated measures, supplement S1). Before the fifth and sixth trials, we introduced a conspecific of slightly smaller body size into a side compartment to simulate intrusion of a subordinate individual. We then scored the number of approaches and bites towards the intruder, and the time spent in proximity to the intruder. Together these three scores were again collapsed

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with PCA to one aggression score (two repeated measures, supplement S1). For a detailed description of procedures see [28]. All fish were moved back to communal holding tanks.

Tissue sampling and fish size measures

Telomere attrition is known to vary among tissue types due to tissue-specific proliferation with age, telomerase activity, or exposure to oxidative stress [19]. We therefore chose to score telomere length in two tissue types thought to be important for active behaviours, the fin and the muscle. Because muscle tissues required terminal sampling, our experimental design allowed fin samples to be collected at similar times as behavioural scores but muscle samples only 94 to 123 days later. Before release, each fish was anaesthetised (0.5ml/l 2-phenoxyethanol), measured for fork length (± 1 mm) and injected with a passive integrated transponder tag in the peritoneal cavity with a hypodermic syringe, enabling individual recognition (PIT, ID100, Trovan Ltd., UK). At this occasion we also collected the outermost 3mm of the adipose fins (stored in 95% ethanol) from all fish to determine pre-release telomere length. Adipose fin clipping is a common practice in release of salmonid fish and unlikely to have affected behaviour or survival of fish [29, 30]. Due to natural growth in the wild, batches differed slightly in size (ANOVA; df = 2, F = 8.7, P < 0.001; mean +/- SE: first batch = 71 +/- 2 mm, second batch = 77 +/- 2 mm, third batch = 82 +/- 2 mm). Four weeks after capture and transport to the laboratory, fish were released at a single location per batch within 40m of their capturing location (22 May to 19 June). On the 20th and 21th of September we sampled the whole experimental stream section using electrofishing, starting 130m downstream the release location of batch one and ending 130 m upstream the release location of batch three. To ensure a high recapture rate, we performed three consecutive electric fishing bouts. We recorded the identity, wet weight, and fork length of each recaptured tagged individual (total N=48 or 67%). Recaptured individuals were then euthanized with a lethal dosis of 2-Phenoxyethanol and a sample of muscle tissue was stored at -80 ˚C for analysis of post-release telomere length. Muscle tissues were dissected

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from the same location on the caudal peduncle and contained a mixture of red and white muscle tissues.

Telomere length determination

Telomere length in both tissues was analyzed using the the so-called gold standard TRF method [31]. Due to the high cost and handling time of TRF analysis per sample we were only able to analyze 35 samples per tissue. As a result, we selected a sample of 35 amongst the 48 recaptured fish by random sampling methods. Recaptured individuals did not differ in behaviour from non-recaptured individuals [28] and restricting our sample as such is therefore not expected to a bias our conclusions. tTelomere fragments were prepared as previously described [32]. Fin and muscle samples from each individual (taken 4-6 months apart) were analyzed next to each other during gel electrophoresis for optimal comparability, and pairs were distributed randomly across 3 gels. Gels did not differ in estimates of telomere length (supplement S2). After standard Southern blotting, telomere fragments were detected by hybridization to an alkaline phosphatase-linked telomere probe and use of chemoluminescence (AlkPhos labeling and detection kit, GE Healthcare). Digitized signals were analyzed within a window of approximately 4-30 kb as previously described [32].

Statistical analysis

We previously established that the individuals in this study consistently differed in exploration behaviour (mixed model, individual-specific random intercepts) and the plastic response of exploration to experience (individual-specific random slopes for trial number) [28]. Further, fish showed a shared mean response of exploration behaviour to experience leading to more active exploration in later trials (fixed effect trial number). Aggression also differed consistently among individuals (individual-specific random intercepts) but individuals showed *no* change of aggression with experience (no individual-specific or shared slope for trial). Yet individuals with a shorter body length behaved more aggressively towards the slightly smaller intruder (fixed effect length). We therefore first built two mixed-effects models

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including only these significant effects ('null models' H_0) and ran these on the data from the present study, one for exploration and one for aggression. We then added telomere length estimates from either fin (alternative model 1, H_{a1}) or muscle samples (alternative model 2, H_{a2}) as continuous fixed effects to each model, including also the second order interactions. Alternative and null models were evaluated with respect to significance of the additional fixed effects, explained variance (R^2) and individual repeatability scores (see supplement 3 for details). The presence of significant individual-specific slopes for changes in exploration with experience implies that individual rank orders for exploration are somewhat trial-specific (H_0, cross-context correlation trial 1 vs. 4 = 0.770, [33]). We therefore calculated repeatabilities for exploration at each level of trial following [34].

All models were built using R v.3.2.2 and the 'lmer' function of the 'lme4' package in the R statistical computing environment [35] and validated by inspection of residual plots and Cook's distances. Critical values for significance were set at 0.05. Markov chain Monte Carlo methods were used to represent individual-specific estimates of exploration and aggression throughout all trials and their uncertainty in the figures (supplement S4).

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Results

Individuals with shorter fin telomeres behaved consistently more exploratively and aggressively (table 1, fig 1 & 2). Regression coefficients between telomere length and scores of aggressive and bold behaviour were also negative for muscle samples collected 3-4 months later, but were non-significant. Throughout, adding telomere length as a fixed predictor increased the variance explained by the fixed effects in the model (R^2_m) and reduced unexplained among-individual repeatability of behaviours (repeatability), without large effects on the overall variance explained by the model ($R^2_{c,}$ see table 1). Differences amongst the three batches caught at different fishing instances were not found to affect our conclusions (supplement 5). Telomere length in the fin samples did not covary with telomere length in muscle samples 3-4 months later (Spearman's rho = 0.262, p = 0.127).

Figure 1 caption: Individual estimates of exploration as a function of fin telomere length for each behavioural trial. To obtain estimates of exploration and their uncertainty we fitted the null models from table 1 with Markov Chain Monte Carlo methods (package MCMCglmm) instead of Laplace approximation (package lmer) and used the posterior chains of the random effect predictors to calculate individual and trial specific Bayesian posterior means and credibility intervals. Since individuals differed in how they changed exploration behaviour through trials, all estimates were calculated by summing the random intercept posterior to

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(random slope posterior*trial number).

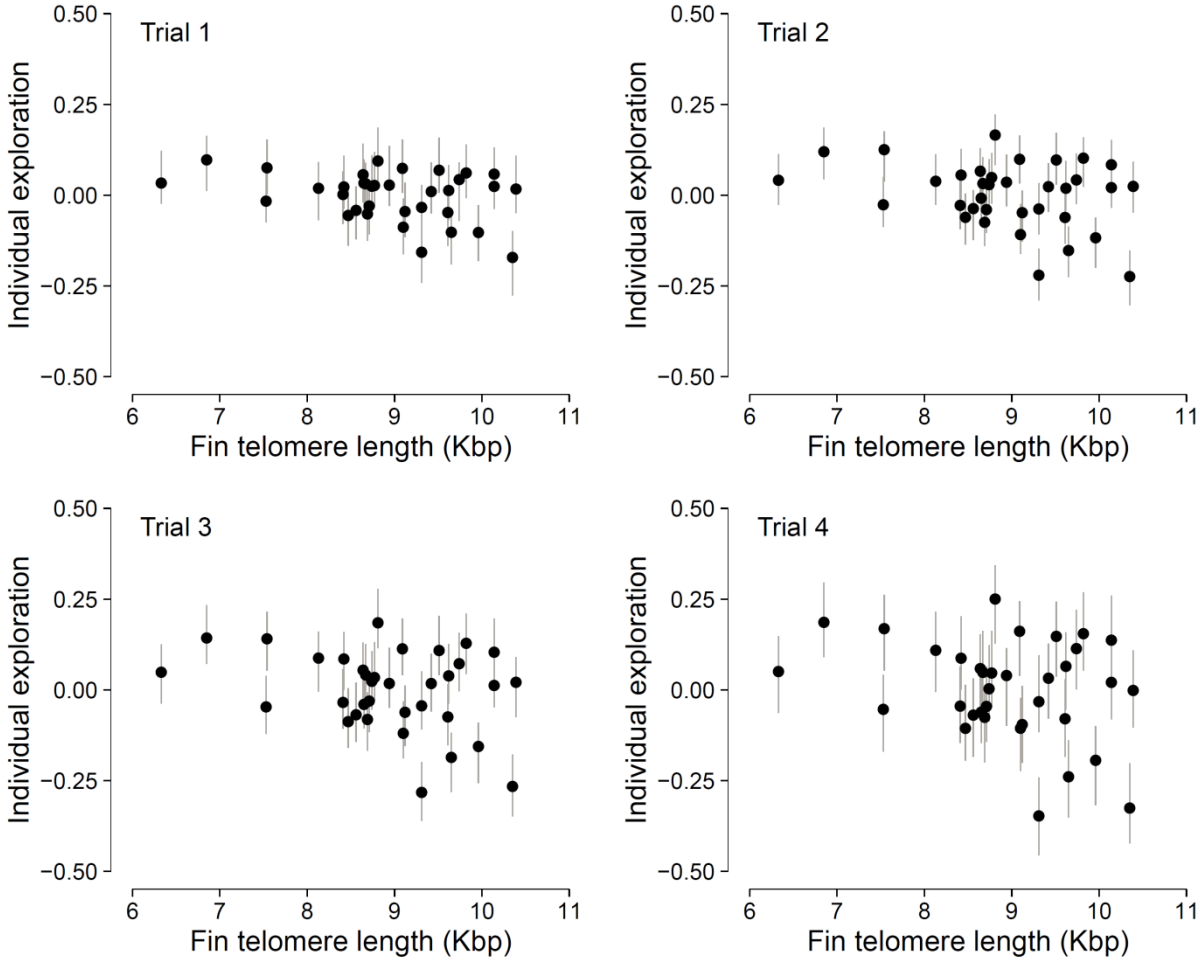

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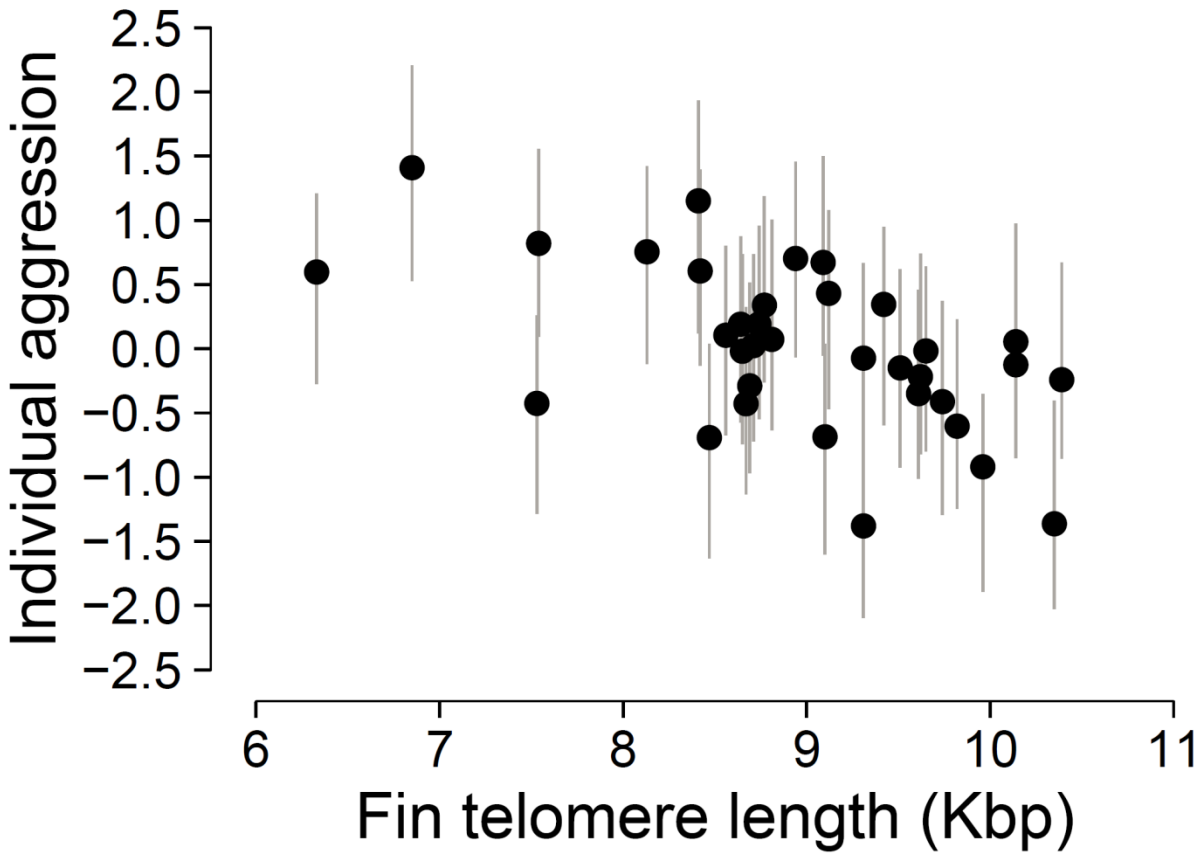
Figure 2 caption: Individual estimates of aggression as a function of fin telomere length. Estimates of aggression and their uncertainty are represented by the Bayesian posterior mean and credibility intervals of their random effect predictors calculated with methods similar to these outlined in figure 1. Since individuals did not differ in the extent they changed aggression with trials individuals maintained their rankings throughout both trials and one posterior mean represents behavioural outputs during both aggression trials.



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Discussion

Wild brown trout yearlings with shorter fin telomeres behaved consistently more boldly and aggressively under controlled conditions in the laboratory. Though not significant, muscle telomere length from samples collected 3-4 months after behavioural assays tended to show similar negative associations with bold and aggressive behaviour. Our results seem consistent with earlier findings by [20] showing that manipulations shortening juvenile telomere length caused European starlings to make more impulsive foraging decisions when adult. Indirect evidence also stems from research on knock-out mouse strains for superoxide dismutase (SOD), an antioxidant known to slow telomere erosion in vitro [36], showing that SOD deficiency leads to elevated aggression [37]. Individual differences in laboratory scores of behaviour similar to those scored in the present study tend to be highly stable across time and positively predict behaviour of brown trout in the wild [28, 38, 39]. We therefore believe our study provides the first evidence that wild populations may display similar associations between natural variation in telomeric and consistent behavioural traits.

Assuming that telomere length predicts lifespan, these results fit with theoretic predictions that individual differences in expected lifespan may promote the emergence of individual differences in risk-taking behaviour [40]. A plausible argument can be made for fitting telomere dynamics within existing integrative models of personality variation, such as the model implied by the POLS hypothesis, where higher metabolic rate in more active individuals may lead to greater exposure to oxidative stress and faster erosion of telomeres, thereby requiring a fast life-history in comparison with more shy, low-energetic individuals [13, 18].

Telomere length appears to have a substantial heritable component in many species [14, 41, 42]. As a state variable, telomeres may further fill the requirements of positive state-behaviour feedback loops required in state-dependent models of personality behaviour if state variables are not inherently stable [2, 4]. Such feedback loops are thought to be

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important in stabilizing differences in state, behaviour and life-history and thus maintain individual differences over time. If individuals born with short telomeres have a reduced lifespan [43], they may counteract this by growing fast and maturing early [19]. This may be achieved by adopting a bold and aggressive lifestyle fueled by a high-energy metabolism [6], exposing them to more oxidative stress and faster telomere erosion [18]. Whereas results from [20], and to some extent also [37], suggest that experimentally reduced telomere length stimulates individuals to behave boldly and aggressively, many of the abovementioned links between behaviour, metabolism, stress and life-history remain unresolved and are likely subject to compensation mechanisms [44-46]. Likewise in brown trout, where studies suggest a more variable link between bold behaviour, metabolism and growth in more heterogeneous environments [28, 39, 47], a negative relationship has been observed between individual metabolism and oxidative stress [48]. Resolving these likely complex pathways among physiology, behaviour and life-history in trout and other models will be an interesting area for further research.

We found no evidence for a relationship between telomere length estimates in fin and muscle samples. While inter-individual differences in telomere length within a single tissue type tend to be highly stable in a range of species, rates of telomere erosion may differ between tissues [15, 16, 49, 50] but see [17] . Our experimental design does not allow us to discern whether the absence of a relationship between fin and muscle telomere length is due to low stability of individual differences or tissue-specific processes. Yet, previous work on similar-aged brown trout suggests repeatable inter-individual differences in telomere length from two pectoral fins sampled one year apart (*Rho* = 0.463, p<0.0001, N=93, unpublished results from [51]).

Currently, the POLS hypothesis is the dominant model integrating physiological and life-history traits with personality and suggests simple, linear covariance among traits across organizational levels [13]. Whereas conceptually attractive, this model has received mixed

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empirical support, and links among behaviour, physiology and life-history often show context- dependence [39, 44, 45, 52] or higher order relationships between behaviour and physiology [53]. This calls for development of alternative models accommodating these complexities. We think telomere dynamics may play an important role in these efforts to understand the complex relationships between physiology, behaviour and life-history.

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Ethics

The experiments were approved by the Ethical Committee for Animal Research for Animal Research in Gothenburg (License 132/2005) and comply with the laws in Sweden.

Data accessibility

The datasets supporting this article have been uploaded as part of the supplementary material.

Authors' contributions

BA, AP, DB and JIJ conceived the experiment. BA conducted the experiment and collected tissue samples which AP analyzed. BA analyzed the data and drafted the manuscript. All authors contributed revisions to the manuscript. All authors gave final approval for publication.

Competing interests

We have no competing interests.

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Table 1 caption: Model parameters for univariate mixed models excluding (H_0) and including estimates of fin (H_{a1}) and muscle telomere length (H_{a2}) for response variables exploration and aggression. R^2 = R squared, R^2_m = marginal R^2, R^2_c = conditional R^2, Loglik = log likelihood, expl = exploration, agr=aggression, finTL = fin telomere length, len= body length, muscleTL = muscle telomere length, ind = individual.

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Table 1

			Fixed effects				Repeatability				R^2		Loglik
Model formula			Effect	Beta [95%CI]	$F_{(df1,df2)}$	p	trial 1	trial 2	trial 3	trial 4	R^2_m	R^2_c	
Exploration													
	H_0	expl ~ trial + (trial|ind)	Trial	0.041 [0.027,0.056]	$30.480_{(1,34)}$	**<0.0001**	0.601	0.679	0.762	0.826	0.110	0.771	130.432
	H_{a1}	expl ~ trial + finTL + (trial|ind)	Trial	0.041 [0.026,0.056]	$30.480_{(1,34)}$	**<0.0001**	0.567	0.656	0.749	0.819	0.166	0.773	132.632
			Fin telomere length (Kbp)	-0.037 [-0.071,-0.002]	$4.423_{(1,33)}$	**0.043**							
	H_{a2}	expl ~ trial + muscleTL + (trial|ind)	Trial	0.041 [0.027,0.056]	$30.480_{(1,34)}$	**<0.0001**	0.571	0.660	0.752	0.822	0.159	0.775	132.392
			Muscle telomere length (Kbp)	-0.040 [-0.080,0.0001]	$3.911_{(1,33)}$	0.056							
Aggression													
	H_0	agr ~ len + (1|ind)	Body length (mm)	-0.044 [-0.072,-0.016]	$8.981_{(1,33)}$	**0.005**	0.627	0.627			0.175	0.692	-83.800
	H_{a1}	agr ~ len + finTL + (1|ind)	Body length (mm)	-0.051 [-0.076,-0.027]	$16.404_{(1,32)}$	**0.0003**	0.520	0.520			0.362	0.694	-77.687
			Fin telomere length (Kbp)	-0.488 [-0.752,-0.227]	$13.381_{(1,32)}$	**0.0009**							
	H_{a2}	agr ~ len + muscleTL + (1|ind)	Body length (mm)	-0.043 [-0.073,-0.015]	$8.981_{(1,33)}$	**0.005**	0.630	0.630			0.183	0.698	-83.477
			Muscle telomere length (Kbp)	-0.138 [-0.483,0.221]	$0.596_{(1,32)}$	0.446							

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Highlights

- Telomeres likely play a crucial role in regulating organismal senescence and intrinsic lifespan
- The role of telomeres in regulating state-dependent personality variation is currently overlooked
- Wild juvenile brown trout (Salmo trutta) with shorter fin telomeres behaved consistently more boldly and aggressively
- We suggest telomere dynamics are important in integrating personality traits with other state variables

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