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► To cite this version:

Robin Le Balle, Julien Cote, Fernando Antonio Santos Fernandez. Evidence for animal personalities in two Brazilian tortoises (*Chelonoidis denticulatus* and *Chelonoidis carbonarius*) and insights for their conservation. *Applied Animal Behaviour Science*, 2021, 241, pp.105400. 10.1016/j.applanim.2021.105400 . hal-03342195

HAL Id: hal-03342195

<https://hal.science/hal-03342195>

Submitted on 29 Sep 2021

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Evidence for animal personalities in two Brazilian tortoises (*Chelonoidis denticulatus* and *Chelonoidis carbonarius*) and insights for their conservation

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Abstract

Animal personality, the consistent between-individual differences in e.g., risk-taking, exploration, antipredator or mating behaviours, has major impacts on the fitness of individuals in many species. Understanding how to quantify animal personality should help us predicting how species interact with their environment and with the current environmental changes. We adapted existing behavioural assays to quantify the personality of two Brazilian tortoises, *Chelonoidis carbonarius* and *C. denticulatus*. We recorded behavioural responses to stress, novel environments, novel objects and social encounters. Behavioural components were consistent through time, supporting the existence of personality in both species. These behaviours were further correlated and could be summarized into two behavioural axes with recognizable biological meanings. One axis was related to responses to threats and novelty, as well as interest and interaction behaviours towards conspecifics and one to submission. The behavioural dimensions were similar in both species, suggesting that they share the same behavioural syndromes, but *C. carbonarius* had greater frequency of risk taking behaviours. This pattern can be related to differences in resource availabilities and

predator pressures in their respective natural habitats. Within each species, however, the individual variation in morphology only had a weak effect on personality and males tended to show more signs of submission. Further studies are needed to investigate the role of habitat features (resource availabilities and predation risk) on individual behavioural variation in each species in order to improve conservation and translocations programs.

Keywords: Animal personality; Conservation; *Chelonoidis*; Behavioural syndrome.

1 Introduction

During the last 300,000 years, 23% of the world's chelonian species went extinct (Rhodin et al., 2015). This loss may have an important impact on the environment and the biodiversity, as tortoises can serve several ecological functions such as herbivory (Hansen and Galetti, 2009), seed dispersal (Linero, 2018) and nutrient cycling (Kaczor and Hartnett, 1990) and are thus responsible for major top-down regulation of functions that structure plant communities and the soil (Owen-Smith, 1989). This role of keystone species makes the conservation of tortoises of important not only for the species themselves, but also for the ecosystem where they live. However, because of their ectothermy, their conservation faces many challenges in an era of climate change (Falcón and Hansen, 2018). Therefore, there is an urgent need for improving the success of conservation programs using cutting-edge approaches. The growing recognition of inter-individual variation in animal behaviour can help conservation managers and policy makers to progress down this path.

Referred to as personality, temperament or behavioural syndrome, the inter-individual variation is a matrix of behavioural components consistent through time and/or contexts, ranked on gradients such as risk-takers to risk-avoiders. The personality of an individual is the value for the individual along each of these gradients (Réale et al., 2007; Sih et al., 2012). Animal personality has usually been described by five dimensions: boldness, reactivity, exploratory behaviour, curiosity and aggressiveness/sociability, even if the definition has recently been widened to consistent inter-individual variation in any behaviours (Beekman and Jordan, 2017; David and Dall, 2016).

Personality can shape the response of individuals to threats (e.g. predators, human infrastructures) and novel environments and therefore have important fitness consequences (Moiron et al., 2020; Møller and Garamszegi, 2012; Smith and Blumstein, 2008). In a context of translocation, personality is thus useful to predict individual responses to environmental challenges such as those imposed by releasing animals into novel areas. Thus, personality can affect an individual's translocation success in a given environment (Baker et al., 2016; Bremner-Harrison et al., 2004) and could be considered as a new parameter to take in account in translocation programs. For example, personality has been used to predict dispersal behaviour (Cote et al., 2010; Sih et al., 2012), a determinant of translocation success (Germano et al., 2017; Tuberville et al., 2005). Moreover, other studies have highlighted the importance of personality in translocation success by influencing growth rate, reproduction and body condition (May et al., 2016; Sinn et al., 2014). Conservation managers would therefore largely benefit from considering consistent individual variation in behaviours while developing reintroduction, translocation and conservation programs.

However, behavioural assays, and in the case of personality, measuring behaviours repeatedly on each individual, are time consuming and require standardized and fastidious procedures. Easily measurable proxies of behavioural types, such as morphological differences, may help the selection of individuals for translocations or the habitat to receive them, or at least improve the prediction about translocation success. Personality traits have been related to dominance status and individual competitiveness in several species (e.g. birds: David et al., 2011; Fox et al., 2009; crickets: Rudin et al., 2017), and also to early food provisioning and sibling competition (Carere et al., 2005). In the colour polymorphic tree lizard *Urosaurus ornatus*, boldness, dominance and territoriality have been linked to colour morphs (Taylor and Lattanzio, 2016). In desert tortoises *Gopherus agassizii*, size have been shown to impact dominancy (Niblick et al., 1994). In other chelonian species, personality can have an impact on food competition hierarchy (Froese and Burghardt, 1974) and food acquisition (Davis and Burghardt, 2007) and thus can indirectly affect size and body condition. We thus hypothesized that personality traits could be predicted by morphology components and body condition differently according to sex and species. In this study, we investigated the personality components of

two Brazilian tortoises: the red-footed tortoise *Chelonoidis carbonarius*, locally known as “jabuti piranga”, and the yellow-footed tortoise *Chelonoidis denticulatus*, called “jabuti tinga”. The latter had been chosen for a translocation in Brazil (Galetti et al., 2017) and the results of this study may help understanding the links between personality and morphology in order to facilitate the selection of individuals for improving translocation success.

These two species are widely distributed in South America. They are very similar in morphological, behavioural and reproductive traits. However, the two species differ in distribution and habitat choice (Farias et al., 2007; Starling-Manne, 2020). *C. denticulatus* occurs preferentially in humid tropical forests, while *C. carbonarius* prefers clearings and dry areas typical of savanna (such as the “cerrado” in Brazil) and caatinga. However, the two species often occur in sympatry, mainly in transition areas between humid forests and the cerrado (Farias et al., 2007; Jerozolinski, 2005; Moreira, 1989; Moskovits and Kiester, 1987). The environmental differences between their habitats could select different behavioural responses for the two species and thus shape distinct personality types. For example, *C. carbonarius* could be more exploratory in response to the reduced density of food resources in dry areas and *C. denticulatus* could be shyer in response to predatory pressure in forested areas. Being able to detect and describe personality types may help future translocation programs to select the best suited individuals for a given environment and thus improve the success of the first steps of population establishment.

The aims of this study are 1) to provide a protocol suited to evaluate the behavioural responses of two tortoise species in captivity to threats, novel environment, novel object and social encounters; 2) to estimate the consistency of these responses across time, a feature of animal personality; 3) to apply matrices of quantifiable personality components to describe the personality of each individual; and 4) to create predictive models of those components depending on morphological factors, sex and species.

2 Material and Methods

Two populations of tortoises were used to assess personality in captivity, both kept at the CETAS (Wild Animal Screening Centre) of Seropédica, Rio de Janeiro state. The populations consisted of 59 *C. carbonarius*, collected from unknown sources around Rio de Janeiro, and 59 *C. denticulatus* (scheduled to be translocated), selected from various zoos and wildlife care facilities in central Brazil. As part of a delayed-release protocol, the animals were kept and fed in an acclimatization pen, in order to decrease their stress and increase their probability of survival (Parker et al., 2012). We therefore used this time to carry out the behavioural tests in captivity. The sex and body mass were recorded for each individual as well as their morphological traits and behavioural responses. Both populations were maintained in separate pens with similar captivity condition. While being homogenous between the two species, these artificial conditions were different from their natural habitats in term of resource availability and coverage. Both pens consisted in fenced enclosures that allowed rain and sun light. Plastic shelters and drinkers were arranged to provide partial shade and water. Food was not freely available, as all individuals were fed simultaneously every two days and each test trial was performed within a day for all individuals, to ensure the homogeneity of the tests' conditions. The population of *C. denticulatus* was brought to the centre two weeks before the tests in order to allow the tortoises to acclimate to their new environment. Before that, they were kept for several months in another centre in central Brazil in similar conditions. The individuals of *C. carbonarius* had already been at the centre for one to six months before the study started. Although captivity may alter the behavioural response of the animals, its total duration and condition were equivalent for both populations. Since the different centres had not recorded the dates of arrival of the animals, it was not possible to assess the exact period of captivity of each individual, which could have an impact on their personality.

The main characteristics used to distinguish the two species are the inguinal scute form, the relationship between the femoral and humeral suture sizes and the growth form of the carapace and prefrontal scales (Barros et al., 2012). Head and limb colour is another trait commonly used to differentiate between the species; however, because of the wide variation in colour patterns, this characteristic may lead to misinterpretations.

2.1 Morphology

We determined the sex of individuals based on plastron hollow, anal scute gap and tail shape (Pritchard and Trebbau, 1984). For *C. carbonarius*, the sex ratio was 31 males for 28 females and for *C. denticulatus*, 23 males for 36 females. We measured the body mass of each individual, as well as another 13 morphological factors, using measuring tape (± 1 mm): linear carapace length (LCL); curved carapace length (CCL); carapace width at the junction of the 5th and 6th marginal scutes (CW 5/6); carapace width at the junction of the 7th and 8th marginal scutes (CW 7/8); linear plastron length (LPL); curved plastron length (CPL); distance between axillary and inguinal scute (AX-IN); gular suture length (GSL); humeral scute width (HSW); width of suture between pectoral scute and abdominal scute (PS-AS); humeral suture length (HSL); femoral suture length (FSL) and inguinal scute width (ISW) (Barros et al., 2012). Finally, we estimated the body condition (BC) as the residuals from the regression of log (mass) on log (LCL) (Willemssen and Hailey, 2002). All individuals were adult; however we did not have access to their age, since age estimation methods are currently inefficient in most chelonian species (Wilson et al., 2003).

2.2 Personality

We assayed each individual for the behavioural responses to several contexts (Table 1). The arena consisted of a 1.5 x 1.5m plain square delimited by 40cm high walls. The tests 1 to 3 were performed in a row; the test 4 was performed separately. The tests were as follows:

1) Stress: the tortoise was put in a random corner of the arena and forced to tuck by slightly touching its nose. Only two different observers participated in this test. We determined if the tortoise took less than 10 seconds to untuck and then the latency to make the first step. After a 20-minute period, if the individual had not moved, the maximum score of 1200 seconds was attributed (trial 1: N=7, trial 2: N=12).

- *Untuck*: untucking or not within 10 seconds.
- *Move*: latency to move (log-transformed).

- 2) Exploration: after its first step the tortoise was allowed to freely explore the arena. Each explorative behaviour was recorded during a 5-minute period (see behaviour description in appendix for details).
- *Exploration*: number of explorative behaviours. Some individuals did not express any explorative behaviour during this test (trial 1: N=7, trial 2: N=12); those individuals were attributed the value of 0 for the corresponding variable and kept in the analysis. Each occurrence of a behaviour was counted as one as long as it was continuous. If the expression of a behaviour was interrupted for more than 5 seconds, it was considered as two occurrences. Likewise, walking was considered as one occurrence as long as it was in the same direction. If the individual changed its course while walking, this was considered as two occurrences.
- 3) Novel object: after the exploration test, the individual was put in the nearest corner and a plastic ball was placed in the arena on the opposite side of the tortoise, and we determined whether or not the individual had inspected this object within a 5-minute period.
- *Object*: inspection or not of the object within 5 minutes.
- 4) Conspecific presence: separately, two individuals were put together in the arena. During a 10-minute period every social behaviour was noted and identified (see behaviour description in appendix for details).
- Presence or absence of each selected behaviour: *sniff*, *trail*, *walk to*, *ram*, *tuck*, *circle*, *spin*, *head bob*, *scratch*, *bite* and *backup*. Each time a behaviour was displayed, it was considered present for the individual expressing it. When a behaviour was expressed by both individuals at the same time (e.g. *walking to* or *sniff*) it was considered present for both of them. In tortoises, aggressive behaviours such as ramming and biting only have the effect of subduing the conspecific and not of harming it. No injuries resulted in any of those aggressive interactions.

Tests 1 to 3 were performed twice for each individual at a 5 days interval to evaluate behavioural consistency. The response to conspecific presence was tested three times: each individual

faced three different conspecifics: 1) randomly selected unknown individual, 2) known male and 3) known female, in order to maximize the variability of the behavioural response. The randomly selected individual facing a female was another female in 46 occasions and a male in 18 occasions. Facing a male, it was a female in 24 occasions and a male in 30 occasions. Both sexes combined, in 70 occasions the randomly selected individual faced another of the same sex and in 48 occasions another of the opposite sex. For each sex we performed a paired Student t-test to evaluate if the sex of the facing conspecific had an impact on each behaviour. The expressions of all observed behaviours were independent of the sex of the facing individual in both sexes (Table 9 supplementary material). The order of the three encounters was randomly selected (Table 10, supplementary material) and each individual spent between 40 and 60 minutes in isolation between two encounters. We checked the effects of familiarity on the encounters outcomes using t-tests.

We checked the inter-observer reliability using a one-way analysis of variance and the observer did not had an impact on any behaviour (Untuck: p-value=0.514, Move: p-value=0.271, Exploration: p-value=0.494, Object: p-value=0.134). All social behaviours were assessed by the same observer.

2.3 Statistical analysis

2.3.1 Factor analyses of morphology and responses to social encounters

We first used Principal Components Analysis (PCA) with the R package ade4 (Dray and Dufour, 2007) to summarize morphological components and Multiple Correspondence Analysis (MCA) with the R package FactoMineR (Lê et al., 2008) to summarize responses to social encounters respectively into a smaller number of independent components (MC components for morphology and SC components for social responses). We divided each morphometric parameter by the straight carapace length in order to remove the effect of size on form (Bonnet et al., 2001; Willemsen et al., 2002). Morphometric parameters were log-transformed for normalization, centred and scaled to zero mean and unit variance before running the PCA.

We then investigated the relevance of sex and species to predict tortoise morphology using linear models and a model averaging selection by AIC (Akaike's Information Criterion) to select the best predicting model for each morphological component. We used the function `model.avg` of the R package MuMIn (Bartoń, 2020), a $\Delta AIC < 2.0$ threshold and provided the relative importance and the conditional estimate for each retained parameter. We further provided the R^2 of the model structured as the average best model. The full model included species, sex and their interaction. When the interaction was retained in the average best model, we further ran separate models for the two species.

2.3.2 Structure and consistency of animal personality

We analysed the behavioural consistency with the Intra-class Correlation Coefficient (ICC), commonly used to assess repeatability (Hayes and Jenkins, 1997; Nakagawa and Schielzeth, 2010), with the R package rptR (Stoffel et al., 2017). Since variables had different distributions, we used the appropriated function for each one of them: we used the `rptPoisson` function for the variable *exploration*, the `rptBinary` function for the variables *untuck* and *object*, and the `rptGaussian` function for the variable *move* (after log-transformation) and for the social response variables SC1 and SC2. Each of these functions estimates repeatability from a generalized linear mixed model (GLMM) fitted by restricted maximum likelihood for data with the appropriated distribution. We chose to keep the non-moving individuals with a maximum latency, considering their low proportion, because the risk of using maximum latency (i.e. imprecise estimates for the lowest activity score) was less important than the bias towards high activity level created by removing the least active individuals from the main analysis on PCA scores.

Then, we calculated the mean behavioural response by averaging the behavioural scores among all trials for the tests 1 to 3 and among encounters for test 4.

We first studied the correlations among behavioural responses to threats, novel environment, novel object and social components (SC) (i.e. behavioural syndromes) using Pearson or Spearman correlations among quantitative variables, depending on their distribution, t-test between quantitative and qualitative variables (see Table 1), and a χ^2 test between qualitative variables. Due to the presence

of both quantitative and qualitative variables, we then performed a Factor Analysis of Mixed Data (FAMD) with the R package FactoMineR (Lê et al., 2008) on these behavioural responses to obtain a limited number of personality traits (PT). We first performed those analyses on both species together, then on each species separately. Behavioural responses were log-transformed for normalization, centred and scaled to zero mean and unit variance before running the FAMD.

Finally, we investigated the relevance of morphological factors, sex and species, to predict tortoise personality using the same method as for the morphology. The full models included morphology components, and body condition, as well as all their two-way interactions with sex and species. Three-way interactions were not included.

Statistical analyses were performed using R 4.0.2 (R Core Team, 2020).

2.4 Ethical statement

This study was carried out in strict accordance with the recommendations of the Brazilian Agency for Wildlife Protection (ICMBio). The protocol was approved by the SISBIO (Permit Number: 62939-1) and the committee of ethics 01200.001568/2013-87.

3 Results

3.1 Morphology

The PCA performed on the 13 morphological variables for both species together showed that three independent components (i.e. morphology components) explain 65.79% of the variance (Table 2). The first morphology component (MC1) was related to the length (LCL), the convexity (CCL) and the constriction (CW 5/6, CW 7/8) of the carapace and to the dimensions of the plastron scutes (GSL, HSL, HSW, PSAS, FSL, ISW, AXIN). The second morphology component (MC2) was related to the size of the plastron (CPL, LPL), the length of the humeral scute (HSL) and the width of the suture between pectoral scute and abdominal scute (PSAS). The third morphology component (MC3) was

related to the concavity of the plastron (CPL), the length of the gular suture (GSL) and the distance between axillary and inguinal scute (AXIN).

The averaged best models showed that MC2 is well predicted by the species but not by the sex, MC1 by the species and the interaction between species and sex and MC3 by the sex and the interaction between species and sex (Table 3, both species). *C. carbonarius* is smaller and have higher CCL and CW due the dome-like shape of the carapace and its roundness in this species, while *C. denticulatus* tends to be flatter and narrower. On the other hand, males have overall a higher CPL, describing the concavity of the plastron, but this effect varied between species.

The model selection further reveals an interaction between sex and species in the models predicting MC1 and MC3, suggesting that the sexual dimorphism is different in the two species. Separate models per species showed that MC1 is not different between sexes for each species, but males in *C. carbonarius* tended to have a smaller value for MC1 than females while males in *C. denticulatus* tended to have higher values for MC1 than females. The sexual dimorphism for MC3 is similar in both species, but stronger in *C. denticulatus*. In *C. denticulatus*, sexual dimorphism in concavity of the plastron is more pronounced and the differences of the size of gular suture and of the distance between auxiliary and inguinal scute are greater (Table 3, separate species).

3.2 Personality

3.2.1 Response to social encounter

The MCA for social behaviours produced two components that together accounted for 31.19% of the variance (Table 4). The first sociability component (SC1) was mostly linked to the number of occurrences of *trailing*, *walking to*, *head bobbing* and *sniffing* which describe behaviours of attraction and interaction towards conspecific. The second sociality component (SC2) was mostly linked to the number of occurrences of *biting*, *tucking* and *spinning*, which describe submission behaviour. We checked the effect of the order of the encounters on the social components by using linear models and a model averaging selection by AIC. The full models included the sex of the individual, the order in

which it encountered the facing individuals (categorical variable with six levels: FFM, FMF, FMM, MFF, MFM, MMF) and the interaction of both. The first model including the order had a $\Delta AIC > 2.0$ with the best model for both SC (Table 11, supplementary material).

3.2.2 Consistency

For both species together, *untuck*, *move*, *exploration*, *object* were repeatable across the two trials separated by five days and SC1 was repeatable across encounters (Table 5), indicating consistent individual variation in behaviour, a feature of animal personality. The comparison of repeatability between species shows that *object* was only repeatable in *C. denticulatus* while SC1 was only repeatable in *C. carbonarius*. SC2 was not repeatable for both species (Table 5). Familiarity had an effect only on the behaviours *spin*, *tuck* and *ram* (respective t-values: 0.0027, 0.0022 and 0.0133).

3.2.3 Structure

The correlation analyses showed that all variables except SC2 were correlated (all the pairwise correlations between *untuck*, *object*, *move*, *exploration* and SC1 showed significant correlations with p-values < 0.001 ; correlations between SC2 and any other variable were not significant) (Table 6).

Because behaviours were almost all correlated, we performed a FAMD on the four behavioural responses to threat, novel environment, novel object and social context, commonly for both species. The FAMD led to two components that together accounted for 67.82% of the variance (table 7). Hereafter, these components will be referred to as “personality traits”. The first personality trait (PT1) was mostly linked to risk-taking behaviours (i.e., latency to move, whether or not it untucked and found the object, and number of explorative behaviours) as well as behaviours of attraction and interaction toward conspecific (SC1). The second personality trait (PT2) was mostly linked to submission behaviours (SC2).

3.3 Predicting personality components from morphology, sex and species

The averaged best models performed on both species together showed that PT1 was predicted only by species and tended to be predicted by an interaction between species and sex and between sex

and MC1 (Table 8, both species). All other retained variables in the averaged best model were weak predictors of PT1. *C. denticulatus* had lower score in PT1, meaning they tended to have higher latencies for moving, did not untuck and found the object in time and had fewer occurrences of exploration and behaviour of attraction and interaction toward conspecific, suggesting a higher neophobia. The analysis for each species (Table 8, separate species) further show that MC1 had indeed an effect on PT1 only in *C. carbonarius* in interaction with sex. PT2 was predicted by the sex, the species and MC1 when analysing both species together, with males, *C. denticulatus* and larger individuals expressing more submissive behaviour toward conspecifics. Overall, the percentages of variance explained by morphology, sex and species are small with the notable exception of PT1 when the two species are analysed together (see R^2 in Table 8). When analysing species separately, PT2 was well predicted by the sex, again with males showing more submission in *C. carbonarius*. The behaviour of *C. denticulatus* was poorly explained by morphology and sex even if the interaction between MC3 and sex was retained in the best averaged model. However, despite a significant estimate, the low relative importance for this interaction and R^2 of the model suggest no strong effect of this interaction.

4 Discussion

In this study, we investigated the existence of personality components in two Brazilian tortoises and how morphological components would allow us to predict them in males and females of both species. Our final goal is to provide effective and realistic tools for conservation stakeholders to easily estimate behavioural types of individuals to be released and monitored. While the two species are different for two morphological dimensions, confirming that *C. carbonarius* is smaller and have a rounder carapace shell and *C. denticulatus* is bigger with a flatter and more elongated carapace, the morphology also vary within species. Males have a more concave plastron which reflects an adaptive trait for copulating and mounting on females; morphological components additionally vary above and beyond sex differences. These results corroborate a previous investigation (Barros et al., 2012) and give some ground for predicting consistent individual variation in behaviours, a.k.a. animal personality, from morphological variation.

We indeed found that the behavioural responses of the two species to novelty, threats and social contexts were repeatable, suggesting the presence of animal personality. However, the first social component, describing behaviours of attraction and interaction toward conspecific, was repeatable in *C. carbonarius* and not in *C. denticulatus*. The other component, describing the submission towards conspecific, was not repeatable. This low repeatability of social components could be explained by an expected high dependency of behavioural responses to the sex of and the familiarity with the individual in interaction. Indeed, two of the behaviours included in SC2 (*spin* and *tuck*) were dependent of the familiarity with the interacting individuals. This result corroborates studies on other species showing a weaker repeatability of individual sociability and a stronger dependency on the experienced social context, the ecological context and the individual characteristics (e.g., familiarity, group size, predation risk, conspecific's personality or focal individual reproductive state) (Cote et al., 2012, 2011; Le Galliard et al., 2015; Menz et al., 2017; Strickland and Frère, 2018).

Further, we found that most behaviours were correlated with each other, again with the exception of the social components describing the submission towards conspecifics. This pattern matches the common behavioural syndrome observed in several species (Sih et al., 2004). Accordingly, all behaviours but this social component are summarized in a single FAMD axis. This axis describes a gradient from individuals that take greater risks and also express a greater number of interaction behaviours to individuals that take less risk and express less interaction behaviours. The other personality dimension was related to the remaining social component, i.e. submission toward conspecifics.

The comparison of the three personality dimensions between species showed us that *C. carbonarius* tends to be bolder than *C. denticulatus*, with lower latency to move, untucking and finding the object in time and a higher number of explorative behaviours than *C. denticulatus*, describing a higher propensity to take risks. Potential explanations relate to resource availability, seasonality and predation risk in the preferred habitats of both species. *C. carbonarius* forage in an environment with fewer resources than *C. denticulatus*, which could have selected for bolder and more explorative individuals. Additionally, the high seasonality in areas inhabited by *C. carbonarius* leads

363 to shifts in resources locations, forcing the tortoises to migrate among different foraging areas along
364 the year (Jerozolinski, 2005), thus enhancing their exploration abilities. Moreover, the only predator
365 of adult tortoises, the jaguar (*Panthera onca*), occurs more frequently in lowland areas of relatively
366 dense forest cover with permanent water sources, inhabited by *C. denticulatus*, than in open,
367 seasonally dry forests inhabited by *C. carbonarius* (Nowell and Jackson, 1996). This predatory
368 pressure could have also shaped *C. denticulatus* personality to be shy.

369 Another main objective was to investigate whether morphological traits could be good
370 predictors of individual personality types allowing managers to estimate individual behaviours without
371 running behavioural assays. Pooling the two species, the main personality dimension, describing all
372 behaviours but submission to conspecific, is the dimension whose variation was best explained by
373 predictors (i.e. with highest R^2). However, this effect is mainly due to a large difference between
374 species and small effects of sex and morphology. The number of submissive behaviours toward
375 conspecifics was also related to the species, with *C. denticulatus* showing more submission, and to the
376 sex, with females being less submissive than males. While running analyses for each species
377 separately, it appears that personality dimension are better predicted by morphology and sex in *C.*
378 *carbonarius* than in *C. denticulatus*. For *C. carbonarius*, the sex of individuals predicts the submission
379 towards conspecifics, with males being more submissive.

380 A better knowledge of how the environmental conditions, such as resource availability or
381 predator pressure, shape personality differently between communities and populations, and how to
382 highlight and describe it, should help us predict individual fitness and thus population stability in order
383 to improve our conservation strategies. For example, animal translocations are widely used in wildlife
384 conservation and management (IUCN/SSC, 2013), for reintroducing locally extinct species in their
385 natural habitat (IUCN, 1987), for diminishing the extinction risk for endangered species (Germano et
386 al., 2015; Sullivan et al., 2014), to restore ecosystem function (Seddon et al., 2014) or to assist
387 colonization (Hoegh-Guldberg et al., 2008). As suggested by recent studies, individual variation in
388 behaviour could have a significant influence on translocation programs outcomes (McDougall et al.,
389 2006). Detection and description of personalities of captive animals could enhance the selection for the

best-suited individuals for translocation, thus improving the success of translocation programs. Individuals with a higher propensity to take risks could be preferred for translocation to an area with low resources. On the contrary, individuals that express less risky behaviours could be preferred for translocation to an area with high predation pressure. The personality of individuals has been shown to correlate with individual life history traits, including reproductive outcomes, growth rate and survival prospects (Sinn et al., 2014). In the context of reintroduction, these effects translate into a better survival to predators (López et al., 2005) and human infrastructures (Hertel et al., 2019), and to a better ability in finding food (Patrick et al., 2017) and mates (Martin-Wintle et al., 2017) in a novel habitat. Our results show that both tortoise species display consistent behavioural differences among individuals and even a behavioural syndrome, i.e. correlations among personality dimensions (Sih et al., 2004). A next step should aim at testing the influences of personality types on the survival, growth and reproduction of individuals in general and, more specifically, in the context of reintroduction.

Despite the evidences of animal personality in these species and a few relationships with morphology, we did not find such good predictors of the personalities of individuals which would make behavioural assays unnecessary. The high level of effort needed to assess personality might restrain managers to implement this important behavioural aspect into the selection of individuals to release. An alternative is to develop simplified behavioural assays, such as scoring behavioural reaction when capturing individuals (Bonnot et al., 2015) and when temporary maintaining individuals in a care centre. Here, we found that whether it took more or less than 10 seconds for the individual to untuck after a disturbance was related to all the other risk-taking behaviours. Since it is relatively easy to assess, it would be a good proxy of general neophobia.

While being central in our study, a remaining important question is whether a subset of personality types should be selected when reintroducing a species. The selection of a subset of available personalities in a translocation program could indeed be risky in terms of behavioural and genetic diversity and could lead to the extinction of the population especially in a fluctuating environment. As any phenotypic traits, behavioural traits are variable within a species, a population and even a social group. The field of animal personality departs from the classical “noise around the

adaptive mean” by attributing evolutionary and ecological functions to behavioural variation. Behavioural types may have different functions in a natural system, e.g., eating different prey, softening predation pressures through the use of variable ecological niches (Dall et al., 2012) and maintaining social games (e.g. hawk-dove or producer–scrounger game) (Kурvers et al., 2010). The other way around, the behavioural variation may be maintained through a balance between fitness costs and benefits of each behavioural type (Stamps, 2007), frequency-dependent selection and a fluctuating selection for types in spatio-temporally variable environments (Dall et al., 2004; Dingemanse and Wolf, 2010). All in all, behavioural variation can contribute to the persistence of populations on a large spatial and temporal scale and in the growth of newly established populations (Sih et al., 2012). Long term and conservation programs should take this important aspect into account. As the success of a translocation primarily relies mostly on the dispersal and survival of the founding individuals, the release of individuals more explorative and more adapted to a given environment could help the population to expand and grow on the short term; the population should later be reinforced by additional releases of other behavioural types. Alternatively, managers may opt to maximize the diversity of behavioural types at any release event, optimizing short-term reintroduction success with the risk of decreasing longer-term establishment probability. The added value of different strategies regarding the diversity of individuals to be released should be examined in the light of the growing knowledge on eco-evolutionary dynamics of animal personality and validated on the focal species to be introduced.

Declaration of interest

None

Acknowledgements

This work was supported by a PhD Scholarship from the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, part of the Brazilian Ministry of Education (MEC/BR), to RLB; by the Instituto Luisa Pinho Sartori, Fundação Grupo Boticário de Proteção à Natureza [grant number 0010_2014]; by National Geographic Society [grant number NGS-64305C-19]; and by a Research Grant from CNPq

443 (National Research Council), part of the Brazilian Ministry of Science and Technology [grant number
444 305991/2018-3], to FASF.

445 We thank the Laboratório de Ecologia e Conservação de Populações, part of the Universidade Federal
446 do Rio de Janeiro (LECP-UFRJ), who created and organized the reintroduction project and
447 participated to the behavioural tests in captivity, and especially Carolina Starling-Manne who
448 orchestrated the recruitment and transportation of the animals. We also thank the Laboratoire
449 Evolution et Diversité Biologique (CNRS, UPS, UMR 5174), part of the Laboratoire d'Excellence
450 (LABEX TULIP, ANR -10-LABX-41) for the advices and expertise on the data analysis and on the
451 redaction of this manuscript. We also thank the professors Daniela Rodrigues and Marcus Vinícius
452 Vieira for their proofreading and advices. Finally, we thank the staff of the Centro de Triagem de
453 Animais Silvestres of Seropédica (RJ), for the care and housing of the animals.

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648 Tables:

Variables	Type	Description	Relevance
Untuck under 10 sec.	Logical, 0 or 1	Response to threatening situations	Predator recognition and avoidance
Latency to move	Integer, range: 0 – 1200 mean: 190.765 ± 28.241		

Number of explorations	Integer, range : 0 – 27 mean: 6.188 ± 0.355	Response to novel environment	Translocation induced stress
Inspection of object under 5 min.	Logical, 0 or 1	Response to novelty	Ability to adapt to new resources.
Presence/Absence of listed behaviours (14)	Logical, 0 or 1	Response to the presence/absence of conspecifics	Establishment of social dominance, ability to mate

Table 1: Description and relevance of potential tortoise personality components with their associated tests. “Description” and “ecological relevance” columns are based on a previous study (May et al., 2016).

	MC1	MC2	MC3
LCL	0.8339	-0.2078	-0.0450
CCL	-0.7344	0.1994	-0.2890
CW.5.6	-0.6495	-0.4022	0.1968
CW.7.8	-0.7580	-0.2399	0.0841
CPL	-0.0811	-0.7603	-0.4780
LPL	-0.0384	-0.8592	-0.2725
GSL	-0.4607	0.1465	-0.6314
HSL	0.4622	-0.4495	-0.0343
HSW	-0.9084	0.1474	0.0481
PSAS	-0.3533	-0.5601	0.3668
FSL	-0.7136	0.1033	-0.2278
ISW	-0.7502	0.1141	0.0252
AXIN	-0.5249	-0.2907	0.5289
Eigenvector	4.9631	2.2862	1.3034
Proportion of total	38.17%	17.58%	10.02%
Total explained	38.17%	55.76%	65.79%

Table 2: Component loadings of morphological variables observed on 3 principal components for the two species together (Principal Components Analysis). Behaviours with a loading above 0.3 are shown in bold.

	Morphology component	Parameter	Estimate (se)	Test*	p-value	Relative importance
Both species	MC1	Intercept	-1.7552 (0.2373)	7.328	< 0.001	
		Species	3.4388 (0.3611)	9.456	< 0.001	1.00
		Sex	-0.2165 (0.3831)	0.561	0.575	0.58
		Species x Sex	1.0346 (0.4896)	2.090	0.036	0.58

<i>C. carbonarius</i>	MC2	Intercept	0.5988 (0.1992)	2.974	0.002	
		Species	-1.2783 (0.2548)	4.889	< 0.001	1.00
		Sex	0.1676 (0.2623)	0.632	0.527	0.30
	MC3	Intercept	0.6206 (0.1578)	3.896	< 0.001	
		Sex	-1.3092 (0.2643)	4.919	< 0.001	1.00
		Species	0.2283 (0.2193)	1.029	0.303	0.61
		Species x Sex	-0.7294 (0.3310)	2.179	0.029	0.61
	MC1	Intercept	-1.6562 (0.2878)	-5.755	< 0.001	
		Sex	-0.3248 (0.3970)	-0.818	0.417	
		Model: $F_{1,57} = 0.669$, p-value = 0.4166, $R^2 = -0.0057$				
	MC2	Intercept	0.6613 (0.2743)	2.411	0.019	
		Sex	0.0100 (0.3784)	0.026	0.979	
		Model: $F_{1,57} = 0.0006$, p-value = 0.959, $R^2 = -0.0175$				
<i>C. denticulatus</i>	MC3	Intercept	0.5712 (0.1797)	3.179	0.003	
		Sex	-1.1769 (0.2478)	-4.748	< 0.001	
		Model: $F_{1,57} = 22.55$, p-value = < 0.001, $R^2 = 0.2709$				
	MC1	Intercept	1.5528 (0.1579)	9.834	< 0.001	
		Sex	0.7032 (0.2529)	2.780	0.007	
		Model: $F_{1,57} = 7.731$, p-value = 0.0073, $R^2 = 0.104$				
	MC2	Intercept	-0.8349 (0.2147)	-3.888	< 0.001	
		Sex	0.4317 (0.3439)	1.255	0.214	
		Model: $F_{1,57} = 1.576$, p-value = 0.2145, $R^2 = 0.0098$				
	MC3	Intercept	0.7856 (0.1235)	6.360	< 0.001	
		Sex	-1.8942 (0.1978)	-9.574	< 0.001	
		Model: $F_{1,57} = 91.67$, p-value = < 0.001, $R^2 = 0.6099$				

Table 3: Summary of the models predicting each morphology component depending on the sex for both species together and separately (model averaging). Estimates are given for *C. denticulatus* for the species and for males for the sex. For both species together, R^2 for best models are 0.67, 0.17 and 0.43 for MC1, MC2 and MC3 respectively. *: z-test for both species together, t-test for each species separately.

	SC1	SC2
Sniff	0.4087	0.0401
Trail	0.3798	0.0106
Walk to	0.5111	0.0060
Ram	0.0015	0.1579
Tuck	0.1294	0.3975
Circle	0.0966	0.0147
Spin	0.0601	0.3016
Head bob	0.3453	0.0050
Scratch	0.0352	0.0105
Bite	0.0015	0.3186
Back	0.0023	0.1960

Eigenvector	1.9722	1.4590
Proportion of total	17.92%	13.26%
Total explained	17.92%	31.19%

669

670 Table 4: Component loadings of social behaviours observed on 2 principal components for the two
671 species together (Multiple Correspondence Analysis). Behaviours with a loading above 0.3 are shown
672 in bold.

		R	SE	CI	P [LRT]
Both species	Untuck	0.6119	0.1483	[0.267 , 0.959]	1.1249e-07
	Move	0.6117	0.0575	[0.493 , 0.711]	2.3042e-13
	Exploration	0.4706	0.0723	[0.318 , 0.605]	6.6236e-08
	Object	0.3499	0.1028	[0.061 , 0.452]	5.1062e-04
	SC1	0.2960	0.0598	[0.176 , 0.406]	1.5433e-07
	SC2	0.0000	0.0327	[0 , 0.104]	1.0000
C. carbonarius	Untuck	0.7902	0.0527	[0.867 , 0.993]	9.7692e-03
	Move	0.3659	0.1143	[0.122 , 0.568]	2.7814e-03
	Exploration	0.3317	0.1314	[0.035 , 0.543]	0.0086
	Object	0.0637	0.1006	[0 , 0.315]	2.9177e-01
	SC1	0.4246	0.0827	[0.25 , 0.575]	9.5342e-08
	SC2	0.0186	0.0541	[0 , 0.188]	4.3464e-01
C. denticulatus	Untuck	0.4360	0.1873	[0.032 , 0.762]	3.1129e-03
	Move	0.4933	0.1016	[0.271 , 0.667]	4.3436e-05
	Exploration	0.4994	0.1224	[0.225 , 0.69]	0.0002
	Object	0.2517	0.2507	[0 , 0.923]	3.9432e-02
	SC1	0.0000	0.0472	[0 , 0.155]	4.9999e-01
	SC2	0.0000	0.0477	[0 , 0.157]	4.9999e-01

673 Table 5: Repeatability estimates between trials for the four behavioural responses and for the
674 sociability components (Intra-class Correlation Coefficient). R = repeatability, SE = standard error, CI
675 = 95% confidence interval, P = error probability (P-value), LRT = likelihood ratio test.

	Untuck	Object	Move	Exploration	SC1
Obj.	Chi ² p< 0.001				
Move	t-test p< 0.001	t-test p< 0.001			
Expl.	t-test p< 0.001	t-test p< 0.001	Pearson -0.66, p<0.001		
SC1	t-test p< 0.001	t-test p< 0.001	Pearson -0.41, p<0.001	Pearson 0.37, p< 0.001	
SC2	t-test p=0.5354	t-test p=0.4839	Pearson -0.03, p=0.7304	Pearson 0.12, p=0.1946	Pearson 0.20, p=0.0339

Table 6: Correlation table of all behavioural responses. (Each corresponding test appears above the value).

	PT1	PT2
Move	0.7346	0.0319
Exploration	0.6894	0.0015
SC1	0.3749	0.1169
SC2	0.0299	0.8621
Untuck	0.6017	0.0291
Object	0.5923	0.0044
Eigenvector	3.0230	1.0463
Proportion of total	50.38%	17.43%
Total explained	50.38%	67.82%

Table 7: Component loadings of all behaviours observed on 2 principal components for the two species together (Factor Analysis of Mixed Data). Behaviours with a loading above 0.3 are shown in bold.

Behavioural component		Parameter	Estimate (se)	z-test	p-value	Relative importance
Both species	PT1	Intercept	1.2203 (0.3033)	3.992	<0.001	
		Species	-2.4224 (0.4289)	5.597	<0.001	1.00
		MC1	0.1225 (0.2043)	0.597	0.550	0.52
		Sex	-0.2805 (0.5275)	0.528	0.597	0.48
		MC1:Sex	-0.4123 (0.2245)	1.824	0.068	0.38
		MC1:Species	-0.3662 (0.2215)	1.634	0.102	0.15
		Sex:Species	1.5663 (0.9375)	1.654	0.098	0.26
		BC	0.0781 (0.1201)	0.643	0.520	0.11
	PT2	Intercept	-0.3289 (0.1961)	1.667	0.095	
		Sex	0.5295 (0.2325)	2.256	0.024	1.00
		Species	0.4742 (0.2311)	2.033	0.042	0.44
		BC	0.1484 (0.1047)	1.403	0.160	0.31
		MC1	0.1117 (0.0567)	1.951	0.051	0.56
		Sex:Species	-0.5005 (0.3789)	1.306	0.191	0.11
		MC3	0.1137 (0.1081)	1.041	0.298	0.19
		MC2	-0.0813 (0.0688)	1.17	0.242	0.24
		MC1:Sex	-0.1015 (0.0866)	1.159	0.246	0.18
C. carbonari	PT1	Intercept	1.2976 (0.3301)	3.859	<0.001	
		MC1	0.2227 (0.1744)	1.251	0.210	0.65
		Sex	-0.5212 (0.424)	1.201	0.229	0.65
		MC1:Sex	-0.4616 (0.1869)	2.414	0.015	0.65

<i>C. denticulatus</i>	PT2	MC2	0.1673 (0.128)	1.276	0.201	0.27
		MC3	-0.1644 (0.1235)	1.302	0.192	0.16
		Intercept	-0.5121 (0.1781)	2.813	0.004	
		Sex	0.6811 (0.2463)	2.705	0.006	1.00
		BC	0.1665 (0.1334)	1.22	0.222	0.33
		MC2	-0.0622 (0.0864)	0.704	0.481	0.19
	PT1	Intercept	-1.1736 (0.2778)	4.149	<0.001	
		MC1	-0.1689 (0.1924)	0.858	0.391	0.179
		MC3	0.1187 (0.1652)	0.702	0.483	0.157
		MC2	-0.097 (0.1499)	0.633	0.527	0.149
		BC	0.1149 (0.1847)	0.608	0.543	0.147
	PT2	Intercept	-0.004 (0.4009)	0.01	0.992	
		MC1	0.2583 (0.2038)	1.246	0.212	0.35
		MC2	-0.2055 (0.1727)	1.163	0.244	0.14
		BC	-0.1009 (0.1343)	0.734	0.463	0.13
		Sex	0.4747 (0.4856)	0.962	0.335	0.23
		MC3	-0.1636 (0.2392)	0.668	0.504	0.11
		MC3:Sex	0.7825 (0.3908)	1.956	0.050	0.11

Table 8: Summary of the models predicting each behavioural component depending on the species, the sex, the mass, the body condition and the morphology components on both species together and separately (model averaging). Estimates are given for *C. denticulatus* for the species and for males for the sex. For both species together, R^2 for best models are 0.4927 and 0.0513 for PT1 and PT2 respectively. For *C. carbonarius*, R^2 for best models are 0.0896 and 0.1104 for PT1 and PT2 respectively. For *C. denticulatus*, R^2 for best models are -0.0549 and 0.0051 for PT1 and PT2 respectively.

Supplementary materials

Description of the behaviours:

Based on Moskovits (1985) and on Ruby and Niblick (1994).

Exploration:

- LOOK AROUND: Head level, slow side-to-side scan of surroundings.
- SUBSTRATE SNIFF: Head oriented down, nostril open, taking deep audible breaths. In sniffs while walking, head is extended out further and down.
- SLOW WALKING: Slowest pace.
- NORMAL WALK: Typical pace when moving and foraging.

- 700 • FAST WALK: Pace when moving purposely.
- 701
- 702 Social behaviour:
- 703 Attraction
- 704 • EXPLORATORY SNIFF: Sniff limb, cloaca or head of other tortoise.
- 705 • WALK TO: Walks closer to another tortoise.
- 706 Interaction
- 707 • TRAILING: One tortoise follows closely behind another tortoise moving away.
- 708 • FRONT RAM (epiplastral): One tortoise butts another face to face, gular projections connect.
- 709 Action usually coordinated by both animals.
- 710 • CIRCLING: Male walks around female who ROTATES away from his attention.
- 711 • HEADBOBS: Quick lateral motions of the head, seen in courtship and aggression; can be
- 712 done by only one animal, or occurs simultaneously or sequentially during encounters with
- 713 another animal.
- 714 • BITE: Bites and holds at least momentarily.
- 715 • SHELL SCRATCH: Individual scratches the shell of other individual.
- 716 Submission
- 717 • HEAD TUCK: Protective response by one tortoise approached by another tortoise.
- 718 • SPIN AWAY: Individual turns on a pivot as a submissive response to approach by another
- 719 tortoise.
- 720 • BACK UP: Submissively backs up.

721

	males	females
Sniff	0.8401	0.0766
Trail	0.4264	0.4219
Walk To	0.8701	0.0831
Ram	0.1855	0.6610
Tuck	0.1334	0.7368
Circle	0.3281	0.3241
Spin	0.4917	0.2539
Head Bob	0.1095	0.2040
Scratch	0.2001	0.0581
Bite	0.3281	0.3223
Back	0.2660	0.5710

722 Table S9: p-values of paired t-tests between the behavioural responses facing the same sex and
 723 opposite sex, for males and females.

724

725

Sex of the focus individual	Order of encounters	Number
Female	FFM	21
	FMF	17
	FMM	6
	MFF	8
	MFM	8
	MMF	4
Male	FFM	11
	FMF	8
	FMM	10
	MFF	5
	MFM	12
	MMF	8

Table S10: distribution of the encounters order for each sex.

	Parameters	df	logLik	AICc	ΔAIC	weight
SC1	Sex	3	-155.32	316.9	0	0.838
	Null	2	-158.15	320.4	3.55	0.142
	Sex+order	8	-153.677	324.8	7.89	0.016
	order	7	-156.454	328	11.12	0.003
	Sex*order	13	-150.383	330.5	13.62	0.001
SC2	Sex	3	-156	318.2	0	0.652
	Null	2	-158.016	320.1	1.92	0.249
	Sex*order	13	-146.707	323.1	4.91	0.056
	Sex+order	8	-153.559	324.5	6.29	0.028
	order	7	-155.335	325.7	7.53	0.015

Table S11: selection table of the models predicting social components depending on the sex and the order of the encounters. Models are ranked by AICc.