Original Article

Exploration is dependent on reproductive state, not social state, in a cooperatively breeding bird

Hannah A. Edwards,[a] Hannah L. Dugdale,[b,c] David S. Richardson,[d,e] Jan Komdeur,[c] and Terry Burke[a]

[a]Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK, [b]School of Biology, The Faculty of Biological Sciences, University of Leeds, Leeds LS2 9JT, UK, [c]Behavioural Ecology and Physiological Group, Groningen Institute for Evolutionary Life Sciences, University of Groningen, PO Box 11103 9700 cc, Groningen, The Netherlands, [d]School of Biological Sciences, University of East Anglia, Norwich Research Park, Norwich, Norfolk NR4 7TJ, UK, and [e]Nature Seychelles, PO BOX 1310, Mahe, Republic of Seychelles

Personality is an intriguing phenomenon in populations because it constrains behavioral flexibility. One theory suggests that personality could be generated and maintained if dependent on asset protection. It is predicted that trade-offs with fitness expectations and survival probability encourage consistent behavioral differences among individuals (personality). Although not mutually exclusive, the social niche specialization hypothesis suggests that a group of individuals that repeatedly interact will develop personality to avoid costly social conflict. The point at which behavioral consistency originates in the social niche hypothesis is still unclear, with predictions for development after a change in social status. In the facultative cooperatively breeding Seychelles warbler (*Acrocephalus sechellensis*), residing on Cousin Island, breeding vacancies are limited and this forces individuals into different social roles. We used this system to test whether reproductive and social state predicted among-individual differences in exploration. We had 2 predictions. First, that an individual's start in life can predict personality, whereby young individuals with a good start to life (associated with early age reproduction and earlier onset survival senescence) are fast explorers, suggesting reproductive state-dependence. Second, that an individual's social status can predict personality, whereby dominant individuals will be fast explorers, suggesting that the behavior is social state-dependent. Neither of the behaviors was associated with social state and social state did not affect behavioral consistency. However, novel object exploration was associated with a proxy of reproductive state. Our results provide further support for state being a mechanism for generating individual differences in behavior.

Key words: **cooperative breeder, personality, Seychelles warbler, reproductive state, social state, state-dependent.**

INTRODUCTION

The occurrence of consistent differences in behavior among individuals, known as animal personality (Sih et al. 2004; Réale et al. 2007), is an intriguing phenomenon considering that a flexible behavioral response should enable individuals to adapt to varying environments (Wolf et al. 2007; Réale et al. 2010). Personality can be highly heritable (Dochtermann et al. 2015) and can affect fitness (Smith and Blumstein 2008), but little is known about how it is maintained at the individual or population level (Bell 2007).

To gain further evolutionary understanding as to why personality is generated and maintained, we require longitudinal studies of personality in the wild. This is because captive environments can alter an individual's behavioral expression and longitudinal studies on free-living organisms in the natural environment are a way to circumvent this (Stamps and Groothuis 2010).

Circumstances or properties that alter the costs and benefits associated with behavior are known as states (Dall et al. 2004; Wolf et al. 2007; Biro and Stamps 2008; Dingemanse and Wolf 2010). States are inherently slow changing but can encourage long-term stability in behavior if associated in a positive feedback loop (Luttbeg and Sih 2010). Behavior dependent on asset protection predicts that individuals with a high future reproductive state

(i.e., high assets) will be consistently slow explorers and risk averse (behaviors that are often positively correlated, e.g., Quinn et al. 2012), in order to prevent predation, compared with those that have a low future reproductive state (Dall et al. 2004; Stamps 2007; Wolf et al. 2007). Although more study is needed, a few empirical studies have found support for this prediction. Slow exploratory behavior was associated with increased survival probability and hence high future reproductive states in wild great tits (*Parus major*, Nicolaus et al. 2012) and reduced risk-taking behavior was exhibited by young individuals with high future reproductive states in gray mouse lemurs (*Microcebus murinus*, Dammhahn 2012).

A less explored avenue of research is the potential for personality to be dependent on social state. Reproductive state and social state are not mutually exclusive because social status is often associated with breeding benefits, although in some species subordinates do have opportunities to breed (Richardson et al. 2002). The social niche specialization hypothesis suggests that a group of individuals in a social group that repeatedly interact will benefit by developing social niches (Bergmüller and Taborsky 2010; Montiglio et al. 2013). Social niches, such as social status, cause individuals to behave differently by reducing social conflict and encouraging behavioral consistency through positive feedback mechanisms such as learning and costs incurred by changing social niches (Bergmüller and Taborsky 2010; Wolf and Weissing 2010). The relationship between social status and behavioral differences among individuals is still unclear (Gómez-Laplaza 2002; Fox et al. 2009). However, a few studies have shown that a dominant social status correlates with fast exploration and bold and aggressive behavior in a territorial context (Verbeek et al. 1996; Dingemanse and de Goede 2004; Favati et al. 2014). Also, in a cooperatively breeding system, immature individuals that showed lower levels of a subordinate helping behavior were aggressive and fast exploring (Bergmüller and Taborsky 2007).

Investigating how social state may affect individual differences in behavior among individuals does not give any insight into how it may affect within-individual consistency in a population (Dingemanse et al. 2010). For example, it is still unclear at what point behavioral consistency within individuals originates under the social niche hypothesis (Carter et al. 2014). It has been postulated that within-individual behavioral consistency could occur after a change in social status, termed the "transition" hypothesis (Carter et al. 2014). Further studies are needed, but in support of this theory, meerkat (*Suricata suricata*) subordinate females that later became dominant exhibited different cooperative personalities after social status change compared with those that remained subordinate (Carter et al. 2014). Also, male domestic fowl (*Gallus gallus*) showed increases in vigilance, activity, and exploration when changed from a subordinate to a dominant social position (Favati et al. 2014).

Facultative cooperative breeders, such as the Seychelles warbler (*Acrocephalus sechellensis*), provide an excellent system in which to test the state dependency of personality. In this species, individuals can forego reproduction to raise offspring that are not their own (Cockburn 1998). They are highly territorial, and the limited number of breeding vacancies in the Cousin Island population forces many individuals into a subordinate social status indefinitely or until there is a dominant breeding vacancy (Komdeur 1991). A subordinate social status can bear a cost through the loss of direct breeding benefits and reduced body condition when helping to rear young (Richardson et al. 2002; van de Crommenacker et al. 2011). These social states could consequently encourage behavioral differences among individuals through character displacement or

trade-offs with future reproductive state (Bergmüller and Taborsky 2010). Furthermore, individuals born in years of high food availability (high insect abundance at year of birth) reproduce at an earlier age but have an earlier onset of survival senescence compared with those born into years of low food availability (Hammers et al. 2013). This good or bad start could influence an individual's future reproductive state and generate behavioral differences among individuals (e.g., Dingemanse et al. 2002; Wolf et al. 2007).

In this study, we investigate whether exploration (exploration of a novel environment and exploration of a novel object) is associated with current social state or future reproductive state. In an attempt to tease these 2 states apart, we tested 2 predictions. First, that an individual's start in life can predict personality, whereby young individuals that have a good start to life, and thus breed at an earlier age and have early onset survival senescence, will be faster explorers than old individuals that have a bad start to life, suggesting that personality is associated with reproductive state. Second, that an individual's social state can predict personality, whereby dominant individuals are faster explorers than subordinates, suggesting that personality is associated with current social state (e.g., social conflict and aspects of the social niche environment such as resource holding potential). Furthermore, we will investigate whether social state affects within-individual behavioral consistency, thus providing support to the "transition" hypothesis.

METHODS

Ethics statement

Local ethical regulations and agreements were followed for fieldwork. Nature Seychelles permitted us to work on Cousin Island Nature Reserve. The Seychelles Department of Environment and the Seychelles Bureau of Standards authorized fieldwork and sampling.

Study system and site

Seychelles warblers were monitored on the main study island of Cousin (0.29 km^2; 04°20′S, 55°40′E) during the winter (January–February) and summer (June–September) breeding seasons in 2010–2015, where they have been monitored intensively since 1981 (Komdeur 1991). During this time, social status and group memberships were identified, individuals were ringed with a metal British Trust for Ornithology ring and color ringed if necessary, and blood sampled (for sexing and genotyping). The sex of each individual is determined using molecular sexing methods (Griffith et al. 2002). The population experiences virtually no immigration and emigration between surrounding islands (Komdeur et al. 2004, 2015), and there is a 0.92 ± 0.02 probability of annually resighting in the first 2 years of life and 0.98 ± 0.01 probability of annually resighting in adults (Brouwer et al. 2010). Subsequently, birds are presumed dead if not seen after 1 year. On average, annual survival probability in the first year of life is 0.61 ± 0.09 and 0.84 ± 0.04 for adult birds (Brouwer et al. 2006). The mean life span of an individual is 5.5 years, and a maximum life span of 17 years has been recorded (Komdeur 1991; Barrett et al. 2013).

To determine territory boundaries, breeding status, and to observe interactions with other warblers, dominant females were followed for a minimum of 15 min on a weekly basis throughout each summer and winter season. A subordinate status was assigned to individual birds (>5 months old) that were consistently seen in a territory and interacted with group members, but did not engage in dominant pair behavior. Subordinates may or may not help defend

territories and may or may not help to raise offspring (Komdeur 1991). Dominant status was assigned when a pair of individuals was observed in a territory over multiple weeks and the individuals within the pair stayed within close proximity of one another and had frequent vocal interactions. The age of the first breeding attempt has been shown to range from 1 to 8 years old, with 48% breeding in their first year (Hammers et al. 2013). The Seychelles warblers are insectivorous and take 98% of their food from the underside of leafs of predominately *Pisonia grandis*, *Morinda citrifolia*, and *Ficus* sp. (Komdeur 1991, 1994). Insect abundance was thus measured over 14 locations across the island during the main breeding season (Komdeur 1992). Using this data, we then averaged insect abundance over these 14 locations per year to get an estimate of annual variation in food availability (Spurgin LG, Bebbington KL, Fairfield EA, Komdeur J, Burke T, Dugdale HL, et al., unpublished data).

Personality assays

Birds were caught in mist nets throughout the summer of 2010 and the winter and summer breeding seasons of 2012–2015 for exploration of the novel environment and of 2013–2015 for exploration of a novel object. Once a bird was caught in a mist net it was extracted, measured for morphometric traits, taken back to the field station, given 5 min in a bird bag, assayed for personality, and then released back at its territory. Exploration of a novel environment was tested in an Oxygen 4 tent (L322 × W340 × H210 cm, Gelert Ltd Wigan). The tent contained 3 artificial trees each with 2 branches 45 cm long (one attached at 95 cm and the other at the top of the trunk) and a trunk 148 cm high (adapted from Verbeek et al. 1994). By observing through a small opening (15.24 cm long by 6.35 cm wide) in the gauze of the tent door, the number of flights, hops, and the total number of trees visited were recorded during a 5-min period. A flight denoted a transfer between branches on the same tree, between trees or between floor and tree, or any movement greater than a branch length that involved flapping of the wings. A hop was described as both feet off the ground with no wing flapping, either on the same branch or on the floor. The combined number of hops, flights, and trees visited was totaled to give a measure of exploration (Edwards et al. 2015).

Exploration of a novel object was then tested 2 min after the exploration assay to allow for habituation to the novel environment of the tent (see acclimation test, Edwards et al. 2015). A novel pink toy attached to a tree branch (95 cm long) was inserted and positioned in the center of the tent (adapted from Verbeek et al. 1994). For each bird, we included a control assay with the novel toy excluded to confirm that the behavioral reaction resulted from the novel toy and not the tree branch it was attached to (Edwards et al. 2015). Behavior scores (hops, flights, and trees visited in 5 min) in the novel object assay were therefore used as a measure of exploration (Edwards et al. 2015).

Personality assays were collected on 312 individuals (1 measure = 175 birds; 2 = 96; 3 = 25; 4 = 8; 5 = 5; 6 = 3; female = 150, male = 166) for novel environment exploration and 177 individuals (1 measure = 120 birds; 2 = 52; 3 = 4; 4 = 1; female = 84, male = 96) for novel object exploration. Plots of both traits after repeat testing can be found in Supplementary Figure S1 and S2. Novel environment exploration and novel object exploration are repeatable in this study species (Edwards et al. 2015; Edwards et al. forthcoming).

Statistical analyses

All statistical analyses were performed in R 3.0.2. (R Development Core Team 2013).

Social or reproductive state-dependence

Generalized linear mixed models using a Poisson error distribution with a log link were run in the package MCMCglmm 2.17 (Hadfield 2009). For all models, we specified an Inverse Wishart prior ($V = 1$, $n = 0.2$), the posterior distribution was sampled every 100 iterations, with a burn-in period of 3000 iterations and a run of 203 000 iterations. Convergence was assessed by autocorrelation values ($r < 0.1$), visual inspection of time series plots of the model parameters and using the heidel.diag and geweke.diag functions. We ran 2 models, with the responses of exploration of a novel environment and exploration of a novel object. The fixed effects included variables known to influence personality: social status at testing (subordinate or dominant) and an interaction with insect abundance at year of birth (mean = 4.61, variance = 3.76), age (novel environment age range: 36–5687 days, novel object age range: 60–1432 days, e.g., Fisher et al. 2015) and an interaction with insect abundance at year of birth (both a proxy for an association with reproductive state), assay number (to control for habituation, e.g., Dingemanse et al. 2012), sex (e.g., Schuett and Dall 2009), and body mass (standardized for time of day). Age (days) was mean centered (Gelman and Hill 2006) and included as a linear term. Tent color was also included as a fixed effect in the novel environment exploration model because it was shown to have an effect in previous analyses (Edwards et al. forthcoming). The model also included observer identity and bird identity as random effects to account to repeat observations. To facilitate visualization of the interaction term between insect abundance and age, we subset insect abundance into good and bad years (defined as above and below the mean [4.61] insect abundance across all years) and used lm to calculate the smoothed regression in ggplot2 (Wickham 2009).

Behavioral consistency at social status transition

Hierarchical generalized linear models (HGLM; Cleasby and Nakagawa 2011; Cleasby et al. 2014) allow for individual/group differences in the residual variance to measure how an individual's behavior changes when measured repeatedly, and hence its predictability. Therefore, only individuals with repeat personality measures were included in this analysis. We included assay number, age, and sex as fixed effects and fitted the difference of status between measures into the dispersion part of the standard Poisson HGLM using the package HGLM 2.0-11 (Ronnegard et al. 2010). The social status differences were grouped as 1) individuals that remained subordinate (novel environment exploration $n = 49$ [female = 26 and male = 23]; novel object exploration $n = 15$ [female = 9 and male = 6]); 2) individuals that remained dominant (novel environment exploration $n = 74$ [female = 29 and male = 45]; novel object exploration $n = 31$ [female = 13 and male = 18]); or 3) individuals that transitioned from subordinate to dominant social status between behavioral measures (novel environment exploration $n = 36$ [female = 17 and male = 19]; novel object exploration $n = 11$ [female = 3 and male = 8]). No individuals transitioned from dominant to subordinate status. Bird identity was also included as a random effect to control for repeat measures. To assess the effect of social status difference on the residual variance, we compared the fit of a model with and without the social status fixed effect in the dispersion part of the HGLM, using the conditional Akaike information criterion (AIC) values (Cleasby et al. 2014). The model with the smaller conditional AIC value and a difference greater than 7 was interpreted as a better fit (Burnham et al. 2011). Modeling variance often requires a large sample size (Martin et al. 2011; van

de Pol 2012). To ensure the small sample size of the novel object exploration assay was not biasing our estimates, we ran a simulation analysis with a Poisson HGLM. We then changed the sample sizes ($n = 11$–500) to investigate the effect on 2 simulated models' parameter estimates. Simulated sample sizes of 11 individuals per group (representative of our social status grouping) did not sufficiently bias the model parameters, suggesting our sample sizes were sufficient to detect an effect (see Supplementary Table S1).

RESULTS

Social or reproductive state-dependence

Social state and insect abundance at year of birth were not associated with novel environment exploration (Figure 1 and Supplementary Table S2). Novel environment exploration instead increased with assay number. The marginal effects explained 0.19 (0.12–0.31) of the variance and the conditional effects explained 0.53 (0.27–0.73) of the variance in the novel environment exploration model. Social state was not associated with novel object exploration but with insect abundance at year of birth and the interaction with age (Figure 2 and Supplementary Table S3). There was a negative relationship between insect abundance and age, whereby young individuals born into years of high food abundance were associated with faster exploration of the novel object compared with individuals born into years of low food abundance (Figures 2 and 3). Males were faster explorers than females and novel object exploration also increased with assay number and age (Figure 2 and Supplementary Table S3). The marginal effects explained 0.22 (0.15–0.28) of the variance and the conditional effects explained 0.52 (0.39–0.62) of the variance in the novel object exploration model.

Behavioral consistency at social status transition

For novel environment exploration, the standard Poisson model and the model with social status fixed in the dispersion were of similar fit (standard Poisson HGLM cAIC = 2864.63, h-likelihood = 2891.61 and modified dispersion HGLM cAIC = 2871.01, h-likelihood = 2896.68). Similarly, for novel object exploration, the 2 models were of similar fit (standard Poisson HGLM cAIC = 1137.75, h-likelihood = 1102.13 and modified dispersion HGLM cAIC = 1135.46, h-likelihood = 1105.94). Thus, there was no evidence for within-individual behavioral consistency being affected by social state.

DISCUSSION

Asset protection could encourage consistent behavioral differences through trade-offs with future fitness expectations and survival probability (Wolf et al. 2007). The social niche specialization hypothesis further suggests that in a group where individuals repeatedly interact, consistent behavioral differences will develop in order to avoid costly social conflict (Bergmüller and Taborsky 2007; Laskowski and Pruitt 2014). In our study, we found that between-individual differences in exploration were not associated with social state and that within-individual behavioral consistency was unaffected by social state. However, insect abundance at year of birth, a proxy of reproductive state, and the interaction with age did predict novel object exploration.

Young individuals born in years of greater food abundance were associated with fast exploration of the novel object. This finding is in line with the asset protection theory that suggests individuals should adjust their risk-taking/exploratory behavior when there
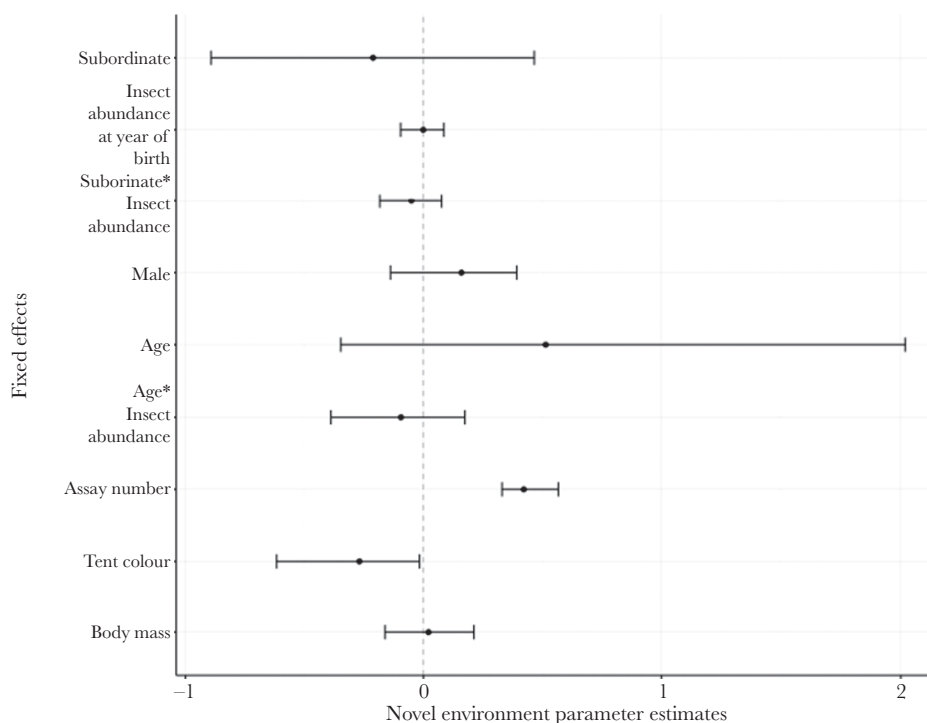

Figure 1

Posterior modes and associated 95% credible intervals of social status (contrast level = dominant, N: subordinates = 167, dominants = 145), insect abundance at year of birth and the interaction with social status, sex (contrast level = female, N: female = 149, male = 163), age and the interaction with insect abundance at year of birth, assay number*, tent color (contrast level = blue, N: blue = 244, green = 88)* and body mass in the novel environment exploration model. *Posterior modes whose 95% credible intervals do not overlap zero.
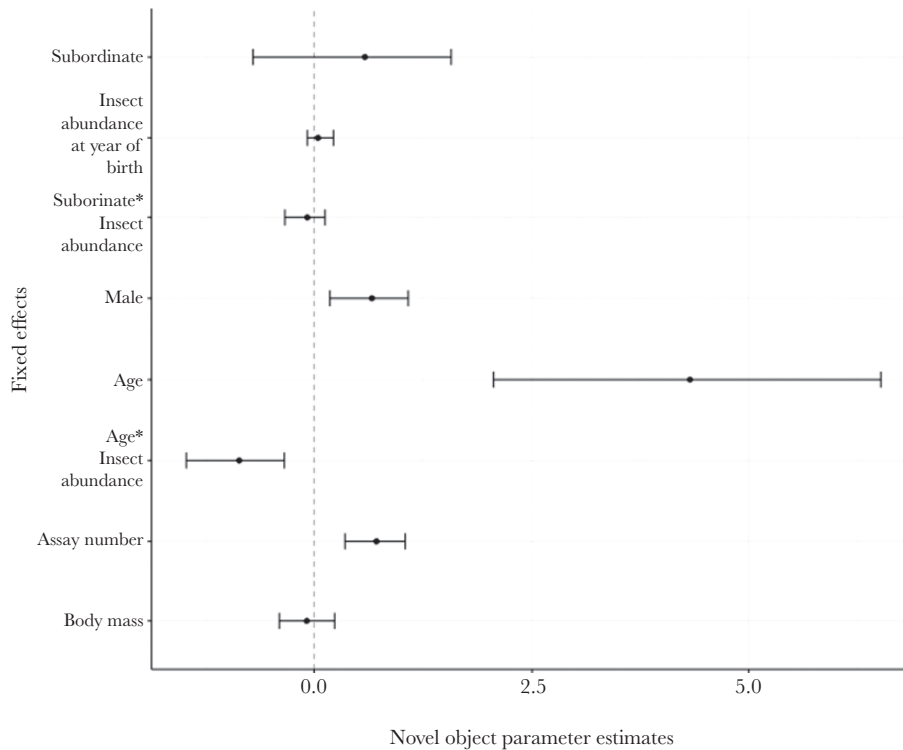
Figure 2

Posterior modes and associated 95% credible intervals of social status (contrast level = dominant, N: subordinate = 76, dominant = 101), insect abundance at year of birth and the interaction with social status, sex (contrast level = female, N: female = 81, male = 96)*, age and the interaction with insect abundance at year of birth*, assay number* and body mass in the novel object exploration model. *Posterior modes whose 95% credible intervals do not overlap zero.

are trade-offs with future fitness expectations and survival probability (Wolf et al. 2007). This relationship has also been confirmed in empirical studies, where slow exploratory and reduced risk-taking behaviors are associated with individuals with high future reproductive states (Dammhahn 2012; Nicolaus et al. 2012). In the Seychelles warbler, greater food abundance at year of birth causes individuals to reproduce for the first time at an earlier age but results in earlier survival senescence (Hammers et al. 2013). Reproductive tactics are thus modified to suit environmental conditions to maintain survival (Hammers et al. 2013) and reproductive output is age dependent, with an initial increase followed by a decline in old age (Hammers et al. 2012). Young individuals born into good insect abundance years (low future reproductive states) may exhibit risky behavior, such as territory guarding and novel foraging, to ensure the success of current reproductive attempts. Long-term studies should look at how novel object exploration may be linked with aspects of the Seychelles warblers' ecology, such as predator susceptibility or resource holding.

Novel object exploration was also associated with age, with older individuals exhibiting faster exploration. Previous studies have found that among-individual variance in personality traits increase later in life (Roberts and DelVecchio 2000; Fisher et al. 2015). It could be that older individuals have experienced greater environmental variation (novel prey or novel conspecifics) and are faster explorers than younger individuals. Furthermore, processes such as stimulus generalization (transfer of a response learned from one stimulus to a similar stimulus) in older individuals may encourage fast exploration. These 2 processes coupled together could result in age-related behavioral differences.

We also show that assay number affected between-individual differences in exploration. Differences in how individuals habituate to

a novel environment are associated with individual differences in learning (Light et al. 2011) and fearfulness (File 2001). After repeat testing, individuals are thought to overcome fear and explore novel environments more superficially compared with previous experiences (Verbeek et al. 1994). This effect is particularly pronounced in slow explorers (Carere et al. 2005). Clearly, repeat testing is conflated with habituation, and therefore, assay number should be accounted for when repeatedly measuring traits that are associated with learning and fearfulness.

Novel object exploration also differed between the sexes, with males being faster explorers than females. The direction of among-individual differences in exploration between the sexes can vary, and it has been postulated that sexual selection may play a role in encouraging these differences (reviewed in Schuett et al. 2010). Exploratory behavior has been correlated with spatial response to territory intrusion, with fast explorers spending more time in proximity to the intruder in great tits (Snijders et al. 2015). In the Seychelles warbler, attack frequencies toward a simulated predator were higher in males, than in females (Veen et al. 2000). Exploration may therefore be associated with territorial defense, and if selected for in males would result in these sex differences.

Behavioral consistency of exploration was unaffected by social state, although this has been suggested as a mechanism for within-individual behavioral consistency in meerkats (Carter et al. 2014). In the Seychelles warbler, it could be that individuals decide on a life-history trajectory early in life and this is why social state had no effect (e.g., Bergmüller and Taborsky 2007). There are, however, some limitations to our study. We were unable to distinguish causation because we did not experimentally manipulate individuals and relied on natural changes in social status. Individuals
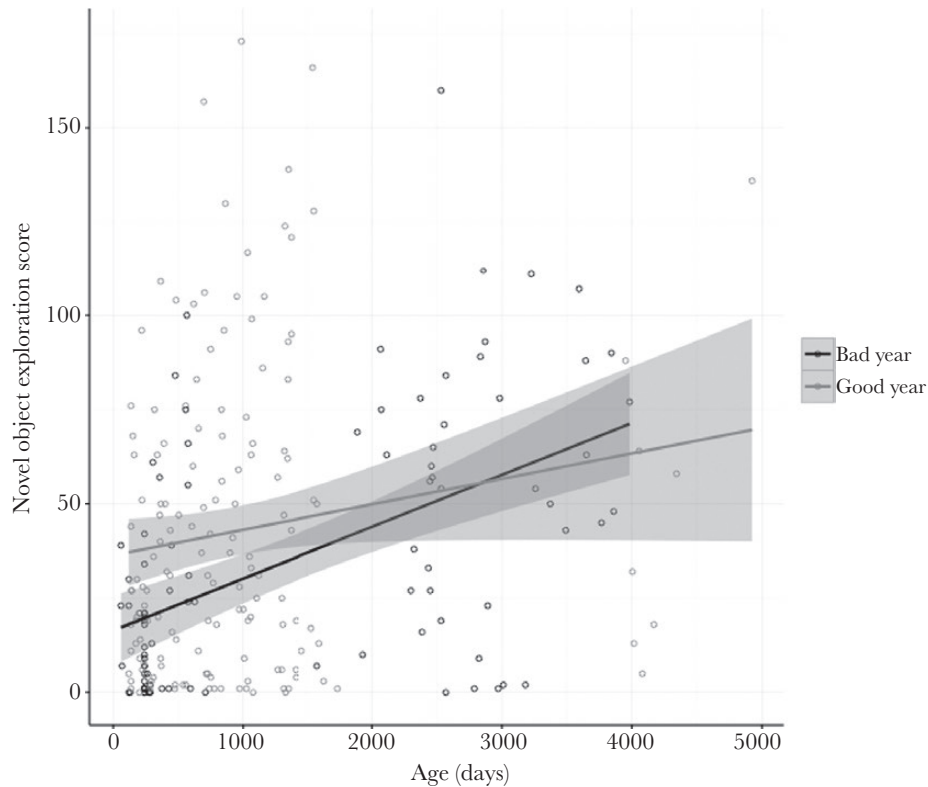
Figure 3

Novel object exploration scores of the Seychelles warblers of different ages (days), for individuals born into bad years ($n = 30$ individuals, black line and circles), and good years ($n = 35$ individuals, dark gray line and circles) of food abundance (defined as above or below the mean [4.61] insect abundance across all years). Insect abundance was a continuous effect in the model but is split into 2 categories on the graph to facilitate visualization of the interaction between insect abundance and age. 95% confidence intervals around the regression lines are in light gray.

could therefore have been predisposed to certain changes in social statuses caused by environmental, physiological or experiential factors. Also, behavioral variation within individuals was not captured over a lifetime (personality tested birds had an average age of 2.98 years, but Seychelles warblers have a mean life span of 5.5 years, Komdeur 1991). For example, subordinates that remained subordinate between personality measures could potentially transition to dominance at a later stage, and dominants that remained dominant may not have been assayed when subordinate. It is difficult to decipher whether the 3 social status groups (individuals that remained subordinate, individuals that remained dominant, or individuals that transitioned from subordinate to dominant social status between behavioral measures) were equally plastic or equally consistent, because variation within all the groups was the same. Both scenarios have their advantages for an individual. Behavioral plasticity can be adaptive (Sih et al. 2004; Kontiainen et al. 2009; Betini and Norris 2012) and allow individuals to display costly behaviors only when required. On the other hand, consistent behavior can allow individuals to specialize in different social niches and avoid costly social conflict (Bergmüller and Taborsky 2007).

SUMMARY

We have shown that social state does not explain behavioral differences in exploration nor affect behavioral consistency. Instead we show that a proxy of reproductive state, sex, and age affect individual differences in novel object exploration, and repeat testing affects

individual differences in novel environment exploration. Our results provide further support that exploration can be reproductive state-dependent and that this may be a mechanism for generating individual differences. We suggest that future work should look directly at survival probability as a mechanism for encouraging personality and sex-specific behavior such as territorial defense, which may encourage sex differences.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

FUNDING

Handling editor: Francisco Garcia-Gonzalez

REFERENCES

Barrett EL, Burke TA, Hammers M, Komdeur J, Richardson DS. 2013. Telomere length and dynamics predict mortality in a wild longitudinal study. Mol Ecol. 22:249–259.

Bell AM. 2007. Future directions in behavioural syndromes research. Proc Biol Sci. 274:755–761.

Bergmüller R, Taborsky M. 2007. Adaptive behavioural syndromes due to strategic niche specialization. BMC Ecol. 7:12.

Bergmüller R, Taborsky M. 2010. Animal personality due to social niche specialisation. Trends Ecol Evol. 25:504–511.

Betini GS, Norris DR. 2012. The relationship between personality and plasticity in tree swallow aggression and the consequences for reproductive success. Anim Behav. 83:137–143.

Biro PA, Stamps JA. 2008. Are animal personality traits linked to life-history productivity? Trends Ecol Evol. 23:361–368.

Brouwer L, Barr I, van de Pol M, Burke T, Komdeur J, Richardson DS. 2010. MHC-dependent survival in a wild population: evidence for hidden genetic benefits gained through extra-pair fertilizations. Mol Ecol. 19:3444–3455.

Brouwer L, Richardson DS, Eikenaar C, Komdeur J. 2006. The role of group size and environmental factors on survival in a cooperatively breeding tropical passerine. J Anim Ecol. 75:1321–1329.

Burnham K, Anderson D, Huyvaert K. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behav Ecol Sociobiol. 65:23–35.

Carere C, Drent PJ, Privitera L, Koolhaas JM, Groothuis TGG. 2005. Personalities in great tits, *Parus major*: stability and consistency. Anim Behav. 70:795–805.

Carter AJ, English S, Clutton-Brock TH. 2014. Cooperative personalities and social niche specialization in female meerkats. J Evol Biol. 27:815–825.

Cleasby IR, Nakagawa S. 2011. Neglected biological patterns in the residuals. Behav Ecol Sociobiol. 65:2361–2372.

Cleasby IR, Nakagawa S, Schielzeth H. 2014. Quantifying the predictability of behaviour: statistical approaches for the study of between-individual variation in the within-individual variance. Method Ecol Evol. 6:27–37.

Cockburn A. 1998. Evolution of Helping Behavior in Cooperatively Breeding Birds. Annu Rev Ecol Syst. 29:141–177.

van de Crommenacker J, Komdeur J, Richardson DS. 2011. Assessing the cost of helping: the roles of body condition and oxidative balance in the Seychelles warbler (*Acrocephalus sechellensis*). PLoS One. 6:e26423.

Dall SRX, Houston AI, McNamara JM. 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. Ecol Lett. 7:734–739.

Dammhahn M. 2012. Are personality differences in a small iteroparous mammal maintained by a life-history trade-off? Proc Biol Sci. 279:2645–2651.

Dingemanse NJ, Both C, Drent PJ, van Oers K, van Noordwijk AJ. 2002. Repeatability and heritability of exploratory behaviour in great tits from the wild. Anim Behav. 64:929–938.

Dingemanse NJ, Bouwman KM, van de Pol M, van Overveld T, Patrick SC, Matthysen E, Quinn JL. 2012. Variation in personality and behavioural plasticity across four populations of the great tit (*Parus major*). J Anim Ecol. 81:116–126.

Dingemanse NJ, de Goede P. 2004. The relation between dominance and exploratory behavior is context-dependent in wild great tits. Behav Ecol. 15:1023–1030.

Dingemanse NJ, Kazem AJN, Réale D, Wright J. 2010. Behavioural reaction norms: animal personality meets individual plasticity. Trends Ecol Evol. 25:81–89.

Dingemanse NJ, Wolf M. 2010. Recent models for adaptive personality differences: a review. Philos Trans R Soc Lond B Biol Sci. 365:3947–3958.

Dochtermann NA, Schwab T, Sih A. 2015. The contribution of additive genetic variation to personality variation: heritability of personality. Proc Biol Sci. 282:20142201.

Edwards HA, Burke T, Richardson DS, Komdeur J, Dugdale HL. Forthcoming. Repeatable and heritable behavioural variation in a wild cooperative breeder. Behav Ecol.

Edwards HA, Hajduk GK, Durieux G, Burke T, Dugdale HL. 2015. No association between personality and candidate gene polymorphisms in a wild bird population. PLoS One. 10:e0138439.

Favati A, Leimar O, Radesäter T, Løvlie H. 2014. Social status and personality: stability in social state can promote consistency of behavioural responses. Proc Biol Sci. 281:20132531.

File SE. 2001. Factors controlling measures of anxiety and responses to novelty in the mouse. Behav Brain Res. 125:151–157.

Fisher DN, David M, Tregenza T, Rodríguez-Muñoza R. 2015. Dynamics of among-individual behavioral variation over adult lifespan in a wild insect. Behav Ecol. 26:975–985.

Fox RA, Ladage LD, Roth TC, Pravosudov VV. 2009. Behavioural profile predicts dominance status in mountain chickadees, *Poecile gambeli*. Anim Behav. 77:1441–1448.

Gelman A, Hill J. 2006. Data analysis using regression and multilevel/hierarchical models. Cambridge (UK): Cambridge University Press.

Gómez-Laplaza L. 2002. Social status and investigatory behaviour in the angelfish (*Pterophyllum scalare*). Behaviour. 139:1469–1490.

Griffith SC, Owens IP, Thuman KA. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. Mol Ecol. 11:2195–2212.

Hadfield J. 2009. {MCMC} Methods for multi-response generalized linear mixed models: the {MCMCglmm} {R} Package. J Stat Softw. 33:1–22.

Hammers M, Richardson DS, Burke T, Komdeur J. 2012. Age-dependent terminal declines in reproductive output in a wild bird. PLoS One. 7:e40413.

Hammers M, Richardson DS, Burke T, Komdeur J. 2013. The impact of reproductive investment and early-life environmental conditions on senescence: support for the disposable soma hypothesis. J Evol Biol. 26:1999–2007.

Komdeur J. 1991. Cooperative breeding in the Seychelles warbler [dissertation]. [Cambridge (UK)]: University of Cambridge.

Komdeur J. 1992. Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. Nature. 358:493–495.

Komdeur J. 1994. Conserving the seychelles warbler *Acrocephalus sechellensis* by translocation from Cousin Island to the islands of Aride and Cousine. Biol Conserv. 67:143–152.

Komdeur J, Burke T, Dugdale HL, Richardson DS. 2015. Seychelles warblers: the complexities of the helping paradox. In: Koenig WD, Dickinson JL, editors. Cooperative breeding: studies of ecology, evolution and behaviour. 1st ed. Cambridge (UK): Cambridge University Press. p. 197–216.

Komdeur J, Piersma T, Kraaijeveld K, Richardson DS. 2004. Why Seychelles warblers fail to recolonize nearby islands: unwilling or unable to fly there? Ibis. 146:298–302.

Kontiainen P, Pietiäinen H, Huttunen K, Karell P, Kolunen H, Brommer JE. 2009. Aggressive Ural owl mothers recruit more offspring. Behav Ecol. 20:789–796.

Laskowski KL, Pruitt JN. 2014. Evidence of social niche construction: persistent and repeated social interactions generate stronger personalities in a social spider. Proc Biol Sci. 281:20133166.

Light KR, Grossman H, Kolata S, Wass C, Matzel LD. 2011. General learning ability regulates exploration through its influence on rate of habituation. Behav Brain Res. 223:297–309.

Luttbeg B, Sih A. 2010. Risk, resources and state-dependent adaptive behavioural syndromes. Philos Trans R Soc Lond B Biol Sci. 365:3977–3990.

Martin JGA, Nussey DH, Wilson AJ, Réale D. 2011. Measuring individual differences in reaction norms in field and experimental studies: a power analysis of random regression models. Method Ecol Evol. 2:362–374.

Montiglio PO, Ferrari C, Réale D. 2013. Social niche specialization under constraints: personality, social interactions and environmental heterogeneity. Philos Trans R Soc Lond B Biol Sci. 368:20120343.

Nicolaus M, Tinbergen JM, Bouwman KM, Michler SP, Ubels R, Both C, Kempenaers B, Dingemanse NJ. 2012. Experimental evidence for adaptive personalities in a wild passerine bird. Proc Biol Sci. 279:4885–4892.

van de Pol M. 2012. Quantifying individual variation in reaction norms: how study design affects the accuracy, precision and power of random regression models. Method Ecol Evol. 3:268–280.

Quinn JL, Cole EF, Bates J, Payne RW, Cresswell W. 2012. Personality predicts individual responsiveness to the risks of starvation and predation. Proc Biol Sci. 279:1919–1926.

R Development Core Team. 2013. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. Available from: http://www.R-project.org/.

Réale D, Dingemanse NJ, Kazem AJ, Wright J. 2010. Evolutionary and ecological approaches to the study of personality. Philos Trans R Soc Lond B Biol Sci. 365:3937–3946.

Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ. 2007. Integrating animal temperament within ecology and evolution. Biol Rev Camb Philos Soc. 82:291–318.

Richardson DS, Burke T, Komdeur J. 2002. Direct benefits and the evolution of female-biased cooperative breeding in Seychelles warblers. Evolution. 56:2313–2321.

Roberts BW, DelVecchio WF. 2000. The rank-order consistency of personality traits from childhood to old age: a quantitative review of longitudinal studies. Psychol Bull. 126:3–25.

Ronnegard L, Shen X, Alam M. 2010. hglm: a package for fitting hierarchical generalized. R J. 2:20–28.

Schuett W, Dall SRX. 2009. Sex differences, social context and personality in zebra finches, *Taeniopygia guttata*. Anim Behav. 77:1041–1050.

Schuett W, Tregenza T, Dall SR. 2010. Sexual selection and animal personality. Biol Rev Camb Philos Soc. 85:217–246.

Sih A, Bell A, Johnson JC. 2004. Behavioral syndromes: an ecological and evolutionary overview. Trends Ecol Evol. 19:372–378.

Smith BR, Blumstein DT. 2008. Fitness consequences of personality: a meta-analysis. Behav Ecol. 19:448–455.

Snijders L, van Rooij EP, Henskens MFA, van Oers K, Naguib M. 2015. Dawn song predicts behaviour during territory conflicts in personality-typed great tits. Anim Behav. 109:45–52.

Stamps JA. 2007. Growth-mortality tradeoffs and 'personality traits' in animals. Ecol Lett. 10:355–363.

Stamps JA, Groothuis TG. 2010. Developmental perspectives on personality: implications for ecological and evolutionary studies of individual differences. Philos Trans R Soc Lond B Biol Sci. 365:4029–4041.

Veen T, Richardson DS, Blaakmeer K, Komdeur J. 2000. Experimental evidence for innate predator recognition in the Seychelles warbler. Proc Biol Sci. 267:2253–2258.

Verbeek MEM, Boon A, Drent PJ. 1996. Exploration, aggressive behaviour and dominance in pair-wise confrontations of juvenile male great tits. Behaviour. 133:945–963.

Verbeek MEM, Drent PJ, Wiepkema PR. 1994. Consistent individual differences in early exploratory behaviour of male great tits. Anim Behav. 48:1113–1121.

Wickham H. 2009. ggplot2: elegant graphics for data analysis. New York: Springer-Verlag.

Wolf M, van Doorn GS, Leimar O, Weissing FJ. 2007. Life-history trade-offs favour the evolution of animal personalities. Nature. 447:581–584.

Wolf M, Weissing FJ. 2010. An explanatory framework for adaptive personality differences. Philos Trans R Soc Lond B Biol Sci. 365:3959–3968.