

1           **Exploratory personality is independent of telomere**  
2                           **dynamics in a wild bird population**

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4   **Running title:** Exploratory personality traits and telomere length

5  
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25 **Abstract**

26 Numerous studies have demonstrated that individuals within a species will consistently vary  
27 between one another in behavioural traits. A prominent adaptive explanation for such ‘animal  
28 personalities’ relates to an individual’s intrinsic state driving and/or being driven by  
29 behaviour. Telomeres – the protective caps at the end of chromosomes which exist in most  
30 organisms – have been proposed as a biomarker of an individual’s intrinsic state and mortality  
31 risk. It is, however, unclear the extent to which telomere dynamics are associated with  
32 repeatable behavioural traits, with only a handful of studies exploring this relationship to date.  
33 Here, we examined the relationship between relative telomere length and exploration of both  
34 a novel environment and novel object in a wild population of Seychelles warblers  
35 (*Acrocephalus sechellensis*). We tested for between-individual covariation between  
36 exploratory traits, as well as between-individual covariation among exploratory traits and both  
37 relative telomere length and change in telomere length over time. We found that individuals  
38 who explored a novel environment more, also explored a novel object more, and that there  
39 was a strong quadratic age effect on both exploratory measures. However, there was no  
40 between-individual relationship between exploratory traits and either relative telomere length  
41 or change in relative telomere length over time. When assessing covariation between intrinsic  
42 state and personality, our findings demonstrate the importance of: (1) considering longitudinal  
43 evidence, where there is an opportunity for environmental stressors to influence telomere  
44 dynamics; (2) considering potentially confounding factors related to within-individual vs  
45 between-individual processes; and, (3) investigating covariation across many taxa.

46

47 **Keywords**

48 animal personality; biomarker; intrinsic state; Seychelles warbler; telomeres; wild population

49 **Introduction**

50 Individuals within a population will differ consistently from one another in their behavioural  
51 traits (i.e. repeatable ‘animal personalities’), and these behavioural traits often correlate with  
52 one another to form ‘behavioural syndromes’ (Dall et al., 2004; Dingemanse & Wolf, 2010;  
53 Sih et al., 2004; Wilson, 1998). Animal personalities are typically described in the context of  
54 a proactive–reactive continuum, where individuals express varying levels of aggression,  
55 boldness, exploration and sociality (Réale et al., 2007). Research highlighting the prevalence  
56 and ecological implications of animal personalities is extensive (e.g. movement; Cote et al.,  
57 2010, mating; Schuett et al., 2010, and population dynamics; Griffen & Dinuzzo, 2020);  
58 however, there is comparatively less empirical evidence describing the mechanisms that  
59 generate and/or maintain animal personalities.

60

61 Many theoretical models explain the prevalence of animal personalities from an adaptive  
62 perspective (Dall et al., 2004; Dingemanse & Wolf, 2010; Wolf & Weissing, 2012), with  
63 particular emphasis on an individual’s ‘intrinsic state’ (Houston & McNamara, 1999; Mathot  
64 et al., 2019; Wolf & Weissing, 2010). Under an adaptive framework, consistent within-  
65 individual behavioural traits can occur if an optimal behaviour is connected to a slow-  
66 changing intrinsic state variable, such as metabolism (e.g. resting and basal metabolic rate;  
67 Careau et al., 2015), plasma hormone levels (e.g. glucocorticoids; Dosmann et al., 2015)  
68 and/or body condition (e.g. body mass; Bijleveld et al., 2014). If these intrinsic state variables  
69 also differ between individuals, then repeatable behavioural traits can arise (Sih et al., 2015).  
70 For instance, an individual with a high level of physiological stress and/or poor body  
71 condition may be more likely to perform risky behaviours depending on how much the  
72 individual stands to gain or lose (‘asset-protection principle’: Clark, 1994; Wolf et al., 2007),

73 particularly if they are on the verge of starvation or facing high levels of competition (Clark &  
74 Mangel, 2000; Luttbeg & Sih, 2010). Alternatively, individuals with a higher body condition  
75 may be more inclined to take more frequent risks if they are better at maximising the benefits  
76 of risky behaviour ('state-dependent safety hypothesis', Luttbeg & Sih, 2010). Both  
77 frameworks are supported by a recent meta-analysis by Niemelä & Dingemanse (2018a),  
78 which shows risk-taking behaviour increased with metabolic activity and hormone levels  
79 (asset-protection principle), as well as body mass and size (state-dependent safety  
80 hypothesis).

81

82 One measure of intrinsic state that is rarely studied alongside repeatable behaviour, but is  
83 often used in evolutionary ecology as a biomarker of somatic stress, is telomere length  
84 (Wilbourn et al., 2018). Telomeres are repetitive nucleotide sequences that cap the ends of  
85 eukaryotic chromosomes and maintain genomic integrity (Blackburn, 2000). As a result of the  
86 'end replication problem', telomeres shorten with each cell division (Watson, 1972), meaning  
87 greater rates of telomere attrition occur during periods of high cellular division i.e., during  
88 growth and with age (Frenck et al., 1998; Hall et al., 2004). Telomeres are also susceptible to  
89 degradation through exposure of an individual to environmental stressors that trigger  
90 pathways of cellular damage, such as oxidative stress (Hausmann & Heidinger, 2015;  
91 Metcalfe & Alonso-Alvarez, 2010; von Zglinicki, 2001). However in some cells and/or  
92 tissues, telomere length can also increase, for example via the restoration of telomeric DNA  
93 by the enzyme telomerase (Blackburn et al., 1989), as well as other lengthening pathways  
94 (Cesare & Reddel, 2010; Mendez-Bermudez et al., 2012). These factors result in between-  
95 individual variation in telomere dynamics. Telomeres are therefore often utilised as  
96 biomarkers of the conditions an individual has experienced over their lifetime, and the

97 associated somatic stress (Monaghan et al., 2022; Spurgin et al., 2018; Young, 2018), and  
98 thus are a good candidate for studying intrinsic state-dependent personality.

99

100 Recent reviews suggest that telomeres should either correlate with, or function as, an adaptive  
101 mediator of an individual's behaviour in a state-dependent manner (Bateson & Nettle, 2018;  
102 Young, 2018). The direction of associations identified in these studies indicates that  
103 individuals with poorer intrinsic state (i.e. shorter telomeres) tend to possess risk-taking  
104 behaviours (Sih et al., 2015), as shown with smoking behaviour in humans (Bateson & Nettle,  
105 2018) and impulsive foraging behaviour in juvenile starlings, (*Sturnus vulgaris*) (Bateson et  
106 al., 2015). However, comparatively less research has focused on the association between  
107 telomeres and repeatable behavioural traits. In wild brown trout (*Salmo trutta*), individuals  
108 with shorter telomere length have higher boldness and aggression (Adriaenssens et al., 2016),  
109 whereas Eastern chipmunks (*Tamias striatus*) with longer telomere length at first breeding  
110 attempt were faster explorers (Tissier et al., 2022). While these studies provide valuable  
111 insights into the importance of intrinsic state in behaviour, it is unclear whether there is a  
112 general positive or negative association between telomeres and behaviour, or whether these  
113 relationships are isolated to a handful of taxa. Therefore, it is important that further empirical  
114 evidence is gathered, particularly in free-living species, and populations that possess repeat  
115 trait measures.

116

117 Here, we use longitudinal data from an island population of individually-marked Seychelles  
118 warblers (*Acrocephalus sechellensis*), to investigate whether intrinsic state, measured using  
119 relative telomere length (RTL), is associated with exploratory behaviour, measured as  
120 exploration of a novel environment and exploration of a novel object. In this population,

121 exploratory behaviour is repeatable: individuals consistently vary between one another in  
122 their levels of exploration over time and across contexts (Edwards et al., 2017). Further, short  
123 RTL and/or greater RTL shortening in individuals is associated with poor body condition  
124 (Barrett et al., 2013), lower food availability (Spurgin et al., 2018), increased inbreeding  
125 (Bebbington et al., 2016) and increased antagonistic interactions with conspecifics  
126 (Bebbington et al., 2017). RTL also declines with age, and adult survival is positively  
127 associated with telomere length and attrition, independent of age (Barrett et al., 2013).  
128 Further, assessments of repeated within-individual measures of RTL show that 46% of  
129 consecutive measurements demonstrate telomere lengthening (Brown et al., 2021; Spurgin et  
130 al., 2018), which is related to periods of reduced stress in females (Brown et al., 2021). As  
131 several studies support the concept that telomere dynamics reflect the costs of life-history  
132 stress in this system, it provides an excellent opportunity to determine whether there are also  
133 somatic costs associated with explorative behaviour.

134

135 To gain understanding of the covariation between Seychelles warbler exploratory behaviour  
136 and relative telomere length, we assess correlations between the two traits by partitioning the  
137 total phenotypic covariance into its between-individual components (Dingemanse et al., 2012;  
138 Niemelä & Dingemanse, 2018b). Based on the general negative associations shown between  
139 intrinsic state and exploratory behaviour (Adriaenssens et al., 2016; Bateson et al., 2015;  
140 Niemelä & Dingemanse, 2018a), we expect negative between-individual correlations between  
141 exploration and RTL, which would indicate that more exploratory individuals have, on  
142 average, shorter relative telomere lengths than those who do not (Niemelä & Dingemanse,  
143 2018b). We also assess whether there is a between-individual association between exploratory  
144 traits and telomere length change (lengthening or shortening; hereafter,  $\Delta$ RTL). We predict

145 that individuals with higher exploratory scores will have shorter telomeres and will  
146 experience a more pronounced loss of telomere length over time compared to their less  
147 exploratory counterparts.

148

## 149 **Materials and Methods**

### 150 *Study site and system*

151 The Seychelles warbler is a small insectivorous passerine endemic to the Seychelles  
152 archipelago. Our study population resides on Cousin Island (29 ha; 04°20'S, 55°40'E), where  
153 it has been monitored intensely since 1997 (Richardson et al., 2002). This population has been  
154 at carrying capacity since 1982, with ca. 320 adult individuals resident in ca. 115 territories  
155 (Hammers et al., 2019). Territories are occupied year-round by a single socially monogamous  
156 breeding pair, that normally produce one-egg clutches (91% of clutches) (Brouwer et al.,  
157 2006). Individuals may adopt a subordinate status by either remaining in their natal group as  
158 non-breeders or, less frequently, dispersing to a neighbouring territory (Groenewoud et al.,  
159 2018). Approximately 50% of territories contain 1–5 adult subordinates (Hammers et al.,  
160 2019; Kingma et al., 2016), and ca. 35% of subordinates (mainly females) help raise offspring  
161 of the dominant pair (Hammers et al., 2019; Richardson et al., 2003). Subordinate females  
162 sometimes (ca. 11% of all maternities; Sparks et al., 2022) also gain maternity by laying an  
163 egg within the dominant female's nest ('cobreeding'). However, virtually no (< 0.6%)  
164 subordinate males gain paternity (Sparks et al., 2021), either within or outside their resident  
165 territory (Richardson et al., 2001).

166

167 Fieldwork is conducted during the minor (January – March) and major (June – August)  
168 breeding seasons. In each season as many individuals as possible are caught with mist nets

169 and blood sampled via brachial venepuncture (ca. 25  $\mu$ l stored in absolute ethanol at 4°C) for  
170 later molecular work including sexing (Richardson et al., 2001). Body mass is measured using  
171 either a Pesola or electronic scale ( $\pm$ 0.1 g) and body size is determined by measuring the  
172 length of the right tarsus using sliding callipers ( $\pm$ 0.1 mm). Any newly-caught individuals are  
173 fitted with a unique combination of three plastic colour rings and a metal British Trust for  
174 Ornithology (BTO) ring, resulting in ca. 96% of the adult population being ringed in any  
175 given year (Raj Pant et al., 2020; Richardson et al., 2001). Most individuals are first ringed at  
176 <5 months of age while still dependent in their natal territory. For individuals who had  
177 unknown lay, hatch, or fledge dates, age was estimated at time of capture using eye colour,  
178 where fledglings have grey eyes (1–5 months), subadults have light brown eyes (6–12  
179 months) and adults (>12 months) have dark brown eyes (Komdeur, 1992). Therefore, age is  
180 known for all individuals included in the study. During both breeding seasons, each territory  
181 is checked at least once a week to identify resident birds, as well as determine their social and  
182 breeding status (Richardson et al., 2002). As the annual resighting probability is close to one  
183 ( $0.98 \pm 0.01$  SE; Brouwer et al., 2010) and inter-island dispersal is virtually absent (Komdeur  
184 et al., 2004), individuals not observed during two consecutive breeding seasons can be  
185 confidently assumed to be dead (Brouwer et al., 2010; Hammers et al., 2021).

186

### 187 *Personality assays*

188 We assayed two measures of exploration (Edwards et al., 2017). Novel environment  
189 exploration was assayed during major and minor breeding seasons 2012–2015, 2019 and  
190 2021, as well as the minor breeding seasons in 2020 and 2022. Assays for novel object  
191 exploration were conducted during all of these seasons apart from the major and minor  
192 seasons in 2012. Personality assays were conducted as described previously (Edwards et al.,



193 2017). In brief, individuals were assayed for personality after being caught in a mist net,  
194 blood sampled and left to rest for five minutes in a bird bag. Individuals were then placed into  
195 an Oxygen 4 tent (L322 × W340 × H210 cm; Gelert Ltd Wigan) containing three artificial  
196 trees, where the number of hops, flights and trees visited were recorded for 5 minutes and  
197 summed to create a measure of novel environment exploration. After a 2-minute break (see  
198 acclimation and randomisation tests, Edwards et al., 2017), a novel pink toy was introduced  
199 for 5 minutes and the exploration of that object was scored. Both novel environment  
200 exploration score and novel object exploration score are repeatable (0.23, 95% credible  
201 interval [CrI] = 0.08–0.36, and 0.37, 95% CrI = 0.04–0.59, respectively; Edwards et al.,  
202 2017), where repeatability is calculated as the proportion of between-individual variance  
203 relative to the total phenotypic variance of the population when using repeat trait measures  
204 per individual (Nakagawa & Schielzeth, 2010). Novel environment exploration in this  
205 population is heritable (0.17, 95% CrI = 3e-4–0.33) while novel object exploration is not  
206 (Edwards et al., 2017). A total of 334 individuals were tested for both novel environment and  
207 object exploration (Table S1).

208

### 209 *Telomere length measurements*

210 RTL (measured as the amount of telomeric DNA sequence relative to the amount of the  
211 reference gene glyceraldehyde-3-phosphate dehydrogenase, GAPDH) was estimated using  
212 qPCR (quantitative polymerase chain reaction) for birds caught and blood sampled between  
213 1995 and 2014, as summarised in Spurgin et al., (2018). qPCR geometric efficiency (mean ±  
214 SD) for the telomere and GAPDH plates was  $1.78 \pm 0.05$  and  $1.92 \pm 0.04$ , respectively  
215 (Spurgin et al., 2018). Within-plate repeatability of GAPDH and telomere cycle quantification  
216 (Cq) values were 0.74 (95% confidence intervals [CI] = 0.74–0.75) and 0.73 (95% CI = 0.71–

217 0.74) for the GAPDH and telomere Cq values, respectively (Spurgin et al., 2018). Between-  
218 plate repeatability of RTL, calculated using 422 samples measured at least twice, was 0.68  
219 (95% CI = 0.65–0.70; Spurgin et al., 2018). The within-individual variance of RTL (i.e., from  
220 multiple samples across an individual's lifetime) is greater than the variance among repeated  
221 measurements of the same sample (Levene's test:  $F = 43.63$ ;  $p < 0.001$ ; Brown et al., 2021).  
222 There were no storage time effects of the blood samples on telomere length (Spurgin et al.,  
223 2018).

224

225 We used RTL measures of individuals that were tested for novel environment exploration  
226 and/or novel object exploration at least once in their lives. After removing outlier samples  
227 with very large Cq values using the QC steps outlined in Spurgin et al. (2018), our final data  
228 set included 921 samples from 295 individuals tested for novel environment exploration and  
229 516 samples from 159 individuals tested for novel object exploration (Table S2–3). For  
230  $\Delta$ RTL, we measured the difference in RTL between two consecutive measures. This included  
231 478 paired measures from 214 individuals tested for novel environment exploration and 271  
232 paired measures from 117 individuals tested for novel object exploration (Table S4–5). Where  
233 multiple RTL measures were collected for the same bird within the same field season, we  
234 selected a single RTL measure at random for each field season to assess  $\Delta$ RTL. As Seychelles  
235 warblers are caught opportunistically, the interval between two consecutive RTL measures  
236 ranges from 0.5 (i.e. a consecutive measure of RTL between the minor and major breeding  
237 seasons) to 7.7 years (mean: 1.9 years  $\pm$  1.3 SD).

238

239 *Statistical analyses*

240 We performed analyses using R v.4.0.2 (RStudio Team, 2022) and the package MCMCglmm  
241 v 4.2.1 (Hadfield, 2010). For all analyses, we employed bivariate Markov chain Monte Carlo  
242 (MCMC) generalised linear mixed models (GLMMs) to estimate between-individual  
243 correlations. Using a Bayesian multivariate framework allowed us to fit the fixed effects  
244 impacting on both traits, thereby avoiding the error associated with using best linear unbiased  
245 predictors (Houslay & Wilson, 2017).

246

247 Each model included two response variables. The first model included exploration of a novel  
248 environment and exploration of a novel object (both fitted as Poisson GLMM: see Figure S1  
249 for distributions). The remaining models included exploration score (novel environment or  
250 novel object) and either RTL or  $\Delta$ RTL (Gaussian distributions) as the other response variable.  
251 RTL was square-root transformed to be consistent with previous work on this system  
252 (Spurgin et al., 2018), and for each model subset we subsequently z-transformed RTL (mean  
253 centred and divided by 1 SD) to improve comparability between RTL studies (Verhulst,  
254 2020). We adjusted  $\Delta$ RTL for regression-to-mean effects by subtracting the mean difference  
255 between successive samples, estimated by the correlation between successive samples  
256 (Verhulst et al., 2013). Positive values indicate telomere lengthening and negative values  
257 indicate telomere shortening, relative to the population mean RTL. Distributions of non-  
258 transformed and the square-root and z-transformed RTL, as well as raw  $\Delta$ RTL and adjusted  
259  $\Delta$ RTL data are provided in Figures S2–3. As fewer individuals possessed measures for  $\Delta$ RTL  
260 compared to RTL, and fewer individuals were tested for novel object exploration relative to  
261 novel environment exploration (Table S1–S5), we could not run multivariate models with  
262 more than two response variables, and so ran four bivariate models instead.

263

264 We included methodological fixed effects for novel environment and novel object  
265 exploration, including tent colour for novel environment exploration (factor: blue/green,  
266 Edwards et al., 2017), branch orientation for novel object exploration (factor:  
267 diagonal/parallel), assay number to control for habituation (Edwards et al., 2017), sex (factor:  
268 male/female) and age in years as both linear and quadratic terms to model for senescence  
269 (Patrick & Weimerskirch, 2015). For RTL, we included laboratory technician ID (factor: 2  
270 levels) and age in years (mean:  $0.85 \pm 0.35$  SD) (log-transformed following Spurgin et al.,  
271 2018). For  $\Delta$ RTL, we included log transformed age at first RTL measurement (years,  
272 continuous), duration of interval between the two RTL measures (years, continuous, hereafter  
273  $\Delta$ RTL period) and technician ID (factor: 3 levels). As it was possible for different technicians  
274 to process the first and second RTL, we created three levels for technician ID: one for either  
275 technician, and a third composite level that indicated that both technicians processed one  
276 sample each. Collinearity between the continuous fixed effects was checked by calculating  
277 variance inflation factors (VIFs); all VIFs were  $< 3$ . To allow estimation of (co)variance on  
278 the level of individuals, we included bird identity (bird ID) as a random effect for all response  
279 variables. Observer identity (observer ID) was included as a random factor for novel  
280 environment (factor: 16 levels) and novel object exploration (factor: 12 levels). As telomere  
281 length shows cohort (Spurgin et al., 2018) and plate (Sparks et al., 2021) effects, both were  
282 included in RTL models as random effects (factor: 17 levels and 71 levels for cohort and plate  
283 ID, respectively). Cohort year was not included as a random factor for  $\Delta$ RTL models since  
284 Spurgin et al. (2018) found no support for cohort effects. Plate identities for both RTL  
285 measurements used to calculate  $\Delta$ RTL were included as two random effects (as per Brown et  
286 al., 2021).

287

288 Unstructured variance–covariance matrices were estimated using the posterior distribution for  
289 the random effects of bird ID for each response variable for between-individual estimates:

$$\begin{bmatrix} \sigma_{trait1}^2 & \sigma_{trait2,trait1} \\ \sigma_{trait1,trait2} & \sigma_{trait2}^2 \end{bmatrix} \quad (1)$$

290 Between-individual correlation estimates were subsequently calculated by dividing the focal  
291 between-individual covariance by the square-root of the product of the between-individual  
292 variances of the two focal traits (see Houslay and Wilson, 2017). From this, we determined  
293 the mean slope estimate and its corresponding 95% highest posterior density (HPD) credible  
294 interval, where a HPD credible interval that did not overlap zero denoted a significant  
295 correlation. We also considered fixed effects to have a significant effect if the HPD credible  
296 interval did not overlap zero. In all cases, models were run for  $4.6 \times 10^6$  iterations, with a  
297 burn-in of  $6 \times 10^4$  and thinning interval of 500. We applied priors with a weakly informative  
298 distribution ( $V = \text{diag}(n)$ ,  $\nu = n + 0.002$ , where  $n =$  number of response variables). We  
299 visually checked time-series plots of model parameters and assessed multiple convergence  
300 diagnostics, including autocorrelation ( $< 0.1$ ) values, effect sizes ( $\geq 1,000$ ), Geweke tests (Z-  
301 score  $< 2$ ) and Heidelberg and Welch (pass) diagnostics.

302

### 303 *Ethical note*

304 All relevant national, institutional, and/or international regulations for the handling and use of  
305 animals were adhered to. For fieldwork, ethical guidelines and agreements were observed  
306 locally. We had access to the Cousin Island Nature Reserve thanks to Nature Seychelles. All  
307 fieldwork and sample protocols were approved and permissions given by the Seychelles  
308 Department of Environment and Seychelles Bureau of Standards. Fieldwork procedures were

309 approved by the University of East Anglia's Ethical Review Committee and ratified by the  
310 University of Leeds.

311

## 312 **Results**

313 Male warblers had significantly higher novel environment and novel object exploration scores  
314 compared to females (Table 1). There was a quadratic effect of age on both measures of  
315 exploration: younger and older individuals had lower exploration scores than middle-aged  
316 individuals (Table 1, Figure 1). However, for novel environment this decline at older ages  
317 was driven by a few data points: without these points scores appear to increase with age  
318 before plateauing or declining slightly in older ages (Figure 1A). There was a negative effect  
319 of age on RTL (Table S6), but there was no effect of age at first RTL measurement, or the  
320 duration of interval between two consecutive RTL measures, on  $\Delta$ RTL (Table S7). While we  
321 found no effect of technician on RTL, we did find a technician effect on  $\Delta$ RTL (Table S7).

322

323 There were also significant methodological effects for exploration tests: individuals tested in a  
324 blue tent for novel environment exploration produced higher exploration scores than those  
325 tested in a green tent (Table 1). Individuals tested for novel object exploration using artificial  
326 trees with diagonal branches also had a higher exploration score than individuals tested with  
327 parallel branches (Table 1). Both novel environment and novel object exploration scores had a  
328 positive association with exploration test number (Table 1).

329

330 Novel environment exploration and novel object exploration displayed significant positive  
331 between-individual correlations (0.600, 95% credible interval = 0.353–0.777; Table 2, Figure  
332 2). Individuals that were more exploratory of a novel environment were also more exploratory

333 of a novel object. We found no significant between-individual correlations between either  
334 Seychelles warbler novel environment or novel object exploration with either RTL or  $\Delta$ RTL  
335 (Table 2, Figure S4).

336

### 337 **Discussion**

338 Here, we tested for between-individual covariation in exploratory traits and telomere  
339 dynamics using long-term data from a wild population of Seychelles warblers. While we  
340 found a positive between-individual correlation between the two exploratory traits, which  
341 aligns with previous Seychelles warbler research (Edwards et al., 2017), we found no  
342 between-individual covariation in exploration of either a novel environment or novel object,  
343 with either telomere length or change in telomere length. However, both traits were age-  
344 dependent: exploration score increased during early-life, then decreased in later life, while  
345 relative telomere length decreased with age.

346

347 The asset-protection principle suggests that individuals who are in a poorer intrinsic state (i.e.  
348 shorter telomeres and greater telomere shortening) have less to lose, and so are more likely to  
349 undertake risky behaviour (Clark, 1994; Wolf et al., 2007). Alternatively, the state-dependent  
350 safety hypothesis posits a positive relationship between intrinsic state and behaviour,  
351 individuals that already have high intrinsic state (i.e. long telomeres) should express risk-  
352 taking behaviours (i.e. more exploratory), and thus gain more resources that maintain their  
353 high state (McElreath et al., 2007). However, we found support for neither hypothesis, which  
354 may suggest that exploratory traits do not facilitate net asset gain in this system. If being  
355 exploratory did facilitate acquisition of more resources (e.g. acquiring a better quality  
356 territory, which can reduce telomere attrition; Brown et al., 2022), then individuals with short

357 telomeres are expected to have high (asset-protection principle) or low (state-dependent safety  
358 hypothesis) exploration scores. Instead, different personality traits, such as those shown to  
359 covary with alternative measures of intrinsic state in other species (Niemelä & Dingemanse,  
360 2018a), may form a stronger association with telomere dynamics in this system. For instance,  
361 male Seychelles warblers who engage in a higher frequency of territorial disputes have been  
362 shown to express higher rates of telomere attrition than their less confrontational counterparts  
363 (Bebbington et al., 2017). This indicates that aggression plays a functional role in facilitating  
364 asset gain in the Seychelles warbler, resulting in a detectable cost to intrinsic state.

365

366 Previous studies have documented mixed associations between behaviour and telomere  
367 length. These include a negative association between telomere length and both exploration  
368 and aggression in brown trout (Adriaenssens et al., 2016), a negative association between  
369 telomere length and impulsive foraging decisions in European starlings (Bateson et al., 2015),  
370 as well as a positive association between exploration and telomere length in Eastern  
371 chipmunks (Tissier et al., 2022). However, in contrast to our research, these previous studies  
372 use either juvenile (Adriaenssens et al., 2016), or fairly short-term data (<15 months, Bateson  
373 et al., 2015; Tissier et al., 2022), where the opportunity for environmental stressors to  
374 influence telomere dynamics is limited. In this Seychelles warbler population, telomere length  
375 and dynamics are influenced by stochastic environmental factors experienced throughout an  
376 individual's lifetime, such as early-life conditions, food abundance and malaria infections  
377 (Brown et al., 2021; Spurgin et al., 2018; van de Crommenacker et al., 2022). Therefore, it is  
378 possible that the complexity of these accumulated experiences throughout an individual's life  
379 make it difficult to partition relevant drivers of intrinsic state and behaviour, which is why we  
380 were unable to detect a relationship between exploration and telomere dynamics. Further,



381 Bateson et al. (2015) monitored individuals in captive experimental environments, where  
382 extrinsic factors other than those manipulated in their study, could be controlled. This could  
383 subsequently increase the likelihood of detecting associations between behaviour and  
384 telomeres compared to wild populations.

385

386 Importantly, recent meta-analyses (Mathot et al., 2019; Moran et al., 2021) have highlighted  
387 that many empirical studies testing for between-individual correlations between risk-taking  
388 behaviour and putative measures of intrinsic state often only report unpartitioned phenotypic  
389 estimates (113 out of 145 studies; Niemelä and Dingemanse, 2018a). Consequently, such  
390 studies, including those conducted in brown trout, starlings and Eastern chipmunks  
391 (Adriaenssens et al., 2016; Bateson et al., 2015; Tissier et al., 2022), often risk confounding  
392 within-individual and between-individual processes ('the individual gambit', Brommer,  
393 2013), which can produce potentially biased correlation estimates (Dochtermann &  
394 Dingemanse, 2013). Here, we avoided taking the individual gambit by opting to partition  
395 phenotypic variation into its between-individual components. Nonetheless, we found no  
396 between-individual correlations between exploration and telomere dynamics, indicating that  
397 the lack of association between exploration and telomere length is not a product of the  
398 individual gambit, but instead due to a lack of an association between exploration and  
399 telomere length.

400

401 We predicted that more exploratory individuals would be in poorer intrinsic state, resulting in  
402 a negative association with telomere length and a higher rate of telomere shortening over  
403 time. However, it may be that telomere length alone is an insufficient biomarker of intrinsic  
404 state (Young, 2018). In our system, telomere length can fluctuate (i.e. both shorten and

405 lengthen) within an individual's lifetime (Spurgin et al., 2018) and individual repeatability of  
406 telomere length is low (Sparks et al., 2021). These fluctuations are indicative of an  
407 individual's somatic stress within a given timeframe (Brown et al., 2021), which may,  
408 consequently, weaken associations with both long-term intrinsic state and consistent  
409 behavioural traits. Furthermore, telomere dynamics can also be driven by other intrinsic  
410 differences between individuals, such as individual quality and biological age. Therefore,  
411 alternative markers may be more appropriate for investigating the link between personality  
412 and intrinsic state. Body mass is a commonly adopted measure of intrinsic state used in  
413 animal personality research (Niemelä & Dingemanse, 2018a). However, the literature  
414 indicates that the relationship between body mass and exploration score is inconsistent, with  
415 positive (Kelleher et al., 2017), negative (Bijleveld et al., 2014) and an absence (Royauté et  
416 al., 2015) of associations, and can be dependent on other measures of intrinsic state, such as  
417 hormones (Seltmann et al., 2012). While body mass is positively associated with individual  
418 condition in the Seychelles warbler (Brown et al., 2021), in supplementary analyses (where  
419 telomeres were substituted for body size and mass) we found no association between  
420 exploratory behaviour and body size or mass (Tables S8–12, Figure S5). That neither  
421 telomere dynamics nor body mass are associated with exploratory behaviour strengthens the  
422 possibility that there is no inter-play between exploration and intrinsic state in this system,  
423 and that alternative mechanisms (e.g. extrinsic factors) may be more important (Sih et al.,  
424 2015).

425

426 One intrinsic factor that was associated with both exploration and telomere length was age.  
427 Exploration scores were highest in prime-aged individuals, whereas telomere length was  
428 highest in early-life. Similar increases in risk-taking behaviour with age have been

429 demonstrated in superb fairy-wrens (*Malurus cyaneus*) (Hall et al., 2015), male grey mouse  
430 lemurs (*Microcebus murinus*) (Dammhahn, 2012), and field crickets (*Gryllus campestris*)  
431 (Fisher et al., 2015). These linear, positive relationships between exploration and age may  
432 reflect processes related to life-history, such as residual reproductive value, where older  
433 individuals that have fewer prospective offspring have less to lose, and so increase their  
434 expression of risk-taking behaviour (i.e. asset protection hypothesis, Roff, 2002; Wolf et al.,  
435 2007). Alternatively, the association with age may reflect changes in other measures of  
436 intrinsic state with age, such as an increase in sex hormone titres (Boulton et al., 2015). For  
437 instance, testosterone levels often increase in early-life in passerines (Hau & Goymann, 2015;  
438 Těšický et al., 2022). However, it is not clear why exploration of a novel object shows a  
439 decline towards the end of an individual's life. Future studies in this system should examine  
440 whether the age-related changes in exploratory behaviour are a result of behavioural plasticity  
441 (i.e. within-individual variation) or a product of selective disappearance of individuals with  
442 less exploratory behaviour (van de Pol & Verhulst, 2006).

443

#### 444 *Summary*

445 We have shown that telomere dynamics do not covary with exploratory behavioural traits in  
446 the Seychelles warbler. Our results do not concur with the few existing published studies that  
447 have tested this relationship, which demonstrate either positive or negative relationships  
448 between risk-taking behaviour and telomeres. This highlights the importance of studying  
449 personality-dependent intrinsic state across a variety of taxa, across different age groups and  
450 in both wild and captive populations. Future research should aim to further explore whether  
451 this associations exist between telomeres and repeatable behavioural traits in other model  
452 systems, and if so, directly manipulate either intrinsic state or behavioural traits to determine

453 whether forced changes in state variables cause directional changes in behaviour, or vice  
454 versa.

455

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763 **Data Accessibility and Benefit-Sharing**

764 *Data Accessibility Statement*

765 Data will be deposited in the Dryad Digital Repository upon acceptance.

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767 *Benefit sharing Statement*

768 A research collaboration was developed with members of Nature Seychelles, where data were  
769 collected, which is included as a co-author.

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771 **Author contributions**

772 The study was designed by TC and HLD and developed with TJB. TC, TJB, AMS, DSR, TB,  
773 JK, and HLD collected the data. Statistical analyses were conducted by TC with input from  
774 TJB and AMS. TC wrote the manuscript and all authors contributed critically to drafts and  
775 gave final approval for publication.

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790 **Table 1.** Bivariate MCMC model results investigating the covariation between novel  
791 environment exploration and novel object exploration as response variables. Reported are the  
792 posterior modes and their 95% credible intervals of all fixed and random effects in the model.  
793 Fixed effects for exploration include: sex (contrast level = males), age at exploration test  
794 (years; quadratic and linear terms), and assay number, plus tent colour (contrast level = blue)  
795 for novel environment exploration, and branch orientation (contrast level = diagonal) for  
796 novel object exploration. Observer ID was included as a random effect. Variance components  
797 attributed to bird ID for each response variable, as well as the covariance between the two are  
798 also shown. Statistical significance of fixed effects is indicated by 95% credible intervals not  
799 overlapping zero and these are denoted in bold.

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	Novel environment exploration	Novel object exploration
Fixed effects		
Sex (male)	<b>0.298 [0.071, 0.515]</b>	<b>0.433 [0.165, 0.734]</b>
Age	<b>1.960 [1.175, 2.711]</b>	<b>1.705 [0.765, 2.711]</b>
Age <sup>2</sup>	<b>-1.317 [-2.055, -0.632]</b>	<b>-1.251 [-2.169, -0.272]</b>
Assay number	<b>0.746 [0.543, 0.958]</b>	<b>0.705 [0.422, 0.965]</b>
Tent colour (blue)	<b>0.307 [0.051, 0.585]</b>	
Branch orientation (diagonal)		<b>0.450 [0.150, 0.781]</b>
Random effects		
Bird ID	0.607 [0.367, 0.848]	0.699 [0.344, 1.065]
Observer ID	0.265 [0.096, 0.490]	0.217 [0.067, 0.432]
Residual	0.961 [0.746, 1.165]	1.123 [0.783, 1.464]
Covariance (Bird ID)		0.404 [0.166, 0.651]
Covariance (Residual)		0.666 [0.440, 0.884]

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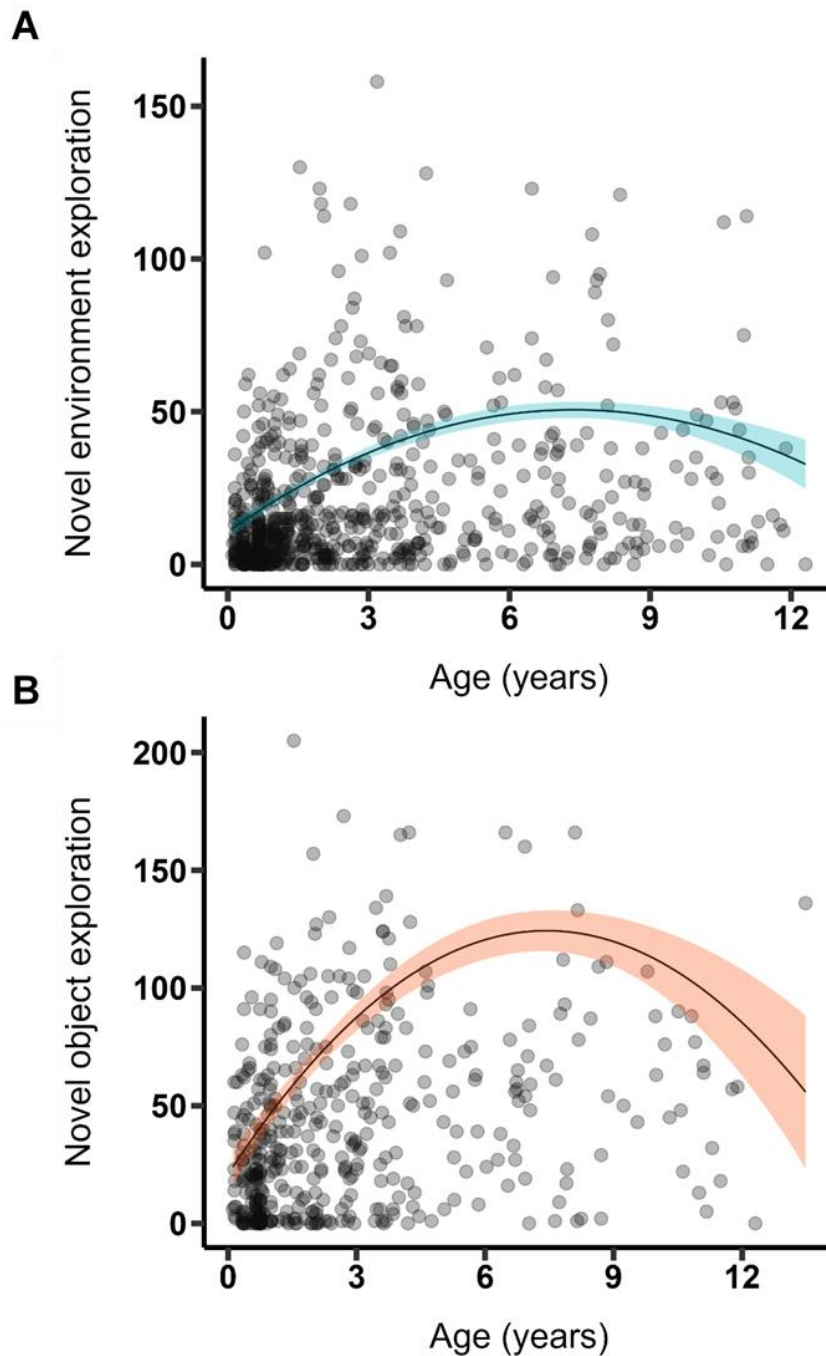
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813 **Table 2.** Correlation coefficients ( $r_i$ ) and corresponding 95% credible intervals extracted  
 814 from bivariate MCMCglms between two exploration traits, and between exploration and  
 815 relative telomere length (RTL) or rate of change of RTL ( $\Delta$ RTL). Statistical significance is  
 816 indicated by 95% credible intervals not overlapping zero and these are denoted in bold.

Trait 1	Trait 2	$r_i$	95% Credible intervals	$N_{individuals}$
<b>Novel environment</b>	<b>Novel object</b>	<b>0.614</b>	<b>0.415, 0.807</b>	<b>334</b>
Novel environment	RTL	0.100	-0.098, 0.256	295
Novel object	RTL	-0.058	-0.232, 0.121	159
Novel environment	$\Delta$ RTL	-0.061	-0.278, 0.130	214
Novel object	$\Delta$ RTL	0.107	-0.105, 0.312	117

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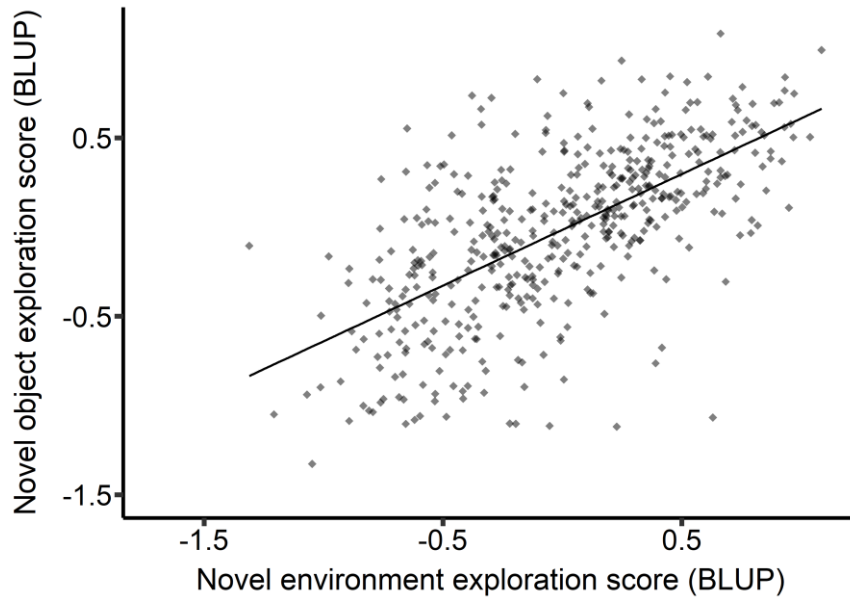
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840 **Figure 1.** (A) Novel environment exploration and (B) novel object exploration scores show a  
 841 quadratic age effect in 334 individuals ( $N=536$ ;  $N=430$  scores for novel environment and  
 842 novel object, respectively). The points show raw data, the black lines show predictions and  
 843 shaded areas represent 95% higher posterior density credible intervals from the bivariate  
 844 model including both exploration scores (see Table 1).

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849 **Figure 2.** The relationship between novel environment exploration and novel object  
850 exploration scores. Posterior means of the random intercepts (BLUPs) are shown here for  
851 visualisation purposes only. A solid trendline indicates a meaningful effect.

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