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Personality in non-human primates: methods of assessment, cross-species comparisons and reproductive performance

Ph.D. Thesis

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Annotation

This thesis is focused on the stable individual behavioural tendencies, i.e. personality, in non-human primates. The studies included in the thesis address questions related to the methods of personality assessment and evolutionary bases of personality. The personality structures in three callitrichid species in captivity, including common marmosets (*Callithrix jacchus*), cotton-top tamarins (*Saguinus oedipus*), and golden-handed tamarins (*Saguinus midas*), were investigated using common behaviour coding and trait rating. More specifically, the minimum length of observation necessary to describe the personality structure, the similarities and differences between personality structures of two related tamarin and one more distantly related marmoset species, and the links between personality and reproductive success, were investigated.

Declaration [in Czech]

Prohlašuji, že svoji disertační práci jsem vypracovala samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

Prohlašuji, že v souladu s § 47b zákona č. 111/1998 Sb. v platném znění souhlasím se zveřejněním své disertační práce, a to v úpravě vzniklé vypuštěním vyznačených částí archivovaných Přírodovědeckou fakultou elektronickou cestou ve veřejně přístupné části databáze STAG provozované Jihočeskou univerzitou v Českých Budějovicích na jejích internetových stránkách, a to se zachováním mého autorského práva k odevzdanému textu této kvalifikační práce. Souhlasím dále s tím, aby toutéž elektronickou cestou byly v souladu s uvedeným ustanovením zákona č. 111/1998 Sb. Zveřejněny posudky školitele a oponentů práce i záznam o průběhu a výsledku obhajoby kvalifikační práce. Rovněž souhlasím s porovnáním textu mé kvalifikační práce s databází kvalifikačních prací Theses.cz provozovanou Národním registrem vysokoškolských kvalifikačních prací a systémem na odhalování plagiátů

České Budějovice, 25.11.2019

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Michaela Másílková

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List of papers and author's contribution

The thesis is based on the following papers (listed chronologically):

I. **Masilkova, M.**, Weiss, A., Konečná, M. (2018). How long does it take? Reliable personality assessment based on common behaviour in cotton-top tamarins (*Saguinus oedipus*). Behavioural Processes, 157, 59-67. https://doi.org/10.1016/j.beproc.2018.08.009 (IF = 2.008)

Michaela Másílková collected the data, prepared the data for analyses, analyzed the data and wrote the manuscript with the help of co-authors.

II. **Masilkova, M.**, Weiss, A., Šlipogor, V, Konečná, M. Comparative assessment of behaviorally-derived personality structures in three callitrichid species. *manuscript*

Michaela Másílková collected the data, prepared the data for analyses, conducted most of the analyses and wrote the manuscript with the help of co-authors.

III. **Masilkova, M.**, Boukal, D., Ash, H., Buchanan-Smith, H. M., Konečná, M. Marmoset match-making: linking personality traits to reproductive performance. *manuscript*

Michaela Másílková designed the study, prepared the data for analyses and wrote the manuscript with the help of co-authors.

Content

CHAPTER I

General introduction

Animal personality

Behaviour is often considered as one of the most flexible traits in animals because it enables individuals to appropriately react to daily-life situations and to changes in their environment, and thus maximize their survival. Individuals are, however, often constrained in their behaviours as a result of their personality. Animal personality is broadly defined as individual differences in behaviours that persist through time (Gosling, 2001; Réale, Reader, Sol, McDougall, & Dingemanse, 2007) and are frequently correlated among each other (Sih, Bell, & Johnson, 2004; Wolf & Weissing, 2012). This phenomenon has been found in a whole range of taxa from invertebrates to non-human primates (reviewed in Bell, Hankison, & Laskowski, 2009; Finger, Dhellemmes, & Guttridge, 2017; Freeman & Gosling, 2010; Gartner & Weiss, 2013; Gosling, 2001; Kralj-Fišer & Schuett, 2014; Réale et a., 2007; van Oers & Naguib, 2013; Waters, Bowers, & Burghardt, 2017).

Why to study personality in animals?

Personality differences influence almost every aspect of an individual's life (reviewed in Réale et al., 2007; Wolf & Weissing, 2012). Personality has been demonstrated to affect fitness outcomes such as reproduction or survival (Smith & Blumstein, 2008), psychological well-being (Inoue-Murayama, Yokoyama, Yamanashi, & Weiss, 2018), health (Robinson et al., 2018), cognitive performance (Carter, Marshall, Heinsohn, & Cowlishaw, 2014), and social interactions among individuals (Weinstein & Capitanio, 2008). Moreover, personality has been related to habitat choice (Holtmann, Santos, Lara, & Nakagawa, 2017), migratory behaviours (Found & St. Clair, 2016), dispersal propensity (Luna, Palma, Sanz-aguilar, Tella, & Carrete, 2019), and invasion success (Pintor, Sih, & Bauer, 2008). It can thus have far-reaching ecological consequences on the level of populations, species, and communities (Canestrelli, Bisconti, & Carere, 2016; Ingley & Johnson, 2014).

The knowledge of individual behavioural differences can be applied in wildlife conservation, animal management, husbandry of captive animals, and in any research including living animals (Gartner & Weiss, 2018; Powell & Gartner, 2011). In fact, ignoring the individual differences in behaviour or personality types in animal research could violate the assumption of random sampling and cause selection bias (Biro & Dingemanse, 2009; Carter, Heinsohn, Goldizen, & Biro, 2012; Mathot et al., 2013; Morton, Lee, & Buchanan-Smith, 2013a). Therefore, animal personality is nowadays an essential component of animal behaviour research.

Recent advances in the field of animal personality

Although animal personality is a rapidly expanding research area, there are still conceptual and empirical discrepancies resulting mainly from two divergent approaches or research traditions (Carter, Feeney, Marshall, Cowlishaw, & Heinsohn, 2013; Koski, 2011; Weiss & Adams, 2013). These approaches differ in the way they conceptualize animal personality, in terms of the methods they use and the questions they investigate. Behavioural ecologists (i.e. biological or reductionist approach) tend to measure individual variability on a single or a few strictly defined personality traits such as boldness, exploratory tendency, activity, aggressiveness, or sociability and use terms such as behavioural syndrome or type (Réale et al., 2007; Sih et al., 2004). Behavioural syndromes are quantified by measuring the behavioural response to stimulus in experimental situations, such as novel environments, objects, or predator models. Behavioural ecology studies the ultimate mechanisms underlying personality variation and the links with ecological variables (Koski, 2011).

In contrary, comparative psychologists (i.e. psychological or holistic approach) examine simultaneously multiple traits of animal personality considering its hierarchical structure (Carter et al., 2013; Koski, 2011). The resulting personality model that reflects latent underlying psychological constructs describes patterns of individual variation in the broadest sense, covering complex associations of behaviours (Digman, 1990; Koski, 2014), represented in different dimensions. Dimensions resembling dimensions of the human Five-Factor personality model, that includes Agreeableness, Openness, Extraversion, Neuroticism, and Conscientiousness (Costa & McCrae, 1995; Digman, 1990), have been identified in non-human primates as well as other species (Gosling & John, 1999; Weiss, 2017). Terms as personality structure or model, domain, dimension, factor, or component are often used. The personality is assessed via trait ratings or observations of behaviours in daily situations. Comparative psychology aims to investigate the similarities and differences in personality structures across species, their adaptive significance, and underlying neuropsychological mechanisms (Koski, 2011).

The two fields have been trying to find a common ground, as is demonstrated in several studies of primate personality that combined methods of personality assessment from both approaches (Šlipogor, Burkart, Martin, Bugnyar, & Koski, 2019; Tkaczynski et al., 2018; Uher, Addessi, & Visalberghi, 2013; see also study on deer by Bergvall, Schäpers, Kjellander, & Weiss, 2011). There is now a broad consensus on the definition of personality and its multi-trait character (see, e.g., Fox & Millam, 2010; Gosling, 1998; Seltmann, Helle, Adams, Mar, & Lahdenperä, 2018). The research has also moved from purely descriptive (which still represent an integral part of personality research) to hypothesis-driven studies (Dall & Griffith, 2014; Henke-Von Der Malsburg & Fichtel, 2018), and from the laboratory to the field (Eckardt et al., 2015; Mella et al., 2016; Nachev & Winter, 2019). The spectrum of studied species has broadened to previously understudied species such as marine mammals (Bubac et al., 2018), elusive species (Hertel et al., 2019), night animals (Mella et al., 2016), amphibians (Brodin, Lind, Wiberg, & Johansson, 2013), elasmobranchs (Finger et al., 2017), or insects and other invertebrates (Walton & Toth, 2016). Apart from the above mentioned traditionally assessed personality components, species ecologically valid personality dimensions have been explored, for instance related to cooperation in cooperatively-breeding species (Sanderson et al., 2015). Moreover, new statistical tools, such as network analyses (Costantini et al., 2014), factor analyses adjusted for small samples (Jung & Lee, 2011), fuzzy set analyses (Adams et al., 2015), repeatability calculations (Nakagawa & Schielzeth, 2010), or frameworks using mixed-effects modelling (Cleasby, Nakagawa, & Schielzeth, 2015), have been adopted. The development in the field is depicted in Figure 1 (Fig 1).

Despite the progress in the field of animal personality, two questions, relevant to both behavioural ecology and comparative psychology, still persist: What are the most efficient methods of personality assessment and what are the ultimate causes of personality?

Personality assessment

Despite the long research tradition of animal personality (reviewed in Whitham & Washburn, 2017), debate how to best capture and quantify animal personality is still ongoing (Carter et al., 2013; Tkaczynski et al., 2018; Uher & Visalberghi, 2016). Although there are many ways to measure personality (e.g. Hertel et al., 2019; Petelle & Blumstein, 2014), currently three methods predominate in the animal personality literature, each of them having its own advantages and disadvantages (Freeman, Gosling, & Schapiro, 2011; Vazire, Gosling, Dickey, & Schapiro, 2007): (1) experimental coding, (2) trait rating, and (3) common behaviour coding (in more detail described in the next section). All of them have been successfully applied on species in captive and field conditions. The decision which method to use is influenced partly by the scientist's research background (behavioural ecology vs comparative psychology), research question, species of interest, time, feasibility, and comparability across species. Irrespective of the method used, the measures must meet the criteria of validity and reliability (Gosling, 2001).

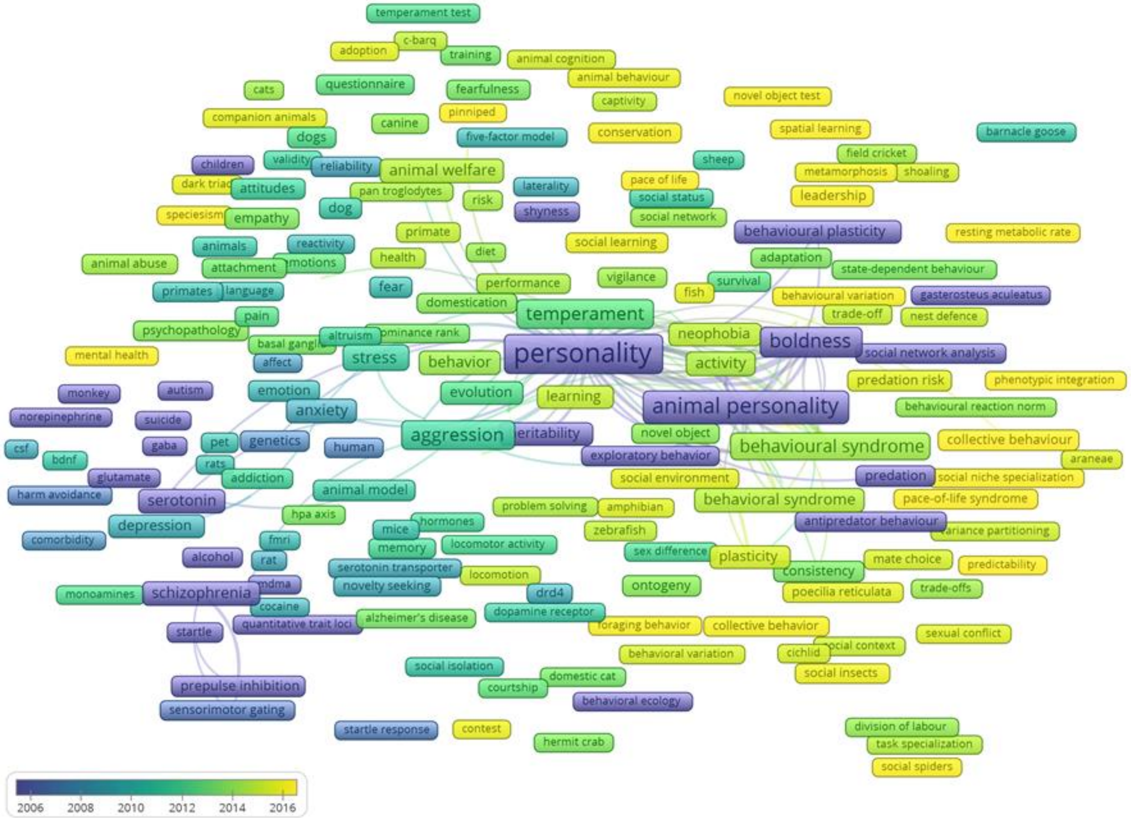

Figure 1. Advances in the field of animal personality. In colours are illustrated the keywords used across years. The network was based on bibliographic data from Web of Science database. The search of studies on topic "animal personality", years 1990-2019 in Web of Science Core Collection generated 3 705 studies (19th November 2019). This figure was created in VOSviewer (version 1.6.10 2019).

Methods of personality evaluation

Experimental coding is a method of personality assessment that quantifies behavioural responses of individuals to experimental situations using standardized tests like the open-field or novel object test (reviewed in Réale et al., 2007). The experimental approach allows one to control for testing conditions, manipulate contexts, and elicit specific behaviours that may be difficult to capture by using other methods of personality assessment (Freeman et al., 2011). However, it is not always clear whether the behavioural response in a testing situation reflects the trait that researchers think they are measuring (Beckmann & Biro, 2013; Carter, Marshall, Heinsohn, & Cowlishaw, 2012; Perals, Griffin, Bartomeus, & Sol, 2017; for detailed discussion see Carter et al., 2013). This might arise either as a result of artificial laboratory environments and isolation of individuals from their group members (Dall & Griffith, 2014; Fisher, James, Rodríguez-Muñoz, & Tregenza, 2015; Niemelä & Dingemanse, 2014), or ecological irrelevance of the test (Bell, 2007; Dall & Griffith, 2014; Larke, Toubiana, Lindsay, Mendoza, & Bales, 2017). As individuals are studied in isolation, the experimental method is also biased towards studying non-social personality components. Thus, the experimental assay risks neglecting potentially important behaviours that might be more relevant to species or might be part of more complex dimensions (Bell, 2007; Koski, 2011, 2014; Weiss & Adams, 2013).

Trait rating is based on employing questionnaires. Raters who are familiar with individual animals rate the animals on a set of predefined traits or adjectives that are supplemented with short descriptions (for different rating instruments see Freeman & Gosling, 2010; Freeman et al., 2011; Itoh, 2002; Uher & Asendorpf, 2008; Uher & Visalberghi, 2016). The raters assess the degree (from minimum to maximum) to which the individuals express personality characteristics using scales such as the Likert scale (as e.g. in Weiss et al., 2009). Trait rating is effective as it enables to measure personality in relatively high numbers of individuals in a comparatively short period of time (Freeman et al., 2011). Because the rater’s judgement is based on experience with an animal over time, trait rating allows to take cross-situational consistency (Koski, 2011) and rare but meaningful behaviours into consideration (Stevenson-Hinde & Hinde, 2011). Nonetheless, this method also has drawbacks. There is a risk of subjective biases and misinterpretation of the meaning of assessed items and it can be difficult to acquire raters who are experienced and well-acquainted with the rated animals (Freeman et al., 2011; Uher & Visalberghi, 2016). Furthermore, species comparisons can be complicated if the questionnaires differ too much (Freeman et al., 2011).

The common behaviour coding targets the observation of a broad range of everyday, naturally occurring behaviours. Behavioural coding is based on classical ethological recording of frequencies and durations of behaviours, where the behaviours are predefined in ethograms, employing different methods of data collection (Altmann, 1974). As with trait rating, the common behaviour coding allows to understand the associations between traits by considering behaviours in a more complex way and thus to reveal the general personality structure of species (Itoh, 2002; Koski, 2014). Common behaviour coding is an ecologically relevant method as the behaviour of individuals can be measured in their natural environment and group settings. It therefore allows to compare individuals based on actual quantifiable frequencies and durations of behaviours (Koski, 2011). One of the main limitations of this method is the possible variation in the manifestation of behaviour caused by daily or seasonal fluctuations, and changes in the social or physical environment (Vazire et al., 2007). Also, behavioural observations might not capture behaviours that occur at low frequencies. This method can be time consuming and demanding (Freeman et al., 2011; Itoh, 2002). The issue of time demanding character of common behaviour coding was addressed and examined in the Chapter II.

Each of the three methods aim at slightly different aspects of personality and combining those methods can create the most comprehensive picture of individual behavioural variation. Using several different methods can serve as cross-validation of results and compensate for the methodological limitations among them. Studies using multimethod approaches are recently on the increase (e.g. Ebenau, von Borell, Penke, Ostner, & Schülke, 2019; Fox & Millam, 2010; Horback, Miller, & Kuczaj, 2013; Konečná et al., 2008; Massen & Koski, 2014); however, studies combining all three methods are still scarce (but see Šlipogor et al., 2019; Tkaczynski et al., 2018).

Top-down vs bottom-up approach

The top-down approach (also "etic" approach) refers to using measuring instruments designed for one species and applying it to another (Freeman et al., 2011). This strategy is commonly employed in trait rating but also in experimental testing (see Fig 2). Thus, for example, a questionnaire developed for evaluating personality of great apes (Hominoid personality questionnaire; Weiss, 2017; Weiss et al., 2009), derived from the aforementioned human Big Five, was successfully applied to macaques (Robinson et al., 2018), squirrel monkeys (Wilson, Inoue-Murayama, & Weiss, 2018), or capuchins (Morton et al., 2013b). The open-field test, an experimental paradigm developed for quantifying locomotor activity, exploratory tendencies, and anxiety in rodents (Hall & Ballachey, 1932), was employed in a modified versions in studies of carpenter ants (d'Ettorre et al., 2016), mosquitofish (Polverino, Ruberto, Staaks, & Mehner, 2016), common mynas (Perals et al., 2017), domestic horses (Seaman, Davidson, & Waran, 2002), or titi monkeys (Larke et al., 2017). In the top-down approach, researchers investigate the presence of particular components or implementations of a particular personality evaluation instrument to species of interest (Uher, 2008). The greatest benefit of this strategy is that it facilitates cross-species comparisons. Moreover, it enables using questionnaires that were already validated (Freeman et al., 2011). Nevertheless, this approach also has its pitfalls. In the case of experiments, comparing species on *a priori* pre-defined component explicitly anticipates the universal presence of such component across studied species. The component, however, doesn´t have to be ecologically valid for the species, might have a different structure (i.e. species differ in the way they manifest the specific trait), or the test might measure different traits (e.g. Perals et al., 2017). In the case of trait ratings, the scale might miss traits meaningful for the species under study or include irrelevant traits and thus obscure species differences (Freeman et al., 2011).

The bottom-up approach (also called “emic” approach), on the other hand, refers to methods of personality assessment developed for particular species (Freeman et al., 2011; Uher, 2008). This approach can be applied to trait rating as well as common behaviour coding (Uher, 2008) (see Fig 2). Constructing species-specific rating scales or choosing behaviours for observations involves detailed knowledge of the behavioural repertoire of species and often builds on previous research (Uher & Asendorpf, 2008; Uher & Visalberghi, 2016). The list of adjectives or behaviours should be an exhaustive representation of a species behavioural spectrum. This approach enables to study personality differences of species in a comprehensive and species-relevant way and can reveal dimensions that are ecologically valid and unique for a given species (Uher, 2008). Employing species-specific methods of personality evaluation, however, prevents the comparability across species.

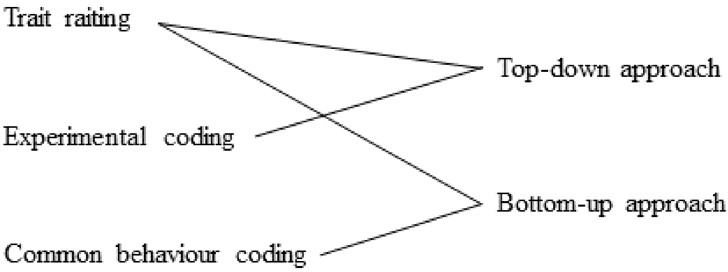

Figure 2. Top-down and Bottom-up approaches to the personality differences and their connection with the methods of personality assessment.

A rarely adopted combination of both top-down and bottom-up approaches allows to directly compare species and investigate species-specific traits. This was, for example, employed in a study of captive chimpanzees (Freeman et al., 2013). First, the authors assembled a list of adjectives used to describe the personality of other non-human primate species in previous studies (top-down). Then, experts on chimpanzee behaviour nominated descriptors unique to chimpanzee behaviour, based on their experience and previously published studies on chimpanzees (bottom-up). With this information at hand, the researchers could assess the overlap between these two lists and remove redundant items. The resulting personality model comprised components comparable to components previously described in chimpanzees and also new component labelled “Methodical” (for discussion see Freeman et al., 2013).

Reliability and validity

Methods of personality assessment should meet two fundamental requirements: reliability and validity (Gosling, 2001; John & Benet, 2000). Reliability refers to the agreement between raters or observers (Gosling, 2001; Shrout & Fleiss, 1979) or to repeatability of behaviour in time (Bell et al., 2009; Lessells & Boag, 1987). In rating studies, an adjective is considered a personality descriptor only if the raters agree on the rating of individuals on that specific adjective. The reported agreement between raters in animal personality studies is comparable to human personality studies (Eckardt et al., 2015). In the case of common behaviour coding, different observers should code the behaviour in a consistent manner (Tkaczynski et al., 2018). Consistency of behaviour in time is a fundamental prerequisite of personality (Réale et al., 2007; Sih et al., 2004). Yet, behavioural coding studies based on everyday common behaviours often do not report any measure of repeatability (Vazire et al., 2007; but see, e.g., Neumann, Agil, Widdig, & Engelhardt, 2013; Tkaczynski et al., 2018). Moreover, repeated measures control for behavioural variation that is due to within- and between-individual variance (Bell et al., 2009). Experimental studies usually take the repeatability into consideration by repeating the experiments at least once with varying time breaks between the tests (test-retest) (Gosling, 2001). The methods of assessing reliability and their values are reviewed in Gosling (2001) and Gosling, Lilienfeld, & Marino (2003).

The second requirement, validity, is associated with the degree to which a method measures an intended trait (convergent and discriminant validity) and whether the intended trait reflects the real world outcome (ecological and biological validity; for different types of validities see Carter et al., 2013; Cronbach & Meehl, 1955; Gosling, 2001; Itoh, 2002). The former refers to positive or negative correlations of behavioural measures obtained by different methods of personality assessment. This can be illustrated by a study of wild mountain gorillas, where Sociability and Dominance (derived from trait raiting) correlated positively with observed grooming time and rates of interventions, respectively (Eckardt et al., 2015). Similarly, personality structures based on common behaviour coding correspond to those derived from trait rating in wild bonobos and Hanuman langurs (Garai et al., 2016; Konečná et al., 2008). In a biological and ecological context, validity expects correlations between behavioural traits and physiological or socio-ecological parameters. For instance, correspondence between personality trait and hormonal profile (Capitanio, Mendoza, & Bentson, 2004; Inoue-Murayama et al., 2018) or general health (Capitanio, 2011; Robinson et al., 2018) have been documented.

Evolution of animal personality

Personality differences have been shown to have a genetic basis (e.g. Ariyomo, Carter, & Watt, 2013; Staes et al., 2016) and affect various fitness outcomes (longevity: Altschul et al., 2018; survival: Niemelä, Lattenkamp, & Dingemanse, 2015; mating success: Sih, Chang, & Wey, 2014; fecundity: Wilson, Godin, & Ward, 2010; reproductive success: Bubac et al., 2018). One would thus expect that selection would act on the most advantageous trait maximizing the fitness and thus would reduce behavioural variation. Hence, one of the main questions in the field of animal personality is why individuals in the same population consistently differ in their behaviour and how this behavioural variation is maintained in wild populations? And why is it that individuals also differ in several traits at once?

Evolutionary mechanisms maintaining personality differences

Although studies of the ultimate causes of animal personality are still scarce (reviewed, e.g., in Dingemanse & Réale, 2013), there is empirical evidence of natural selection acting on personality in wild populations and such studies are increasing in numbers. Various theories have been advanced to explain the presence of behavioural variation (Biro & Stamps, 2008; Dall, Houston, & McNamara, 2004; Wolf & Weissing, 2010).

Behavioural variation might be maintained as a result of life-history trade-offs (Biro & Stamps, 2008). In this case, some personality traits are associated with particular life-history strategies and represent alternative strategies within a population (Stamps, 2007; Wolf, van Doorn, Leimar, & Weissing, 2007). The variation in personality traits is therefore maintained by trade-offs that lead to similar fitness consequences. For example, docile males of bighorn sheep survived longer but reproduced at an older age compared to less docile males that reproduced earlier in their lives and had a short life expectancy (Réale, Martin, Coltman, Poissant, & Festa-Bianchet, 2009). Similar relationships were revealed between reproduction, longevity, and boldness (Smith & Blumstein, 2008). The theory of life-history trade-offs received considerable attention and to date a growing body of evidence supporting this theory is available (Biro & Stamps, 2008; Boon, Réale, & Boutin, 2008).

Another frequently studied mechanism responsible for maintaining behavioural variation is fluctuating (heterogenous) selection caused by spatial (e.g. resource abundance) or temporal (e.g. predator presence, population density) variability in the environment (Dingemanse, Both, Drent, & Tinbergen, 2004; Nicolaus, Tinbergen, Ubels, Both, & Dingemanse, 2016; Réale et al., 2009). For instance, in years of low food availability, bolder chipmunks had higher reproductive success as a result of more efficient food acquisition or access to females but the reverse was true for shy chipmunks during years of high food availability (Le Cœur et al., 2015). In another study, Réale & Festa-Bianchet (2003) found that in the years with frequent predation by cougars, bold bighorn sheep had higher survival. In years with low predation pressure, no evidence of selection on personality was observed.

Recent studies have demonstrated that sexual selection also contributes to generating and maintaining animal personality differences (e.g. Collins, Hatch, Elliott, & Jacobs, 2019; Dzieweczynski, Russell, Forrette, & Mannion, 2014; Pogány et al., 2018). Among other characteristics such as physical features, individuals can choose their partners based on their personality type if it is connected with some benefits (reviewed Schuett, Tregenza, & Dall, 2010). Individuals might have a universal preference for certain personality types as was documented, for example, in females of Siamese fighting fish that prefer males with behavioural strategy "lover" and avoid overly aggressive "fighter" males (Dzieweczynski et al., 2014; see Godin & Dugatkin, 1996 for other example). However, individuals might differ in their preferences and their selection can be affected by their own personality and personality of their partner resulting in non-random pair combinations. Assortative pairing has been documented in a number of bird species (e.g. Both, Dingemanse, Drent, & Tinbergen, 2005; Clermont, Réale, & Giroux, 2019; Collins et al., 2019; Schuett, Dall, & Royle, 2011). Behaviourally similar partners are more compatible, which might be advantageous, for example, in species with long-term partners. Disassortative pairing of behaviourally dissimilar partners was also documented (Dingemanse et al., 2004; Fox & Millam, 2014; Martin-Wintle et al., 2017; Scherer, Kuhnhardt, & Schuett, 2017). The form of mate choice is, however, dependent on the specific benefits linked to the personality types (Schuett et al., 2010), the level of paternal care, the mating system of species, or current environmental conditions (Dingemanse et al., 2004). The personality combinations of partners and their consequences for reproductive success were investigated in detail in Chapter IV.

Several further evolutionary mechanisms and theories have been linked with maintaining polymorphism in personality traits, but supporting empirical evidence is scarce. Among them are, for instance, frequency-dependent selection, where the fitness of a particular behavioural type depends on the abundance of other types in a population (Kralj-Fišer & Schneider, 2012; Wolf, van Doorn, & Weissing, 2008; Wolf & McNamara, 2012), or antagonistic selection, acting differently across sexes or life stages (Dingemanse et al., 2004; Pruitt & Riechert, 2009). Correlational selection, occurring when fitness of one trait depends on another trait due to genetic correlation, could explain covariance of behavioural traits. However, the evidence supporting this theory is rare (Eaves, Martin, Heath, Hewitt, & Neale, 1990; Montiglio, Wey, Chang, Fogarty, & Sih, 2017) or circumstantial (Dingemanse et al., 2007), and several studies could not detect correlational selection at all (Boon, Réale, & Boutin, 2007; Réale et al., 2009). Personality differences might be shaped also by the social environment. The theory of social niche specialization suggests that strong within-species social competition for a specific social niche can select on consistent differences between individuals and thus reduce the conflict between them (Bergmüller & Taborsky, 2010). Considering personality differences to be not adaptive, accumulation of mutations or mutation-selection balance might also be involved in creating polymorphism in personality (Penke, Denissen, & Miller, 2007).

Finally, these mechanisms are not mutually exclusive. Because the studies of evolutionary mechanisms in wild populations are obstructed by methodological difficulties, the scope of ultimate consequences is not yet fully understood (Dingemanse & Réale, 2013). Similarly, the question why behavioural traits are correlated has not been fully answered yet. Moreover, it is not known in detail in which situations selection favours plasticity of behaviour, and in which consistency. Studies and theories explaining why individuals are consistent in their behaviour are, however, on the increase (Dall et al., 2004; Dingemanse, Kazem, Réale, & Wright, 2010; Dingemanse & Wolf, 2010).

Studying personality differences as adaptations

Natural selection is often measured as covariance of behavioural traits and fitness components (Biro & Stamps, 2008). Experimental studies on wild populations providing the most informative account of evolutionary mechanisms behind personality are, however, extremely rare, since they are challenging to conduct (Dingemanse & Réale, 2013; Niemelä & Dingemanse, 2014). First, to capture how selection acts on personality, longitudinal data on personality, fitness, as well as environmental conditions must be collected. This is only possible only for species with short life span (e.g. rodents Le Cœur et al., 2015 or invertebrates Niemelä et al., 2015) or at field sites with ongoing long-term projects (e.g. Réale et al., 2009). Hence, the range of studied species and our knowledge is limited to few well-studied model species (Boon et al., 2007; Dingemanse et al., 2004; Réale & Festa-Bianchet, 2003). Second, repeated measures of personality are often difficult to collect in the wild. Furthermore, studies usually focus on a limited set of personality traits such as activity, aggressiveness, boldness, or exploration, traits prone to sampling bias, and ignoring other potentially important traits (Biro & Dingemanse, 2009; Dingemanse & Wolf, 2010). The same applies to estimating fitness components. Research focuses usually on selected fitness measures such a survival or reproductive success and does not take into account other measures or their combinations (Smith & Blumstein, 2008). To reveal the heritability of personality traits, genetic analyses must be involved (Bengston et al., 2018). Finally, examining the effect of the ecological or social environment on personality requires either detailed knowledge of species habitats, predator pressure, resource fluctuations, social systems, and others, or experimental manipulations of the environment (Lapiedra, Schoener, Leal, Losos, & Kolbe, 2018).

Selective pressures acting on personality differences can be studied on the level of individuals or populations within a species (Brodin et al., 2013; Giles & Huntingford, 1984) as well as on the level of species (Gosling & Graybeal, 2007; Uher, 2008). Comparisons of species enable to investigate the associations between personality traits and other variables such as ecological or social factors and phylogenetic relationships. Such comparative approaches thus allow to study the evolutionary origins of personality on a broader scale. For instance, revealing personality traits in species that are closely related but evolved under different socio-ecological conditions might suggest that traits were inherited from a common ancestor (i.e. homologous). Identifying a trait common to distantly related species that are similar in their ecologies and social systems, on the other hand, might suggest that such trait might have evolved as an adaptive response to similar selection pressures (i.e. analogous) (Gosling, 2001; Gosling & Graybeal, 2007). The comparative approach has proven to be instrumental, yet, it has been applied mostly in primates (e.g. Henke-Von Der Malsburg & Fichtel, 2018; Weiss, Adams, Widdig, & Gerald, 2011) and birds (e.g. Brown & Jones, 2016; Miller, Bugnyar, Pölzl, & Schwab, 2015), with few exceptions (Benhaïm et al., 2017; Carter & Feeney, 2012; von Merten, Zwolak, & Rychlik, 2017).

There are two approaches how to compare the personality across species differing in the question they address. The first approach investigates whether species differ in the mean value they reach on a particular pre-defined personality component, e.g., exploration, quantified in experimental set-ups. For example, resident species of parrots and parrots feeding predominantly on fruits explored the space more in detail than nomadic species and species with a different diet (Mettke-Hofmann, Wink, Winkler, & Leisler, 2005). The second approach examines several personality components at once using either trait rating or common behaviour coding. Researches then assess the absence or presence of particular components but also their content and organization across species, i.e. personality structure. This approach has also potential to uncover species-specific ecologically valid components corresponding to the complexity of a species’ niche and can be used for comparing humans to non-human primates (Uher, 2008). For example, personality models of humans lack the separate component of Dominance that is found in chimpanzees, and is otherwise universally present in non-human primates and other animals as well (Gosling & John, 1999; Weiss et al., 2011). This, however, does not mean that humans cannot be dominant. Instead, the traits related to dominance are included in the Agreeableness dimension in humans (King & Figueredo, 1997). The personality structures of three species of New World primates were compared in the Chapter III.

Nevertheless, even this approach is not without its drawbacks. Comparing species with different lifestyles or physiologies could yield results that are not comparable across species (Réale et al., 2007). Furthermore, when interpreting the results, researchers should bare in mind that present selective pressures don´t have to be necessarily the same as pressures in the past. Sometimes also components which might be potentially inherited from common ancestors might be underpinned by other variables which were not evaluated (Réale et al., 2007). Finally, researchers must balance between comparability and uniqueness of personality traits, i.e. between top-down and bottom-up approach (described in the section “Personality assessment”). Despite these limitations, comparative assessments of personality structures across species can be evolutionary informative.

Personality in callitrichids

The first attempts to quantify personality differences in primates have been made already in the late 1930s (Crawford, 1938) and since then the field of primate personality has received considerable attention (reviewed in Freeman & Gosling, 2010). However, most of the studies were conducted on great apes and Old World monkeys. New World monkeys have been ignored until very recently (Ferreira et al., 2016; Morton et al., 2013b; Robinson et al., 2016; Uher et al., 2013; Uher & Visalberghi, 2016; Visalberghi, Janson, & Agostini, 2003; Wilson et al., 2018; Witczak, Ferrer, & Bales, 2018).

Due to their small body size, fast reproduction, and relatively low husbandry requirements, callitrichids are a group of New World primates commonly held in captivity (Hampton, 1964). In the past, attempts were made to quantify behavioural variation of different callitrichid species in experimental situations (novel environment: Cameron & Rogers, 1999; novel food: Addessi, Chiarotti, Visalberghi, & Anzenberger, 2007; novel objects: Menzel & Menzel, 1979; novel foraging tasks: Kendal, Coe, & Laland, 2005). Although these studies explained their results in terms of exploration or neophobia, they rarely controlled for individual consistency of behaviour in time, i.e. did not address personality.

The first personality model of the common marmoset *(Callithrix jacchus)* based on trait rating and behavioural coding (Iwanicki & Lehmann, 2015) revealed a personality structure that resembled the human personality model including Extraversion, Agreeableness, Openness, and the separate dimension of Conscientiousness otherwise typical for hominoids and capuchins. Subsequently, two more independent studies of common marmoset personality models derived from trait ratings emerged (Inoue-Murayama et al., 2018; Koski, Buchanan-Smith, Burkart, Bugnyar, & Weiss, 2017). These studies confirmed the existence of the domains previously identified by Iwanicki & Lehmann (2015) but also revealed additional ones such as Neuroticism (Inoue-Murayama et al., 2018) and Patience (Koski et al., 2017). Patience is a domain unique to marmosets related to focus, socio-positive behaviour, and attentiveness (Koski et al., 2017). Moreover, Inoue-Murayama et al. (2018) documented the associations between the personality domains and subjective well-being, cortisol levels, and genotype. Further studies on common marmosets assessed personality differences using a battery of tests and revealed additional dimensions of Boldness-Shyness, Stress-Activity, and

Exploration-Avoidance, as well as the presence of group-level similarity in personality traits, i.e. group-personality (Koski & Burkart, 2015; Šlipogor, Gunhold-de Oliveira, Tadić, Massen, & Bugnyar 2016). Additionally, a study validating personality assessment methods (Šlipogor et al., 2019) and a study using a novel statistical framework (Martin et al., 2018) based on data from common marmosets were published.

Callitrichids represent ideal model species for studying methodological aspects of personality assessment (Šlipogor et al., 2019). Due to their small body size, callitrichids are frequently held in captivity in large numbers and are easy to subject to experimental situations (Šlipogor et al., 2016). Moreover, they can be housed in stable family groups in socially valid settings supporting the expression of the species' full behavioural repertoire (Schultz-Darken, Ace, & Ash, 2019). Callitrichids are also ideal model species for studying personality in terms of ultimate and proximate mechanisms (Inoue-Murayama et al., 2018; Yokoyama & Onoe, 2011). They have relatively short life-spans and high reproductive potential which enables investigating various components of fitness. Callitrichids are also easy to train via positive reinforcement to, for instance, provide saliva or urine samples for physiological analyses (McKinley, Buchanan-Smith, Bassett, & Morris, 2003).

Personality studies, however, have focused primarily on common marmosets. Systematic personality studies of other callitrichid species and genera (tamarins, lion tamarins, Goeldi's monkeys, pygmy marmosets, Amazonian marmosets), and relevant topics are missing.

Aims of the thesis

The main aims of the studies included in this thesis were to investigate questions related to the two unsettled issues in animal personality research - methods of personality assessment and the evolution of personality differences. The three studies presented below were conducted in captive settings on laboratory- or zoo-housed individuals of three callitrichid species using common behaviour coding or trait rating as method of choice for personality evaluation.

The main objectives of the first study (Chapter II: Masilkova, Weiss, & Konečná, 2018) were to systematically examine the method of common behaviour coding in a sample of cotton-top tamarins and test the minimum length of observation necessary to obtain stable personality models and individual personality scores. The study questioned the general assumption that behavioural coding is a time-consuming method of personality assessment.

In the second study (Chapter III: Masilkova, Weiss, Šlipogor, & Konečná, under review) we investigated the differences and similarities in the personality structures across three callitrichid species and discussed the possible selective forces (including ecology, sociality and phylogenetic relatedness) shaping these structures and species typical personality models.

In the last study (Chapter IV: Masilkova, Boukal, Ash, Buchanan-Smith, & Konečná, manuscript), we examined the links between personality and various variables of reproductive success in common marmosets. The main aim was to test whether certain personality combinations of partners have higher reproductive performance than others suggesting the possible benefits of non-random mating by personality.

Findings of studies included in this thesis contribute to the discussion of two unsettled questions in animal personality research related to the methods of personality evaluation, possible underlying evolutionary mechanisms of personality variation and adaptive significance of personality traits.

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CHAPTER II

How long does it take? Reliable personality assessment based on common behaviour in cotton-top tamarins (*Saguinus oedipus*)

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ABSTRACT

Individual variation in behaviour has been shown to have important ecological and evolutionary consequences. Research on animal personality has therefore received considerable attention, yet some methodological issues remain unresolved. We tested whether assessing personality by coding common behaviours is as time-consuming method as some researchers believe it to be. Altogether, 300 hours of observation were collected on 20 captive cotton-top tamarins (*Saguinus oedipus*). We first examined the repeatability of behavioural indices that represented the behavioural repertoire of cotton-top tamarins. We then compared the personality structures, based on different lengths of observation time, of these behavioural indices. The minimum observational time necessary to obtain a stable personality structure was 5 to 7 hours per individual. This stable structure included two components: Extraversion and Confidence, which were similar to those described in great apes, Old World monkeys, and other New World monkeys. Our findings suggest that, at least in the case of cotton-top tamarins, behavioural coding over relatively short periods of time can be used to assess personality and that longer observation periods may yield diminishing returns.

Keywords: Animal personality, Behavioural observation, Callitrichidae, Consistency, Continuous focal recording

1. INTRODUCTION

Personality traits have been described in species throughout the animal kingdom (reviewed in Bell et al., 2009; Freeman and Gosling, 2010; Gosling, 2001) and have far-reaching ecological and evolutionary consequences (reviewed in Réale et al., 2007). However, methodological issues relating to personality assessment remain unresolved (e.g. Carter et al., 2013).

Despite personality in animals having been studied since the 1970s (e.g. Chamove et al., 1972; Huntingford, 1976; Stevenson-Hinde et al., 1978) and earlier (reviewed in Whitham and Washburn, 2017), currently animal personality research is pursued predominantly by behavioural ecologists and comparative psychologists. Although there is overlap between these disciplines, they differ in how they conceptualise animal personality, which species they study, and which methods they use (Carter et al., 2013; Koski, 2011a; Weiss and Adams, 2013). To summarise, behavioural ecologists typically measure individual variation in a single trait and so assess narrow aspects of personality; their study subjects are usually small mammals (Kanda et al., 2012), birds (Carere and van Oers, 2004), fish (Wilson et al., 2010), or invertebrates (Stanley et al., 2017), all of which are easily subjected to experimental tests of personality, such as the open field test (Perals et al., 2017). The personality traits that behavioural ecologists study most often include activity, aggressiveness, boldness, exploration and sociability (Réale et al., 2007; Sih et al., 2004). Comparative psychologists, on the other hand (like human personality psychologists) tend to examine multiple, structured traits (e.g. Garai et al., 2016). The resulting models, derived from data reduction techniques, such as factor analysis (FA) or principal components analysis (PCA), reflect latent constructs that describe patterns of covariation among these traits (Digman, 1990). The human Five-Factor Model or “Big Five”, consisting of personality dimensions labelled Agreeableness, Conscientiousness, Extraversion, Neuroticism, and Openness (Digman, 1990), has been a useful framework for comparing species (Gosling and John, 1999; Weiss, 2017), especially when applied to nonhuman primates, to humans and one another (e.g. Weiss et al., 2011).

There are several methods of personality assessment (see Freeman et al., 2011 and Vazire et al., 2007 for reviews). One method is to gather ratings of traits by knowledgeable informants. Another method is to conduct behavioural tests and to record (or code) the behaviours performed by the animals in the experiments (hereafter "experimental coding"). A third method is to record naturally occurring everyday behaviours (hereafter "common behaviour coding"). These three methods overlap to a certain degree and have been used to validate one another as in, for example, a study of hanuman langurs (Konečná et al., 2008). These methods also can complement one another as in a study of common marmosets (*Callithrix jacchus*) where behavioural coding revealed a "Neuroticism" that did not emerge from trait-ratings in the same sample (Iwanicki and Lehmann, 2015).

Common behaviour coding is based on methods used in classical ethology. It therefore involves recording frequencies and durations of behaviours that are predefined in ethograms by means of different methods of observation, such as continuous focal recording, instantaneous sampling, or scan sampling (Martin and Bateson, 2007). By recording a broad range of everyday, naturally occurring, behaviours and subjecting them to data reduction analyses one can identify how behavioural traits within a species are organised by seeing how they "cluster" in the same components or factors (Itoh, 2002; Koski, 2014). Therefore, this method is potentially useful for studying personality structure and conducting cross-species comparisons. Moreover, common behaviour coding is an ecologically relevant method as the behaviour of an individual is measured in its natural environment and in natural social settings (Koski, 2011a). Yet, so far, not many animal personality studies have involved common behaviour coding in personality model assessment (some exceptions include Anestis, 2005; Freeman et al., 2013; Garai et al., 2016; Iwanicki and Lehmann, 2015; Konečná et al., 2008; Neumann et al., 2013; Pederson et al., 2005; Robinson et al., 2018; Sussman et al., 2014, 2013).

Assessing personality variation via observations of behaviours can benefit both behavioural ecology and comparative psychology. For example, behavioural observations can be used to validate other measures such as personality questionnaires (Konečná et al., 2008) or experiments (Neumann et al., 2013). Behavioural observations can also be used to measure personality in species that are difficult to study in laboratory settings (e.g. large or endangered species), species that are not found in sufficient numbers in the field (e.g. solitary species), or species that are prone to stress when separated from conspecifics for the purpose of individual testing (e.g. group-housed laboratory animals). Common behaviour coding can also be used to study personality in captive or wild individuals when there are no potential raters available.

Although it has been shown that common behaviour coding can contribute to animal personality research, the perception that long periods of time need to be devoted to gathering these observations (Freeman et al., 2011; Itoh, 2002) may have led some researchers to prefer trait rating or behavioural experiments. However, it is not clear how much time needs to be devoted to behavioural observations if one is to obtain representative data for constructing stable personality models. Indeed, the length of behavioural observations reported for personality studies varies substantially from 2 (Vazire et al., 2007) to 66 h (Neumann et al., 2013) of mean observation per individual. In some studies, the observation time can be highly variable as it depends on the visibility of focal individuals. For example, Neumann et al. (2013) reported between 0.6 and 130 h of observation time per individual. Observation time that is too short might miss meaningful but rare behaviours and may be susceptible to bias arising from temporal fluctuations in an animal’s state, its environment, or in the situations in which it finds itself (Freeman et al., 2011; Vazire et al., 2007). Extensive observational hours, on the other hand, might be an unnecessary investment of scientific resources. Ideally, then, researchers need to spend enough time to obtain an adequate sample of behavioural data but not spend time or scientific resources that could be invested elsewhere.

The present study sought to determine how much sampling effort was needed to derive stable personality traits and individual variation in each trait from common behaviours in captive cotton-top tamarins, a cooperatively breeding primate species from the family Callitrichidae. Although evidence for the existence of consistent personality traits has been already demonstrated within this clade (Addessi et al., 2007; Day et al., 2003; Franks et al., 2013; Koski and Burkart, 2015; Šlipogor et al., 2016), personality structure based on common behaviour coding has so far only been examined in common marmosets (Iwanicki and Lehmann, 2015). In our study, we tested the repeatability of each behaviour within our dataset and then proceeded subject reliable behaviours to data reduction analyses (PCA and REFA) to derive a personality structure for our subjects. We then compared how this personality structure, i.e., the number and characteristics of the components or factors, differed as a function of varying levels of observation length.

2. METHODS

2.1. Subjects

Subjects were 20 captive-born cotton-top tamarins that lived in five zoos located in the Czech Republic and Slovakia: Zoo Bojnice, Zoo Bratislava, Zoo Jihlava, Zoo Ostrava, Zoo Ústí nad Labem. The subjects included eight females (mean age in months ± SD = 75.7 ± 46) and 12 males (mean age in months ± SD = 59.4 ± 54.5). With the exception of the tamarins in Ostrava, each group consisted of a breeding pair and their offspring (see Table 1 for group composition and demographic data). Only adults and subadults were observed as focal individuals.

All facilities are members of the European Association of Zoos and Aquaria and meet the conditions of animal welfare (Bairrão Ruivo and Stevenson, 2017). Tamarins were housed in indoor enclosures equipped with branches, ropes, shelves, sleeping boxes and other sources of enrichment. One group (Zoo Ostrava) also had access to an outdoor enclosure at the time of data collection. Tamarins were fed a mixture of commercial prepared food and fresh food two to four times each day. Water was always available.

Table 1. Composition and demography of observed groups.

Zoo	Adult	Subadult	Juvenile	Infant
Bojnice	**1F, 1M**	2M	2F	2F
Bratislava	**1F, 1M,** 1M			1F
Jihlava	**1F, 1M**	1F, 1M	1M	1F,1M
Ostrava	**1F,** 1F, 2M			
Ústí nad Labem	**1F, 1M,** 2M	1F		1M

Note. Breeding individuals are shown in bold. F = female, M = male. Adults > 21 mo, subadults 14–21 mo, juveniles 7–14 mo, infants < 7 mo (Cleveland and Snowdon, 1984).

2.2. Behavioural data collection

For the common behaviour coding, we created an ethogram consisting of a broad range of behaviours previously described in tamarins (Coates and Poole, 1983; Edwards et al., 2010; Knox and Sade, 1991; Peñate et al., 2009; Price, 1991; Vogt, 1978). The complete ethogram of 122 items with the 47 behaviours selected for the analyses in bold is presented in Supplementary materials (Table S1).

A combination of focal continuous recording with 30-minute periods and focal instantaneous sampling with 2-minute intervals was used to collect behavioural data (Martin and Bateson, 2007). This enabled us to obtain frequencies from continuous recording and proportions from instantaneous scans. During focal observations, all behaviours of the focal individual were recorded, including the identity of social partners, which included infants, and the direction of social interactions. In instantaneous samples, the location (type of substrate) was also recorded. Not all of the study groups included infants, and as such any interactions with infants were omitted from the analyses. The order of focal individuals was counterbalanced so that focal periods for individuals were distributed evenly throughout the day and the study period. There were 12 focal sessions per day with each focal animal being observed from 2 to 4 times depending on the group size. Each individual was observed for 15 h in total within 8 to 13 days.

Altogether, 300 h of observation were collected from July 2011 to February 2012 by MM using a voice recorder (Olympus VN-8700PC Digital Voice Recorder). The observations were conducted from an area for visitors. Each group was given 2 days to acclimatise to the presence of the observer. MM identified individual tamarins using distinct facial or body features, such as body size, face shape, the presence of scars or warts, the size and shape of white head tufts and the shape of the tail.

2.3. Behavioural indices

Twenty-three behavioural indices (see Table 2) representing behaviours ranging from activity to social interactions were created from recorded behaviours. Using behavioural indices to assess personality provides a more detailed account of behaviour than simple behaviours as they take relations between different behaviours into account and correspond more to the use of questionnaire items (Konečná et al., 2008) (for examples, see Tables S19–S20). Indices based of frequency, proportions and diversity indices (Shannon and Weaver, 1963) were computed. The selection of indices was based on previous studies (Anestis, 2005; Garai et al., 2016; Iwanicki and Lehmann, 2015; Konečná et al., 2008) and on the frequency of the observed behaviours. The latter was important to demonstrate interindividual variation, especially when dividing the observation times into relatively short periods (see section 2.6. *Time-constrained models*). The indices were transformed into *z*-scores for all analyses.

Table 2. List of behavioural indices and their definitions used in principal components analysis.

Behavioural category	Index	Type of observation	Calculation
activity	*Resting*^{P}	I	(rest + look + watch + sit + lie) / (move + jump + cling + hang)
	Activity diversity^S	I	Shannon diversity index of activity types
	Substrate diversity^S	I	Shannon diversity index of substrate types
self-directed	*Self-grooming*^{F}	C	self-groom/hour
	Scratching^F	C	scratch/hour
surroundings dirrected	*Object sniffing*^{F}	C	object sniffing/hour
	Exploration^F	C	(exploration + object manipulation + search)/hour
	Vigilance^F	C	alert/hour
	Monitoring^P	I	watch/sample
socio-positive	*Affiliation*^{P}	I	[contact + proximity + social play + groom(in) + groom(rec)]/hour
	Passive affiliation^P	I	(contact + proximity)/[contact + proximity + social play + groom(in) + groom(rec)]
	Grooming(in)^F	C	groom(in)/hour
	Grooming(rec)^F	C	groom(rec)/hour
	Invite grooming(in)^F	C	groom invite(in)/hour
	Invite grooming(rec)^F	C	groom invite(rec)/hour
	Approaches(in)^F	C	approach(in)/hour
socio-negative	*Contact aggression(in)*^{F}	C	(general aggression + bite + beat + grab + grasp + chase + fight + face + push + displace)/hour
	Threats(in)^F	C	(facial threat + open mouth display + headshake + body display + tongue flick)/hour
dominance	*Scent marking*^{F}	C	scent marking/hour
	Carrying food away(in)^F	C	carry food away(in)/hour
	Terminate grooming^F	C	terminate grooming(in)/hour
	Grimace^F	C	grimace/hour
	Departures(in)^F	C	departure(in)/hour

Note. P = based on proportion of time, S = computed as Shannon diversity index measuring and explaining the variation in diversity of a particular variable with higher values indicating higher variability (Shannon and Weaver, 1963), F = calculated as frequency, (in) = behaviour initiated by focal individual, (rec) = behaviour received from an individual, C = continuous recording, I = instantaneous sampling.

2.4. Repeatability

Consistency of behaviour over time (e.g. whether an individual is consistently more aggressive than others) is a fundamental aspect of animal personality (Gosling, 2001; Réale et al., 2007; Sih et al., 2004). To examine the consistency of behaviour in time, and thus appropriateness of the behaviour for personality analyses, we determined the repeatability of each behavioural index. Repeatability is the proportion of behavioural variation that is due to interindividual differences compared to within individual variation (Bell et al., 2009). High repeatability estimates imply that individuals behave differently from each other and at the same time behave consistently over two or more observation periods (Bell et al., 2009). To do so, we divided the observation into 3 5-hour time blocks and computed the behavioural indices for each time block. The reasoning for dividing observations into 3 time blocks was two-fold. First, we wanted to test the repeatability of behaviours collected over several time periods long enough to enable reasonable data aggregation within each period. Second, the time blocks enabled us to cover several days of observation (3–5 days per block) and so to reduce measurement error (Epstein, 1983). The repeatability was analysed using linear mixed-effects models (Nakagawa and Schielzeth, 2010). The 95% confidence intervals and p-values were calculated by means of 1000 bootstrap runs and 1000 permutations, respectively. As recommended by previous studies (Schuster et al., 2017), we interpreted the estimates of repeatability regarding both the confidence interval and *p*-values simultaneously.

2.5. Data reduction

To determine the number of components to retain for personality models, we performed a parallel analysis (Dinno, 2012; Horn, 1965) and examined the scree plot (Cattell, 1966). Parallel analysis compares eigenvalues derived from observed data to eigenvalues of randomly generated matrices with the same numbers of variables and subjects as the observed data. Eigenvalues of data that exceed the 95th percentile of eigenvalues derived from parallel analysis are retained (Zwick and Velicer, 1986).

Given our small sample size, to examine personality structure, we performed a PCA and a regularised exploratory factor analysis (REFA; Jung and Lee, 2011), as recommended for samples below 50. To improve interpretability of the component or factor structure, we applied a promax (oblique) and varimax (orthogonal) rotation. The oblique rotation produces components that are correlated with one another, whereas the orthogonal rotation provides components that are independent. To interpret the structure, we defined absolute loadings of indices ≥ |0.4| as salient. In the case of cross-loadings, indices were assigned to the component or factor with the highest absolute loading.

2.6. *Time-constrained models*

To estimate the minimum number of observational hours needed to obtain a stable personality structure, we split our data, which was based on 15 h of observation, into 14 subsets based on various amounts of observation time. Each subset contained one hour of observation per individual less than the previous subset, therefore observation times for subsets ranged from 14 h to 1 h per individual. For each subset, we used the data reduction methods described above. This resulted in generating 14 time-constrained personality models.

2.7. *Comparison of models*

We first compared the personality structure of the full 15-hour model based on PCA and REFA to assess whether our sample size was satisfactory to obtain a stable structure (Jung and Lee, 2011). Second, we compared the promax and varimax solutions of the full model to determine whether we should interpret the correlated or independent dimensions. Third, we compared all 14 time-constrained models to full model based on

15 h of observation to determine the minimal length of observation needed to get a stable personality structure. We then interpreted the personality structure identified in the full model.

To compare the models' loadings and structure we used targeted orthogonal Procrustes rotations (McCrae et al., 1996), which yield Tucker's congruence coefficients for each factor and for the entire loading pattern (Lorenzo-Seva and ten Berge, 2006).

2.8. Individual variation assessment

To evaluate how well the individual personality scores on each component based on time-restricted models describe the behavioural variation in comparison to full model, we computed three sets of unit-weighted scores for each individual. These scores were computed using time-restricted personality models based on 5, 10, and 15 h of observation. We then used Pearson's correlation coefficients for those scores to compare whether the rank orders of scores were consistent, making sure to adjust *p*-values for multiple tests using a procedure described by Holm (1979).

All statistical analyses were performed in R (version 3.3.3, 2017) using the psych (Revelle, 2017), paran (Dinno, 2012), and rptR (Stoffel et al., 2017) packages. REFA was computed using MATLAB (version 9.4., 2018).

3. RESULTS

3.1. Repeatability of behavioural indices

The repeatability of the behavioural indices ranged from 0.25 for *Invite grooming(rec)*^{F} to 0.93 *Approaches(in)*^{F} and *Departures(in)*^{F} with a mean repeatability of 0.62 (SD = 0.23) (Table S2). These values were in the range of repeatability reported for other species (Bell et al., 2009). Five indices, however, had lower repeatability, and although the *p*-value indicated significance, the confidence interval included zero. We conducted the same analyses without these indices and the results (personality models, the recommended length of observation) did not change considerably (data not shown). Therefore, we decided to consider all indices as acceptable for further data reduction analyses (Freeman et al., 2013).

3.2. Model comparison

Parallel analysis and the scree plot indicated that there were 2 components in the full data set. The component solution derived from PCA was equal (congruence coefficients 1.00 for both components) to the REFA solution (see Table S3). Therefore, we decided to interpret the PCA structure as it is reported more frequently in the literature (Konečná et al., 2012). Since the correlations between components were negligible, and the structure of components from both solutions were nearly identical, we retained component solution from varimax rotation. For the promax-rotated solution see Table S4.

In subsets based on 2–14 h of observation, parallel analyses and scree plots suggested retaining 2 components. In the subset based on 1 h of observation per animal, the parallel analysis and scree plot indicated that there was 1 component. Given this result, we considered 1 h of observation as insufficient and did not examine it further. Time constrained personality models are provided in Tables S5–S18.

Congruence coefficients comparing the loadings of 14 time-constrained models to loadings from the model derived from 15 h of observation are presented in Table 3. The structure of time-constrained models based on 2 to 3 h of observation did not replicate the structure of the full model. At 4 h of observation, only 1 of the components replicated. The components derived from data based on 5 or 6 h of observation time, however, replicated those derived from the full data set (all congruence coefficients > 0.89). From 7 h onward, both components and the structure can be considered equal to full model (congruence coefficients > 0.97). It took less observation time to replicate the second component, which we labelled Confidence, than it took to replicate the first component, which we labelled Extraversion. Specifically, a stable Confidence dimension was obtained after 4 h and was replicable at 6 h; to derive a stable and replicable Extraversion dimension required 1 additional hour (Fig. 1).

Although the overall model structure of datasets based on shorter observation periods was replicable, there were minor inconsistencies with respect to assignment of certain indices to dimensions. *Monitoring*^{P} for example, only had a salient loading in models based on ≥10 h. For *Vigilance*^{F} this was true only with ≥ 6 h of observation time. Only three indices were assigned to different components (*Grooming(rec)*^{F}, *Invite grooming(in)*^{F}, *Resting*^{P}) in the models based on 6 and 5 h in comparison to the full model.

Table 3. Congruence between models based on different length of observation and full model based on 15 hours of observation.

	Congruence coefficient		
Observation length (h)	Extraversion	Confidence	Model total
1	0.86	0.61	0.74
2	0.72	0.86	0.79
3	0.75	0.81	0.78
4	0.82	0.89	0.85
5	0.89	0.93	0.91
6	0.94	0.97	0.96
7	0.97	0.98	0.98
8	0.98	0.99	0.98
9	0.99	0.99	0.99
10	1.00	0.99	0.99
11	1.00	1.00	1.00
12	1.00	1.00	1.00
13	1.00	1.00	1.00
14	1.00	1.00	1.00

Note. >0.95 models are equal, 0.85 – 0.94 models display fair similarity, <0.85 no similarity (Lorenzo-Seva and ten Berge, 2006).

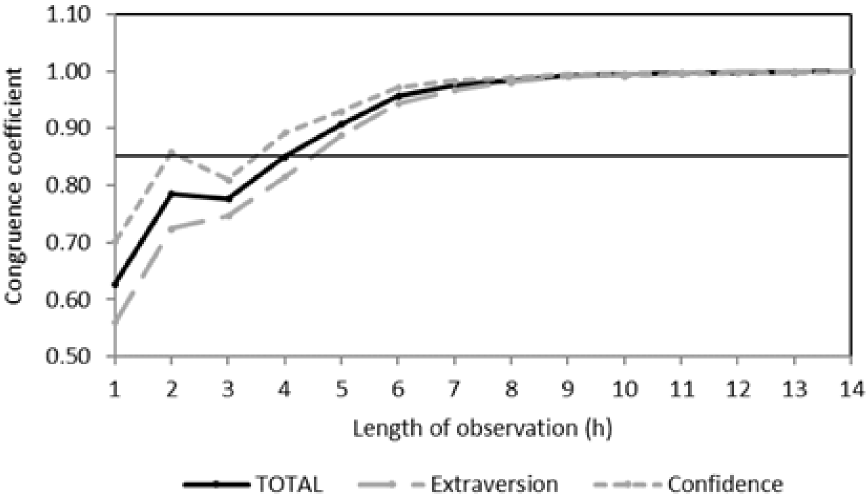

Fig. 1. The relationship between congruence coefficients and the length of observation (hours). Reference line refers to threshold of fair similarity.

3.3. Individual variation

Table 4 shows the correlations of unit-weighted scores for each component of three time-restricted models. Correlations between scores based on 5 and 10 h and between 5 and 15 h are slightly lower but still reasonably high and significant ($p < 0.01$). Thus, 5 h of observation is sufficient for description of individual variation on personality components (Fig. 2).

Table 4. Pearson’s correlations of individual personality scores for each component of three time-restricted models.

Observation length (h)	Extraversion (95% CI)	Confidence (95% CI)
15 vs 10	0.98 (0.95, 0.99)	0.99 (0.98, 1.00)
15 vs 5	0.87 (0.70, 0.95)	0.93 (0.82, 0.97)
10 vs 5	0.87 (0.70, 0.95)	0.92 (0.81, 0.97)

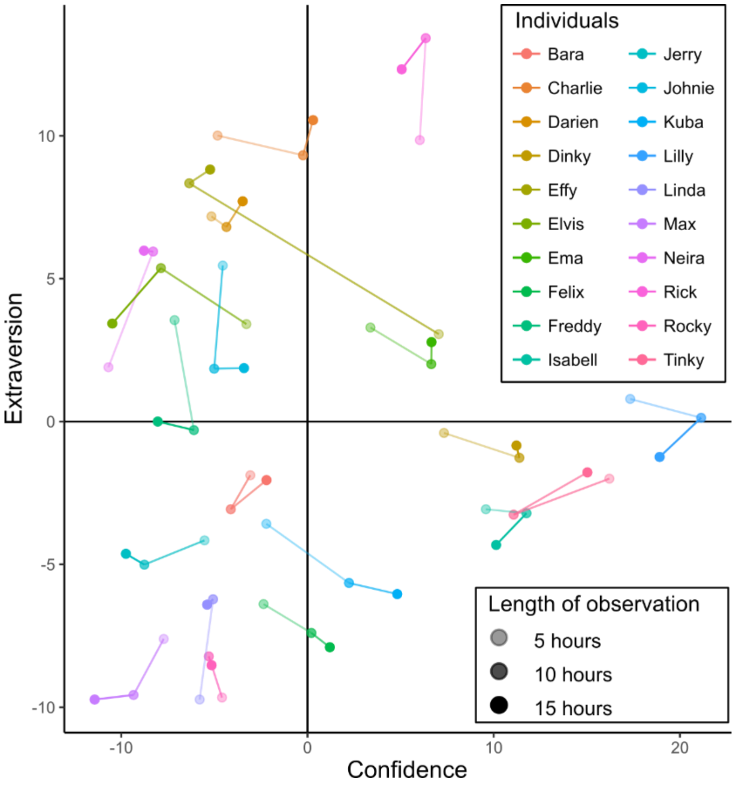

Fig. 2. Individual PCA scores based on the components Extraversion and Confidence for 5, 10 and 15 hours of observation. Scores of each individual are represented by 3 dots connected with a line. Shading indicates the length of observation.

3.4. Full personality model

The full personality model with the two components is presented in Table 5. The components explained 54% of the variance. Only one index (*Scent marking*^{F}) did not load on any component. The indices *Vigilance*^{F}, *Terminate grooming*^{F}, and *Resting*^{P} loaded on both components. The first component loaded on indices related to physical and social activity. Individuals who scored high on this component performed a wide range of behaviours (*Activity diversity*^{S}) and preferred active affiliation, such as grooming and social play, to sitting in contact or proximity with conspecifics (*Grooming(in)*^{F}, negative *Passive affiliation*^{P}). This

Table 5. Personality model of cotton-top tamarins. Varimax rotated solution of principal components analysis.

	Component		
Behavioural index	Extraversion	Confidence	Communalities
Activity diversity^S	**0.89**	0.29	0.87
Passive affiliation^P	**-0.88**	0.09	0.79
Exploration^F	**0.88**	0.00	0.77
Threats(in)^F	**0.88**	-0.06	0.77
Vigilance^F	**0.72**	**-0.42**	0.69
Grooming(in)^F	**0.71**	0.35	0.62
Invite grooming(rec)^F	**0.68**	0.04	0.46
Terminate grooming^F	**0.64**	**0.41**	0.58
Resting^P	**-0.63**	**-0.44**	0.59
Grimace^F	**0.59**	-0.12	0.36
Object sniffing^F	**0.49**	-0.34	0.36
Monitoring^P	**0.43**	-0.09	0.19
Self-grooming^F	**0.40**	-0.22	0.21
Departures(in)^F	-0.17	**0.92**	0.88
Approaches(in)^F	-0.07	**0.85**	0.72
Scratching^F	-0.12	**-0.84**	0.72
Affiliation^P	-0.25	**0.80**	0.70
Contact aggression(in)^F	-0.05	**0.76**	0.58
Carrying food away(in)^F	-0.17	**0.65**	0.45
Grooming(rec)^F	0.05	**0.62**	0.38
Substrate diversity^S	0.30	**0.58**	0.42
Invite grooming(in)^F	0.21	**0.45**	0.25
Scent marking^F	0.34	0.10	0.12
Explained variability	29%	25%	

Note. N = 20. Salient loadings are in boldface. P = index based on proportion of time, S = index computed as Shannon diversity index, F = index calculated as frequency, (in) = behaviour initiated by focal individual, (rec) = behaviour received by focal individual.

component consisted also of indices related to exploration and active interest in surroundings (*Exploration*^{F}). Therefore, we labelled this component “Extraversion”.

The second component was characterized by dominance-related behaviours. Individuals scoring high on this component were confident in their interactions with others (*Approaches (in)*^{F}, *Contact aggression(in)*^{F}) and could acquire resources (*Carrying food away(in)*^{F}, *Grooming(rec)*^{F}). Furthermore, *Scratching*^{F}, which is often identified as an indicator of anxiety and stress in callitrichids (Caperos et al., 2011), loaded negatively on this component. Given these features, we labelled this component “Confidence”.

4. DISCUSSION

A PCA of commonly observed behaviours that had moderate to high repeatability unveiled two personality components, Extraversion and Confidence, in cotton-top tamarins. Comparisons of the personality structures based on different lengths of observation indicated that 5 h of observation time per individual were sufficient to obtain a replicable personality structure and a stable description of individual variation.

4.1. Common behaviour coding method

Behavioural coding has often been considered time-consuming and thus has not been used as often as other methods of collecting personality data (Freeman et al., 2011; Itoh, 2002). Our results, however, indicate that long observations might not be necessary for assessing personality. In cotton-top tamarins, stable personality structure was revealed after 5 h of observation per individual. After 7 h of observation time, both components and the overall structure were nearly identical to the full model.

The minimum length necessary to obtain stable personality assessment might differ across personality dimensions. Our results indicate that Confidence takes less time to assess than Extraversion.

Similarly, research on humans reported that some traits are more “visible” and thus easier to judge than others (Funder, 2012). Behaviours related to Confidence could have been easier to observe due to their higher frequency, as these behaviours are important in social animals that have to cope with complex individualized social relationships on a daily basis. Confidence-related behaviours also play a crucial part in callitrichid social groups, where reproductive suppression can impose intense competition (Digby et al., 2006).

For this study, we analysed behaviours that occurred more frequently which could have also contributed to significant reduction of the overall sampling effort. Recording rare but species relevant behaviours, such as food sharing in tamarins, would probably extend the length of observation. Age-sex classes should also be considered as certain behaviours might be more prevalent in males or females or in different age categories. For example, severe aggression is more common among male cotton-top tamarins (Snowdon and Pickhard, 1999). Similarly, individuals in larger groups might have more opportunities to express social behaviours than individuals in smaller groups or pairs of individuals, thus the behaviour is more rapidly accumulated. The effect of those variables on data accumulation in the context of animal personality, however, remains to be tested.

The overall sampling effort in terms of observation length can also be influenced by the selection of the sampling method and the design of observation. In our study, we used a combination of continuous and instantaneous focal sampling methods, which together enabled us to record different types of information and thus collect the data more efficiently. Scan sampling of the group could further reduce the workload of observers as it allows one to measure behaviours in several animals within one period (Martin and Bateson, 2007). Furthermore, the length of the focal observational period or scan interval can influence how fast the data accumulate, with shorter periods and intervals possibly accumulating data faster (Edwards et al., 2010; Kawanaka, 1996). Scheduling the focal periods across several days (in our study the minimum of 5 h was accomplished within 3–5 days) eliminates the influence of unexpected situations (such as severe fights or management intervention in captivity) that may affect the behaviour of an animal on a particular day. The effects of the distribution of focal periods over time, the length of focal period, and the sampling method on personality assessment remain to be tested as well.

It is important to emphasize, however, that the minimum length of observation might be specific to nonhuman primates, New World monkeys, callitrichids, cotton-top tamarins or even just captive populations of cotton-top tamarins. A study on wild chimpanzees, for example, reported 25 h of observation as the critical length of observation needed for reliable scoring of behaviours and social relationships (Kawanaka, 1996). On the other hand, results from a study on rhesus macaques in captivity suggested that 6 h of data collection per group were sufficient to provide a reliable group time budget (Nyström et al., 2001). Given that callitrichids are small bodied, active, and have a relatively high metabolism rate, behaviours in this species might accumulate more quickly compared with larger, less active species that have a relatively slow metabolism (Careau and Garland, 2012). Furthermore, the type and quality of a species' diet as well as feeding habits can be directly connected to activity patterns (Baldwin and Baldwin, 1978; Masi et al., 2009), and thus affect the accumulation of different behaviours. For instance, "energy minimising" folivores, such as howler monkeys (*Alouatta* sp.), spend up to 80% of their daily activities resting (Estrada et al., 1999), compared with the frugivorous-insectivorous black-handed tamarins, which spend only 10% of the day resting (da Silva et al., 2007). However, more data is needed from a wider variety of species in order to determine whether body size or feeding ecology, indeed influence the rate of accumulating behaviours related to personality.

Finally, depending on group size, 5 h of observation per individual can be considered time-consuming and requiring more effort compared to other methods. However, preparation of experiments, from designing an apparatus, habituating animals, conducting the experiments to necessary pauses between tests, can also take up a considerable amount of time, in particular when researchers seek to evaluate several personality dimensions. Using questionnaires for trait rating might seem to be the quickest method, however, it is only shorter if well-acquainted raters are available. In other cases (e.g. Konečná et al., 2008), raters must spend several months observing individuals before they can even begin rating. Moreover, long forms (e.g. HPQ with 54 adjectives; Weiss et al., 2009) can take considerable time to complete. Interestingly, the time demands of different personality assessment methods have only been discussed but not empirically examined (Freeman et al., 2011; Vazire et al., 2007).

4.2. Repeatability of behaviours

The majority of behavioural indices used in the current study were either highly or moderately reliable across three observation periods, representing a short time span. Still, there was some variation. Indices with lower repeatability included those related to grooming interactions, namely *Grooming(rec)*^{F}, *Invite grooming(rec)*^{F}, *Grooming(in)*^{F}, *Terminate grooming*^{F}, and self-grooming (*Self-grooming*^{F}). One possible explanation of lower stability estimates is that social grooming indices are, by definition, a function of the social environment. Therefore, the lower stability of social indices might be attributable to the fact that their occurrence is dependent on the behaviour of the focal individual and its social partners at the same time. Some studies have found that grooming-related indices were repeatable (Blaszczyk, 2018; Koski, 2011b; Neumann et al., 2013), although the indices based on received social interactions were less repeatable than the indices based on initiated social interactions (Blaszczyk, 2018; Koski, 2011b). Alternatively, grooming behaviours might be context specific and therefore represent several different traits (Carter et al., 2013; Gosling, 2001). Grooming is most often thought of as an affiliative action but in cooperative breeders it can also be used to induce helpers to stay in the group (pay-for-help strategy) (Ginther and Snowdon, 2009) or to reduce the tension of these helpers (Caperos et al., 2011).

Other indices that could have been influenced by context are *Scent marking*^{F} and *Monitoring*^{P}. *Scent marking*^{F}, which did not have a salient loading on any component in our study, has been suggested to be a contagious behaviour in marmosets (Massen et al., 2016) and so it is not possible to determine whether this behaviour was spontaneous, or triggered by the behaviour of others. Moreover, scent marking might have several functions (Roberts, 2012) and might be affected by sex (French and Cleveland, 1984) or breeding position (Heistermann et al., 1989). *Monitoring*^{P} could have merged several types of scanning as social scanning, curiosity or alertness (Gosselin-Ildari and Koenig, 2012). Therefore, we recommend using indices related to scent marking and monitoring with caution. The context specificity and the true motivation of an animal, however, is not always possible to record during focal behavioural coding (for discussion see Freeman et al., 2011; Iwanicki and Lehmann, 2015; Vazire et al., 2007). To overcome the effect of context it would be necessary either to record the context they occurred in or aggregate those behaviours sufficiently in time by means of longer observation periods (Epstein, 1983).

4.3. Cotton-top tamarin personality model

One set of behaviours that defined Extraversion in tamarins included indices related to physical and social activities. Extraversion in this sense has been described in great apes (Weiss et al., 2009, 2006) and as part of the human Five-Factor Model (McCrae and John, 1992). A second set of behaviours defining cotton-top tamarin Extraversion included indices related to individuals' tendencies to explore their environment. In this way, tamarin Extraversion partly resembled common marmoset Inquisitiveness (Koski et al., 2017) and Openness dimensions (Iwanicki and Lehmann, 2015) identified by questionnaires (for details see

Table S19), and Exploration-Avoidance (Koski and Burkart, 2015; Šlipogor et al., 2016) measured by experimental coding. There are three possible reasons why exploratory behaviours were subsumed under cotton-top tamarin Extraversion. First, exploratory behaviours that we observed might be those more connected to physical activity and thus loaded on the same dimension. Second, exploratory behaviour might be rare in stable predictable captive conditions where animals do not have to forage and do not encounter novel stimuli as often. Third, the species-specific socioecology might also play a role. Marmosets live in more diverse habitats than tamarins, and so a distinct Openness dimension in marmosets could reflect an evolved response to spatial variation in habitats (Digby et al., 2006).

Confidence included dominance-related behaviours, low levels of scratching and indices connected to using the space and resources. Tamarin Confidence corresponded to the Assertiveness dimension in one ratings-based study of common marmosets (Koski et al., 2017). It also corresponded to a dimension labelled "Extraversion", which mainly comprised of dominance-related traits, as described in another study (Iwanicki and Lehmann, 2015) (Table S20). Our results therefore support the general interpretation of dimension, usually labelled as Confidence, Dominance, or Assertiveness as an important part of primate personality that reflects the individuals' need to cope with social interactions and relationships in highly complex social groups.

Many studies have demonstrated that behaviour-based personality models correspond to questionnaire-based models (Garai et al., 2016; Iwanicki and Lehmann, 2015; Konečná et al., 2008; Murray, 2011). This suggests that both methods assess the same underlying constructs. However, the resulting cotton-top tamarin personality model remains to be validated against other personality measures, underlying physiological indicators (e.g. hormones), or other outcomes (e.g. survival or reproductive success).

The fact that we did not obtain further personality dimensions does not necessarily imply that only two personality dimensions characterize tamarin behaviour. Using trait ratings, Iwanicki and Lehmann (2015) and Koski et al. (2017) identified a Conscientiousness dimension in marmosets, which appears to be connected to the advanced socio-cognitive skills necessary for cooperative breeding and therefore it might be an important domain to callitrichids. It is possible that we might have omitted behaviours relevant to Conscientiousness, such as infant care (Delgado and Sulloway, 2017) and other traits otherwise present in questionnaires. Similarly, using controlled experiments it might be possible to assess reactions to novelty or other exploratory tendencies in more detail. For the identification of the whole personality model of a species, we recommend the utilisation of the broader behavioural spectrum and a selection of behaviours relevant to species typical socio-ecology.

5. CONCLUSION

We described a personality model of cotton-top tamarins, consisting of Extraversion and Confidence. The model corresponds with results of previous studies in primates and can serve as a basis for future comparative personality research in callitrichids. Our findings suggest that common behaviour coding is a useful tool for assessing complex personality structure and may be less time-consuming than previously believed. For cotton-top tamarins, stable personality structure was obtained only after 5 hours of observation per individual. The recommended length of observation in this species can be used as a guide not only in personality studies but also in studies assessing individual variation in behaviour in general. The minimum length of observation recommended in this study for personality assessment should, however, be treated as species-specific before data from other species differing in body size and feeding ecology are tested.

Conflict of interest

None.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.beproc.2018.08.009.

Original source: https://doi.org/10.1016/j.beproc.2018.08.009

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SUPPLEMENTARY MATERIAL

Table S1. Ethogram of cotton-top tamarin *(Saguinus oedipus)*

Behavioural category	Behaviour	Description
Continuous focal sampling		
Locomotion	**Move**	horizontal or vertical movement of more than 50 cm; including walking running and climbing; excluding chasing and playing
	Jump	focal individual jumps to overcome gaps between substrates in the enclosure (i.e. branches, trunks, shelves, walls, …); including change of substrate
	Resting	sitting or lying in relaxed position with closed eyes; individual may be in proximity or contact with other individual
Food interactions	**Eating**	handling, chewing and active ingestion of food by swallowing it
	Drinking	ingestion of liquids by drinking from water bowl/dispenser, licking wet surfaces or hands dipped in water
	Floor scanning	visual inspection of ground in order to find food; individual might be on the ground or on substrate above the ground
	Prey catching	catching invertebrates moving freely in the enclosure
	Prey catching - attempt	unsuccessful attempt to catch invertebrates moving freely in the enclosure
	Taking food from keeper	individual takes food from the zookeeper’s hand
	Approach – food	oriented approach towards individual possessing food item
	Contact - food	initiation of contact with individual possessing food item
	Follow – food	individual follows the movement of another individual that possesses food to its proximity
	Co-feeding	joining other individual eating from the same feeding bowl
	Carrying food away	taking food away from feeding bowl where other individual is eating
	Begging	scrounging the food from individual that is eating by fixing the food item with sight; may involve characteristic vocalization (squeak), touching or attempting to take the food item
	Sharing food	voluntary sharing of food item with other individual resulting in eating together the same food item the possessor holds in hand or yielding the food item; often after begging
	Stealing food	taking food from other individual’s hand or mouth
	Stealing food - attempt	unsuccessful attempt to steal food from hand or mouth of other individual
Object interactions	**Attention**	individual fixes its stare to the object of interest to examine it; usually followed by moving in direction of object
	Surface licking	individual licks surface of substrate

	Substrate searching	sitting on the ground and looking for the food in the substrate by using hands
	Object manipulation	manipulation with object (e.g. twigs, leaves, bark; excluding food) using hands or mouth; including looking at, sniffing and biting into the object
	General exploration	manipulative investigation of objects, enrichment or equipment of enclosure using hands or mouth
	Approach - object	oriented approach towards individual possessing object of interest
	Contact – object	initiation of contact with individual possessing object of interest
	Follow - object	individual follows the movement of another individual that possesses object to its proximity
	Stealing object	taking an object (e.g. twig, leaf, bark) from individual possessing it
	Stealing object - attempt	unsuccessful attempt to possess an object that is hold by other individual
Comfort	**Scratching**	rapid rubbing of body using the claws of hand or foot; individual does not have to be visually focused on the scratched area
	Face scratching	rubbing muzzle with hand
	Self-grooming	using claws of hands or mouth to pick through its own skin or fur; including removing of particles; individual is visually focused on the groomed area
	Stretching	stretching of entire body or limbs
Olfactory	**Object sniffing**	smelling the surface of substrate, objects, scent marks or food
	Sniffing individual	smelling the body, face or anogenital region of other individual
	Muzzle rubbing	pressing the oro-facial region onto the substrate and rubbing it with movements of head
	Scent marking	rubbing the anogenital area against the substrate in a sitting position or the suprapubic pad or sternal area either by pulling itself forward with hands or pushing with legs; may be accompanied by urine discharge
	Allomarking	scent marking over the body of another individual that can carry infants
	Urine tasting	individual licks urine drops of another individual either left on substrate or while the individual is urinating or scent marking
Play	**Solitary play**	repeated jumping and falling from one branch to another, swinging and bouncing on branches; excluding play with object
	Play with object	manipulation or biting into an object in the context of play
	Social play	non-aggressive and active interaction of 2 or more individuals, including play chasing, play wrestling, displaying, repeated jumping/ falling from one branch to another together with others
	Joining the play	individual engages in ongoing social play of other individuals
	Solicit play	attempt to attract the attention and involve other individual in playing; including tongue flicking, staring, pushing the individual or jumping in front of the individual
Affiliative	**Proximity**	individual is in the distance of max. 30 cm from other individual

	Contact	individual is in body contact with another or in the comfortable reach of arm (<9 cm)
	Allogrooming	individual picks slowly through the fur or skin of other individual using the claws of 1 or both hands or mouth; including removing particles
	Invite grooming	individual lowers its body or stretches out on its back or side requesting grooming
	Nuzzling	individual gently rubs its muzzle against other individual; may be accompanied by sniffing and licking
	Kiss	muzzle-muzzle contact of 2 animals; may involve tongue flicking
	Arm over	placing arm around other individual's upper body or shoulders
	Waist clasping	placing both arms from behind around other individual's waist
	Huddling	animal lies across or sits or lies next to other individual in tight body contact; limbs can be intertwined
Sexual	**Copulation**	male mounts a female, including penile insertion and thrusting, sometimes accompanied by tongue flicking
	Mounting	individual gets on back of other individual with arms around its waist; may include pelvic thrusts and tongue flicking
Infant care	**Climb on**	infant climbs on the back or side of potential carrier (from substrate or another carrier); limbs of infant are not in the contact with substrate; initiative of infant
	Climb off	infant climbs from the carrier to substrate or another carrier
	Solicit carrying	infant approaches potential carrier trying to climb on its back squeaking; potential carrier is not interested
	Invitation to carry	potential carrier attempts to entice the infant in order to carry it; including tongue flicking or lowering its body
	Taking infant on	potential carrier gathers infant from substrate or back of current carrier in order to carry it; initiative of potential carrier
	Taking infant on – attempt	unsuccessful attempt of potential carrier to gather infant from substrate or back of the current carrier in order to carry it; infant refuses to climb on or the carrier refuses to transfer the infant; sometimes resulting in aggression between caretakers
	Infant rejection	caretaker dislodges infant clinging to it or prevents infant to climb on by using scratching, biting, pushing, pulling infant's extremities or rolling the infant against substrate
	Infant rejection - attempt	unsuccessful attempt to dislodge infant from back or prevent infant to climb on
	Nursing	infant is from the ventral side of the female suckling; infant's mouth is on the nipple of female
Dominance	**Grimace**	lip corners are pulled back, lower lip is retracted so the mouth is slightly open revealing dentition with pressed jaws; accompanied by vocalization
	Avoiding	individual while travelling changes the direction of its move in order to avoid another individual
	Grasp	individual places its arm over the other individual's shoulder, head, upper body or touches other individual's face in dominant manner while slightly raising its body or head
	Displacement	individual chases other individual away from potential source, e.g. food, water, sleeping box
Agonistic non-contact	**Facial threat**	staring and frowning at other individual, may involve tongue or ear flicking

	Open mouth display	individual stares at another with mouth widely open exposing its teeth
	Headshake	rapid turning of head from side to side; might be accompanied by teeth chattering
	Body display	individual stares at other individual, limbs flexed, vertebral column bent into high arch, fur piloerected; often accompanied by facial threat; individual might be moving or vocalizing
	Chase	chasing other individual that is fleeing and trying to hide; rapid locomotion
Agonistic contact	**Face pressing**	individual grabs the head of other individual and presses its open mouth to oponent’s mouth
	Bite	individual bites another individual with its teeth; teeth may or may not penetrate the skin
	Push	individual aggressively hits other individual using its hand; may push the other animal away
	Grab	individual grabs hair of other individual; may pull out strand of hair
	Beating	repeated pushing and hitting other individual using arms; other individual usually beats back
	Fight	aggressive physical confrontation of individuals; short fast struggle involving biting, wrestling, hitting, scratching, kicking; victim may scream
	General aggression	any fast aggressive act of behaviour that observer was not able to register in detail
Other	**Alert**	vigilant observing of environment; individual is stationary and may turn its head from side to side
	General alarm	individual vocalizes (Type E or H chirp) when startled or frightened
	Vomiting	throwing up, usually after eating insect
	Head twist	stereotypic behaviour when individual stretches its head by tilting it back
	Out of sight	individual disappears from sight of observer to the box or separate part of enclosure
Other social	**Approach**	individual comes in proximity to other individual
	Departure	leaving from contact or proximity of other individual; excluding fleeing or displacement
	Following	individual follows the movement of other individual to its proximity
	Attention to other	fixed gaze at individual of interest; in context of hostility or curiosity
	Tongue flick	protrusion and rapid rhythmical movements of the tongue tip up and down; in sexual, aggressive or infant care context
	Teeth cleaning	individual uses its hands to open mouth of other individual and clean its teeth by using tongue; does not usually last long as groomee tries to recoil; often followed by aggression from groomee
	Terminate grooming	individual ends the allogrooming
Instantaneous focal sampling		
Substrate type	**Branch**	branch or stem of a tree or bush; excluding vertical stems
	Trunk	vertical trunk or stem of any diameter
	Sleeping box	nesting box providing shelter
	Shelf	horizontal surfaces wider and longer than 10 cm, e.g. shelves, top of sleeping box

	Ground	floor of the enclosure
	Wall	vertical wall (wire mesh, artificial rockwork) of enclosure enabling clinging and locomotion
	Ceiling	roof or ceiling of enclosure enabling hanging or moving
	Other	other equipment of enclosure, e.g. ropes, pipes, toys, enrichment
Locomotion/ postures	**Move**	
	Jump	
	Sitting	individual is in stationary position sitting on horizontal substrate
	Lying	individual places its body in horizontal position, with both limbs hanging down or rested; on horizontal or slightly inclined substrate
	Clinging	individual hangs on tightly to vertical substrate using claws of both hands and feet (i.e. wire mesh, wall, large tree trunks)
	Hanging	individual is suspended from wire mesh ceiling of enclosure or branch holding on using all limbs or legs
	Resting	
Food interactions	**Eating**	
	Drinking	
	Co-feeding	
Object interactions	**Substrate searching**	
	Object manipulation	
	General exploration	
	Play with object	
Social interactions	**Social play**	
	Allogrooming	
	Proximity	
	Contact	
Other	**Solitary play**	
	Self-grooming	
	Looking	individual is stationary and calmly looks around
	Watching	individual observes particular object, place, animal or person
	Alert	

Table S2. Repeatability estimates of behavioural indices across three time blocks

	R ± SE	95% CI	*p*
Approaches(in)^F	0.93 ± 0.04	[0.83, 0.96]	0.001
Departures(in)^F	0.93 ± 0.03	[0.85, 0.97]	0.001
Substrate diversity^S	0.88 ± 0.05	[0.75, 0.94]	0.001
Affiliation^P	0.84 ± 0.06	[0.67, 0.92]	0.001
Scratching^F	0.82 ± 0.07	[0.64, 0.91]	0.001
Scent marking^F	0.79 ± 0.08	[0.60, 0.89]	0.001
Exploration^F	0.77 ± 0.08	[0.57, 0.88]	0.001
Object sniffing^F	0.77 ± 0.08	[0.57, 0.88]	0.001
Contact aggression(in)^F	0.76 ± 0.09	[0.54, 0.88]	0.001
Carrying food away(in)^F	0.73 ± 0.10	[0.47, 0.86]	0.001
Resting^P	0.73 ± 0.09	[0.51, 0.85]	0.001
Activity diversity^S	0.69 ± 0.10	[0.44, 0.83]	0.001
Grimace^F	0.69 ± 0.10	[0.43, 0.82]	0.001
Monitoring^P	0.63 ± 0.12	[0.35, 0.79]	0.001
Threats(in)^F	0.60 ± 0.12	[0.32, 0.77]	0.001
Vigilance^F	0.51 ± 0.13	[0.19, 0.71]	0.001
Passive affiliation^P	0.45 ± 0.14	[0.15, 0.67]	0.002
Invite grooming(in)^F	0.37 ± 0.14	[0.07, 0.62]	0.004
Grooming(in)^F	0.29 ± 0.14	[0, 0.54]	0.02
Self-grooming^F	0.28 ± 0.14	[0, 0.55]	0.02
Grooming(rec)^F	0.26 ± 0.15	[0, 0.55]	0.03
Terminate grooming^F	0.26 ± 0.14	[0, 0.53]	0.03
Invite grooming(rec)^F	0.25 ± 0.14	[0, 0.52]	0.04

Note. P = index based on proportion of time, S = index computed as Shannon diversity index, F = index calculated as frequency, (in) = behaviour initiated by focal individual, (rec) = behaviour received by focal individual

Table S3. Full model. Varimax rotated solution of REFA

	Component		
Behavioural index	F1	F2	Communalities
Activity diversity^S	**0.86**	0.28	0.81
Passive affiliation^P	**-0.85**	0.09	0.73
Threats(in)^F	**0.84**	-0.05	0.72
Exploration^F	**0.84**	0.00	0.71
Vigilance^F	**0.69**	**-0.40**	0.64
Grooming(in)^F	**0.68**	**0.33**	0.57
Invite grooming(rec)^F	**0.65**	0.04	0.43

Resting^P	**-0.61**	**-0.42**	0.54
Terminate grooming^F	**0.61**	**0.39**	0.53
Grimace^F	**0.57**	-0.11	0.33
Object sniffing^F	**0.47**	**-0.32**	0.33
Monitoring^P	**0.41**	-0.08	0.17
Self-grooming^F	**0.39**	-0.21	0.19
Scent marking^F	**0.32**	0.09	0.11
Departures(in)^F	-0.16	**0.88**	0.80
Approaches(in)^F	-0.06	**0.81**	0.66
Scratching^F	-0.11	**-0.80**	0.65
Affiliation^P	-0.24	**0.76**	0.64
Contact aggression(in)^F	-0.05	**0.73**	0.53
Carrying food away(in)^F	-0.16	**0.62**	0.41
Grooming(rec)^F	0.05	**0.59**	0.35
Substrate diversity^S	0.29	**0.55**	0.39
Invite grooming(in)^F	0.20	**0.43**	0.23
Explained variability	27%	23%	

Note. N = 20. Factor loadings ≥ |0.3| are considered salient and indicated in bold-face.

Table S4. Promax rotated solution of PCA and the component correlation: full model

	Component		
Behavioural index	PC1	PC2	Communalities
Activity diversity^S	**0.90**	0.22	0.87
Exploration^F	**0.88**	-0.07	0.77
Passive affiliation^P	**-0.88**	0.16	0.79
Threats(in)^F	**0.88**	-0.13	0.77
Grooming(in)^F	**0.72**	0.29	0.62
Vigilance^F	**0.70**	**-0.47**	0.69
Invite grooming(rec)^F	**0.68**	-0.02	0.46
Terminate grooming^F	**0.65**	0.36	0.58
Resting^P	**-0.65**	-0.39	0.59
Grimace^F	**0.58**	-0.16	0.36
Object sniffing^F	**0.48**	-0.38	0.36
Monitoring^P	**0.42**	-0.12	0.19
Self-grooming^F	0.39	-0.25	0.21
Scent marking^F	0.34	0.07	0.12
Departures(in)^F	-0.13	**0.93**	0.88
Approaches(in)^F	-0.03	**0.85**	0.72
Scratching^F	-0.15	**-0.83**	0.72

Affiliation^{P}	-0.22	**0.81**	0.70
Contact aggression(in)^{F}	-0.02	**0.76**	0.58
Carrying food away(in)^{F}	-0.14	**0.66**	0.45
Grooming(rec)^{F}	0.08	**0.61**	0.38
Substrate diversity^{S}	0.32	**0.55**	0.42
Invite grooming(in)^{F}	0.23	**0.43**	0.25
Explained variability	29%	25%	

Note. The correlation of components was 0.04. Tables S4 – S18: N = 20. Salient loadings ≥ |0.4| are in bold-face.

Table S5. Varimax rotated solution of PCA: 14-hour model

	Component		
Behavioural index	PC1	PC2	Communalities
Activity diversity^{S}	**0.89**	0.27	0.86
Exploration^{F}	**0.87**	0.00	0.76
Passive affiliation^{P}	**-0.87**	0.12	0.78
Threats(in)^{F}	**0.87**	-0.05	0.76
Vigilance^{F}	**0.72**	**-0.41**	0.69
Grooming(in)^{F}	**0.72**	0.33	0.63
Invite grooming(rec)^{F}	**0.71**	0.07	0.50
Terminate grooming^{F}	**0.66**	0.38	0.58
Resting^{P}	**-0.61**	**-0.43**	0.56
Grimace^{F}	**0.58**	-0.12	0.35
Object sniffing^{F}	**0.49**	-0.31	0.34
Self-grooming^{F}	**0.47**	-0.21	0.27
Monitoring^{P}	**0.44**	-0.14	0.21
Scent marking^{F}	0.35	0.09	0.13
Departures(in)^{F}	-0.17	**0.91**	0.86
Scratching^{F}	-0.11	**-0.86**	0.75
Approaches(in)^{F}	-0.09	**0.82**	0.68
Affiliation^{P}	-0.24	**0.80**	0.70
Contact aggression(in)^{F}	-0.08	**0.74**	0.56
Grooming(rec)^{F}	0.09	**0.62**	0.40
Carrying food away(in)^{F}	-0.19	**0.62**	0.42
Substrate diversity^{S}	0.29	**0.59**	0.43
Invite grooming(in)^{F}	0.20	**0.49**	0.28
Explained variability	30%	24%	

Table S6. Varimax rotated solution of PCA: 13-hour model

Behavioural index	Component PC1	Component PC2	Communalities
Activity diversity^{S}	**0.89**	0.25	0.86
Threats(in)^{F}	**0.88**	-0.07	0.78
Exploration^{F}	**0.88**	-0.06	0.77
Passive affiliation^{P}	**-0.87**	0.08	0.76
Vigilance^{F}	**0.72**	**-0.41**	0.68
Grooming(in)^{F}	**0.70**	0.36	0.63
Invite grooming(rec)^{F}	**0.65**	0.09	0.44
Resting^{P}	**-0.63**	**-0.41**	0.56
Terminate grooming^{F}	**0.63**	**0.45**	0.59
Grimace^{F}	**0.55**	-0.14	0.32
Object sniffing^{F}	**0.51**	-0.28	0.34
Self-grooming^{F}	**0.47**	-0.20	0.26
Monitoring^{P}	**0.46**	-0.16	0.24
Scent marking^{F}	0.33	0.09	0.12
Departures(in)^{F}	-0.19	**0.91**	0.87
Scratching^{F}	-0.10	**-0.87**	0.76
Approaches(in)^{F}	-0.09	**0.83**	0.69
Affiliation^{P}	-0.26	**0.79**	0.70
Contact aggression(in)^{F}	-0.07	**0.74**	0.56
Grooming(rec)^{F}	0.02	**0.63**	0.39
Carrying food away(in)^{F}	-0.20	**0.61**	0.42
Substrate diversity^{S}	0.28	**0.59**	0.43
Invite grooming(in)^{F}	0.15	**0.47**	0.25
Explained variability	29%	25%	

Table S7. Varimax rotated solution of PCA: 12-hour model

Behavioural index	Component PC1	Component PC2	Communalities
Activity diversity^{S}	**0.89**	0.24	0.86
Passive affiliation^{P}	**-0.88**	0.08	0.78
Exploration^{F}	**0.88**	-0.07	0.78
Threats(in)^{F}	**0.88**	-0.03	0.77
Grooming(in)^{F}	**0.74**	0.36	0.67
Vigilance^{F}	**0.71**	**-0.41**	0.67
Terminate grooming^{F}	**0.66**	**0.45**	0.64

Invite grooming(rec)^F	**0.64**	0.09	0.42
Resting^P	**-0.61**	**-0.40**	0.54
Grimace^F	**0.54**	-0.13	0.31
Object sniffing^F	**0.51**	-0.26	0.33
Self-grooming^F	**0.48**	-0.19	0.26
Monitoring^P	**0.48**	-0.13	0.24
Scent marking^F	0.30	0.09	0.10
Departures(in)^F	-0.19	**0.92**	0.88
Scratching^F	-0.12	**-0.84**	0.73
Approaches(in)^F	-0.09	**0.83**	0.70
Affiliation^P	-0.26	**0.79**	0.70
Contact aggression(in)^F	-0.06	**0.75**	0.57
Grooming(rec)^F	0.07	**0.64**	0.42
Substrate diversity^S	0.25	**0.57**	0.39
Carrying food away(in)^F	-0.21	**0.56**	0.36
Invite grooming(in)^F	0.16	**0.48**	0.25
Explained variability	29%	25%	

Table S8. Varimax rotated solution of PCA: 11-hour model

	Component		
Behavioural index	PC1	PC2	Communalities
Activity diversity^S	**0.89**	0.25	0.85
Threats(in)^F	**0.88**	-0.02	0.77
Exploration^F	**0.85**	-0.03	0.72
Passive affiliation^P	**-0.83**	0.08	0.70
Grooming(in)^F	**0.70**	**0.41**	0.66
Vigilance^F	**0.69**	**-0.42**	0.66
Resting^P	**-0.64**	-0.37	0.55
Invite grooming(rec)^F	**0.62**	0.13	0.40
Terminate grooming^F	**0.62**	**0.51**	0.64
Object sniffing^F	**0.57**	-0.24	0.38
Grimace^F	**0.49**	-0.14	0.26
Monitoring^P	**0.46**	-0.10	0.23
Self-grooming^F	**0.46**	-0.19	0.25
Scent marking^F	0.35	0.10	0.13
Departures(in)^F	-0.19	**0.92**	0.88
Approaches(in)^F	-0.10	**0.84**	0.71
Scratching^F	-0.11	**-0.83**	0.70

Affiliation^{P}	-0.28	**0.78**	0.68
Contact aggression(in)^{F}	-0.07	**0.75**	0.56
Grooming(rec)^{F}	0.07	**0.67**	0.45
Substrate diversity^{S}	0.25	**0.56**	0.38
Carrying food away(in)^{F}	-0.18	**0.56**	0.34
Invite grooming(in)^{F}	0.19	**0.51**	0.29
Explained variability	28%	25%	

Table S9. Varimax rotated solution of PCA: 10-hour model

	Component		
Behavioural index	PC1	PC2	Communalities
Activity diversity^{S}	**0.89**	0.24	0.85
Threats(in)^{F}	**0.85**	-0.03	0.72
Passive affiliation^{P}	**-0.83**	0.09	0.69
Exploration^{F}	**0.79**	-0.04	0.63
Grooming(in)^{F}	**0.74**	0.39	0.70
Terminate grooming^{F}	**0.66**	**0.49**	0.67
Vigilance^{F}	**0.65**	**-0.45**	0.62
Invite grooming(rec)^{F}	**0.62**	0.22	0.44
Resting^{P}	**-0.60**	-0.36	0.49
Object sniffing^{F}	**0.54**	-0.30	0.38
Grimace^{F}	**0.50**	-0.15	0.27
Self-grooming^{F}	**0.48**	-0.11	0.24
Monitoring^{P}	**0.42**	-0.07	0.18
Scent marking^{F}	0.37	0.05	0.14
Departures(in)^{F}	-0.22	**0.91**	0.88
Approaches(in)^{F}	-0.13	**0.82**	0.70
Scratching^{F}	-0.16	**-0.81**	0.67
Affiliation^{P}	-0.25	**0.75**	0.63
Contact aggression(in)^{F}	-0.12	**0.71**	0.52
Grooming(rec)^{F}	0.13	**0.67**	0.46
Carrying food away(in)^{F}	0.10	**0.60**	0.37
Invite grooming(in)^{F}	0.20	**0.56**	0.35
Substrate diversity^{S}	0.25	**0.56**	0.37
Explained variability	28%	24%	

Table S10. Varimax rotated solution of PCA: 9-hour model

	Component		
Behavioural index	PC1	PC2	Communalities
Activity diversity^S	**0.88**	0.27	0.85
Passive affiliation^P	**-0.80**	0.11	0.66
Exploration^F	**0.80**	0.04	0.65
Threats(in)^F	**0.79**	-0.03	0.62
Grooming(in)^F	**0.72**	**0.45**	0.72
Terminate grooming^F	**0.64**	**0.54**	0.70
Invite grooming(rec)^F	**0.62**	0.24	0.45
Vigilance^F	**0.60**	**-0.42**	0.53
Object sniffing^F	**0.56**	-0.30	0.40
Resting^P	**-0.56**	**-0.42**	0.49
Grimace^F	**0.52**	-0.10	0.28
Self-grooming^F	**0.45**	-0.17	0.23
Monitoring^P	0.36	-0.06	0.14
Scent marking^F	0.34	0.05	0.12
Departures(in)^F	-0.27	**0.90**	0.88
Scratching^F	-0.16	**-0.82**	0.71
Approaches(in)^F	-0.18	**0.82**	0.71
Affiliation^P	-0.23	**0.78**	0.65
Contact aggression(in)^F	-0.17	**0.73**	0.57
Carrying food away(in)^F	-0.07	**0.62**	0.39
Grooming(rec)^F	0.16	**0.59**	0.37
Substrate diversity^S	0.17	**0.58**	0.36
Invite grooming(in)^F	0.16	**0.51**	0.29
Explained variability	26%	25%	

Table S11. Varimax rotated solution of PCA: 8-hour model

	Component		
Behavioural index	PC1	PC2	Communalities
Activity diversity^S	**0.89**	0.18	0.82
Grooming(in)^F	**0.82**	0.29	0.76
Threats(in)^F	**0.80**	-0.01	0.65
Passive affiliation^P	**-0.80**	0.20	0.68
Exploration^F	**0.76**	0.06	0.58
Terminate grooming^F	**0.75**	0.39	0.71
Invite grooming(rec)^F	**0.67**	0.28	0.53

Grimace^F	**0.54**	-0.08	0.30
Vigilance^F	**0.54**	**-0.45**	0.50
Resting^P	**-0.53**	-0.38	0.43
Object sniffing^F	**0.51**	-0.28	0.34
Self-grooming^F	**0.41**	-0.19	0.20
Scent marking^F	0.36	0.07	0.13
Monitoring^P	0.27	-0.09	0.08
Departures(in)^F	-0.25	**0.90**	0.87
Scratching^F	-0.18	**-0.83**	0.72
Approaches(in)^F	-0.18	**0.81**	0.69
Affiliation^P	-0.15	**0.79**	0.65
Contact aggression(in)^F	-0.19	**0.74**	0.58
Substrate diversity^S	0.23	**0.59**	0.40
Carrying food away(in)^F	0.03	**0.58**	0.34
Invite grooming(in)^F	0.14	**0.58**	0.35
Grooming(rec)^F	0.25	**0.54**	0.35
Explained variability	27%	24%	

Table S12. Varimax rotated solution of PCA: 7-hour model

	Component		
Behavioural index	PC1	PC2	Communalities
Activity diversity^S	**0.87**	0.22	0.80
Grooming(in)^F	**0.87**	0.22	0.80
Passive affiliation^P	**-0.80**	0.21	0.69
Terminate grooming^F	**0.79**	0.33	0.73
Threats(in)^F	**0.77**	-0.01	0.59
Exploration^F	**0.73**	0.09	0.54
Invite grooming(rec)^F	**0.64**	0.28	0.48
Grimace^F	**0.61**	-0.06	0.38
Resting^P	**-0.49**	**-0.44**	0.44
Vigilance^F	**0.49**	**-0.42**	0.42
Object sniffing^F	**0.48**	-0.25	0.29
Self-grooming^F	**0.43**	-0.18	0.22
Scent marking^F	0.36	0.12	0.14
Monitoring^P	0.18	-0.08	0.04
Departures(in)^F	-0.28	**0.89**	0.88
Scratching^F	-0.20	**-0.83**	0.74
Approaches(in)^F	-0.21	**0.81**	0.70

Contact aggression(in)^F	-0.19	**0.79**	0.66
Affiliation^P	-0.09	**0.78**	0.62
Substrate diversity^S	0.24	**0.60**	0.42
Invite grooming(in)^F	0.17	**0.58**	0.36
Carrying food away(in)^F	0.03	**0.53**	0.29
Grooming(rec)^F	0.33	**0.47**	0.33
Explained variability	27%	23%	

Table S13. Varimax rotated solution of PCA: 6-hour model

	Component		
Behavioural index	PC1	PC2	Communalities
Grooming(in)^F	**0.88**	0.01	0.78
Passive affiliation^P	**-0.88**	0.14	0.79
Activity diversity^S	**0.85**	0.19	0.76
Terminate grooming^F	**0.83**	0.10	0.70
Threats(in)^F	**0.80**	-0.02	0.64
Invite grooming(rec)^F	**0.68**	0.22	0.51
Exploration^F	**0.65**	-0.08	0.43
Grimace^F	**0.61**	-0.11	0.38
Grooming(rec)^F	**0.52**	**0.40**	0.44
Object sniffing^F	**0.50**	-0.33	0.36
Self-grooming^F	**0.49**	-0.19	0.27
Resting^P	**-0.48**	**-0.44**	0.42
Scent marking^F	0.28	0.03	0.08
Departures(in)^F	-0.25	**0.87**	0.82
Scratching^F	-0.19	**-0.83**	0.72
Affiliation^P	0.04	**0.80**	0.65
Approaches(in)^F	-0.20	**0.79**	0.67
Contact aggression(in)^F	-0.19	**0.78**	0.64
Substrate diversity^S	0.14	**0.67**	0.47
Carrying food away(in)^F	0.10	**0.55**	0.32
Invite grooming(in)^F	0.32	**0.44**	0.29
Vigilance^F	0.35	**-0.40**	0.29
Monitoring^P	0.19	-0.21	0.08
Explained variability	28%	22%	

Table S14. Varimax rotated solution of PCA: 5-hour model

	Component		
Behavioural index	PC1	PC2	Communalities
Grooming(in)^F	**0.87**	-0.10	0.77
Terminate grooming^F	**0.85**	-0.03	0.73
Passive affiliation^P	**-0.84**	0.26	0.77
Activity diversity^S	**0.81**	0.20	0.70
Invite grooming(rec)^F	**0.72**	0.13	0.53
Threats(in)^F	**0.67**	0.09	0.46
Grooming(rec)^F	**0.65**	0.20	0.46
Self-grooming^F	**0.55**	-0.11	0.32
Grimace^F	**0.53**	-0.06	0.28
Object sniffing^F	**0.52**	-0.38	0.42
Invite grooming(in)^F	**0.51**	0.23	0.31
Exploration^F	**0.45**	0.00	0.20
Scent marking^F	0.33	-0.01	0.11
Departures(in)^F	-0.21	**0.89**	0.84
Approaches(in)^F	-0.17	**0.84**	0.73
Scratching^F	-0.29	**-0.79**	0.71
Contact aggression(in)^F	-0.19	**0.78**	0.64
Affiliation^P	0.14	**0.72**	0.54
Substrate diversity^S	0.21	**0.67**	0.50
Carrying food away(in)^F	0.17	**0.56**	0.34
Resting^P	**-0.41**	**-0.54**	0.46
Vigilance^F	0.05	-0.35	0.13
Monitoring^P	0.10	-0.33	0.12
Explained variability	27%	21%	

Table S15. Varimax rotated solution of PCA: 4-hour model

	Component		
Behavioural index	PC1	PC2	Communalities
Grooming(in)^F	**0.87**	-0.01	0.75
Terminate grooming^F	**0.85**	0.04	0.72
Invite grooming(rec)^F	**0.81**	0.05	0.66
Passive affiliation^P	**-0.81**	0.17	0.68
Grooming(rec)^F	**0.74**	0.08	0.56
Activity diversity^S	**0.67**	0.37	0.59
Object sniffing^F	**0.64**	-0.34	0.53

Grimace^{F}	**0.58**	0.06	0.34
Threats(in)^{F}	**0.57**	0.25	0.39
Invite grooming(in)^{F}	**0.54**	0.05	0.30
Self-grooming^{F}	**0.45**	-0.09	0.21
Scent marking^{F}	**0.40**	0.01	0.16
Exploration^{F}	0.29	0.21	0.13
Departures(in)^{F}	-0.29	**0.85**	0.80
Approaches(in)^{F}	-0.26	**0.82**	0.74
Scratching^{F}	-0.22	**-0.80**	0.68
Contact aggression(in)^{F}	-0.28	**0.79**	0.70
Substrate diversity^{S}	0.10	**0.72**	0.53
Affiliation^{P}	0.13	**0.63**	0.41
Resting^{P}	-0.30	**-0.61**	0.47
Carrying food away(in)^{F}	0.16	**0.55**	0.33
Monitoring^{P}	0.10	-0.35	0.14
Vigilance^{F}	-0.09	-0.26	0.08
Explained variability	26%	21%	

Table S16. Varimax rotated solution of PCA: 3-hour model

	Component		
Behavioural index	PC1	PC2	Communalities
Terminate grooming^{F}	**0.89**	-0.11	0.80
Grooming(in)^{F}	**0.87**	-0.15	0.79
Grooming(rec)^{F}	**0.81**	-0.11	0.67
Invite grooming(rec)^{F}	**0.78**	-0.08	0.61
Passive affiliation^{P}	**-0.75**	0.27	0.63
Threats(in)^{F}	**0.68**	0.00	0.47
Activity diversity^{S}	**0.56**	0.35	0.44
Invite grooming(in)^{F}	**0.55**	-0.13	0.32
Grimace^{F}	**0.49**	0.22	0.29
Vigilance^{F}	-0.32	-0.11	0.12
Scent marking^{F}	0.19	0.03	0.04
Departures(in)^{F}	-0.18	**0.87**	0.79
Approaches(in)^{F}	-0.14	**0.82**	0.70
Scratching^{F}	**-0.42**	**-0.78**	0.79
Contact aggression(in)^{F}	-0.10	**0.72**	0.53
Substrate diversity^{S}	0.08	**0.66**	0.45
Resting^{P}	-0.21	**-0.60**	0.40

Carrying food away(in)^F	0.22	**0.58**	0.39
Affiliation^P	0.39	**0.57**	0.49
Object sniffing^F	0.35	**-0.50**	0.37
Self-grooming^F	0.17	-0.37	0.17
Monitoring^P	0.15	-0.33	0.13
Exploration^F	0.00	0.22	0.05
Explained variability	24%	21%	

Table S17. Varimax rotated solution of PCA: 2-hour model

	Component		
Behavioural index	PC1	PC2	Communalities
Terminate grooming^F	**0.88**	-0.15	0.80
Grooming(in)^F	**0.88**	-0.22	0.82
Invite grooming(rec)^F	**0.83**	0.12	0.71
Grooming(rec)^F	**0.80**	0.09	0.64
Passive affiliation^P	**-0.65**	0.39	0.57
Invite grooming(in)^F	**0.64**	0.08	0.41
Threats(in)^F	**0.63**	0.00	0.40
Activity diversity^S	**0.51**	0.34	0.37
Object sniffing^F	0.34	-0.30	0.21
Grimace^F	0.33	0.12	0.12
Scent marking^F	0.29	0.06	0.09
Self-grooming^F	0.22	-0.22	0.10
Departures(in)^F	-0.33	**0.85**	0.83
Scratching^F	-0.29	**-0.84**	0.80
Approaches(in)^F	-0.29	**0.75**	0.64
Contact aggression(in)^F	-0.10	**0.73**	0.54
Substrate diversity^S	0.15	**0.59**	0.37
Affiliation^P	0.35	**0.58**	0.46
Resting^P	-0.16	**-0.55**	0.33
Carrying food away(in)^F	0.18	**0.43**	0.22
Monitoring^P	0.26	-0.29	0.15
Vigilance^F	-0.21	-0.26	0.11
Exploration^F	-0.07	0.21	0.05
Explained variability	23%	19%	

Table S18. Varimax rotated solution of PCA: 1-hour model

	Component	
Behavioural index	PC1	Communalities
Grooming(in)^F	**0.77**	0.60
Terminate grooming^F	**0.73**	0.54
Departures(in)^F	**-0.72**	0.52
Scratching^F	**0.65**	0.42
Approaches(in)^F	**-0.62**	0.39
Contact aggression(in)^F	**-0.59**	0.35
Monitoring^P	**0.59**	0.35
Substrate diversity^S	**-0.58**	0.34
Object sniffing^F	**0.53**	0.29
Passive affiliation^P	**-0.51**	0.26
Resting^P	**0.51**	0.26
Exploration^F	**-0.44**	0.20
Scent marking^F	**0.42**	0.18
Grooming(rec)^F	**0.42**	0.18
Invite grooming(in)^F	0.36	0.13
Invite grooming(rec)^F	0.31	0.10
Carrying food away(in)^F	-0.28	0.08
Threats(in)^F	0.26	0.07
Affiliation^P	-0.23	0.05
Self-grooming^F	0.21	0.04
Activity diversity^S	-0.19	0.04
Vigilance^F	0.01	0.00
Grimace^F	0.00	0.00
Explained variability	23%	

Table S19. Comparison of cotton-top tamarin behaviour-based Extraversion with common marmoset questionnaire-based dimensions

Cotton-top tamarin		Common marmoset (Koski et al., 2017)		Common marmoset (Iwanicki and Lehmann, 2015)	
Index	Formula	Adjective	Definition	Adjective	Definition
Extraversion		**Inquisitiveness**		**Openness**	
(-)Resting^{P}	(rest + look + watch + sit + lie) / (move + jump + cling + hang)	(-)Lazy	"Monkey has inexpressive reactions, is inactive and slow."	Active	"Spends considerable time moving around or engaging in some energetic behaviour"
Activity diversity^{S}	Shannon diversity index of activity types	Active	"Monkey seeks physical activity, and is fast and agile."		
Exploration^{F}	(exploration + object manipulation + search)/hour	Exploratory	"Monkey is seeking new objects in its environment and seems eager to learn about them as much as possible."	Curious	"Readily explores new situations, seeking out or investigating novel situations"
Object sniffing^{F}	object sniffing/hour				
(-)Passive affiliation^{P}	(contact + proximity)/[contact + proximity + social play + groom(in) + groom(rec)]	(-)Solitary	"Monkey prefers to spend considerable time alone not seeking or even directly avoiding contact with others."		
Grooming(in)^{F}	groom(in)/hour				
Monitoring^{P}	watch/sample	Alert	"Monkey pays attention to other monkeys' behavior and its environment. Monkey does not seem to be tense; it is keeping an eye on the general situation."		
Vigilance^{F}	alert/hour			Vigilant	"Attentive, watchful, notices with special attention; not oblivious to surroundings"
				Extraversion	
Threats(in)^{F}	(facial threat + open mouth display + headshake + body display + tongue flick)/hour			Dominant	"Able to displace, threaten, or take food from other animals"

Note. (-) negative loading on component

Table S20. Comparison of cotton-top tamarin behaviour-based Confidence with common marmoset questionnaire-based dimensions

Cotton-top tamarin		Common marmoset (Koski et al., 2017)		Common marmoset (Iwanicki and Lehmann, 2015)	
Index	Formula	Adjective	Definition	Adjective	Definition
Confidence		**Assertiveness**		**Extraversion**	
Contact aggression(in)^{F}	(general aggression + bit + beat + grab + grasp + chase + fight + face + push + displace)/hour)	Dominant	"Monkey easily gets its own way, is able to control others and decisively intervenes in social interactions"	(-)Submissive	"Gives in readily to others"
		(-)Vulnerable	"Monkey is prone to be physically or emotionally hurt as a result of aggression or assertive behavior by another individual."	Effective	"Gets own way; can control others"
		(-)Sympathetic	"Monkey seems to be considerate and kind towards others as if sharing their feelings or trying to provide reassurance."	Bold	"Daring and fearless, not restrained or tentative. Not timid, shy, or coy."
Substrate diversity^{S}	Shannon diversity index of substrate types	(-)Cautious	"Monkey avoids risky behaviors and situations."	(-)Cautious	"Exhibits a careful, measured approach to investigations; avoids risky behaviors"
		(-)Timid	"Monkey lacks self-confidence, is easily alarmed and is hesitant to venture into new social or non-social situations."		
(-)Scratching^{F}	scratch/hour	(-)Anxious	"Monkey often seems distressed, troubled, or in a state of uncertainty."		
Carrying food away(in)^{F}	carry food away(in)/hour	Selective	"Monkey tries to select the best food or place if having chance to do so, seems picky."	Stingy	"Excessively covetous of favored resources(food, etc.); unwilling to share"
Affiliation^{P}		**Agreeableness**			
	[contact + proximity + social play + groom(in) + groom(rec)]/hour	Sociable	"Monkey seeks, enjoys and keeps the company of other monkeys."	(-)Solitary	"Prefers to spend considerable time alone; avoids contact with other animals"
Invite grooming(in)^{F}	groom invite(in)/hour	Affectionate	"Monkey has a warm attachment or closeness with others. Monkey's	Confident	"Behaves in a positive, assured manner; not restrained or tentative"

Approaches(in)^F	approach(in)/hour		behavior expresses the positive relationship to others.”		
Confidence		**Agreeableness**		**Extraversion**	
Grooming(rec)^F	groom(rec)/hour	Popular	“Monkey is often sought out as a companion by others”	(-)Depressed	“Often appears isolated, withdrawn, has reduced activity; socially unresponsive”

Note. (-) negative loading on component

CHAPTER III

Comparative assessment of behaviorally-derived personality structures in three callitrichid species

Masilkova M., Weiss A., Šlipogor V., & Konečná M.

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ABSTRACT

One way to address questions about the origins and adaptive significance of personality dimensions is by comparing the personality structures of closely-related species that differ in their socioecological circumstances. For the present study, we compared the personalities of captive golden-handed tamarins (*Saguinus midas*; N = 28), cotton-top tamarins (*Saguinus oedipus*; N = 20), and common marmosets (*Callithrix jacchus*; N = 17). All three species are New World monkeys of the family Callitrichidae. They thus share reproductive and behavioral characteristics but differ some in terms of their diet, habitat, and social organization. We expected that personality structures of closely-related tamarin species would overlap more, both in terms of number of dimensions and their content, than either would with the personality structure of common marmosets. We assessed personality using behavioral observations and compared the personality structures by means of cross-species correlations and fuzzy set-analyses. Principal component analyses identified components that we labeled Agreeableness, Assertiveness, and Extraversion in golden-handed tamarins and common marmosets and components labeled Confidence and Extraversion in cotton-top tamarins. The greater personality similarities of the two phylogenetically more distant species suggest that differences in social organization, and both habitat diversity and complexity, contributed to the personality evolution. However, we also found that behaviors clustered in similar ways in the two tamarin species, suggesting that phylogenetic relatedness and genus-specific socioecological characteristics, such as the degree of reproductive competition, shaped personality structure in this way.

Keywords: marmoset, tamarin, primates, temperament, fuzzy set analysis

CHAPTER IV

Marmoset match-making: linking personality traits to reproductive performance

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& Konečná M.

manuscript

ABSTRACT

Animal personality can affect individual fitness and population growth. In species with long-term pairs and biparental care of infants, the combination of personality traits between partners might facilitate their mating and coordination of infant care. Previous studies of personality combinations of partners and their reproductive performance have been limited to birds and fish. This is the first study investigating this link in a non-human primate. We studied the effects of five personality traits, including their absolute and directional differences within pairs, on key components of reproductive performance and reproductive rates in captive common marmosets (*Callithrix jacchus*) (N = 21 pairs; 214 reproductive events). We found that partners with similar scores on Agreeableness and Conscientiousness had shorter inter-birth intervals and optimal litter sizes, respectively. Surprisingly, these effects were not reflected in reproductive rates, measured as total litter size or total number of surviving offspring per year. Reproductive rates increased with mean pair Inquisitiveness and were higher if female was the more inquisitive sex. Our study demonstrates that animal personalities play important role in reproductive performance and should be considered in selection of breeding animals to optimize their well-being and animal welfare.

Keywords: animal personality, animal welfare, *Callithrix jacchus*, infant care, mate matching, reproductive success

CHAPTER V

Summary of results

Summary of results

This thesis focused on personality in primates, specifically on the methods of personality assessment, comparison of personality structures across species, and interplay between personality and reproductive success. We systematically investigated the method of common behaviour coding and determined the minimum length of observation needed for description of personality differences in callitrichids. Studies included in this thesis provide the description of personality structures derived from ecologically valid method of common behaviour coding in three callitrichid species, including common marmosets and two tamarin species (cotton-top tamarins and golden-handed tamarins) for which the personality structure was previously unknown. We also investigated the links between reproductive success and personality of mating partners for the first time in non-human primates. The results of our studies are, thus, instrumental from the methodological point of view, further the understanding of evolutionary bases of personality differences and fitness consequences, and can contribute to the welfare of callitrichids in captive conditions.

I. In the first study, we tested whether the method of common behaviour coding is as time-consuming as usually assumed. We compared the personality models of cotton-top tamarins based on different observational length (from 1 to 15 hours per individual) and found that the model and individual personality scores converged after only 5 to 7 hours of observation per individual. Our results suggest that, at least in small bodied primates, personality can be described in relatively short time and excessively long observations might yield diminishing returns.

II. In the second study, we compared the behaviourally-derived personality structures of three callitrichid species. Based on their close phylogenetic relatedness, we expected that personality structures of two tamarin species will be more similar than to the personality structure of more distantly related common marmosets. However, we found greater similarity between two more phylogenetically distant species, common marmosets and golden-handed tamarins, in which the personality structure consisted of three domains including Extraversion, Assertiveness and Agreeableness. In cotton-top tamarins, the personality structure comprised domains of Extraversion and Confidence. There were, however, also similarities between cotton-top and golden-handed tamarins in the way the behaviours organized into dimensions. These results can be explained in terms of the complexity of social and ecological niche, specifically social organization and habitat diversity.

III. In the third study, we investigated whether the combination of personality traits in partners of captive common marmosets can facilitate their reproductive success. We examined the links between the personality scores on five dimensions derived via trait rating and several measures of reproductive success. We found that partners with similar scores on Agreeableness and Conscientiousness had shorter inter-birth intervals and more optimal litter sizes, respectively. Litter size and number of weaned infants per year increased with mean pair Inquisitiveness. Our results suggest that personality of partners affect their reproductive success and can be used when establishing breeding pairs of marmosets in captive colonies to improve the animal well-being.

APPENDIX

Curriculum vitae

MICHAELA MÁSÍLKOVÁ

Born: 7.4.1988 in Tábor
E-mail: michaela.masilkova@gmail.com

Education

2013 – present	PhD student in Zoology, Department of Zoology, Faculty of Science, University of South Bohemia
2010 – 2013	Master´s degree in Zoology, Faculty of Science, University of South Bohemia
2007 – 2010	Bachelor´s degree in Biology, Faculty of Science, University of South Bohemia

Work experience

Sep 2019 – present	research assistant, Institute of Entomology, Biology Center CAS
Jan 2018 – present	technician, Faculty of Science, University of South Bohemia

Internships and research stays

2016	Department of Cognitive Biology, Faculty of Life Sciences, University of Vienna, Austria (2 months); prof. Thomas Bugnyar
	Zoologischer Garten Magdeburg, Germany (1 month)
2015	Department of Cognitive Biology, Faculty of Life Sciences, University of Vienna, Austria (2 months); prof. Thomas Bugnyar
	Department of Psychology, School of Philosophy, Psychology, and Language Sciences, The University of Edinburgh, UK (2 months); Dr. Alexander Weiss

Funding and awards

2019	ISSABC conference grant; International Student Symposium on Animal Behavior & Cognition, Kyoto
2018	ASAB conference grant; 9th European Conference on Behavioural Biology, Liverpool
2016	Aktion Österreich-Tschechien, Austrian Federal Ministry of Science, Research and Economy – BMWFW: project: Social environment as an important factor in marmoset personality assessment. Under supervision of prof. Thomas Bugnyar
2015	Czech and Slovak Ethological Society: award for the best student talk

Conferences

European Conference on Behavioural Biology (2018 poster, 2016 poster), European Student Conference on Behaviour & Cognition (2018 talk, 2016 talk), Conference of ČSEtS (2019 talk, 2018 poster, 2015 talk), Konferenz der Gesselschaft für Primatologie (2019 poster), Meeting of Primate Society of Great Britain (2017 poster)

Supervision

Maršíková, I. (2019): Olfactory communication and the function of urine washing in golden-handed tamarins (*Saguinus midas*) – defended bachelor’s thesis.

Teaching experience

Methods in animal behaviour research (2019), Field and laboratory exercise in animal behaviour (2018), Primatology (2016, 2015), Animal care and welfare (2014, 2016)

Membership

since 2018	Gesselschaft für Primatologie
since 2017	Primate Society of Great Britain

	Association for the Study of Animal Behaviour
since 2016	Czech and Slovak Ethological Society

Other activities

Sep 2017	organizer of 4th European Student Conference on Behaviour & Cognition in České Budějovice

Publications

Masilkova, M., Weiss, A., Konečná, M., (2018). How long does it take? Reliable personality assessment based on common behaviour in cotton-top tamarins (*Saguinus oedipus*). Behavioural Processes, 157, 59-67.

Upcoming publications

Masilkova, M., Weiss, A., Šlipogor, V., Konečná, M. Comparative assessment of behaviorally-derived personality structures in three callitrichid species. *Under review in Journal of Comparative Psychology*.

Masilkova, M., Boukal, D., Ash, H., Buchanan-Smith, H. M., Konečná, M. Marmoset match-making: linking personality traits to reproductive performance. *In prep for Proceedings of the Royal Society B: Biological Sciences*.

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