Title

Absence of the pace-of-life syndrome in a wild-living population of cooperatively-breeding passerine

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Lay summary

The pace-of-life syndrome hypothesis predicts that differences in behavior are associated with an individual's pace-of-life: risk-takers should "live fast, die young" compared to individuals who are risk averse. Using longitudinal data from a wild population of birds, where there is a known trade-off between reproduction and survival, we show that exploratory behavior is not associated with lifespan or reproduction, and thus no support of the pace-of-life syndrome hypothesis.

Abstract

The pace-of-life syndrome hypothesis posits that consistent between-individual variation in behavioral traits (‘animal personalities’) mediates trade-offs in life-history. Individuals with risk-averse traits are expected to follow a relatively ‘slow’ pace-of-life (long lifespan, delayed reproduction), compared to their riskier, ‘fast’, counterparts. Despite a breadth of empirical research, findings are equivocal, with recent reviews highlighting that the core assumptions of the pace-of-life syndrome hypothesis are likely overlooked. Here, we use long-term data from a closed population of individually-marked Seychelles warblers, whose life-history trade-offs and ecological conditions align with the pace-of-life syndrome framework, but whose risk-averse traits associate negatively, rather than positively with a slow pace-of-life. Specifically, we test for associations between exploratory scores (novel environment and novel object) and three life-history measures (age at first breeding, reproductive lifespan and longevity) as well as lifetime reproductive success as a measure of fitness. We find no evidence for covariation between exploratory personalities and any of the life-history measures or lifetime reproductive success, in either males or females. We thus find no support for the pace-of-life syndrome hypothesis, and demonstrate that whilst preliminary checks prior to testing the pace-of-life syndrome hypothesis are important, alternative mechanisms may loosen selective pressures needed for a pace-of-life syndrome to emerge.

Keywords pace-of-life syndrome, animal personality, exploration, wild population, fitness, cooperative breeder

Introduction

Covariation between life-history traits along a slow–fast continuum is referred to as the pace-of-life, where short lifespan, fast growth rate and early reproduction characterize a ‘fast’ pace-of-life, whilst the opposing traits represent a ‘slow’ pace-of-life (Stearns 1983). Both physiological and behavioral traits covary with the pace-of-life across different levels of biological organization, including between individuals (Réale et al. 2010), populations (Wikelski et al. 2003) and species (Wiersma et al. 2007), to form distinct phenotypes under an evolutionary framework known as the pace-of-life syndrome hypothesis (Stamps 2007; Biro and Stamps 2008).

Consistent between-individual variation in behavioral traits, or animal 'personalities', are a core element of pace-of-life syndromes at the organismal level (Réale et al. 2010). By influencing how an individual interacts with its environment, animal personality traits play a functional role in life-history trade-offs (Stamps 2007; Wolf et al. 2007; Biro and Stamps 2008). For example, behavioral traits can influence strategies related to resource acquisition and monopolization, including foraging (Patrick and Weimerskirch 2014) and dispersal to breeding positions (Cote et al. 2010). Subsequently, fast-living individuals that prioritize current over future reproduction are predicted to express risk-taking behaviors (including high exploration, aggression and boldness) when locating and exploiting the resources needed for rapid growth and reproduction (Réale et al. 2010). In comparison, slow-living individuals should express risk-averse traits that assist with avoiding potentially dangerous situations, such as predation (Biro et al. 2004), and instead prioritize somatic maintenance (Martin et al. 2006) and slower growth rate (Biro et al. 2014), resulting in delayed maturity and longer life (Réale et al. 2010).

Pace-of-life research has gained notable traction since the integration of behavioral traits (Réale et al. 2010; Royauté et al. 2018). However, empirical findings are ambiguous, with many studies providing null results (Royauté et al. 2015) or only partial evidence (Montiglio et al. 2014; Le Cœur et al. 2015; Mariette et al. 2015) supporting the pace-of-life syndrome hypothesis. Whilst such findings bring to question the generality of the pace-of-life syndrome hypothesis, it is possible that these results stem from studies overlooking the two core assumptions needed for pace-of-life syndrome to arise (Dammhahn 2012; Montiglio et al. 2018; Royauté et al. 2018). First, the presence of life-history trade-offs should be imposed by resource-limited environmental conditions (Stearns 1989). In the absence of life-history trade-offs, there is no slow–fast axis for behavior and physiology to covary with, making it impossible for a pace-of-life syndrome to develop. Second, behavioral traits must play a functional role in facilitating life-history trade-offs within the selected study system. For instance, high levels of exploration may promote rapid growth rates and/or lower ages at first breeding, but only in species or populations where exploration determines food intake and/or acquisition of mates (Stamps 2007; Wolf et al. 2007; Réale et al. 2010). Indeed, a recent meta-analysis by Royauté et al. (2018) identified few studies that demonstrated these assumptions had been met, thus highlighting the importance of future empirical research addressing these requirements prior to conducting further analyses.

Recent attempts to review the pace-of-life syndrome hypothesis have highlighted that behavioral, physiological and life-history traits often do not associate in the direction predicted by the traditional framework (Araya-Ajoy et al. 2018; Royauté et al. 2018; Moiron et al. 2020). For instance, a study by Mariette et al. (2015) demonstrated that zebra finches (*Taeniopygia guttata*) that were less exploratory of a novel environment were more likely to disperse earlier than their more exploratory counterparts. Adriaenssens and Johnsson (2011) also observed results that contradicted the pace-of-life syndrome framework: brown trout (*Salmo trutta*) that were faster at exploring a novel environment, had slower growth rates in a mark recapture study. It has been suggested that the assumptions made by Réale et al (2010) and Wolf et al (2007) may be too strict to fit all possible associations between life history, behavior and physiology, and should instead reflect ecologically relevant dimensions of the system and/or population being studied (Salzman et al. 2018). Indeed, any trait facilitating current reproduction at the expense of future reproduction and survival can potentially undergo correlational selection with a fast or slow pace-of-life. Therefore, relaxing assumptions of the pace-of-life syndrome hypothesis to reflect the functional roles of behavioral and physiological traits is an important step forward in fully understanding the pace-of-life syndrome framework.

Until recently, the role of sex in the pace-of-life syndrome hypothesis has been largely overlooked (Hämäläinen et al. 2018; Immonen et al. 2018; Tarka et al. 2018). Males and females often have different optimal life-history strategies as a result of sexual selection, which causes variations in mean optima along the pace-of-life continuum. In anisogamous species, asymmetry in the energetic demands of reproduction between the sexes, e.g. egg production, gestation and lactation compared to sperm production, regularly lead to sex-specific differences in the allocation of resources towards somatic maintenance and reproduction (Bateman 1948; Maynard Smith 1982; Wedell et al. 2006). This occurs in avian species, where females have larger gametes than males, and the energetic cost of egg production is predicted to three times greater than that of ejaculate production (Hayward and Gillooly 2011). To compensate for the larger energetic demands and time needed for reproduction, the sex with higher reproductive costs is expected to possess a relatively slower pace of life, where individuals will engage in less extreme risk-taking behaviors in order to increase their reproductive lifespan (Hämäläinen et al. 2018; Immonen et al. 2018). As a consequence, sex differences in mean trait expression, as well as differences in covariance structures between traits may arise (Smith and Blumstein 2008; Debecker et al. 2016; Moschilla et al. 2019).

Here, we investigate the pace-of-life syndrome hypothesis using a long-term dataset of a closed wild population of Seychelles warblers (*Acrocephalus sechellensis*) on Cousin Island, Seychelles. The study population has been subject to intense monitoring since 1997 (Komdeur 1992; Richardson et al. 2002; Wright et al. 2014), with high annual resighting rates (Brouwer et al. 2006), virtually no inter-island dispersal (Komdeur et al. 2004) and possesses a verified genetic pedigree (Sparks et al. 2021), therefore providing accurate life history and fitness data needed to test the pace-of-life syndrome hypothesis. In this species, there is a trade-off in life history, where individuals that begin breeding at an older age show delayed survival senescence (Hammers et al. 2013). Further, exploratory behavior is positively associated with delayed natal dispersal and distance travelled during dispersal (Cox et al. 2023), a crucial life-history stage that plays a functional role in access to reproduction (Komdeur et al. 2016). Given the importance of sex and early-life conditions (food availability, natal group size and maternal age) on life history and fitness (Hammers et al. 2013; Cox et al. 2022), we can also account for extrinsic ecological conditions and intrinsic sexual dimorphism that may conceal the presence of the pace-of-life syndrome.

Specifically, we test for covariation of exploratory behavior with three life-history traits: longevity, age at first breeding and reproductive lifespan. To determine whether selection favors a particular trait within the population, we also assess covariance between a fitness metric – lifetime reproductive success (LRS), a measure of total number of offspring produced over a lifetime – and exploration. We adapt predictions from the traditional pace-of-life syndrome framework to align with the pre-existing knowledge of Seychelles warbler life history and behavior, specifically the positive association between exploratory behavior and tendency to delay natal dispersal (Cox et al. 2023). Therefore, we predict that slow explorers will have faster life-history strategies, including greater longevity, delayed age at first reproduction and a longer reproductive lifespan. Seychelles warblers are anisogamous and the sexes follow different life-history strategies. Whilst females have the opportunity to reproduce as subordinates, males must first obtain a dominant breeding position (Komdeur 1994). Therefore, we also predict sexual dimorphism in life history and behavioral covariation, where both sexes will show a positive association between slow exploration and fast life history, but that the strength of this relationship will be stronger in males (Hämäläinen et al. 2018). As selection is predicted to remove less fit phenotypes (Wolf et al. 2007; Dingemanse and Wolf 2010), it is likely that phenotypic variation should only persist if all traits have relatively similar fitness outputs (Mangel and Stamps 2001), and so we also expect there to be no relationship between exploration and LRS.

Methods

Study site and system

Seychelles warblers are insectivorous passerines endemic to the Seychelles archipelago. On Cousin Island (0.29 km^2; 4°20′S, 55°40′E), the population has been monitored as part of a long-term study since 1985, and has a carrying of ca. 320 individuals across ca. 115 territories (Busana et al. 2022). Territories are occupied year-round by a single breeding pair that predominantly produce one-egg clutches (87% of clutches; Brouwer et al., 2006). As facultatively cooperative breeders, individuals of either sex may delay independent breeding following sexual maturity and become a subordinate (often in their natal group; Komdeur, 1992). As a result, approximately 50% of territories support 1–5 subordinates; subordinates are ≥6 months old and 55% are female (Hammers et al., 2019; Kingma et al., 2016a). Subordinates of either sex (approx. 20% of males and 42% of females; Hammers et al., 2019) may provide alloparental care to group offspring, where females help to build the nest and incubate, males help nest guard, and both sexes feed nestlings and fledglings (Komdeur 1994; Richardson et al. 2003). Typically, the breeding pair will remain together until one individual dies (but see Richardson et al., 2007), at which point the vacancy is promptly taken over by a subordinate individual from either the natal or an external territory (8.6% of positions are inherited by a subordinate within the territory; Kingma et al., 2017).

Each year, the population is monitored throughout the minor (January–March) and major (June–September) breeding seasons (Komdeur et al. 2016). During each season, as many individuals as possible are caught as either nestlings, or as juveniles using mist nets. Juveniles are aged as fledglings (1–3 months), old fledglings (3–5 months) or subadults (6–12 months) using hatch dates where possible or, alternatively, based on eye colour (Komdeur, 1992) and behavior. Any unringed warblers are provided with a unique combination of leg rings for individual identification (three colour rings and one British Trust for Ornithology metal ring), resulting in virtually all (≥96%) individuals being rung since 1997 (Richardson et al. 2001; Raj Pant et al. 2020). From all caught individuals, ca. 25 μl blood is collected using brachial venipuncture and stored in 100% ethanol for later molecular sexing and genotyping (Griffiths et al. 1998;

Richardson et al. 2001; Spurgin et al. 2014). Each territory is checked at least once every two weeks for pair and courtship behaviors to determine the resident dominant pair and monitor breeding behavior (e.g. nest building, copulations), then checked daily once a nest is found to determine precise hatching and fledging dates. As the resighting probability is almost one (0.98 ± 0.01 SE; Brouwer et al., 2010), and inter-island migration is virtually non-existent (0.10% of all colour-ringed individuals; Komdeur et al., 2004), we can confidently assume that an individual is dead if it has not been observed for two consecutive breeding seasons (mean longevity is 5.5 years, maximum recorded longevity is 19 years; Hammers and Brouwer, 2017; Komdeur, 1991).

To account for the influence of early-life conditions on life history and fitness, we included data for maternal age at the focal individual's hatch date, presence of a helper at the focal individual's natal territory, natal group size , natal territory quality, and natal island-wide food availability (Hammers et al. 2013; Sparks et al. 2022). Helpers are subordinates observed providing alloparental care in a given breeding season, however, as few natal territories possessed >1 helper in our dataset (N = 16/344 individuals tested for reproductive lifespan), helper presence was included as a binary variable (i.e. present/absence: Hammers et al., 2019). Natal group size was the number of independent individuals (i.e. the dominant pair and any subordinates) in the natal territory (range: 2–6). As Seychelles warblers feed almost entirely on arthropods (predominantly insects) gleaned from the underside of leaves (Komdeur et al. 1997), natal territory quality was calculated using an index of insect abundance. Insect abundance was calculated using $A * \sum(Cx * Ix)$, where A is the territory size (in hectares), Cx is the amount of foliage cover for tree species x, and Ix is the mean monthly insect density for tree species x per unit leaf area in dm^2 (Brouwer et al., 2009; Komdeur, 1992). Natal island-wide food availability was calculated as the mean number of insects found per unit leaf area within a season (see Spurgin et al., 2018 for full details on calculations).

Parentage

Genetic parents were assigned for offspring hatched between 1992 and the minor breeding season in 2018 using a pedigree constructed using 30 highly polymorphic microsatellite loci in *MasterBayes* v2.5.2 (Hadfield et al. 2006) with at least 80% confidence (for methods see Sparks et al., 2021). Seychelles warblers are socially monogamous but genetically promiscuous (Richardson et al. 2001; Raj Pant et al. 2019). Approximately 44% of offspring are sired through extra-pair paternity, with almost all of these sires (ca. 97%) being a dominant male from another territory (Richardson et al. 2001; Hadfield et al. 2006). Occasionally, subordinate females will also gain maternity within their own territory through cobreeding (ca. 11% of all maternities; Sparks et al., 2022).

Life history and fitness

We measured three life-history traits: (i) longevity, (ii) age at first breeding, and (iii) reproductive lifespan, and one fitness proxy: (iv) LRS (Figure S1-4). First, longevity (years) was calculated from hatch year until the last year an individual was seen alive, provided two subsequent seasons had passed and the individual had not been translocated to a neighboring island. Second, we defined age at first breeding (years) as the earliest age at which an individual acquired a dominant breeding status. As female subordinates have the opportunity to reproduce prior to gaining dominance (40% of female subordinates cobreed each year: Richardson et al., 2003), we also considered the earliest age at which a female was assigned offspring in the genetic pedigree. As almost all extra pair paternity is gained by dominant males from a neighboring territory (Richardson et al. 2001; Raj Pant et al. 2019), and no subordinate males in our dataset succeeded in reproducing, we did not consider male age at first genetic offspring. Third, reproductive lifespan was measured as the number of years between ages of first and last breeding, where age at last breeding was the latest year an individual was recorded as being a dominant breeder. For females, we also considered first and last dates of genetic offspring. Finally, we calculated LRS as the total number of offspring assigned to an individual in the genetic pedigree over its lifetime that survived to at least one year of age.

Personality assays

As detailed in Edwards et al., (2017), individuals were placed in a novel environment (Gelert Oxygen 4 tent) containing three artificial trees, and their exploratory movement was monitored (total number of flights, hops and trees visited) for five minutes to produce an "exploration score". After a two–minute break (see acclimation and randomization tests, Edwards et al., 2017), a novel pink toy was introduced for five minutes and the exploration of that object scored. During each personality assay, additional parameters including age of the focal individual under test, test number, colour of the tent an individual was tested in (blue or green) and observer identity were noted so that these factors could be controlled for. Assays were conducted between 2012–2014 and 2019–2022. Both novel environment exploration score and novel object exploration score were repeatable (0.23, 95% credible interval [CrI] = 0.08 – 0.36, and 0.37, 95% CrI = 0.04 – 0.59, respectively), correlated (0.60, CrI = 0.35–0.78) and novel environment exploration was heritable (0.17, 95% CrI = 3e-4 – 0.33) though novel object exploration was not (Edwards et al. 2017; Cox et al. 2022).

Statistical analyses

All analyses were performed using R v.4.0.2 (RStudio Team 2022). All continuous fixed effects were standardized by subtracting the mean and dividing by two standard deviations in *arm* v.1.13-2. We also checked there was no collinearity between fixed effects by ensuring Variance Inflation Factors (VIFs) were <3.

Longevity and personality

To determine whether novel environment exploration and novel object exploration impact longevity, we ran Cox mixed effects proportional hazard models using *coxme* v2.2-16 for individuals that survived to at least one year of age (Therneau 2021) (see Figure S1 for data distribution). This method was used so that individuals that were translocated to neighboring islands as part of conservation efforts (4 males, 5 females) and individuals that were still alive at the time of the analysis (Table S1) could be right-censored. The independent variable was either an individual's first recorded novel environment or novel object exploration score. As Cox mixed effects proportional hazards models cannot accommodate the specification of fixed effects to an independent variable, which is required for this study as there are known methodological effects on exploration score (Edwards et al. 2017), we instead used residual exploration score values extracted from negative binomial GLMMs (*lme4* v1.1-29, Bates et al. 2015). The negative binomial GLMMs included either an individual's first novel environment or novel object exploration score as the independent variable, and age as both linear and quadratic terms (Edwards et al. 2017) and either tent colour (factor: blue/green, Edwards et al. 2017) for novel environment exploration or branch orientation (factor: diagonal/parallel) for novel object exploration (Cox et al., 2022).

Additional fixed effects included sex and an interaction between sex and residual exploration score. As individuals born into poorer quality territories had shorter lifespans (Sparks et al. 2022), we included natal territory quality (log transformed to aid interpretation of model coefficients: van de Crommenacker et al., 2011). Whilst older mothers produce female offspring with shorter lifespans (Sparks et al. 2022), adding maternal age at hatching reduced our sample size by 106 and 108 individuals for novel environment exploration and novel object exploration (29% of both datasets), respectively, and the effect of exploration appeared not to change when maternal age was removed from the model (Table S2), so we omitted it from our analyses. We checked the proportional hazards assumptions were met using scaled Schoenfeld residuals (Grambsch and Therneau 1994). In all cases, model assumptions were successfully met. All models were run again using raw novel environment and novel object exploration scores, then compared to the models using residual values and the conclusions were found to be the same (Table S3–S5).

Life history, fitness and personality

We ran bivariate Markov chain Monte Carlo (MCMC) generalized linear mixed models (GLMMs) with Poisson error distributions, including two response variables of exploration score (novel environment or novel object) and either age at first breeding (years), reproductive lifespan (years) or LRS (number of offspring that survived to at least 1 year) using *MCMCglmm* v.2.33 (Hadfield, 2010) (see Figure S2–4 for data distributions). As individuals tested for reproductive lifespan and LRS were required to be dead, whereas those tested for age at first breeding did not, and fewer individuals were tested for novel object exploration (N = 248) relative to novel environment exploration (N = 362) (see Table S6–S8), we could not run multivariate models with more than two response variables, and so ran bivariate models instead. As there are known sex effects in Seychelles warbler exploration scores (Edwards et al. 2017) and life-history strategies (Komdeur 2006), all models were run separately for males and females.

Adopting multivariate Bayesian techniques has become an increasingly popular technique in animal personality research as it partitions total variance into within- and between-individual level (Houslay and Wilson 2017; Dingemanse and Wright 2020). Bivariate models also allow different fixed effects to be specified for each response variable, while also measuring the covariation between the two responses. We therefore fitted the same methodological fixed effects included in the previously mentioned negative binomial GLMMs used for longevity, as well as assay number to control for habituation (e.g., Edwards et al. 2017; Cox et al. 2022) for all bivariate MCMCglmm models.

For the life history and fitness response variables (age at first breeding, reproductive lifespan and LRS), different fixed effects were included as follows. Natal territory quality and natal island-wide food availability increase with age at first breeding (Hammers et al. 2013), and so both were logged and included as a linear covariates. For reproductive lifespan, both natal group size and maternal age decrease with female reproductive lifespan (Sparks et al. 2022), and so both were included as linear covariates. For LRS, we included the maternal age when an individual hatched (linear covariate) and the presence of helpers in the natal territory (binary factor: yes/no) of females (Sparks et al. 2022). Cohort was included as a linear covariate for models including reproductive lifespan and LRS to account for more recently hatched individuals inherently having had shorter lives, and thus fewer opportunities to reproduce, as well as less time to gain a breeding position (Bouwhuis et al. 2015). For random effects, we included bird identity for all traits. We also specified cohort for the life history and fitness traits to account for potential drivers not encompassed in fixed effects, and for exploratory traits we fitted the observer.

From the bivariate models, we extracted variance and covariance of exploration and life-history/fitness traits on the between-individual level (bird identity), which provided the posterior distribution for each slope estimate for the between-individual correlation between exploration and life history/fitness (O'Dea et al. 2021):

$$r = \frac{COV_{(E,Y)}}{\sqrt{V_E}\sqrt{V_Y}} \tag{1}$$

From this, we determined the mode slope estimate and its corresponding 95% highest posterior density (HPD) interval, where a HPD interval that did not overlap zero denoted a significant correlation. We applied priors with an uninformative Inverse-Wishart distribution (V = diag(n), nu = n; where n is the number of response variables) for both the residual and random effects structure (see Figure S5 for similar results achieved using inverse-Gamma prior). As multiple repeats were obtained for exploration score, compared to the single values for the life-history traits, we used 'covu = TRUE' in the primary residual structure specified in the prior to allow covariance between the individual-level random effect for the exploratory trait and the residual variance of the life-history trait (see supplementary material of Thomson et al., 2017). Posterior distributions were sampled every 500 iterations, with a burn-in of 60,000 and a run of 4,600,000 iterations. We visually checked time-series plots of model parameters and assessed multiple convergence diagnostics, including autocorrelation (<0.1) values, effect sizes (≥1,000), Geweke tests and Heidel diagnostics.

Ethics statement

Fieldwork protocols were approved by the BIO Ethical Review Committee, University of East Anglia, and were ratified by the University of Leeds. Fieldwork was in accordance with local ethical regulations and agreements: The Seychelles Department of Environment and the Seychelles Bureau of Standards provided research permits.

Results

We found no relationship between novel environment or novel object exploration on longevity, age at first breeding, reproductive lifespan or LRS in either sex in the Seychelles warbler (Table 1–2). Results for methodological fixed effects aligned with previous studies in this system (Cox et al., 2023): exploration score increased with age, assay number, blue tent colour, diagonal branch orientation and demonstrated a significant quadratic age effect (Table 3–5).

The early-life environmental parameters included in this analysis (presence of a helper at the focal individual's natal territory, natal group size, natal territory quality, or natal island-wide food availability) had no significant effect on longevity, age at first breeding, reproductive lifespan or LRS (Table 1, 3–5). However, there was a sex-specific effect of maternal age on LRS in females, where individuals with older mothers had lower LRS (novel environment exploration: β = -0.611, *pMCM*C = 0.042; novel object exploration: β = -1.020, *pMCMC* = 0.012) (Table 5). Cohort also had a significant effect on reproductive lifespan and LRS in both males and females, where more recently hatched individuals had shorter reproductive lifespans (novel environment exploration, males: β = -0.154, *pMCMC* = <0.001 and females: β = -0.117, *pMCMC* = <0.001; novel object exploration, males: β = -0.170, *pMCMC* = <0.001 and females: β = -0.128, *pMCMC* = <0.001) and lower LRS (novel environment exploration, males: β = -0.256, *pMCMC* = <0.001 and female:

β = -0.236, *pMCMC* = <0.001; novel object exploration, males: β = -0.278, *pMCMC* = <0.001 and females: β = -0.258, *pMCMC* = <0.001) (Table 3–5).

Discussion

We predicted that less exploratory Seychelles warblers would display a faster pace-of-life, including lower longevity, earlier age at first breeding and shorter reproductive lifespan. However, we found no evidence to support our hypothesis, with no significant relationship between either exploration of a novel environment or novel object and the three life-history traits (longevity, age at first breeding and reproductive lifespan). Given that selection favors traits with higher fitness, and thus should maintain variance in behavioral phenotypes that yield equally high fitness outcomes (Mangel and Stamps 2001; Dingemanse and Wolf 2010), we also expected individuals with differing levels of exploratory behavior to express relatively equal LRS. Our results aligned with this prediction: exploratory traits did not affect an individual's LRS in either males or females. However, as exploration was not linked to longevity, age at first breeding or reproductive lifespan, equal LRS did not result from individuals with different behavioral traits adopting alternative life-history strategies with an equal fitness payout, and so is unlikely to be likely unrelated to the pace-of-life syndrome hypothesis.

Whilst our findings conflict with the expectations of the pace-of-life syndrome hypothesis, they are consistent with a recent meta-analysis (Royauté et al. 2018) that demonstrates an overall lack of covariation between exploratory traits and life-history, including survival and timing of reproduction. In their paper, Royauté et al. (2018) suggest the lack of empirical evidence for pace-of-life syndrome hypothesis may result from violation of its assumptions. A core component of the pace-of-life syndrome framework is that behavioral traits play a functional role in facilitating life-history strategies. In the Seychelles warbler, exploratory traits influence the timing of natal dispersal to a dominant breeding position (Cox et al. 2023), and, in turn, an individual's access to opportunities for reproduction. Despite this, we found no evidence linking an individual's novel environment or novel object exploration score with their age at first breeding or reproductive lifespan. This lack of evidence may in part result from the present study including individuals who gain parentage in both dominant and subordinate roles. Although almost all offspring are sired by dominant over subordinate males (97%: Raj Pant et al. 2019), approximately 11% of all maternities (Sparks et al. 2021) and virtually all inherited dominant breeding positions are obtained by subordinate females (Groenewoud et al. 2018). For females who breed as subordinates, high sociality and lower aggression towards conspecifics prevent eviction and provide access to opportunities for cobreeding and inheritance of a dominant breeding position (Bergmüller and Taborsky 2007; Schürch et al. 2010).

Another key assumption of pace-of-life syndrome hypothesis is that behavioral traits affect an individual's risk of mortality (Stamps 2007; Wolf et al. 2007; Réale et al. 2010). Individuals who move superficially and are less cautious (both qualities of exploratory behavior) are predicted to experience higher mortality (Dammhahn et al. 2018). This heightened mortality is expected to result from increased encounters with predators, as well as a higher frequency of interactions with conspecifics (Biro et al. 2006; Boon et al. 2008), which can increase the likelihood of exposure to parasites and/or pathogens (Barber and Dingemanse 2010; Kortet et al. 2010). This was demonstrated in masu salmon *Oncorhynchus masou masou*, where bolder individuals suffered higher predation as they less successful at avoiding ambushes of grey heron *Ardea cinerea* (Miyamoto and Araki 2020), and in deer mice *Peromyscus maniculatus*, where exploratory individuals were three times more likely to be infected with hantavirus (Dizney and Dearing 2013). However, our study population of Seychelles warblers mainly experiences egg and nestling predation (Collar et al. 1985), and there are no known parasites or pathogens that spread through conspecific interactions. Therefore, it is unlikely that exploratory traits contribute to predation- or parasite-related increased mortality. Instead, mortality reduced body condition can occur through agonistic interactions with conspecifics, particularly during extraterritorial forays (Kingma et al. 2016b). Therefore, measures of aggressive behavior, which is often quantified by monitoring fight initiations and contest behavior (Réale et al. 2010; Briffa et al. 2015), may align better within the framework of the pace-of-life syndrome within this system.

Failure to account for environmental conditions has also been proposed as a reason for lack of empirical evidence demonstrating the pace-of-life syndrome (Montiglio et al. 2010; Dammhahn et al. 2018; Montiglio et al. 2018). Under favorable environmental conditions where life-history trade-offs are relaxed, covariation between behavioral and life-history traits can be masked (Montiglio et al. 2018). In our analyses, we accounted for all early-life environmental conditions known to affect Seychelles warbler life history and fitness, including maternal age, food availability and helper presence at the natal nest (Hammers et al. 2013; Sparks et al. 2022). Nonetheless, we obtained no evidence validating the pace-of-life syndrome hypothesis. Instead, it is possible that stochasticity in ecological conditions experienced during adulthood, rather than early-life, may be altering the association between behavior and life history within our study (Montiglio et al. 2018). This has been demonstrated across many taxa, particularly in species whose food availability is dependent on masting events (Bergeron et al. 2013; Cote et al. 2013; Montiglio et al. 2014; Le Galliard et al. 2015; Debecker et al. 2016; Goulet et al. 2016). In our study population, environmental conditions may occasionally become more favorable, resulting in relaxed trade-offs in life history. For example, four separate translocation exercises that removed breeding individuals away from Cousin to neighboring islands temporarily eased intraspecific competition by creating breeding vacancies (Johnson et al. 2018). Therefore, it is possible that some of the Seychelles warblers included in our analyses experienced periods of relaxed pressure for trade-offs, resulting in the potential masking of covariation between behavior and life history.

According to the pace-of-life syndrome hypothesis, natural selection and trade-offs in resource allocation to different biological functions maintain phenotypic variation and adaptive integration of both life-history and behavioral traits to form syndromes (Stearns 1992; Roff 1993; Wolf et al.

2007). Under such conditions, various syndromes that exist along the pace-of-life continuum are expected to possess similar fitness consequences, such as their effect on LRS. Whilst we identified no difference in LRS values between high and low exploratory individuals, we also did not identify covariation between life history and behavior, and so a lack of directional selection of behavior is unlikely to be a consequence of life-history trade-offs. Alternative mechanisms related to internal state, frequency-dependent selection or non-equilibrium dynamics (Wolf and Weissing 2010) may instead play a greater role in maintaining exploratory traits within the population.

Summary

In summary, we have shown that despite conducting preliminary checks to validate the core assumptions of pace-of-life syndrome hypothesis, as well as accounting for early-life ecological conditions that could potentially conceal the prevalence of the pace-of-life syndrome, we found no evidence for covariation between behavioral and life-history traits in the Seychelles warbler. This echoes findings from recent meta-analyses, which also demonstrate the lack of evidence for covariation between exploratory behavior and life history, and provides further understanding of the conditions needed for the pace-of-life syndrome to emerge in a wild population of long-lived passerine. We also found no relationship between behavior and LRS; however, as this did not result from life-history trade-offs, it is likely a result of alternative evolutionary mechanisms maintaining variation in exploratory behavior.

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Tables and table legends

Table 1 Cox proportional hazards mixed model results for the effect of residual (**A**) novel environment exploration score or (**B**) residual novel object exploration score on longevity in the Seychelles warbler. Including parameter coefficients (estimate), standard errors (SE), exponential coefficients (Exp(est)), which represent the hazard ratios, Wald statistic (z) and statistical significance (P). Significant effects denoted in bold. This model uses residual exploration scores corrected for age (linear and quadratic terms) and tent colour (blue/green).

	(a) Novel environment exploration N=466 (dead = 307, alive = 150, translocated = 9)					(b) Novel object exploration N=326 (dead = 186, alive = 139, translocated = 1)				
	Estimate	SE	Exp(est)	z	P	Estimate	SE	Exp(est)	z	P
Fixed effects										
Sex (male)	0.061	0.120	1.062	0.510	0.610	0.022	0.157	1.022	0.140	0.890
Residual exploration score	-0.137	0.872	0.872	-1.070	0.280	-0.090	0.160	0.914	-0.560	0.580
Natal territory quality	-0.189	0.828	0.828	-1.480	0.140	-0.101	0.160	0.904	-0.630	0.530
Random effect										
Cohort	0.415					0.323				

Table 2 Correlation between exploratory traits and life-history/fitness. Includes between-individual correlation coefficients (r_i) and corresponding 95% credible intervals (CrI) extracted from bivariate MCMCglmms between either novel environment exploration or novel object exploration as the behavioral trait and age at first breeding, reproductive lifespan or lifetime reproductive success (LRS) is the life-history/fitness trait.

Exploratory trait	Life-history/ fitness trait	Sex	Correlation coefficient (r_i), 95% CrI	$N_{individuals}$
Novel environment	Age at first breeding	♂	0.138 [-0.311, 0.544]	194
Novel environment	Age at first breeding	♀	-0.238 [-0.547, 0.171]	168
Novel object	Age at first breeding	♂	0.001 [-0.463, 0.465]	137
Novel object	Age at first breeding	♀	0.074 [-0.302, 0.567]	112
Novel environment	Reproductive lifespan	♂	0.174 [-0.199, 0.426]	182
Novel environment	Reproductive lifespan	♀	0.228 [-0.228, 0.450]	169
Novel object	Reproductive lifespan	♂	0.099 [-0.242, 0.458]	121
Novel object	Reproductive lifespan	♀	-0.210 [-0.511, 0.264]	107
Novel environment	LRS	♂	0.023 [-0.352, 0.479]	116
Novel environment	LRS	♀	0.014 [-0.488, 0.441]	113
Novel object	LRS	♂	0.128 [-0.382, 0.636]	65
Novel object	LRS	♀	0.412 [-0.344, 0.752]	64

Table 3 Bivariate MCMC model results investigating the covariation between either (**A**) novel environment exploration or (**B**) novel object exploration and age at first breeding as response variables. Reported are the posterior modes and their 95% credible intervals of all fixed and random effects in the model. Fixed effects include: age (quadratic and linear terms), assay number, tent colour (contrast level = blue), branch orientation (contrast level = diagonal), early-life insect availability, natal territory quality and cohort. Random effects include cohort, observer ID bird ID and residual components. Statistical significance of fixed effects is indicated by 95% credible intervals not overlapping zero and these are denoted in bold.

	(a) Novel environment exploration		(b) Novel object exploration	
	Males	Females	Males	Females
Fixed effects				
Exploration : Age	**2.105 [1.199, 2.948]**	**1.660 [0.560, 2.821]**	**1.107 [0.092, 2.221]**	**3.851 [1.845, 5.794]**
Exploration : Age^2	**-1.283 [-2.047,-0.558]**	**-0.953 [-1.842,-0.090]**	-0.431 [-1.264, 0.453]	**-2.677 [-4.217,-1.105]**
Exploration : Assay number	**0.347 [0.189, 0.505]**	**0.624 [0.423, 0.810]**	**0.413 [0.189, 0.654]**	**0.556 [0.202, 0.921]**
Exploration : Tent colour (blue)	**0.307 [0.017, 0.625]**	0.310 [-0.138, 0.744]		
Exploration : Branch orientation (diagonal)			0.328 [-0.064, 0.692]	0.410 [-0.232, 1.060]
Age at first breeding: Insect availability	-0.036 [-0.324, 0.257]	0.087 [-0.336, 0.478]	-0.021 [-0.354, 0.321]	0.044 [-0.458, 0.513]
Age at first breeding : Natal territory quality	-0.103 [-0.856, 0.603]	-0.309 [-1.154, 0.631]	0.006 [-0.885, 0.877]	-0.125 [-1.277, 1.066]
Random effects				
Exploration : Bird ID	0.511 [0.217, 0.811]	0.669 [0.347, 1.069]	0.526 [0.162, 0.9345]	1.388 [0.466, 2.305]
Exploration : Observer ID	0.063 [0.001, 0.209]	0.480 [0.091, 1.102]	0.023 [0.001, 0.091]	0.392 [0.076, 0.934]
Exploration : Residual	0.846 [0.607, 1.117]	0.998 [0.674, 1.375]	0.929 [0.552, 1.320]	1.171 [0.559, 1.909]
Age at first breeding : Bird ID	0.075 [0.039, 0.116]	0.145 [0.075, 0.222]	0.089 [0.044, 0.142]	0.184 [0.090, 0.290]
Age at first breeding : Cohort	0.015 [0.001, 0.053]	0.146 [0.050, 0.274]	0.013 [0.001, 0.047]	0.1814 [0.052, 0.352]
Covariance (BirdID)	0.023 [-0.065, 0.120]	-0.064 [-0.200, 0.053]	0.003 [-0.105, 0.117]	0.068 [-0.174, 0.306]

Table 4 Bivariate MCMC model results investigating the covariation between either (**A**) novel environment exploration or (**B**) novel object exploration and reproductive lifespan as response variables. Reported are the posterior modes and their 95% credible intervals of all fixed and random effects in the model. Fixed effects include: age (quadratic and linear terms), assay number, tent colour (contrast level = blue), branch orientation (contrast level = diagonal), natal group size, maternal age (years) and cohort. Random effects include cohort, observer ID bird ID and residual components. Statistical significance of fixed effects is indicated by 95% credible intervals not overlapping zero and these are denoted in bold.

	(a) Novel environment exploration		(b) Novel object exploration	
	Males	Females	Males	Females
Fixed effects				
Exploration : Age	**1.750 [0.846, 2.666]**	**1.197 [0.094, 2.280]**	0.676 [-0.545, 1.866]	**3.524 [1.463, 5.539]**
Exploration : Age^2	**-1.098 [-1.924, -0.300]**	-0.677 [-1.658, 0.234]	-0.137 [-1.113, 0.846]	**-2.341 [-3.939,-0.736]**
Exploration : Assay number	**0.612 [0.321, 1.948]**	**1.295 [0.879, 1.742]**	**0.813 [0.263, 1.342]**	0.815 [-0.002, 1.593]
Exploration : Tent colour (blue)	**0.450 [0.094, 0.816]**	0.295 [-0.175, 0.755]		
Exploration : Branch orientation (diagonal)			0.341 [-0.179, 0.846]	0.359 [-0.359, 1.069]
Reproductive lifespan : Natal group size	-0.102 [-0.563, 0.355]	0.020 [-0.430, 0.448]	-0.324 [-0.826, 0.183]	-0.237 [-0.830, 0.363]
Reproductive lifespan : Maternal age	-0.068 [-0.319, 0.177]	-0.229 [-0.504, 0.040]	-0.124 [-0.415, 0.152]	-0.143 [-0.505, 0.212]
Reproductive lifespan : Cohort	**-0.120 [-0.164, -0.075]**	**-0.092 [-0.137, -0.048]**	**-0.128 [-0.177, -0.074]**	**-0.098 [-0.155,-0.037]**
Random effects				
Exploration : Bird ID	0.457 [0.218, 0.725]	0.618 [0.260, 1.016]	0.613 [0.232, 1.037]	1.296 [0.315, 2.328]
Exploration : Observer ID	0.228 [0.066, 0.457]	0.289 [0.060, 0.669]	0.289 [0.060, 0.669]	0.477 [0.067, 1.1669]
Exploration : Residual	0.716 [0.509, 0.951]	1.125 [0.735, 1.513]	0.946 [0.573, 1.381]	1.453 [0.680, 2.362]
Reproductive lifespan : Bird ID	0.368 [0.224, 0.522]	0.055 [-0.102, 0.215]	0.242 [0.128, 0.369]	0.360 [0.188, 0.577]
Reproductive lifespan : Cohort	0.143 [0.050, 0.272]	0.172 [0.062, 0.324]	0.156 [0.050, 0.298]	0.196 [0.052, 0.388]
Covariance (BirdID)	0.050 [-0.132, 0.118]	0.336 [0.195, 0.492]	0.044 [-0.100, 0.181]	-0.081 [-0.366, 0.177]

Table 5 Bivariate MCMC model results investigating the covariation between either (**A**) novel environment exploration or (**B**) novel object exploration and lifetime reproductive success as response variables. Reported are the posterior modes and their 95% credible intervals of all fixed and random effects in the model. Fixed effects include: age (quadratic and linear terms), assay number, tent colour (contrast level = blue), branch orientation (contrast level = diagonal), helper in natal group (yes/no), natal group size, maternal age (years) and cohort. Random effects include cohort, observer ID bird ID and residual components. Statistical significance of fixed effects is indicated by 95% credible intervals not overlapping zero and these are denoted in bold.

	(a) Novel environment exploration		(b) Novel object exploration	
	Males	Females	Males	Females
Fixed effects				
Exploration : Age	**2.087 [1.038, 3.114]**	**1.536 [0.160, 3.051]**	0.743 [-0.889, 2.451]	2.433 [-0.189, 5.270]
Exploration : Age^2	**-1.303 [-2.254,-0.298]**	-0.945 [-2.249, 0.360]	-0.046 [-1.559, 1.459]	-1.514 [-3.888, 0.905]
Exploration : Assay number	**0.599 [0.237, 0.953]**	**1.284 [0.796, 1.736]**	0.405 [-0.391, 1.138]	0.445 [-0.505, 1.367]
Exploration : Tent colour (blue)	0.287 [-0.133, 0.731]	-0.205 [-0.735, 0.332]		
Exploration : Branch orientation (diagonal)			0.052 [-0.706, 0.781]	0.544 [-0.337, 1.449]
LRS : Helper in natal group (no)	0.111 [-0.562, 0.791]	0.233 [-0.408, 0.865]	0.397 [-0.448, 1.257]	0.090 [-0.904, 1.0444]
LRS : Maternal age	0.351 [-0.214, 0.901]	**-0.583 [-1.157,-0.014]**	0.128 [-0.636, 0.869]	**-1.050 [-1.966,-0.200]**
LRS : Cohort	**-0.243 [-0.342,-0.149]**	**-0.249 [-0.346,-0.152]**	**-0.258 [-0.386,-0.137]**	**-0.244 [-0.383,-0.103]**
Random effects				
Exploration : Bird ID	0.449 [0.193, 0.722]	0.659 [0.262, 1.076]	0.678 [0.226, 1.218]	1.471 [0.373, 2.646]
Exploration : Observer ID	0.243 [0.060, 0.514]	0.388 [0.077, 0.861]	0.391 [0.067, 0.959]	0.655 [0.070 1.851]
Exploration : Residual	0.599 [0.382, 0.837]	0.928 [0.577, 1.320]	0.800 [0.344, 1.304]	1.195 [0.495, 2.093]
LRS : Bird ID	0.766 [0.327, 1.288]	0.565 [0.212, 0.977]	0.624 [0.204, 1.160]	0.645 [0.193, 1.237]
LRS : Cohort	0.329 [0.066, 0.735]	0.286 [0.064, 0.637]	0.454 [0.080, 1.066]	0.462 [0.068, 1.106]
Covariance (BirdID)	0.037 [-0.213, 0.299]	-0.019 [-0.308, 0.268]	0.101 [-0.248, 0.480]	0.228 [–0.351, 0.881]