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Tameness does not correlate with the learning of an appetitive association in a wild canid

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Abstract

Individual differences in cognition have been shown to be common in some animal taxa, and recent evidence suggests that an individual's personality can be associated with an individual's cognitive strategy. We tested whether wild bat-eared foxes *Otocyon megalotis* differ in a risk-taking behavior (tameness) and whether this trait correlated with appetitive association learning performance. While our result shows that individuals differed in their tameness, we found no association between this personality trait and learning the appetitive association. This result does not support the framework that differences in cognition are associated with differences in personality; however, our small sample size does not allow us to assert that personality cannot be associated with cognition in this system. This study highlights that measuring cognition and personality in wild systems presents added difficulty and that correlations found in captive animals may not be evident in their wild counterparts.

Key words: carnivore, cognition, bat-eared fox, personality

Individuals differ consistently in behaviors across time and context; a phenomenon generally labeled as animal personality (Réale et al. 2007; Carere and Maestripieri 2013). Personality traits can influence fitness, which may have ecological and evolutionary consequences (Smith and Blumstein 2008; Wolf and Weissing 2012). Recent theoretical and empirical evidence suggests that personality traits are linked to life-history strategies (Stamps 2007; Réale et al. 2010), and may also be associated with individual differences in cognition (Carere and Locurto 2011; Sih and Del Giudice 2012; Griffin et al. 2015; Morand-Ferron et al. 2015; Guillette et al. 2017).

Individual differences in cognition have been reported in several species (Griffin et al. 2015; but see Brust and Guenther 2017; Guillette et al. 2017; Lucon-Xiccato and Bisazza 2017; Matzel et al. 2017), and it appears likely that cognitive abilities and personality traits may have been similarly shaped by natural selection, based on shared underlying mechanisms (Sih and Del Giudice 2012). Cognition is the acquisition, processing, storage, and use of information (Shettleworth 2001; 2009) and covers a wide range of processes including attention, memory, and associative learning. One

hypothesis for this association is that personality and cognition are correlated through a speed-accuracy tradeoff (Chittka et al. 2009; Sih and Del Giudice 2012). For example, individuals that acquire information faster may be able to use resources sooner. However, this may also increase the chances of making a potentially costly mistake. These tradeoffs have been seen in a number of species including bumblebees *Bombus terrestris* (Chittka et al. 2003) and guppies *Poecilia reticulate* (Burns and Rodd 2008). To reduce these potential errors, individuals often develop routines or heuristics (shortcuts), which reduces the ability to respond to rapid environmental changes. The move to acquire information faster may, therefore, be correlated with individuals taking more risks (i.e., bolder or faster explorers). Conversely, individuals who are slower at acquiring information explore a novel environment slowly and more thoroughly and retain behavioral flexibility as environments change because they use cues from the environment (Chittka et al. 2009). For example, slower exploring black-capped chickadees *Poecile atricapillus* were quicker to relearn an acoustic operant discrimination task than faster exploring birds (Guillette et al. 2010).

A personality/cognition correlation has been shown in a number of captive species including insects (Chang et al. 2016), fish (Øverli et al. 2007; Lucon-Xiccato and Bisazza 2017), birds (Biondi et al. 2010; Guillette et al. 2015; de Haas et al. 2017), and mammals (Nawroth et al. 2017). However, how these traits correlate in the wild is still lacking empirical evidence.

Here we use wild habituated bat-eared foxes *Otocyon megalotis* (hereafter foxes) to understand the relationship between personality and cognition in a wild setting. Foxes forage on transient termite *Hodotermes mossambicus* patches (Nel 1978), and thus need to acquire and use environmental cues about resource availability and distribution. We use the framework from Sih and Del Giudice (2012) indicating that bolder individuals are more likely to learn an association first because they are more likely to experience new situations, and thus may form association sooner. Using approach-to-observer data from a population of wild foxes, we first expected foxes to exhibit consistent individual differences in tameness. Tameness is related to wariness toward humans, and can be related to docility or the bold-shy continuum (Réale et al. 2007). Following the above framework, we predicted that more tame (approach humans more readily), or bolder individuals are faster at the learning of an appetitive association. Foxes are not highly sexually dimorphic in morphology or social behavior; however, there may be unknown sex differences in these foxes (Carazo et al. 2014; Lucon-Xiccato et al. 2016). We thus have no a priori hypotheses about potential differences in cognition between the sexes.

Materials and Methods

We studied 12 habituated foxes (5 females and 7 males) at the Kuruman River Reserve (KRR, 28°58'S, 21°49'E) Northern Cape, South Africa, from July 2014 to April 2016. All foxes were considered habituated when we were able to follow them at a distance of 2–5 m for an extended period of time (>1 h). All foxes had been observed multiple times prior to recording latency to approach and associative learning. Foxes are small canids (2–4 kg) that feed predominantly on insects—termites making the bulk of their diet (Maas and Macdonald 2004; Nel 1990). Individuals spend 70–90% of their active time foraging (Nel 1978), while often moving between termite patches—their main food source (Nel 1978). Due to thermally driven changes in termite activity patterns, diurnal activity is more common for foxes in winter, and nocturnal movement in summer (Nel 1978). We conducted 2-h observational sessions on each individual once a week (henceforth a follow), wherein all foraged items, social interactions, and marking events were recorded along with Global Positioning System (GPS) locations. These follows were done as part of a larger study on fox movement and foraging activities (Périquet and le Roux 2017; Welch et al. 2017). The intervals between these sessions were designed to reduce the chance of over-habituation and to avoid excessive disturbance of the foxes or, potentially, their prey.

Measuring tameness

Although foxes were habituated to observers, there may remain differences in how individual foxes perceive humans. Habituation, for the purposes of this study, was the evident tolerance of observers, on foot, whereas foxes foraged and exhibited apparently natural, undisturbed behavior. Tameness, or tolerance of humans, is critical in the domestication of animals (Driscoll et al. 2009), and has been shown to correlate with aggression, activity, and stress response in wild-derived rats *Rattus norvegicus* (Albert et al. 2008). Therefore, after individuals were fully habituated to observer presence, we estimated

tameness as latency to approach an observer with an attractive lure from 114 approaches on 12 individuals from June 2015 to April 2016. These approaches were part of an ongoing study on fox movement and foraging behaviors discussed above. Thus, for each follow, an individual was located between 5:00 PM and 9:00 PM and lured to the observer shaking a small plastic bag and proffering a small food reward (raisins). Individuals initially learned the association between the bag rattle and a food reward during habituation. Handheld spotlights were used to observe individuals as they moved throughout the night. Observers noted the time an individual was 20 m and 2 m away (distances estimated by eye). Latency to approach was calculated as the time difference between the 2 distances in seconds. Latencies that lasted longer than 10 min were excluded from analysis (3 points out of 117).

Associative learning task

To examine associative learning in already-habituated animals, we tested 9 individuals (a subset of the 12 above—6 males and 3 females) over 61 trials from June to October 2015, with a novel stimulus–reward association. Before a follow, we paired a dog whistle (condition stimulus, CS) with a single raisin (unconditioned stimulus, US) 10 times, for example, a dog whistle was blown and a single raisin was given immediately after the whistle; this process was repeated 10 times consecutively with each combination happening within 5–10 s of the previous pairing. Raisins were tossed ∼1 m from individuals. These pairings were considered a training period. This period was necessary as individuals were free to move or leave without hindrance. This necessitated that we call in individuals first using the bag shake, pair the whistle and raisins multiple times, and then test the association. After a 10-min waiting period, the CS was given again while the fox was moving but not actively eating a prey item. If the fox returned to the observer, the US was provided. This whole process constituted 1 trial (CS/US pairing and post-10-min CS presentation). Trials were conducted once before a follow and once after when possible (i.e., 2 h after the pre-follow trial). Once the fox had returned for the US, the individual was noted as successfully associating the CS with the US. Pairings were only done when foxes were in close proximity (<5 m) to the observer ($n = 6$; range of trials = 8–34). To prevent social learning, trials were conducted only when the focal individual was alone.

Statistical analysis

All analyses were done in R (R Core Team 2016) in the package lme4 (Bates et al. 2015). In the following analyses, all 2-way interactions were included in each model and removed from the model if not significant, based on 95% confidence intervals (C.I.). A main effect was also considered significant if the 95% C.I. did not include zero. Individual was included as a random effect in all analyses, and observer was also included as a random effect in the tameness analysis. Repeatability was calculated by dividing the individual variance by the total phenotypic variance. Significance of a random effect was tested using log-likelihood ratio tests (LRT) between models with and without the random effect.

Tameness

We fit a linear mixed-effects model of latency to approach observer as a function of trial number. Individuals had already been habituated to observer presence for some time, but we included trial to control for any further habituation effects. Individual and observer were added as random effects. There were a total of 6 observers in this study.

Associative learning task

We fit a generalized mixed-effects model with a binomial distribution of whether an individual had learned the association between CS and US as a function of trial number, sex, and the last latency to approach (by date) and observer for each individual. A random regression model (Nussey et al. 2007) to test for individual differences in learning (an individual × environment interaction) could not be fit due to restrictions in sample size and model convergence. One individual did not make the association before disappearing from the population. This individual received 4 trials and these trials were included in the analysis. Our small sample size makes it difficult to assert the null between cognition and covariates (see results below). We, therefore, calculated a Bayesian factor (BF) for nonsignificant fixed effects to determine the strength of support for our data given our result (Jarosz and Wiley 2014). Thus, we calculated the Bayesian Information Criterion (BIC) for our full model containing all covariates and for models without specific fixed effects. We then estimated a proxy Bayes factor for each nonsignificant fixed effect by taking the natural log and raising it to the difference between full and nested model BICs divided by 2. It should be noted that this is an approximation to a Bayes factor and does not give a definite answer to whether one can assert the null. However, it can give support for one hypothesis over another (Jarosz and Wiley 2014). A value between 0.33 and 0.10 suggests strong or substantial support for an alternative hypothesis (Jarosz and Wiley 2014).

Results

Tameness

Mean latency to approach for all individuals took ~45 s ($x = 42.76$ s; range = 2–240). Individuals did not increase their habituation to our presence (trial: $\beta = -0.283$; SE = 0.552; 95% C.I. = −1.376 to 0.798). There was significant but low among-individual differences in latency to approach ($R = 0.110$; LRT = 4.389; $P = 0.036$). We also found a significant effect of observer ($R = 0.275$; LRT = 18.867; $P < 0.001$) suggesting that foxes may view observers differently, or a systematic bias by observers in measuring fox approaches. Mean approach for observers varied greatly (range = 9.417–70.273), but when the fox with the highest mean latency to approach was removed from analysis the observer effect was still present ($R = 0.274$; LRT = 16.916; $P < 0.001$). Interestingly, the 2 observers with the highest mean approach were also the only observers that conducted this fox's trials. However, these 2 observers remained as the observers with the highest approach times without this fox in the analysis. This suggests that an unknown observer characteristic still had a large effect even with this extreme fox's approaches excluded.

Associative learning

Mean trials to learn the association was ~4 (range 1–10). Individuals made the association between CS and US as trials increased ($\beta = 0.879$; SE = 0.247; 95% C.I. = 0.476–1.476; Figure 1). There was no sex difference (females as reference: $\beta = -1.700$; SE = 1.295; 95% C.I. = −5.075 to 1.014), and we found no association between tameness ($\beta = -0.024$; SE = 0.023; 95% C.I. = −0.081 to 0.027) and learning (Figure 2). We found no interaction between any variables. We found low support to assert the null for the last latency to approach—our measure of tameness—($BF_{01} = 0.219$). We also found low support to assert the null for no differences in sex ($BF_{01} = 0.307$).
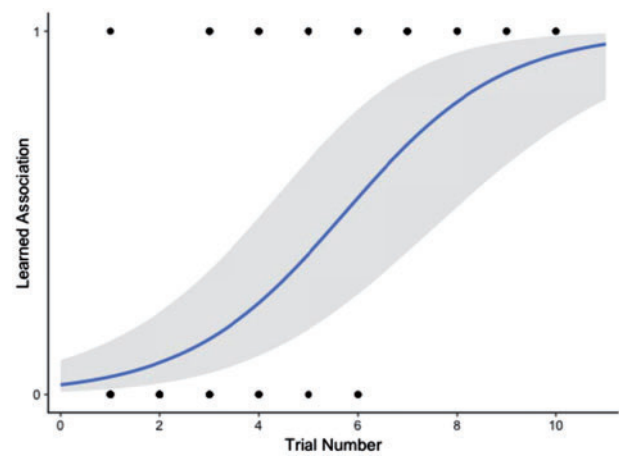

Figure 1. The effect of trial on the learning of an appetitive association. Individuals learned an association between a dog whistle and a food reward. Regression line is from predicted values and points are from raw data. Grey ribbons signify 95% C.I.
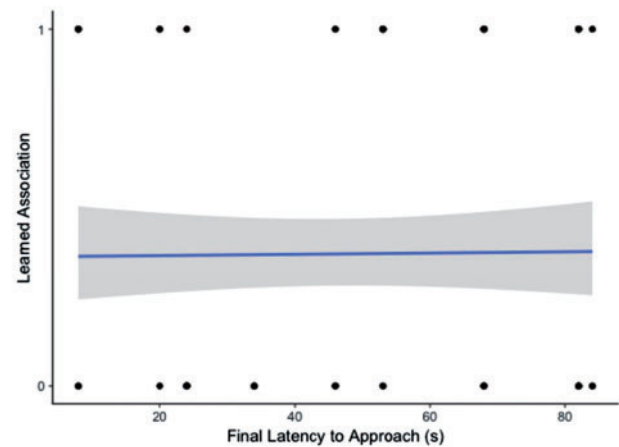

Figure 2. The association between average tameness and the learning of an appetitive association. Regression line is from predicted values and points are from raw data. Grey ribbon signifies 95% C.I.

Discussion

Animal personality is now ubiquitous throughout the behavioral ecology literature (Sih et al. 2012), and our results support the hypothesis that individuals vary consistently in their tameness. Our repeatability estimates are lower than reported in a recent meta-analysis (Bell et al. 2009), but are well within reported estimates of activity and sociability in carpenter ants *Camponotus aethiops* (Udino et al. 2017) and escape behaviors in blue tits *Cyanistes caeruleus* (Kluen and Brommer 2013). It should be noted that working with habituated individuals should reduce the probability of detecting consistent individual differences in tameness. Indeed, we expect bolder individuals to be more likely to be habituated and thus erode among individual variance (Carter et al. 2013). Despite this potential erosion, we still detected consistent individual differences in willingness to approach a human observer. Thus, we believe that our repeatability of tameness is a conservative estimate as we most likely were only able to habituate individuals with certain behavioral types.

Our analysis also shows that foxes react differently to observers, or alternatively there may have been systematic bias in how

observers judged distances. The exact cause of this result is unknown. Determining the exact cause of these differences may be difficult. Salient features of the observers, such as sex, size, and odor, are confounded in this study (only 1 male observer, M.B. Petelle). Furthermore, the male observer had the third highest best linear unbiased predictor (BLUP) suggesting that the larger, male observer did not stand out from the female observers. Past research has shown that observers can have an impact on a species' behavior (Iredale et al. 2010; Nowak et al. 2014). Indeed, research on observer effects within our own fox population shows that foxes are more vigilant toward certain observers during follows (Welch et al. 2018). This result suggests that researchers should take observer effects into account when analyzing behavioral data.

We found no relationship between tameness and learning of an appetitive association. The resulting Bayes factor suggests strong evidence for the alternative hypothesis that personality may be linked to cognitive processes. Although we did not test accuracy in this study, we still expect personality traits to correlate with the speed of learning an association. An individual's last latency to approach, however, was not linked to how quickly this learning occurred, for example, we found no interaction between trial and tameness. The link between cognition and personality in the wild is still ambiguous with relatively few studies on the subject. Importantly, our results are inconsistent with theory and previous empirical support. For instance, learning was associated with neophobia in zebra finches *Taeniopygia guttata* (Gibelli and Dubois 2016), and research on cavies *Cavia aperea* showed that individuals willing to take more risks were quicker in learning an association (Guenther et al. 2014). However, new evidence from cavies suggests that only certain personality traits might be linked to individual differences in cognition (Guenther and Brust 2017), and neophilia in zebra finches was only linked to learning during the simplest discrimination tasks (Gibelli and Dubois 2016). We may, therefore, need to expand future studies to investigate other dimensions of personality such as exploration or aggression. One potential explanation for our results is that hunger levels may have masked the effect of personality when using an appetitive association. In many association studies, a food reward is used as the US, yet individuals are held an appropriate amount of time to limit the effect of hunger (Guillette et al. 2015). It is difficult to control for hunger levels in the wild. It may be possible to test the effect of hunger in masking personality by testing whether personality of individuals that have foraged during the follow has a large effect, but with very few post-follow tests (4 trials) it is difficult to tease apart hunger as a factor.

We found no sex effect in associative learning; however, our Bayes factor does not allow us to make a definitive statement given our data. Previous studies have found sex differences in cognition in a number of cognitive tests. Eastern water skink *Eulamprus quoyii* males performed better at a spatial learning task, and female guppies *P. reticulata* were found to outperform males at a visual discrimination task (shoal size) when that task was harder (Lucon-Xiccato et al. 2016). Foxes are not a morphologically sexually dimorphic species or in terms of social behavior (i.e., males perform much of the parental care—Pauw 2000); males perform remarkably similar roles to females. This may explain why male and female foxes exhibit similar cognitive ability. Nonetheless, an alternative hypothesis is that the cognitive task we presented to the foxes was not complicated enough to display sex-dependent differences. For example, great tits *Parus major* were found to differ in a sex-by-personality interaction only when the learning tasks became harder (Titulaer et al. 2012).

Finally, trial had a significant effect on learning the association. This is not surprising; individuals should learn the association as they received more training. It is, however, interesting that individuals made the association at different speeds. This suggests that individuals may differ in their cognitive abilities. Measuring cognition in the wild can be difficult (Morand-Ferron et al. 2015), and our study highlights this issue. Yet studies showing individual differences in cognition are rare in the wild, and more so for wild carnivores (but see Benson-Amram and Holekamp 2012).

Individuals that live in complex, heterogeneous environments, like the Kalahari Desert, should be adept at detecting environmental cues, which in turn should promote individuals learning new associations quickly. Yet the acquisition of information and the ability to make association can be costly and involves a speed-accuracy trade-off (Chittka et al. 2009). If individuals can access clear cues of environmental resources, or if the costs of accessing these cues are not necessarily high, they may not need to acquire more information and bypass the speed-accuracy tradeoff. We may then not see behavioral flexibility and personality linked in this scenario. Termite patches, the main food of these foxes, are ephemeral, but occur widely throughout the habitat (Périquet and le Roux 2017), which may not lend itself to a speed-accuracy tradeoff. Thus, further investigation of when and how links between differences in behavior and cognition are warranted, as personality may be important only in specific cognitive tests.

Our study highlights that researching cognition in the wild can be challenging, but it is important to understand the potential correlations between behavioral types and cognition. We call for further investigation into why we may see clear links between cognition and personality and when we may not. We expect that personality traits and cognition may be associated based on the ecology or sociality of the species in question. Thus, ecologically or socially functional personality traits (exploration and sociability, respectively) should be linked to cognition if these traits help individuals gather information about their information.

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