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Personality traits in common marmosets (*Callithrix jacchus*, L.)

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ZNAČAJKE OSOBNOSTI U OBIČNIH MARMOZETA (*Callithrix jacchus*, L.)

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Osobnosti (engl. *personalities*) u životinja su definirane kao stalne individualne razlike u skupu koreliranih ponašanja u istome kontekstu ili situaciji, ili u različitim kontekstima ili situacijama. Iako postoji duga povijest istraživanja osobnosti u ljudi, osobnosti u životinja su tek relativno nedavno dobile znatni interes znanstvene zajednice, posebice u različitim disciplinama biologije (od ponašanja životinja i ekologije, preko razvojne biologije i neuroendokrinologije, do genetike i evolucije) te su proučavane u raznim vrstama. Štoviše, smatra se da bi neka ponašanja, korelirana u određenim situacijama ili kontekstima, mogla dijeliti iste fiziološke mehanizme te, umjesto da se razviju neovisno jedno o drugome, razviju zajedno. Ovaj koncept bi tako mogao imati važnih implikacija za naše razumijevanje evolucijskih procesa, posebice mehanizama kao što su prirodna selekcija i održavanje jedinstvenih osobnosti u populacijama i vrstama. Isto tako, ovaj koncept bi nam mogao dati uvid u jedno od pitanja koje zanima ljude od davnina: Zašto svatko od nas ima jedinstvene reakcije na isti podražaj, odnosno jedinstvenu osobnost.

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Graduation Thesis

PERSONALITY TRAITS IN COMMON MARMOSETS (*Callithrix jacchus*, L.)

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Animal personalities are defined as consistent individual differences in sets of correlated behaviours across the same or different contexts or situations. Although personalities have a long history of research in humans, the topic of personalities in animals has in recent years received considerable scientific interest from a wide range of disciplines in biology: animal behaviour, ecology, development, neuroendocrinology, genetics and evolution, and has been studied in a variety of species. This interest may be attributed to a notion that different behaviours, when correlated, might share a common proximate mechanism, so they might not evolve independently from each other, but instead evolve together. Thus, this concept could have major implications on our understanding of the evolutionary processes, specifically its ultimate mechanisms, such as natural selection and the maintenance of unique personalities in populations and species. Also, this concept could give us insight into why each and every one of us has individual reactions to the same stimuli, and a unique personality.

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LIST OF ABBREVIATIONS

NO	Novel Object
cNO	Novel Object Control
tNO	Novel Object Test
NF	Novel Food
cNF	Novel Food Control
tNF	Novel Food Test
FUR	Foraging Under Risk
cFUR	Foraging Under Risk Control
tFUR	Foraging Under Risk Test
P	Predator
cP	Predator Control
tP	Predator Test

1 INTRODUCTION

1.1 THE OBJECTIVE OF RESEARCH

Animal personalities are defined as consistent individual differences in sets of correlated behaviours across the same or different contexts or situations (Sih et al. 2004a,b). Although personalities have a long history of research in humans, only in recent years the topic of personalities in animals has received considerable scientific interest from a wide range of disciplines in biology: behaviour, ecology, development, neuroendocrinology, genetics and evolution, and has been studied in a variety of species (Bell 2007a,b). This interest may be attributed to a notion that different behaviours, when correlated, might share a common proximate mechanism (Koolhaas 2008), so they might not evolve independently from each other, but instead evolve together. Thus, this concept could have major implications for our understanding of the evolutionary processes, specifically its ultimate mechanisms, such as natural selection and the maintenance of unique personalities in populations and species (Wolf et al. 2007). Also, this concept could provide insight into why each and every one of us has individual reactions to the same stimuli, and a unique personality (Nettle & Penke 2010).

1.2 A HISTORICAL OVERVIEW OF THE RESEARCH ON HUMAN & ANIMAL PERSONALITIES

Probably ever since the beginning of time, but certainly since the first written evidence in ancient Greece (3000 years ago), human behaviour, its driving motives, and many aspects of human personality have intrigued philosophers. Thus, it is not surprising that Pythagoreans, Heracliteans, Democriteans, Platonists, Aristotelians influenced many famous personality psychologists and biologists, such as Charcot, Freud or Darwin (Dumont 2010), to name a few. Subtle differences in the behaviour of an individual and a unique way in reacting to diverse stimuli, yielded a hundred year's tradition of psychology research (Nettle & Penke 2010), and the study of human personality was one of its main themes (Réale et al. 2007). In the last decade, a growing body of literature has also focused on personalities in non-human animals (Gosling 2001, Gosling & John 1999, Sih et al. 2004a,b, Réale et al. 2007, Bell 2007a).

To many people who work closely with animals, especially researchers, animal keepers and pet owners, the existence of consistent individual differences in animals, seems more than obvious. However, when applying appropriate terminology in this respect, one needs to be careful (Réale et al. 2007). In human personality studies, researchers are not reluctant to assign terms like “personalities” to different individuals (Briffa & Weiss 2010), because it seems straightforward and almost self-evident (Bell 2007a, Wolf et al. 2007, Sih et al. 2004a). However, when the same terms are to be applied to animals, researchers often hesitate (Briffa & Weiss 2010, Gosling & John 1999). This might be in order to avoid anthropomorphism (Réale et al. 2007, Bouchard & Loehlin 2001, Gosling 2001). Although there is a strong potential of convergence and unification of these two disciplines in the future, the study of personalities in animals has until this day only a little in common with the study of personality in humans (Nettle & Penke 2010, Vazire & Gosling 2003).

At the beginning of the 20th century, Ivan Pavlov was a prominent early animal personality researcher; he identified three “temperaments” in dogs (Pavlov 1906, Weinstein et al. 2008). Similar research continued with studies on apes (Yerkes 1939, according to Wolf 2009) and other animals (Hebb 1946, according to Wolf 2009). In the “Handbook of Social Psychology” (Murchison 1935), 30% of the book was dedicated to the animal research (Weinstein et al. 2008). The attention to animal personality studies has then noticeably decreased, with a few exceptions (Zajonc 1969, Huntingford 1976, Buss 1988). The existence of consistent intra-individual differences was in the following period often treated as a noise, or even completely ignored. The research focused more on the central tendency of animals' behaviour and relied on a group-level approach (Nettle & Penke 2010, Briffa & Weiss 2010, Vazire & Gosling 2003).

Over the past thirty years, and especially in the last decade, it has been widely recognised that consistent individual differences in animals actually represent an interesting research topic (Sih et al. 2004a,b, Muller & Chittka 2008, Réale et al. 2007, 2010b, Koolhaas et al. 2010, Bell 2007a,b, Bell et al. 2009, Wolf et al. 2007, Dingemanse et al. 2009, Dingemanse & Réale 2005; Briffa & Weiss 2010, Gosling 2001, 2002). A number of review papers have gathered data from personality studies. They provided thorough material on the subject and analysed different approaches in studying individual differences (Gosling & John 1999, Gosling 2001, Bouchard & Loehlin 2001, Sih et al. 2004a,b, Dingemanse et al. 2010, Dingemanse & Réale 2005, Réale et al. 2007, Koolhaas 2008, Loehlin 2009, Dingemanse & Wolf 2010, Koolhaas et al. 2010, van Oers & Mueller 2010, Bell & Aubin-Horth 2010). Therefore, it is noticeable that research on animal personalities has come again to the spotlight, and is experiencing growth in many disciplines (behavioural ecology, applied ethology, animal behaviour, behavioural genetics, comparative psychology, biological psychiatry) (Bell 2007b, Weinstein et al. 2008). Clearly, this is mainly due to its important aspects in ecology, evolution and conservation biology (Dingemanse et al. 2009, Bell 2007a), animal production, pharmacology and animal welfare (Coleman 2012, Réale et al. 2007). However, studying animal personalities is still quite challenging, because of discrepant terminology, complicacy in finding appropriate study methods to quantify personalities and difficulties in applying the significance of laboratory based tests to the wild (Réale et al. 2007).

1.3 DEFINITION, EVOLUTION AND PROXIMATE MECHANISMS OF ANIMAL PERSONALITIES

The term “personality” derives from human personality psychology literature, where it defines differences between individuals that are consistent over time and have an effect on the behaviour expressed in different contexts (Stamps & Groothuis 2010a). The definition of personality in animals is similar. Animal personalities (Sih et al. 2004a,b, Gosling 2001), also labelled as “behavioural syndromes” (Sih et al. 2004a,b), “coping strategies” (Dingemanse & Réale 2005), “temperaments” (Dingemanse & Réale 2005, Réale et al. 2007) or “behavioural tendencies, axes, constructs” (Sih et al. 2004a,b), are a group of correlated behaviours; i.e., a consistent way in which individual animals of the same/different sex, age or population differ in their behaviour, throughout the time and/or across different situations and/or contexts (Sih et al. 2004a,b, Dingemanse et al. 2009), and are to some extent heritable (Wolf et al. 2007). Here, a context represents a functional behavioural category (e.g. mating, feeding, foraging, anti-predator context), whereas a situation represents a set of conditions at one time point (e.g. different levels of food availability, surrounding predators) or over a longer time period (e.g. seasonal influence) (Sih et al. 2004a).

These behaviours can be positively or negatively correlated within the same behavioural context (e.g. exploratory behaviour is correlated with general activity in the anti-predator context) and/or across multiple contexts (e.g. correlations across anti-predator context, mating and feeding context) (Sih et al. 2004a). From the evolutionary point of view, this implies that if personalities expressed within/across different contexts are correlated, their personality traits should not evolve in isolation, but instead evolve as suits of correlated behaviours (correlated personality traits), that could generate different trade-offs in the individual (Sih et al. 2004a, Réale et al. 2009). In isolated cases, these trade-offs could seem suboptimal, but actually during the whole lifetime of an individual, they could present optimal life-history trade-offs (Sih et al. 2004b).

Animal personalities are considered to be an integration of genetic, epigenetic (Stamps & Groothuis 2010a), neuroendocrine, developmental (Stamps & Groothuis 2010a,b) physiological, ecological and evolutionary (Dingemanse & Wolf 2010, Réale et al. 2010b, Wolf et al. 2007, Dingemanse et al. 2009) ways to study animal behaviour (Bell 2007a). In this respect, animal personalities ("behavioural syndromes") are characteristics of a population, whereas personality traits ("behavioural types") are set of behaviours that an individual expresses, therefore, characteristics of an individual (Bell 2007b).

One of the most interesting questions that arise in the personality literature is how it is possible for multiple personalities (different sets of genotypes) to co-exist in the same environment and the same population. It seems plausible that natural selection should favour only some configurations of personality traits, or even only a particular configuration of traits. These configurations would eventually "win" all the other configurations of traits, and "erase" any variation in the population (Bell 2007a, Muller & Chittka 2008); then, all the individuals would be optimally fit in every environment (Sih et al. 2004a).

Although the general concept used to be that animals are at any given point infinitely plastic or fit and can adapt to any given situation, it now seems that the plasticity may be less flexible than previously thought (Bell 2007a, Wolf et al. 2007, Dingemanse et al. 2009). Individual animals are in this sense different from each other, but consistent in their individuality to how they react to diverse stimuli (Dingemanse & Réale 2005). Thus, Houston and McNamara (1999) suggested that individual variation may persist because more optima exist simultaneously in the same environment, and they depend on different trade-offs. For example, two fish could differ in the exhibited amount of some personality trait (e.g. boldness). If one fish is consistently more "bold" than the others and spends more time foraging for prey, this also implies that it is for a longer time period away from the shelter and therefore, more exposed to predators. At the same time, a "shy" fish, which stays in the shelter, does not benefit from eating a prey, but on the other hand, it is not exposed to predators and the threat of being eaten. In some particular contexts, both behaviours might be "the best" solution. If there is an abundance of predators, the fish which stays hidden will benefit, and if there are no predators, the fish which forages for prey benefits. In other words, if there is no information about the conditions in the environment, the optimal answer for the maintenance of the population as a whole would be less plastic than the answer given when the complete information about the environment would be present. Therefore, if the future is uncertain, the best option would be to maintain both personality types in the population. Sih and colleagues (2004a) suggested that the evolution of limited plasticity could indeed be favoured by means of natural selection.

This view has also been explained in terms of proximate mechanisms. Sih and colleagues (2004a) and Réale and colleagues (2007) argued that proximate mechanisms determine the existence and stability of behavioural correlations, and put limits on plasticity. In other words, when we observe two correlated behaviours, the arising question is whether there is an underlying mechanism responsible for both observed behaviours (e.g. pleiotropy, a common hormone), or each of the behaviours has its own independent mechanism (e.g. via linkage disequilibrium) (Sih et al. 2004b). There are three proximate mechanisms that induce certain behaviours and thus constitute personalities; i.e. genetic, neuroendocrine and environmental mechanisms (Koolhaas et al. 2010, Sih et al. 2004a,b).

A genetic approach to personalities might reconstruct historical pathways of evolution (van Oers & Mueller 2010), whereas a phenotypic approach measures the present selection on traits. Hence, it is possible now to identify gene interactions and expressions that may be responsible for the natural selection and maintenance of different personalities (van Oers & Mueller 2010). Nowadays, a lot of aspects can be measured, such as the molecular background and correlations of natural selection, gene-gene & gene-environment interactions and inferring micro-evolutionary processes that are responsible for the maintenance of personality trait variation. Also, the trait variation can be linked with polymorphisms that code for the variation (van Oers & Mueller 2010). For instance, two correlated behaviours of a single personality are hard to decouple if the underlying mechanism is pleiotropy (when one gene affects multiple behaviours), but easier to decouple if the mechanism is based on the linkage disequilibrium (as this is only a statistical relationship between genes that are mechanistically independent) (Sih et al. 2004a). This could explain why a bold animal is sometimes also aggressive towards its conspecifics and generally more active than other individuals from a population.

In recent years, the study of animal personality has changed with the improvements of genetic and genomic tools. When we investigate personalities on the genetic level, a goal would be to identify the candidate genes for a certain mechanism, their functions and interactions (with a Quantitative Trait Locus (QTL) Analysis). Also, as suggested recently, many personalities seem to be under polygenic control, so high-throughput methods (such as DNA microarrays) can be used to simultaneously assess gene expression for thousands of loci (Sih et al. 2004a). Some studies take a whole genome approach to this (Bell & Aubin-Horth 2010), while others identify polymorphisms of certain candidate genes that are thought to be responsible for a certain trait (van Oers et al. 2005). Some of the suggested candidates for “personality” genes are DRD4, SERT, MAOA, D2, 5-HT2C, HTR2a, Tyrosine Hydroxylase (van Oers & Mueller 2010). Recently, some quantitative genetic models have also been proposed to accompany the study of personality and have received considerable scientific interest (Wolf 2009).

Some studies have shown that hormones and other neuroendocrine mechanisms might generate personalities. Those mechanisms could be correlated, at least to a certain extent, with some personality traits (e.g. testosterone & aggression, cortisol & aggression, cortisol & boldness) (Koolhaas 2008, 2010, Raoult et al. 2012, Johnson et al. 1996, Saltzman & Abbot 2011, Nunes et al. 2000, Saltzman et al. 2006, Higham et al. 2010, Prudom et al. 2008, Thomson et al. 2011, Beausoleil et al. 2008, Silva et al. 2010, French et al. 2012, Mormède et al. 2007, Cross et al. 2004, Aubin-Horth et al. 2012). As already mentioned above, personalities can form (positively or negatively) correlated traits. Studies have shown that aggressiveness can be positively correlated with boldness and activity (Réale et al. 2009, Sih et al. 2004a), and some argue that this may be due to some underlying proximate mechanisms, such as HPA (hypothalamic-pituitary-adrenal) axis or sympathetic and parasympathetic nervous system (Koolhaas et al. 2010, Øverli et al. 2007). Koolhaas (2008) has reported that bold and aggressive individuals show low HPA reactivity in response to stress (low plasma cortisol) but high sympathetic reactivity (high levels of catecholamine). Hormonal levels depend, however, on many factors, namely, hormonal receptors, synthesis and breakdown of hormones and hormone-hormone interactions. Some authors even suggest that a certain type of personality could be connected to the immune system and the possibility of obtaining a certain disease (Capitanio 2008, Capitanio et al. 2004).

Furthermore, individual experiences seem to have important influence on the personality, e.g. stressful or traumatic events may cause an individual to be fearful for the rest of its life, and this depends on the timing of the stressful experience (Sih et al. 2004a). If it happens early in life of an individual, then it usually has a vast impact on the personality, whereas, if it happens later, the impact is weaker. This could be important especially for animals living in social communities where this event could greatly influence the individual's social behaviour and life history (Sih et al. 2004a).

Proximate explanations do provide an understanding of animal personalities, but only to a certain extent. A thorough understanding of personalities will be only possible when both proximate and ultimate, adaptive mechanisms of maintaining consistent individual differences across time and/or contexts and situations will be resolved (Wolf 2009).

1.4 PERSONALITY TRAITS

Personality traits are considered to be characteristics of organisms shared by some or all individuals of a species and that vary among individuals. These traits can be measured, and the values obtained from personality traits are called phenotypes. As already mentioned, if two traits are associated at a phenotypic level, this might suggest their genetic or hormonal links (Réale et al. 2007, Sih et al. 2004a). It is not a simple task to measure personality traits, starting with the sampling bias, choosing which trait to study and deciding which experimental method to use.

In the wild, it is very important to minimise bias when sampling individuals from the experimental population. As suggested by Biro & Dingemanse (2008), it is rather common to make a mistake, e.g. when sampling fish for the aggressiveness test, to catch only the most aggressive ones. Here, the obtained results would not reflect the real picture, as we would only have the population of the most aggressive fish, while other shy ones would not be captured at all. Also, Koolhaas and colleagues (2010) noted that a bias may also occur in the laboratory bred animals, especially in the strains of mice and rats, through using inbred strains, and rigorous standardisations. These could delete e.g. highly aggressive phenotypes from the population, and keep only the less aggressive ones, therefore making a strong selection bias.

In studying personality in humans, it has been traditionally widely accepted to use a "Five-Factor Model" (or "The Big Five"), which describes five clusters of personality traits; i.e., A ("agreeableness", "altruism", "affection"), C ("conscientiousness", "control", "constraint"), E ("extraversion", "energy", "enthusiasm"), N ("neuroticism", "nervousness", "negative affectivity"), and O ("openness to experience", "originality", "open-mindedness") and assign the related trait values via means such as questionnaires (Blatchley & Hopkins 2010). In some primate studies (e.g. King & Figueredo 1997) the same personality traits were measured, with addition of one trait solely related to chimpanzees (i.e. "dominance"). However, this has to be interpreted carefully. Even within a human population, differences in the five-factor model occur between the Western and Eastern cultures (King & Figueredo 1997), so the extent to which the five-factor model is also applicable to non-human animals is quite questionable. For this reason, there is growing evidence of animal personality literature that takes a different approach, and studies certain traits that are widely distributed (and therefore applicable) in various taxa. Réale and colleagues (2007) suggested five major personality trait categories, namely, "Boldness-Shyness" (reaction to any risky situation e.g. predators in a non-novel situation) (e.g. Blumstein et al. 2006, Armitage & Van Vuren 2003, Álvarez & Bell 2007, Biro et al. 2010, Bell 2005, Schöpf Rehage & Sih 2004; Saltzman & Abbott 2011), "Exploration-Avoidance" (reaction to a new situation, e.g. environment, food or object) (e.g. Dingemanse et al. 2002, 2003, 2007), "Activity" (the level of activity in a non-novel environment) (e.g. Dingemanse et al. 2007), "Sociability" (reaction of an animal to the presence or absence of a conspecific) and "Aggressiveness" (aggressive reaction to a conspecific). Réale and colleagues (2007) also claimed that those traits are heritable and linked to fitness, and therefore also linked to ecology and evolution.

Personality traits are said to be also expressed within a social context (Réale & Dingemanse 2010), although only few studies have been conducted in this respect (Pollard & Blumstein 2011, Krause et al. 2010, Bergmüller & Taborsky 2010). For example, analysing social networks could provide a new way to characterise the structure of a population and to understand the roles individual animals have within their group, and whether this is due to a certain personality type (Réale & Dingemanse 2010, Fox et al. 2009). As suggested by Gosling and John (1999), future research should also examine the links between dominance hierarchy, personality traits and hormones (Briffa & Weiss 2010, Sapolsky 2005).

In the approach to study personalities in animals, most researchers rely on one of two possible methods (Itoh 2002, Uher & Asendorpf 2008); i.e., codings of personality traits in animals over a series of behavioural tests that typically contain a degree of novelty, e.g. a novel object or a conspecific (Uher et al. 2008) or rankings of personality traits in their home environment by human observers (Gosling 2001, Stamps & Groothuis 2010a, b, Coleman 2012). In the first approach, personalities are studied in terms of confronting an individual animal with a specific set-up (a situation or a context) and noting its reaction (e.g. latency to emerge from the home cage, time spent exploring the environment, number of different vocalisations, etc.). The codings are usually done on two or more occasions. Consistency across time, contexts and situations can be measured reliably and quite objectively. Recently, Muller and Chittka (2008) emphasised that research on nonhuman animals should be done by both, measuring the accuracy of decision making of a certain behavioural task and quantifying the time (the speed) of decision making. They stressed that only in this sense, the behaviour can be understood in a meaningful way, because uncertain conditions require a higher sampling time, and thus, accuracy and speed must be correlated.

In the second approach of studying personalities, individual animals are rated at certain time points via questionnaires related to the trait observed. The questionnaires consist of descriptive adjectives and a few sentences to clarify the definition of a particular adjective (e.g. “playful”). Then they are rated on a 7-point scale based on how well the adjective describes the animal (Pederson et al. 2005). This is done by people who are said to know the individual animals well (e.g. animal caretakers) (Gosling & Vazire 2002, Gosling 2001). One problem with this method, especially when the study is on primates and they are rated by naïve and inexperienced observers, is the possibility that results of the study are influenced by anthropomorphism. There is also a problem of the extent to which inter-observers vary in assigning values on a 7-point scale (Briffa & Weiss 2010). Nevertheless, most research on primates has been carried out actually with this method (Pederson et al.

2005, Gosling 2001, King & Figueredo 1997). Some researchers argue that both methods give accurate and comparable results, when the possible drawbacks of methods are circumvented by valid statistical techniques. However, with all of this taken into account, behavioural codings seem to be a more objective method to examine animal personalities.

This study is special in the sense that it does not use behavioural traits that are analogues of "The Big Five" in human personality research for the study questions. Instead, it takes the approach suggested by Réale and colleagues (2007); it allows comparison and validation of the results on the interspecies level, so the same behaviour could be compared between e.g. fish, monkeys, squids and lizards. Furthermore, instead of behavioural rankings, the behavioural codings approach is taken that ensures less bias to the interpretation of a given behaviour. Some primate studies have used a similar approach (e.g. Uher et al. 2008, Koski 2011; Massen et al. (*submitted*)) and showed promising results regarding the applicability of this procedure. The research goal is to study personalities on many different levels (behaviour, neuroendocrine, genetic) and then to extract the possible causalities from the given behavioural pattern (Bell 2007b).

1.5 COMMON MARMOSETS (*Callithrix jacchus,* L.) AS MODEL ORGANISM

Common marmosets (*Callithrix jacchus,* L.) are New World monkeys of the class Mammalia, order Primates, family Callitrichidae. This family includes six genera: tamarins (*Saguinus*, 15 species), lion tamarins (*Leontopithecus*, 4 species), Goeldi's monkeys (*Callimico*, 1 species), eastern Brazilian marmosets (*Callithrix*, 6 species), Amazonian marmosets (*Mico*, 14 species) and pygmy marmosets (*Cebuella*, 1 species) (Perelman et al. 2011, Rylands & Mittermeier 2009).

Callitrichidae are among the world's smallest primates, and members of this family represent the smallest true monkeys (simian primates). Common marmosets are no exception to this. Adult body mass for wild marmosets is on average 320 g−336 g, whereas 283 g-530 g, for captive marmosets (depending on the colony) (Araujo et al. 2000, Tardiff et al. 2009). Head and body length are between 18.5-25 cm, and tail length between 29.5-35 cm. Their furry coat is grey, black, brown and white with a bit of orange parts, and their tail is striped, with alternating dark and pale bands. Distinguishing characteristics are white ear tufts (Figure 1). Claw-like nails grow on all fingers and toes except the big toe. The big toe is opposable to the other fingers (Grzimek 2003).

Figure 1: Common marmoset (*Callithrix jacchus*). (Photo: Tina Gunhold)

They are endemic to Northeast Brazil (Figure 2), but they have also been introduced to areas outside of their natural geographic range in East and Southeast Brazil (Gunhold 2007, Rylands et al. 1993). They inhabit a variety of forest types (Atlantic coastal forests, gallery forests, forest patches within open habitats) (Grzimek 2003), and their home range varies from 0.5 to 6.5 ha (Rylands et al. 1993). According to the Red List of IUCN (2012) conservational status of common marmosets is considered to be at “Least Concern”.

Figure 2: Distribution of endemic common marmosets in Northeast Brazil (*Callithrix jacchus*). (Photo: IUCN)

Common marmosets are diurnal animals, leaving their sleeping sites at sunrise and then usually being active 11 to 12 hours per day (Grzimek 2003, Stevenson & Rylands 1988). During the day they forage, rest and socialise (Stevenson & Rylands 1988). Their diet includes a variety of food sources, such as fruits, plant exudates (gum, sap, latex, nectar), insects, snails, lizards, bird eggs, nestlings, tree frogs, small vertebrates, seeds and flowers (Gunhold 2007). Foraging for prey is the most time-consuming activity (almost 45% of their waking hours) (Grzimek 2003).

They communicate via olfactory, visual and auditory signals (Bezerra & Souto 2008), but it seems that vocal signals are especially important means of communication in arboreal habitats due to poor visibility. Indeed, marmosets are highly vocal species, with their vocal repertoire consisting of approximately 13 different calls, distinguishable both via sonogram and human ear (Bezerra and Souto 2008).

Common marmosets live in extended family groups ranging from 5 to 15 individuals (Gunhold 2007) with a dominance hierarchy, where breeding adults are at the top (Dell'mour et al. 2009, Bezerra et al. 2009). Their within-group behaviour shows much affiliation, and social grooming is the most frequent interaction performed during prolonged resting periods (Figure 3). Also, the animals often huddle together for longer periods. Young individuals are involved in social play (chasing, wrestling, smooth biting). Severe aggression is rare in the wild (Grzimek 2003).

Figure 3: Common marmosets involved in social grooming. (Photo: Vedrana Šlipogor).

In common marmosets, each group includes a single breeding pair (dominant), although the evidence of polyandry has also been observed in the wild (Goldizen 1988). The cooperative breeding system includes both carrying the infants on their back and food transfer (Figure 4). Most of the subadult and adult members participate in infant carrying and food transfer, which is a strong energetic burden during the first months after birth (but it decreases with increasing age of the offspring) (Grzimek 2003).

Figure 4: Subadult male marmoset carrying his infant siblings. (Photo:Tina Gunhold).

All callitrichids are rather susceptible to predators because of their small body size. Attacks have been witnessed from raptorial birds and snakes (anacondas (*Eunectes murinus*), rainbow boas (*Boa constrictor*) and jararacas (*Bothrops jararaca*) (Grzimek 2003). Alarm calls are emitted by marmosets, followed by escaping and hiding. Once the predator is exposed, marmosets may approach and intensively mob the predator with special vocalisations (Cross & Rogers 2005, Bezerra & Souto 2008).

Captive common marmosets have recently received great interest in animal psychology. They are an ideal model species because of their small size, availability and the ease of breeding in captivity (Mansfield et al. 2004). Marmosets have been studied in the laboratory since 1960, and have become widely used alternative species to more traditional nonhuman primates especially for biomedical purposes (Yamazaki & Watanabe 2009), but also for social learning, habit formation, imitation, foraging, cooperative breeding, etc. (e.g.

Bugnyar & Huber 1997, Voelkl & Huber 2000, 2007, Dell'mour et al. 2009, Voelkl et al. 2006). Also, a number of studies on the behaviour and ecology of marmosets have been done in the field (e.g. Pesendorfer et al. 2009, Schiel & Huber 2006, Bezerra & Souto 2008, Hubrecht 1984).

Common marmosets obviously represent a good model species for studying personality because previous studies have already noticed that individual marmosets differ in their reactions to stimuli, and that this is consistent within an individual, through time (Mendes & Huber 2004, Voelkl & Huber 2000, Bugnyar & Huber 1997). Therefore, it would be interesting to investigate whether those individual differences in marmosets are consistent across different contexts, situations and throughout time, and whether they are heritable. The social structure of their family groups makes them also interesting models for obtaining personalities in the social set-up. Furthermore, the Human Genome Sequencing Center (HGSC) is currently running a Marmoset Genome Project and it is expected that the whole genome will soon be sequenced (Mansfield et al. 2004), therefore making it possible to further analyse candidate genes for certain behaviours.

2 AIM OF THE STUDY AND PREDICTIONS

The aim of this research was to examine whether personality traits can be found in common marmosets (*Callithrix jacchus*), on a behavioural level, through a series of behavioural tests.

Specifically, I asked the following questions:

1) Can individual behavioural differences be found in common marmosets?
2) Are individual differences in common marmosets consistent across time and contexts?
3) Which behaviours might share a common proximate mechanism?

I expected that:

1) Individual behavioural differences can be found in common marmosets.
2) Individual differences in common marmosets are consistent across time and contexts.
3) A common proximate mechanism might be shared by boldness, activity and explorative behaviour.

3 METHODS AND DESIGN

3.1 SUBJECTS

Twenty-one common marmosets, 12 males and 9 females, were used as experimental subjects in this study. The animals were maintained in three family groups at the Department of Cognitive Biology at the University of Vienna, Austria. The composition and detailed individual information of each family group is shown in Table 1. All monkeys were born in captivity.

Table 1: Description of the subjects: family group, name, sex and date of birth.

FAMILY GROUP	NAME	SEX	DATE OF BIRTH
1	Kobold	♂	11.04.2005
1	Wichtel	♀	30.10.2005
1	Clever	♂	04.11.2009
1	Smart	♂	04.11.2009
1	Fix	♂	15.06.2010
1	Foxi	♂	15.06.2010
2	Pooh	♂	14.08.1999
2	Augustina	♀	1999
2	Fimo	♂	August 2002
2	Pandu	♀	March 2003
2	Yara	♂	March 2003
2	Locri	♂	August 2003
2	Messina	♀	August 2003
3	Kiri	♀	2000
3	Zaphod	♂	August 2002
3	Veli	♀	14.11.2004
3	Nemo	♀	15.5.2005
3	Mink	♂	15.5.2005
3	Oli	♀	15.10.2005
3	Jack	♂	23.3.2006
3	Sparrow	♀	23.3.2006

The groups lived in indoor-outdoor cages (Figure 5 & 6) of welded mesh (each cage measuring 250 x 250 x 250 cm), equipped with wood shavings, branches, ropes, platforms, pieces of cloth, tunnels, sleeping boxes and other objects for enrichment of captive animals. The visual contact between the family groups was prevented by blinds set between the cages.

Figure 5: The indoor enclosures with experimental cage. (Photo: Tina Gunhold).

Figure 6: The outdoor enclosures. (Photo: Vedrana Šlipogor)

The animals were fed daily a fixed diet of different fruits, vegetables, grains, as well as protein and vitamin supplements and occasionally insects. Water was provided ad libitum. The monkeys were kept at a temperature of 24 – 26 °C during the day and night. The humidity ranged from 50 – 70%. Daylight was the main source of lighting, but additionally solar-coloured lamps were available. The day period was maintained on a stable light-dark cycle that consisted of 12 hours each.

3.2 EXPERIMENTAL SET-UP

All experiments were conducted in an experimental cage (length x width x height; 146cm x 36cm x 110cm) (Figure 7). The monkeys had access to it from visually (but not auditory or olfactory) isolated indoor cages through a passageway system of tunnels. The opaque guillotine doors in the passageway facilitated luring certain subjects to enter the experimental cage.

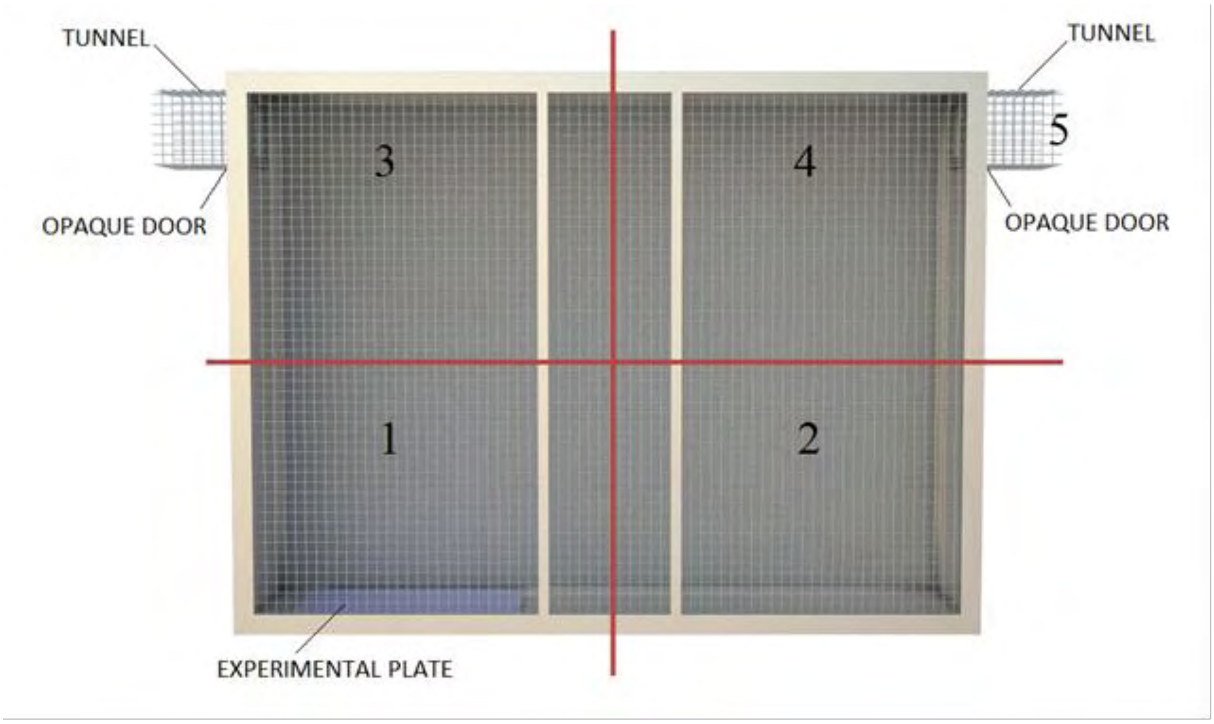

Figure 7: Diagram of the experimental cage. Virtual division of the compartments suggests level of potential danger that the monkey is experiencing (1 – highest level, 5 – lowest level). (Figure: Mauro Milli).

For the purpose of the analyses, the experimental cage was virtually divided in five different compartments (Figure 7). In compartment 1, I placed an experimental plate which was changed among the different groups, in between the tests. This was to control for any olfactory effect that could influence the behaviour during the tests. Compartment 1 was closest to the novelty (predator, novel object, etc.) that the individual was experiencing in the test, therefore I assumed that if the monkey spends time here, at the same time it should be facing the greatest level of possible "danger". The other compartments represented decreasing level of "danger". Compartments 2 and 3 of the experimental cage were assigned in this way because marmosets are usually more likely to "flee" upwards (vertically) when exposed to something potentially dangerous, than to simply run away (horizontally). Compartment 5 was not actually a part of the experimental cage, but represented a "waiting compartment" before the entrance. The side of entering the experimental cage was changed among the individuals of different groups.

3.3 PROCEDURE

Prior to the start of experiments, the subjects were habituated both to the experimental cage and the use of the passageway system. They were given access to the experimental cage with a food reward every day for two weeks, for approximately half an hour; first as a whole family group and then individually.

Two cameras were used to record all experiments. One camera (SONY DCR-SR35E) was placed on a tripod in front of the cage (focusing on the whole experimental plate in compartment 1) and the other camera (SANYO VPC-WH1) was handled by the experimenter (focusing on the subject and its behaviour).

All animals were tested in five different tasks (see below, 3.4). Every experiment was preceded by a control and was done in approximately the same manner. The subjects were lured through a series of tunnels and guillotine doors to the ("waiting") compartment 5. The trial started after opening the dividing opaque door between compartment 4 and 5, and finished after five minutes. The experimental-set up was placed on an experimental plate in compartment 1. All the behaviours exhibited in the experimental cage were recorded with cameras, and later coded (see Appendix 1).

Prior to each test, the monkeys were not fed to increase their motivation for successful cooperation. The order of subjects and of tests was randomised, with exception of the General Activity Test which was done as a first test for all the monkeys (see Appendix 2).

3.4 BEHAVIOURAL TESTS

3.4.1 General Activity Test (GA)

This test measured general activity of the subjects when being individually separated for five minutes in the empty experimental cage (Figure 8). Total movement and all other possible behaviours and vocalisations (see Appendix 1) were recorded.

Figure 8: A snapshot of Pooh performing the General Activity Test.

3.4.2 Novel Food Test (tNF)

The Novel Food Test measured the behaviour of the subjects when they were confronted with a piece of novel food. A novel food item (a macadamia nut in the first test session, a chestnut in the second test session) was placed on a porcelain plate at the furthermost position of the experimental plate (Figure 9 & 10). Different parameters, e.g. total movement, time spent manipulating the food, time spent close to the food, eating the food, etc. (see Appendix 1) were recorded, and later coded. The control for the Novel Food Test (cNF) was performed in the same way, with the difference of placing a familiar food item (a small piece of banana in both test sessions) on the porcelain plate.

Figures 9, 10: A snapshot of Mink and Clever performing the Novel Food Test in Session 1 and 2, respectively.

3.4.3 Novel Object Test (tNO)

The Novel Object Test measured the behaviour of the subjects when a novel object was presented. A novel object item (green spiky ball in the first test session, blue ball with holes in the second test session) was placed at the furthermost position of the experimental plate (Figure 11 & 12). Total movement, time spent manipulating the object, time spent close to the object and all other meaningful behaviours and vocalisations (see Appendix 1.) were recorded. The control for the Novel Object Test (cNO) was done in the same manner, with the difference of placing a familiar object (ball of strings) on the experimental plate.

Figures 11, 12: A snapshot of Pooh and Nemo performing the Novel Object Test in Session 1 and 2, respectively.

3.4.4 Predator Test (tP)

The Predator Test measured the behaviour of the subjects when faced with a predator. A plastic model of a predator (snake) was placed on the experimental plate and partially hidden in leaves (Figure 13). The latency to enter the experimental cage, the alarm calls and other vocalisations, the duration of time spent in different compartments, etc. was measured (see Appendix 1). The control for the Predator Test (cP) was made in a similar manner, with the difference of not having a model of predator hidden, but just the leaves.

Figure 13: The subject's viewpoint in the Predator Test. (Photo: Vedrana Šlipogor).

3.4.5 Foraging Under Risk Test (tFUR)

The Foraging Under Risk Test measured behaviour of subjects when confronted with a food reward and a potentially dangerous stimulus at the same time. The experimental plate was for the purpose of this test covered with saw dust, and on the furthermost part of the experimental plate, a small transparent box with a food reward (five mealworms) was placed. In front of the transparent box a lychee fruit was placed, to represent a potential danger for the monkeys. Due to prior encounters, it was known that the subjects emit “tsik” calls when being in proximity of a lychee fruit. Therefore, we assumed that its skin may resemble a skin part of a predator, most likely a snake (Figure 14). The latency to enter the experimental cage, the alarm calls and other vocalisations, the number of meal worms eaten, the duration of time spent in different compartments, etc. was measured (see Appendix 1). The control for the Foraging Under Risk Test (cFUR) was done in a similar way, but without placing a lychee in front of the transparent box.

Figure 14: A snapshot of Wichtel performing the Foraging Under Risk Test.

3.5 DATA CODING AND STATISTICAL ANALYSES

The videos were first analysed with a program for behaviour coding, *Solomon coder beta v. 12.09.02.* Then the data was exported to *Microsoft Excel 2010* and afterwards evaluated statistically with *IBM SPSS Statistics v. 20.0.*

The intra-class correlation coefficient (ICC) was used to test for consistency over time, to estimate the repeatability of the measures from the first set of experiments (Session 1) with the same measures from the second set of experiments (Session 2) (see Appendix 1) (Hayes & Jenkins, 1997). This coefficient is a mathematical equivalent to the standard repeatability test, and it explains fraction of behavioural variation due to individual differences (Bell et al. 2009). In other words, it accounts for proportion of variation in behaviour that is responsible for inter-individual variation, compared to that of intra-individual variation (Lessells & Boag 1987, Falconer & Mackay 1996). In order to go into further analyses, the ICC value of the two repeatable variables had to show significant repeatability ($p < 0.05$).

Of these variables, an individual mean value over two repeated experiments was calculated. This mean value was assigned to its tentative personality trait category (Table 2). Its consistency within this category (cross-experimental consistency) was tested with Cronbach's alpha (Bland & Altman, 1997) if there were more than two values, or with Spearman rank-order correlation, if there were only two variables. If Cronbach's alpha was above the satisfactory 0.7 (Bland & Altman, 1997), the variable was considered as contextually consistent (Table 3) (Massen et al. *submitted*). In this category, an individual mean value was calculated across the experiments to obtain an individual trait score. The variables that did not reach this value of Cronbach's alpha (> 0.7) or the significance of Spearman's Rho ($p < 0.05$) were excluded from further analyses.

To investigate whether and how these personality traits are associated with each other as syndromes, individual trait scores were entered into a principal component analyses (PCA). The PCA-solution was Varimax rotated and variable loadings >±0.4 were considered salient (Table 4). This rotation was used because of the three major methods of orthogonal rotation (Varimax, Quartimax and Equimax). Varimax rotation provides the clearest separation of the individual factors, by producing the maximum simplification of the factors within the factor matrix (Ho 2006).

The regression method was used to obtain the component scores for the PCA-constructs. The derived component scores were then compared between sexes and among the three family groups. Here, Mann-Whitney U-test was used for two-group and Kruskal-Wallis test for multiple-group comparisons. Post-hoc analyses (Mann-Whitney U-test with Holm-Bonferroni correction to adjust the probability) was performed when Kruskal-Wallis test showed significant differences ($p < 0.05$). All comparisons were graphically presented with box-plot diagrams.

Additionally, Wilcoxon Signed Rank test was used to compare different variables recorded during the tests and the controls per individual, and these comparisons were graphically presented with clustered bar histograms.

4 RESULTS

Using the intra-class correlation coefficient (ICC), I found that across the two test sessions, 88 variables were significantly repeatable (out of a total of 275 variables measured). Only these variables were taken into further analyses. This repeatability indicated temporal consistency between the test sessions and inter-individual behavioural variation. The ICC repeatability values ranged from 0.369 (*"Self-grooming";* tNF) to 0.962 (*"Manual manipulation"*; cNF) (Table 2).

Table 2: Summary of significant variables and their Session 1-Session 2 consistency as intra-class correlation (ICC 3,1) with 95% confidence intervals. Borderline significant ICC values are indicated in italic typeface.

TYPE OF EXPERIMENT	**PERSONALITY TRAIT CATEGORY**	**MEASURE(S)**	**ICC**	**95% CI lower, upper**	***p* - value**
GENERAL ACTIVITY (GA)	ACTIVITY	Scent_marking_duration	0.72	0.428, 0.876	<0.001
		Locomotion	0.458	0.043, 0.738	0.016
		Twitter_duration	0.497	0.094, 0.760	0.009
		Whirr_duration	0.583	0.213, 0.807	0.002
		Ek_duration	0.509	0.110, 0.767	0.008
TEST NOVEL OBJECT (tNO)	EXPLORATION - AVOIDANCE	Self-grooming_frequency	0.6	0.238, 0.816	0.002
		Locomotion	0.438	0.018, 0.726	0.021
		1st Compartment	0.786	0.545, 0.907	<0.001
		Ground	0.511	0.113, 0.768	0.008
		4th+5th Compartment	0.388	-0.042, 0.696	0.037
CONTROL NOVEL OBJECT (cNO)	EXPLORATION - AVOIDANCE	Manual manipulation_target_ Duration	0.435	0.015, 0.725	0.021
		Scratching_duration	0.539	0.151, 0.784	0.005
		Self-grooming_frequency	0.872	0.712, 0.946	<0.001
		Locomotion	0.49	0.084, 0.756	0.01
		1st Compartment	*0.358*	*-0.076, 0.678*	*0.051*
		2nd Compartment	0.414	-0.011, 0.712	0.028
		Compartment alternations	0.44	0.021, 0.727	0.02
		Tsik-ek_duration	0.624	0.273, 0.828	0.001
		See_duration	0.431	0.010, 0.722	0.023
		Whirr_duration	0.411	-0.014, 0.710	0.029
		Phee_duration	*0.355*	*-0.080, 0.676*	*0.053*
TEST PREDATOR (tP)	BOLDNESS - SHYNESS	Focus_target_duration	0.658	0.328, 0.845	<0.001
		Defecation_frequency	0.386	-0.043, 0.695	0.038
		Calls_sum_duration	0.668	0.342, 0.851	<0.001
		2nd Compartment	0.431	0.011, 0.722	0.022
		4th Compartment	0.374	-0..58, 0.688	0.043

		2nd+3rd Compartment	0.465	0.053, 0.742	0.015
		4th+5th Compartment	0.523	0.129, 0.774	0.006
		Compartment alternations	0.722	0.431, 0.877	<0.001
		Tsik_duration	0.71	0.410, 0.871	<0.001
		Tsik-ek_duration	0.621	0.269, 0.827	0.001
		Whirr_duration	0.431	0.011, 0.722	0.023
CONTROL PREDATOR (cP)	BOLDNESS - SHYNESS	Calls_sum_duration	0.717	0.421, 0.874	<0.001
		Piloerection	0.444	0.027, 0.730	0.019
		1st Compartment	0.399	-0.029, 0.703	0.033
		4th Compartment	0.373	-0.059, 0.687	0.044
		4th+5th Compartment	0.381	-0.050, 0.692	0.04
		Compartment alternations	0.605	0.245, 0.818	0.001
		Phee_duration	0.804	0.577, 0.916	<0.001
		Whirr_duration	0.528	0.136, 0.777	0.006
TEST NOVEL FOOD (tNF)	EXPLORATION - AVOIDANCE	Focus_target_duration	0.558	0.178, 0.794	0.003
		Eat_target_duration	0.609	0.251, 0.821	0.001
		Self-grooming_frequency	0.369	-0.063, 0.685	0.045
		Urination	0.6	0.238, 0.816	0.002
		Locomotion	0.447	0.03, 0.731	0.019
		3rd Compartment	0.414	-0.010, 0.712	0.028
		Ground	0.497	0.094, 0.760	0.009
		Latency_touch	0.601	0.228, 0.821	0.002
		Compartment alternations	0.593	0.227, 0.812	0.002
		Phee_duration	0.759	0.495, 0.895	<0.001
CONTROL NOVEL FOOD (cNF)	EXPLORATION - AVOIDANCE	Manual manipulation_target_ Duration	0.962	0.909, 0.984	<0.001
		Eat_target_duration	0.405	-0.021, 0.707	0.031
		Nb eaten_target	0.611	0.254, 0.822	0.001
		Scent_marking_duration	0.535	0.145, 0.781	0.005
		Scratching_duration	0.457	0.042, 0.737	0.016
		Manipulation_cage_frequency	0.416	-0.008, 0.713	0.027
		Defecation	0.466	0.054, 0.743	0.014
		Locomotion	0.577	0.204, 0.804	0.002
		Compartment alternations	0.605	0.245, 0.818	0.001
		Tsik-ek_duration	0.404	-0.023, 0.706	0.031
TEST FORAGING UNDER RISK (tFUR)	BOLDNESS - SHYNESS	Focus_target_duration	0.453	0.038, 0.735	0.017
		Manual manipulation_target_ Duration	0.563	0.185, 0.796	0.003
		Eat_target_duration	0.526	0.133, 0.776	0.006
		Focus target_focus lychee_duration	0.608	0.250, 0.820	0.001
		Scratching_duration	0.895	0.760, 0.956	<0.001
		Defecation	0.386	-0.043, 0.695	0.038
		Calls_sum_duration	0.505	0.105, 0.765	0.008
		Piloerection	0.5	0.098, 0.762	0.009
		1st Compartment	0.698	0.390, 0.865	<0.001
		3rd Compartment	0.405	-0.021, 0.707	0.031
		4th Compartment	0.416	-0.008, 0.714	0.027
		4th+5th Compartment	0.767	0.510, 0.899	<0.001

		Ground	0.671	0.347, 0.852	<0.001
		Latency_touch	0.841	-0.143, 0.989	0.037
		Tsik_durations	0.474	0.064, 0.747	0.013
		Tsik-ek_duration	0.478	0.069, 0.749	0.012
CONTROL FORAGING UNDER RISK (cFUR)	BOLDNESS - SHYNESS	Latency_enter	0.892	0.752, 0.955	<0.001
		Focus_target_duration	0.406	-0.02, 0.707	0.03
		Eat_target_duration	0.66	0.329, 0.846	<0.001
		Defecation	0.492	0.087, 0.757	0.01
		Piloerection	0.842	0.651, 0.933	<0.001
		5th Compartment	0.891	0.751, 0.954	<0.001
		4th+5th Compartment	0.728	0.441, 0.880	<0.001
		Ground	0.594	0.228, 0.812	0.002
		Latency_touch	0.468	0.016, 0.761	0.022
		Ek_duration	0.393	-0.035, 0.700	0.035
		Chirp_duration	0.502	0.100, 0.763	0.009
		Whirr_duration	0.437	0.018, 0.726	0.021

Of these 88 variables, an individual mean value over two repeated experiments was calculated, and assigned to its tentative personality trait category (Table 2). Its internal consistency within this category was tested with Cronbach’s alpha or Spearman rank-order correlation (Table 3). The trait “Activity” was measured by *“Locomotion”* in GA, tNO, cNO, tNF and cNF, which was highly consistent (alpha = 0.836) and by *“Compartment alternations”* in cNO, tNO, cNF, tP and cP, also showing a high repeatability across different experiments (alpha = 0.891). *“Whirr”*calls and *“Focus target”*, failed to show sufficient repeatability in the tests, and were therefore excluded. The trait “Boldness-Shyness” was measured by *“Self-grooming”* in tNO and cNO and in tNF, and was highly consistent (alpha = 0.774). This trait was also assigned to *“Calls sum”* in tP and tFUR, consistent between the experiments ($r_s = 0.455$, $p = 0.038$), and to *“Tsik-ek”* calls in tP and tFUR that were also contextually consistent ($r_s = 0.713$, $p < 0.000$). Additionally, *“1st compartment”*, *“ground”*, *“2nd and 3rd compartment”* and *“4th and 5th compartment*” were indicators for “Boldness-Shyness” in tP and tFUR. However, they were found in only one of the tests, so the contextual consistency could not be measured, and were instead taken as single variables in further analyses. Also, *“Tsik”* calls were measured as an indication for “Boldness-Shyness”, but failed to show sufficient repeatability. The trait “Exploration-Avoidance” was measured in tNF and tNO by *“1st compartment”*, *“4th and 5th compartment”*, *“Focus target”*, *“Eat* *target”* and *“Latency touch”*. Same as with the “Boldness-Shyness” indicators, these variables were the only repeatable measures of their kind, so the contextual consistence could not be measured, but the individual variables were taken into further evaluations. Here, *“Ground”* failed to show a significant contextual consistency and was eliminated from the following analyses (Table 3).

Table 3: The contextual consistency of individuals per trait across the same variable. Only the significantly repeatable variables were used in further analyses.

ASSIGNED TRAIT	VARIABLE	EXPERIMENT	CRONBACH'S ALPHA / SPEARMAN'S RHO*
Activity	Locomotion	General Activity (GA) Novel Object Test (tNO) Novel Object Control (cNO) Novel Food Test (tNF) Novel Food Control (tNF)	0.836
Activity	Compartment Alterations	Novel Object Control (cNO) Novel Food Test (tNF) Novel Food Control (cNF) Predator Test (tP) Predator Control (cP)	0.891
Boldness-Shyness	Self-grooming	Novel Object Test (tNO) Novel Object Control (cNO) Novel Food Test (tNF)	0.774
Boldness-Shyness	Calls Sum	Predator Test (tP) Foraging UnderRisk Test (tFUR)	0.455*
Boldness-Shyness	Tsik-Ek	Predator Test (tP) Foraging Under Risk Test (tFUR)	0.713*

Variables that reached the value of Cronbach’s alpha (> 0.7) or the significance of Spearman’s Rho ($p < 0.05$) were used for further analyses. Hence, an individual mean value was calculated across the experiments of the same category. With this, an individual trait score was obtained. Then, to investigate whether and how these personality traits are associated with each other as syndromes, the individual trait scores were entered in a principal component analyses (PCA). In sum, 12 variables were entered into the PCA to assess the covariance among them. The PCA-solution was Varimax rotated and variable loadings >±0.4 were considered salient (Table 4).

The analyses indicated appropriate sampling adequacy (KMO = 0.583; Barlett's Test of Sphericity, $p < 0.001$), and all variables had communality estimates > 0.678. Four components were extracted, Varimax rotated and explained together 82.28% of variance. The first component itself explained 39.53% of the variance and had high loadings (> 0.7) on *"1st compartment"* and *"Ground"* in tFUR and *"1st compartment"* in tNO, and salient negative loading (> -0.4) on *"4th and 5th compartment"* in tNO and salient positive loading (> 0.4) on *"2nd and 3rd compartment"* in tP. Therefore, it consisted of the traits related to boldness and exploration tendency, and was labelled as "Boldness-Shyness". The second component explained 19.52% of the variance and had very high positive loadings (> 0.9) on *"Locomotion"* and *"Compartment alternations"* in all tests; therefore, it was labelled as "Activity". It also had salient negative loadings (> -0.4) on *"4th compartment"* in tNO, (although weaker than on the first component) and *"Latency touch"* in tNF. The third component explained 14.75% of the variance. It had high positive loadings on *"Focus target"* in tNF (> 0.7) and on *"Self-grooming"* (0.698) and a high negative loading (> -0.7) on *"Eat target"* in tNF. Also, it had a salient positive loading (> 0.4) on *"Latency touch"* in tNF (stronger than on the second component) and a salient negative loading (> -0.4) on *"2nd and 3rd compartment*" in tP (weaker than on the first component). Taken all this into account, the third component was labelled as "Exploration-Avoidance". The fourth component explained 8.48% of the variance and had high loading on *"Calls sum"* in tP and tFUR, and was therefore labelled as "Vocalisations". Also, it had salient negative loadings on *"2nd and 3rd compartment"* in tP (> -0.4).

Table 4: Variable loadings in principal component analysis (PCA), Varimax rotation with Kaiser normalisation. Only loadings > ±0.4 are shown. High loadings (> ±0.7) are indicated in bold. Communalities indicate a proportion of each variable's variance that can be explained by the principal components.

	COMPONENT				
	BOLDNESS - SHYNESS	**ACTIVITY**	**EXPLORATION - AVOIDANCE**	**VOCALISATIONS**	**COMMUNALITIES**
% OF VARIANCE EXPLAINED	39.53	19.52	14.75	8.48	
EIGENVALUE	4.744	2.343	1.770	1.017	
LOCOMOTION		**.916**			0.864
SELF-GROOMING			.698		0.721
COMPARTMENT ALTERATIONS		**.919**			0.865
CALLS SUM (P, FUR)				**.872**	0.853
1^{ST} COMPARTMENT (FUR)	**.830**				0.872
GROUND (FUR)	**.883**				0.832
1^{ST} COMPARTMENT (NO)	**.816**				0.820
4^{TH} AND 5^{TH} COMPARTMENT (NO)	-.602	-.498			0.678
FOCUS TARGET (NF)			**.801**		0.905
EAT TARGET (NF)			**-.772**		0.817
LATENCY TOUCH (NF)		-.614	.650		0.895
2^{ND} AND 3^{RD} COMPARTMENT (P)	.470		-.402	-.606	0.751

To obtain the component scores for the PCA-constructs I used the regression method. Derived component scores were then compared between sexes ($N_{males} = 12$, $N_{females} = 9$), and among three family groups ($N_{Wichtel} = 6$, $N_{Pooh} = 7$, $N_{Kiri} = 8$). Some sex and group differences were found in the component scores.

Males and females did not differ in the Boldness-Shyness component (Mann-Whitney U-test, $N_{males} = 12$, $N_{females} = 9$, Z = -0.92, $p = 0.38$), Activity component (Z = -1.49, $p = 0.148$) or Exploration-Avoidance component (Z = 0.78, $p = 0.464$), but the females scored higher than the males in the Vocalisations component (Mann-Whitney U-test, $N_{males} = 12$, $N_{females} = 9$, Z = -2.49, $p = 0.012$). This difference is also clearly demonstrated in the mean duration of calls emitted in tP and tFUR (Mann-Whitney U-test, $N_{males} = 12$, $N_{females} = 9$, Z = -2.203, $p = 0.028$) (Figure 15).

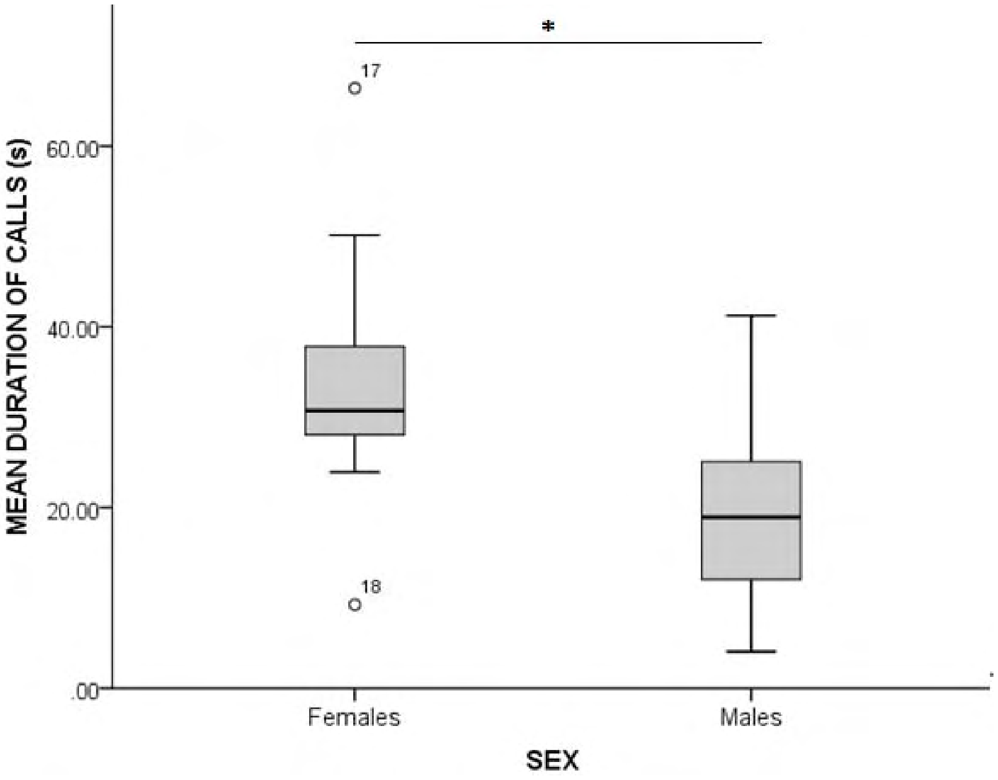

Figure 15: Box-plots showing sex differences in the mean duration of calls emitted *("Calls sum")* in tP and tFUR.

When comparing Boldness-Shyness, Activity or Vocalisations between different family groups, I found no differences (Kruskal-Wallis test, $N_{Wichtel}$ = 6, N_{Pooh} = 7, N_{Kiri} = 8; Boldness-Shyness: KW(2) = 2.52, *p* = 0.28; Activity: KW(2)= 2.32, *p* = 0.31; Vocalisations: KW(2) = 1.327 *p* = 0.53). However, differences were found in Exploration-Avoidance (KW(2) = 10.440, *p* = 0.005; post-hoc Mann-Whitney U-test, Bonferroni corrected, Kiri-Pooh: n.s., Pooh-Wichtel: *p* = 0.004; Wichtel-Kiri: *p* = 0.016) (Figure 16). To be more precise, 12 initial variables were used for the PCA, and the ones that showed significant differences on a group level were *"1st compartment"* in tFUR (KW(2) = 6.76, *p* = 0.048; post-hoc Mann-Whitney U-test, Bonferroni corrected, Kiri-Pooh: n.s., Pooh-Wichtel: *p* = 0.07, Wichtel-Kiri: n.s.), and *"Eat target"* in tNF (KW(2) = 6.31, *p* = 0.024; post-hoc Mann-Whitney U-test, Bonferroni corrected, Kiri-Pooh: n.s., Pooh-Wichtel: p = 0.028, Wichtel-Kiri: n.s.), as shown in Figures 17-18.

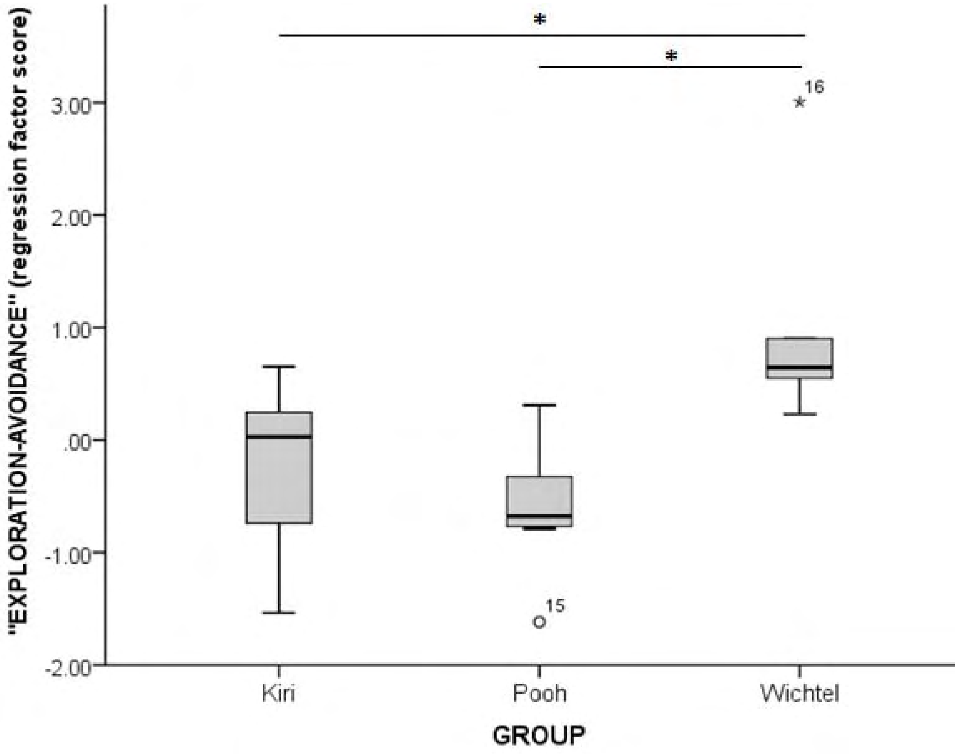

Figure 16: Box-plots showing differences between the groups (Kiri, Pooh, Wichtel) in regression factor scores of "Exploration-Avoidance".

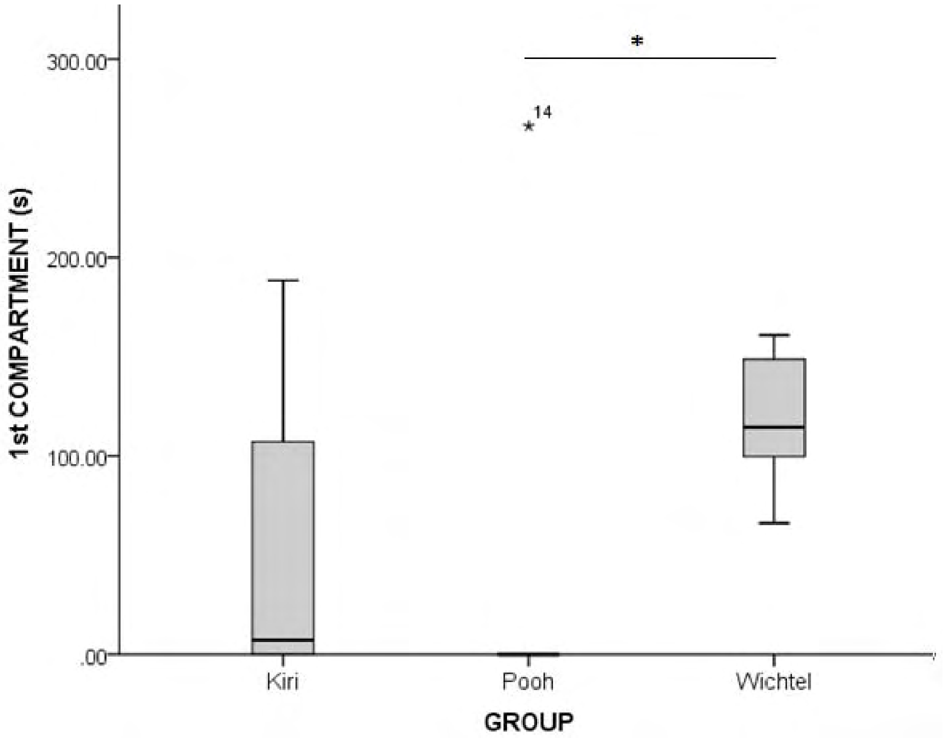

Figure 17: Box-plots showing differences between the groups (Kiri, Pooh, Wichtel) in duration of time spent in the first compartment *("1st compartment")* in tFUR.

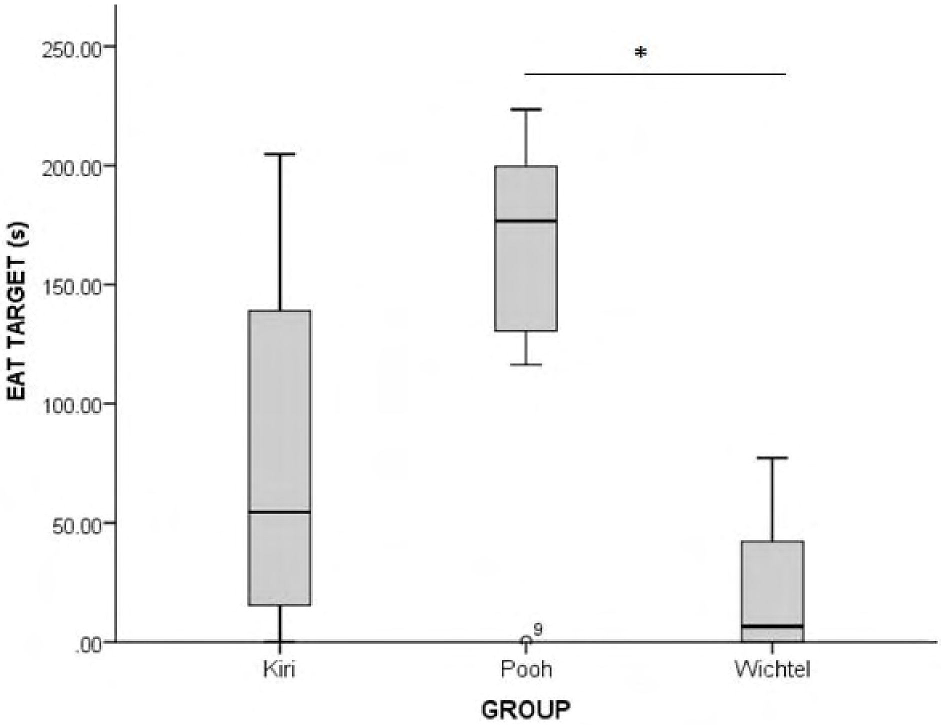

Figure 18: Box-plots showing differences between the groups (Kiri, Pooh, Wichtel) in duration of time spent eating the target (novel food) *("Eat target")* in tNF.

Test vs. Control Conditions

Wilcoxon Signed Rank test was used to compare different variables recorded during the tests and the controls. tP and cP revealed a significant difference in the mean duration of all calls emitted in the experiment (Wilcoxon Signed Rank test, N= 21, $p < 0.001$), with the test condition showing more emitted calls than the control condition (Figure 19).

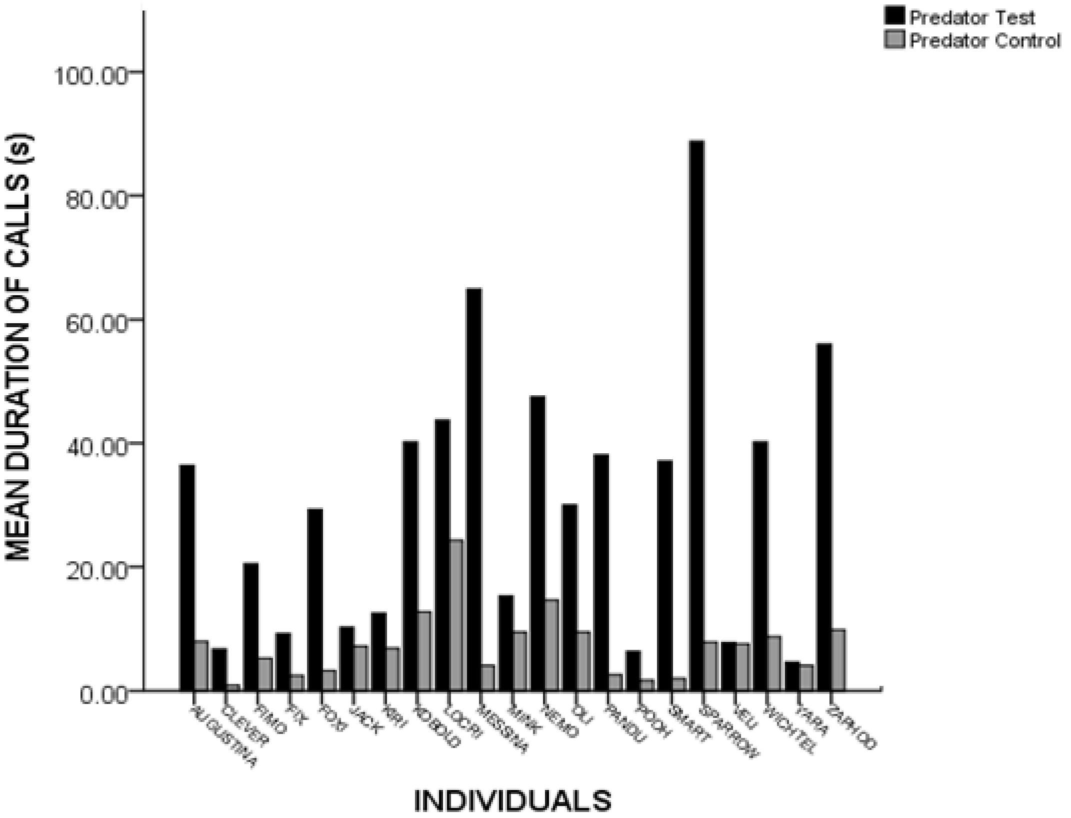

Figure 19: Clustered bar histogram showing the difference in mean duration of calls (*"Calls sum")* between the tP and the cP.

Also, the time spent in different compartments was analysed both in the controls and tests to control for subjects' preference in spending more or less time in certain compartments. In the cP the monkeys spent more time in the first experimental compartment, when compared to the tP (Wilcoxon Signed Rank test, $p < 0.001$). More precisely, only five monkeys (Fix, Kiri, Mink, Pooh and Yara) spent some time in the first compartment when exposed to the predator model in the same compartment (Figure 20). Similarly, in the test condition the subjects spent more time in the fourth and the fifth compartment (*"4th and 5th compartment"*), when compared to the control condition (Wilcoxon Signed Rank test, $p < 0.001$) (Figure 21).

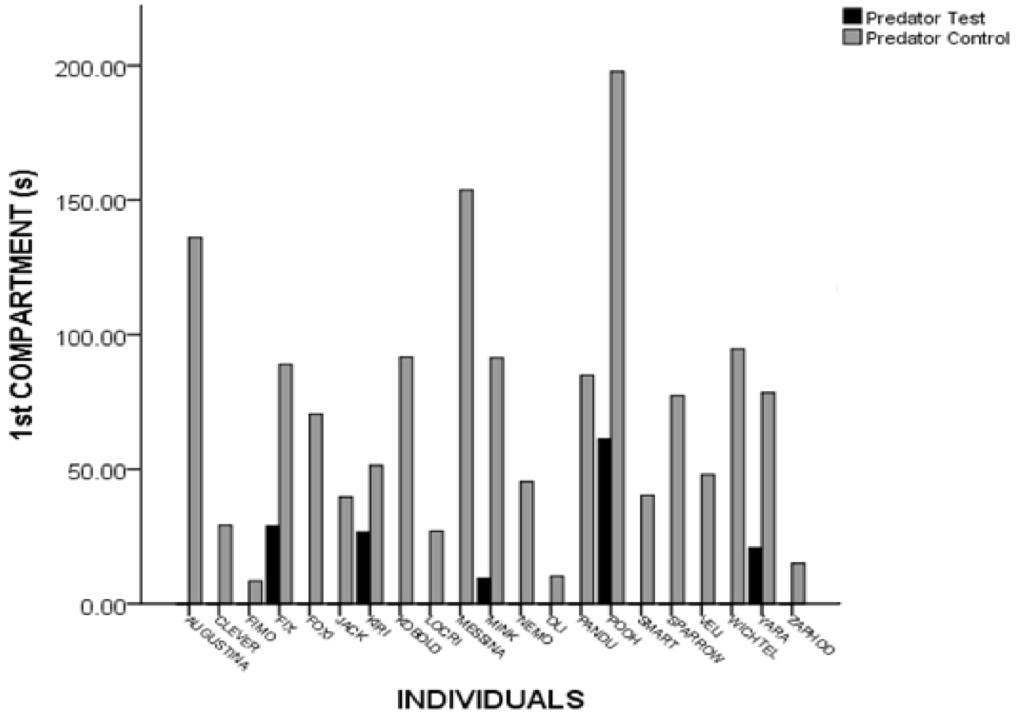

Figure 20: Clustered bar histogram showing the difference in duration of time spent in the first experimental compartment *("1st compartment")* between the tP and the cP.

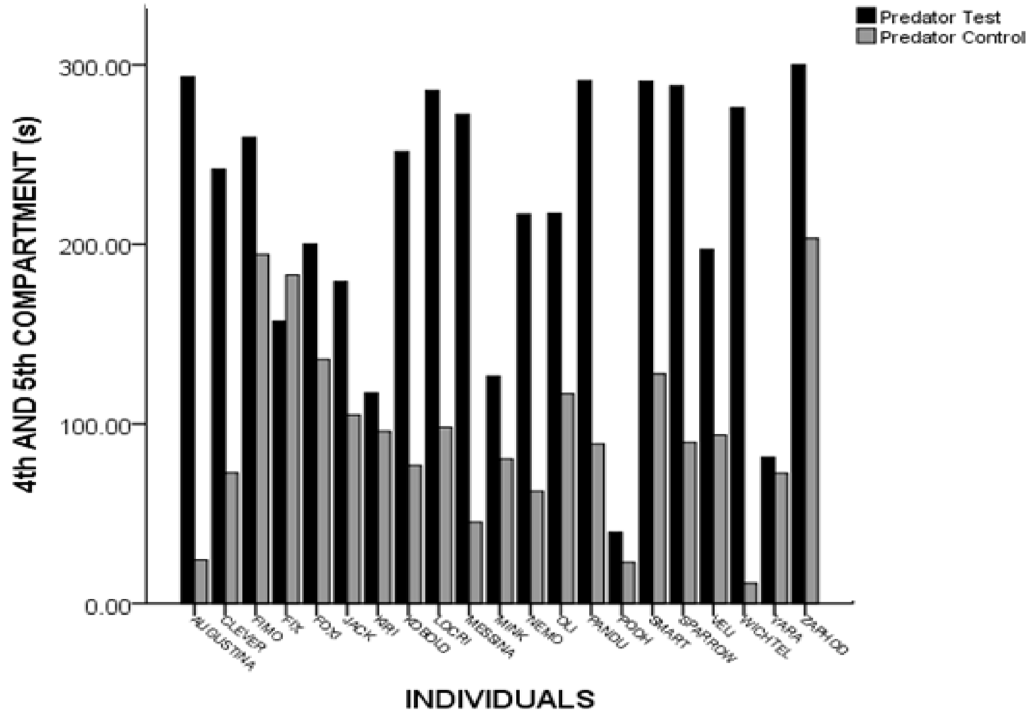

Figure 21: Clustered bar histogram showing the difference in duration of time spent in the fourth and fifth experimental compartment *("4th and 5th compartment")* between the tP and cP.

The latency to touch the transparent bowl with mealworms *(“Latency touch“)*, was also analysed in the tFUR and the cFUR (Figure 22). The subjects needed more time until they touch the reward in the test condition than in the control condition (Wilcoxon Signed Rank test, $p = 0.001$). Ten monkeys never touched the reward in the test condition at all, and therefore, these individuals were assigned with the total duration of the test.

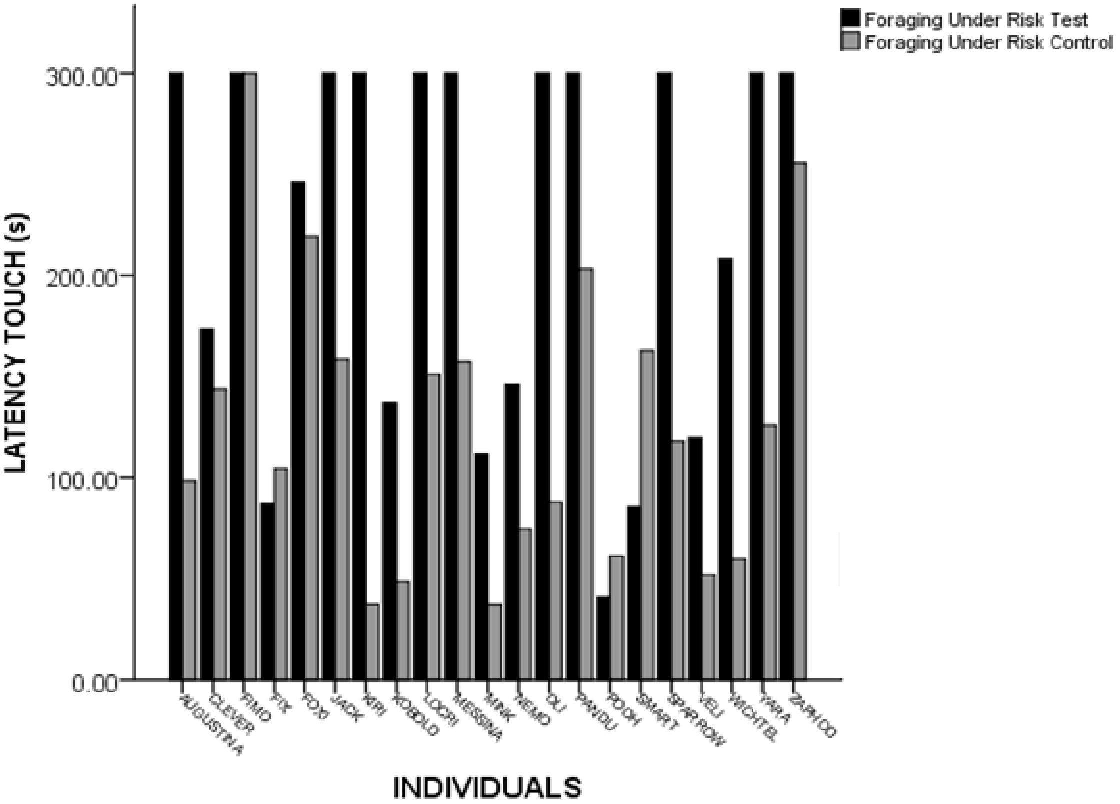

Figure 22: Clustered bar histogram showing the difference in latency to touch the transparent box with mealworms *(“Latency touch“)* between the tFUR and the cFUR.

I also analysed the time spent eating the reward (mealworms in a transparent box), labelled as *“Eat target“*, in the tFUR and the cFUR. In the test condition the subjects spent less time eating the reward than in the control condition (Wilcoxon Signed Rank test, $p < 0.001$), where some of them (e.g. Wichtel) spent more than half of the total time eating the mealworms. Some individuals, although eating for a long time in the control condition, did not eat at all in the test condition (e.g. Kiri, Yara, Oli) (Figure 23). Finally, the time spent focusing on the target *(“Focus target“)* was analysed in the tNO and the cNO (Figure 24). The results show that the subjects focused significantly longer on the object in the test condition than in the control condition (Wilcoxon Signed Rank test, $p < 0.001$).

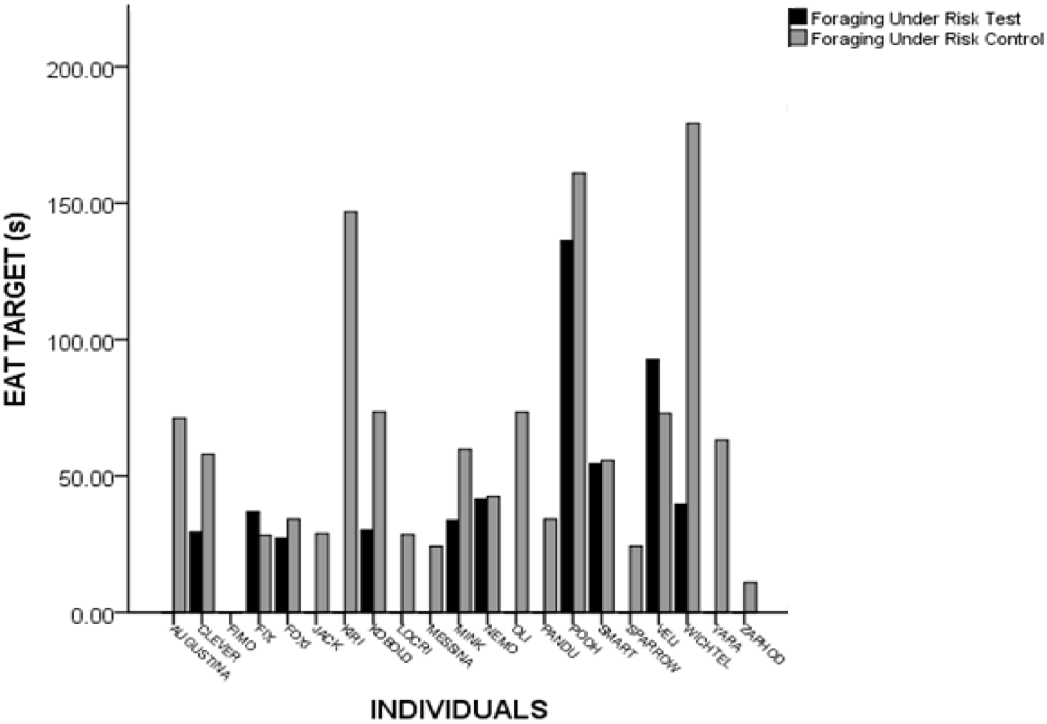

Figure 23: Clustered bar histogram showing the difference in time spent eating the mealworms *("Eat target")* between the tFUR and the cFUR.

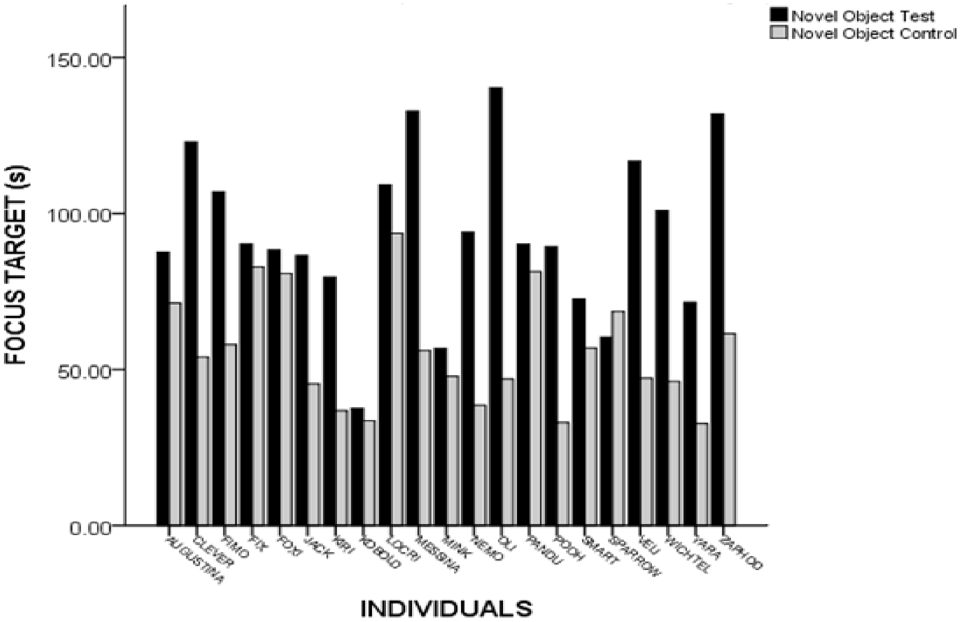

Figure 24: Clustered bar histogram showing the difference in time spent focusing on the target *("Focus target")* between the tNO and the cNO.

5 DISCUSSION

In this study, personality was tested in 21 common marmosets using an approach where the subjects were confronted with the experimental set-up individually. All traits were measured with several variables in five different experiments (General Activity, Novel Food, Novel Object, Foraging Under Risk and Predator).

The control conditions were always done before the test conditions, and were compared afterwards. As expected, behavioural responses were always stronger in the tests than in the controls. For instance, when subjects were exposed to a model of a predator hidden in leaves in the first compartment, they emitted more calls than in the control condition when they were just exposed to leaves in that compartment. The time spent in the first compartment was longer in the control condition, whereas the time spent in the fourth and the fifth compartment (furthest away from a threatening stimulus) was much longer in the test condition. Therefore, it seems that both the number of calls emitted and the location in the experimental cage are connected to a potentially dangerous or threatening situation. Differences between the test and the control conditions were also evident in the novel object tasks. Although novel objects looked similar in size and shape to the familiar object, the monkeys spent more time focusing on the novel objects than on the familiar ones. Additionally, in the foraging under risk tasks, when required to forage close to a lychee fruit (with a snake-like skin), the subjects needed more time to touch the highly valuable reward (mealworms) and they spent less time eating the reward than in the control condition.

Importantly, many variables measured in the experiments (88 in total) showed consistency in the individual behavioural response between temporally separated experiments (Session 1 vs. Session 2). This repeatability was fairly high, and also in accordance with the repeatability range of personality traits found in many other species (Bell et al. 2009). Most of the variables showed a high repeatability both in frequencies and in durations, but, to avoid data redundancy, only the durations were taken into further analyses. Also, many vocalisations showed a temporal repeatability, but for a still unknown nature of some calls (which behavioural response they actually represent), only a total number of all vocalisations was taken into further investigations. Some variables, however, did not show a temporal repeatability, such as latencies in most of the tests. This is in accordance to previous studies. Massen and colleagues (*submitted*) suggested that this temporal inconsistency could be due to a habituation effect, specifically in novelty (here, Novel Object or Novel Food), or a decrease of the perceived threat (here, Predator or Foraging Under Risk). Although some individuals showed a high repeatability in entering latencies across the experiments, this was not generally the case for the majority of individuals, and was, therefore, not evident in the results.

The temporally consistent variables were also tested for their contextual consistency. It was expected that the individuals would have a similar response in behavioural variables across different experiments that were aiming for the same personality trait (Stamps & Groothuis 2010b, Massen et al. *submitted*). To mention some of these variables, *"Locomotion"* aimed to test the personality trait "Activity", and proved to be a salient contextually consistent variable, showing consistency across most of the tests (GA, tNO, cNO, tNF, cNF). Also, *"Compartment alternations"*, a variable that was also aimed to test for "Activity" showed high repeatability across most of the tests (tNF, cNF, tP, cP, cNO). *"Self-grooming"* was highly repeatable across novelty tests and controls (tNO, cNO, tNF), indicating not only "Boldness-Shyness", but also its potential use as a stress indicator in future studies. *"Calls sum"* showed to be highly repeatable in the contexts connected to possible life-threatening situations (tP, tFUR). Time spent in different compartments of the experimental cage proved to be a good temporally and contextually consistent variable describing "Boldness-Shyness" in different experiments. Similarly, Dammhahn and Almeling (2012) tested free-ranging grey mouse lemurs (*Microcebus murinus*) and obtained contextual consistency of behavioural variables expressed in a novel object and foraging under risk task that also aimed to test "Boldness-shyness". To sum up, the monkeys showed temporal and contextual consistency in many (although not all) behaviours.

Using a principal component analysis (PCA), it was investigated whether, and if yes, how personality traits are associated with each other as syndromes. The analysis indicated that all similar behaviours loaded on the same principal components in the PCA. I obtained four independent principal components. Three common personality traits ("Boldness-Shyness", "Activity" and "Exploration-Avoidance") were found, but additionally a new possible personality trait ("Vocalisations") emerged, which was not yet proposed as a personality trait in previous studies.

The first principal component, "Boldness-Shyness", formed a construct where the time spent in different experimental compartments was a predominant variable. The time spent in the first compartment and on the ground (tNO, tFUR) and in the second and the third compartment (tP) loaded highly and saliently on this component, and had a positive value; while the time spent in the fourth and the fifth compartment (tP) also loaded saliently, but had a negative value. This is in accordance with my expectations, and explains that boldness and shyness are different types of the same personality trait. In other words, individuals that spend more time in risky environments will automatically spend less time in safe environments (Sih et al. 2004a). Coleman and Wilson (1998), for instance, looked at boldness in sunfish (*Lepomis gibbosus*) and found that bolder sunfish feed more when they are exposed, acclimate more quickly to the laboratory setting and engage in more predator inspection than shy sunfish. Likewise, Dingemanse et al. (2003) found that bold great tits (*Parus major*) disperse further in the field than shy great tits.

The second component, "Activity", formed a construct where locomotion and compartment alterations were predominant variables and loaded very highly on this component. Additionally, the time spent in the fourth and fifth compartment (tNO) loaded saliently, but negatively and less strongly than on the first component. This is probably due to the fact that the highly active individuals are less prone to spend time statically in a safe environment. General activity as a personality trait in novel/familiar environment studies usually measures the amount of movement as an index of exploration, or as a control (baseline) for a later behaviour when the animal is exposed to experimental conditions (Dingemanse et al. 2002). The same concept was applied in this study, and in a number of other studies that also found activity to be an independent personality trait (e.g. Sih et al. 2003, Bell 2005, Massen et al. (*submitted*)).

The third component, “Exploration-Avoidance”, formed a construct where time spent focusing on the target and eating the target loaded highly on this component. *“Focus target”* (tNF) had a positive value, and *“Eat target”* (tNF) had a negative value, which can be explained in the sense that the individuals that focus on the target are also the ones that avoid risky situations, in contrast to the individuals that spend more time exploring the novelty in a possibly risky environment. Self-grooming and the latency to touch the novel food (tNF) loaded saliently on this component and both had a positive value, whereas time spent in the second and the third compartment (tP) had a negative value. One possible explanation could be that focusing on the target, self-grooming and a longer latency to touch the novel object/food might be avoiding behavioural mechanisms, whereas explorative behaviour could be understood as long time spent in proximity of the novelty. Although most authors describe Exploration-Avoidance as an independent construct (Massen et al. (*submitted)*, Dingemanse et al. 2002), some authors (Koolhaas et al. 1999) include Exploration-Avoidance in a more general component, and label it as “Proactive-Reactive Axis”. This component describes the proactive individuals as being both aggressive and bold, actively engaged in environmental exploration, manipulation and routines formation, and also as being dominant in a stable environment. Reactive individuals are described as being more cautious about external stimuli, less explorative, but better at responding to changing environments.

The fourth component, “Vocalisations”, was not expected to emerge from the PCA as an independent component. However, total duration of all the calls (tP, tFUR) was a predominant variable, loading heavily and positively on the fourth component. Besides this variable, the time spent in the second and the third compartment (tP) also loaded saliently and negatively. Considering that most of the calls emitted in tP and tFUR were calls that the subjects normally exhibit during some alarming situations (“tsik”, “tsik-ek”), it is not surprising that the amount of time spent in the most “risky” environment would load on the opposite side of the “Vocalisations” construct. In other words, if an individual is highly vocal and alert, it is less likely to spend time putting itself in a dangerous position. Also, there is a possibility that this component could be reflecting a personality trait “Sociability”, broadly defined as an individual’s reaction to the presence or absence of conspecifics (Réale et al. 2007, Koski 2011). In this study, all tests were done individually, hence the only possible social interactions of the isolated member and the rest of the family group were through different vocalisations.

Although still little is known about the effects played by social roles, sex and age on personality (Massen et al. (*submitted)*), the comparisons between sexes and among three family groups (Wichtel, Pooh and Kiri) served as additional illustrations of a complete behavioural repertoire of common marmosets, and interesting results were obtained. Sexes did not differ in “Boldness-Shyness”, “Activity” or “Exploration-Avoidance”. However, females scored higher than males in Vocalisations, or more precisely, the mean duration of calls emitted in tP and tFUR was longer for the females than for the males. This is rather surprising because previous studies on common marmosets found no difference between sexes in respect to the rate of different vocalisations (Bezerra et al. 2009) or “phee” call production (Norcross & Newman 1993). In contrast to this, various studies on tamarins showed sex differences in vocalisations (Miller et al. 2004, Weiss et al. 2001). This difference might be due to the fact that subjects were not presented with the same experimental set-up in previously mentioned studies, so this sex difference might be due to specific experimental set-ups used in this study. Here, marmosets mostly vocalised (tP, tFUR) with “tsik” or “tsik-ek”, calls they usually emit only in situations of some alarm (Cross & Rogers 2005). Therefore, in future studies it would be interesting to see whether females really “warn” other members of their group of a potential danger more than males do. Also, new studies should focus on gathering more information on the context and the nature of different calls, since there are still incomplete or even conflicting results from different studies.

The three family groups did not differ in “Boldness-Shyness”, “Activity” and “Vocalisations”. However, the “Exploration-Avoidance” construct yielded a significant difference, which was especially evident for the Wichtel group, having higher regression scores than the Pooh or Kiri group. The Wichtel group spent more time in the first experimental compartment (tFUR). In the same test, the Pooh group spent hardly any time in this compartment and could therefore be considered as being the least explorative of the groups. The Wichtel group consisted of the youngest and least experienced individuals, whereas the Pooh group consisted of older and more experienced individuals. Therefore, experience or age could have had an effect on their behaviour. However, the duration of time spent eating the novel food (what would be considered as an explorative tendency) was longest for the Pooh group, so no congruent conclusions about this can be made. At least in this study, it seems that the group affiliation does not have a large effect on marmosets’ behaviour.

It is rather difficult to compare the results of this study to other non-human primate personality studies. The main reason is that this study used an approach in which the monkeys are subjected to a series of behavioural tests, where they are confronted with different stimuli, in order to evoke a certain personality trait (Boldness-Shyness, Activity, etc.). Although animal personalities have recently received an increasing interest from many disciplines in biology and personality traits have already been studied in various taxa with many specially designed tests (novel object, novel environment, novel food, startle response, predator…) (e.g. Blumstein et al. 2010, Bell & Sih 2007, Dingemanse et al. 2002), there is still an abundance of behavioural rating studies where personality assessments are only made by human observers (Weiss et al. 2009, King & Figueredo 1997). Behavioural observations and/or experimental studies that code the observed/tested behaviour, without previous assumptions given to the emerging personality constructs, are still quite rare (Massen et al. (*submitted)*, Seyfarth et al. 2012, Koski 2011, Uher et al. 2008). In the study of Dammhahn and Almeling (2012), variation in boldness towards a novel object was tested in 36 free-ranging grey mouse lemurs (*Microcebus murinus*) on Madagascar. The results obtained suggested three personality constructs, labelled as “Exploration time”, “Boldness” and “Feeding time”. Also, boldness in the novel object task was correlated with the risk taking in a foraging task. Massen and colleagues (*submitted*) analysed the behaviour of 29 captive chimpanzees (*Pan troglodytes*) in ten different experiments, and found that they express personality in “Exploration tendency”, “Boldness”, “Persistence” and “Tool-orientation”. These traits formed two syndromes, “Exploration-Persistence” and “Boldness”. Koski (2011) observed 75 chimpanzees and found 15 highly repeatable behavioural variables, which suggested social personality traits labelled as “Sociability”, “Positive effect”, “Grooming equitability”, “Anxiety” and “Activity”. Therefore, it might be possible that personalities in chimpanzees consist of a range of both social and non-social personality traits. Uher and colleagues (2008) made a cross-species study on chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), gorillas (*Gorilla gorilla gorilla*) and orang-utans (*Pongo pygmaeus abelii*), and obtained seven personality traits, labelled as “Aggressiveness”, “Arousability”, “Anxiousness”, “Curiosity”, “Friendliness to human impulsiveness”, “Persistency” and “Physical Activity.” Although this study corresponded well to findings in other primate as well as human personality studies, a drawback was the small sample size (only five) per species. Similar future studies should consider, if possible, increasing the number of experimental subjects.

Given all this, there is still a lack of clarity in the world of primate personalities. Vocalisations appeared in my study as an important construct, and it should be analysed in a greater detail. More different vocalisations should be taken into account in future studies. The animals in this study were confronted with the experimental set-up alone, but because of the highly social structure of their family groups, further investigations should design experiments where monkeys would be tested in dyads or in family groups. This is usually how they are confronted with daily life problems, both in the wild and in captivity. Furthermore, a detailed description of the social structure should be entailed in the studies to account for the social roles that animals have in their groups (Krause et al. 2010), especially in highly social species as common marmosets. Additionally, collecting physiological measurements (e.g. level of hormones) (Lutz et al. 2000) would provide more insight into proximate mechanisms of individual behaviour.

6 CONCLUSION

In this study of consistent individual differences, four independent principal components were obtained, labelled as: 1) “Boldness-Shyness”, 2) “Activity”, 3) “Exploration-Avoidance” and 4) “Vocalisations”. The first three obtained personality components were common personality constructs, ubiquitous in the animal kingdom but additionally a new personality construct (“Vocalisations”) emerged, which was not yet proposed as an independent construct in previous animal personality studies. All components but “Vocalisations” showed no difference in sex, and all components but “Exploration-Avoidance” showed no difference in family groups’ affiliation.

Given the extensive list of papers, primate personality studies are momentarily blooming, but are still far away from universal agreement in terminology as well as in methodology. The ultimate task of personality psychology would be a general unification of both human and animal personality theory.

To make this task possible, and to thoroughly understand the evolutionary history and the significance of animal personality, it is becoming increasingly important to be familiar with approaches derived from quantitative genetics (e.g. Falconer & Mackay, 1996), advanced statistical techniques, and the role of proximate factors in life of an individual (e.g. hormones, genes and development). In this way, the evolutionary ecology of individual differences will finally become widely recognised, and as Charles Darwin once accentuated, it should be accepted that: “*Variety is the spice of life*” (Dall et al. 2012).

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8 APPENDICES

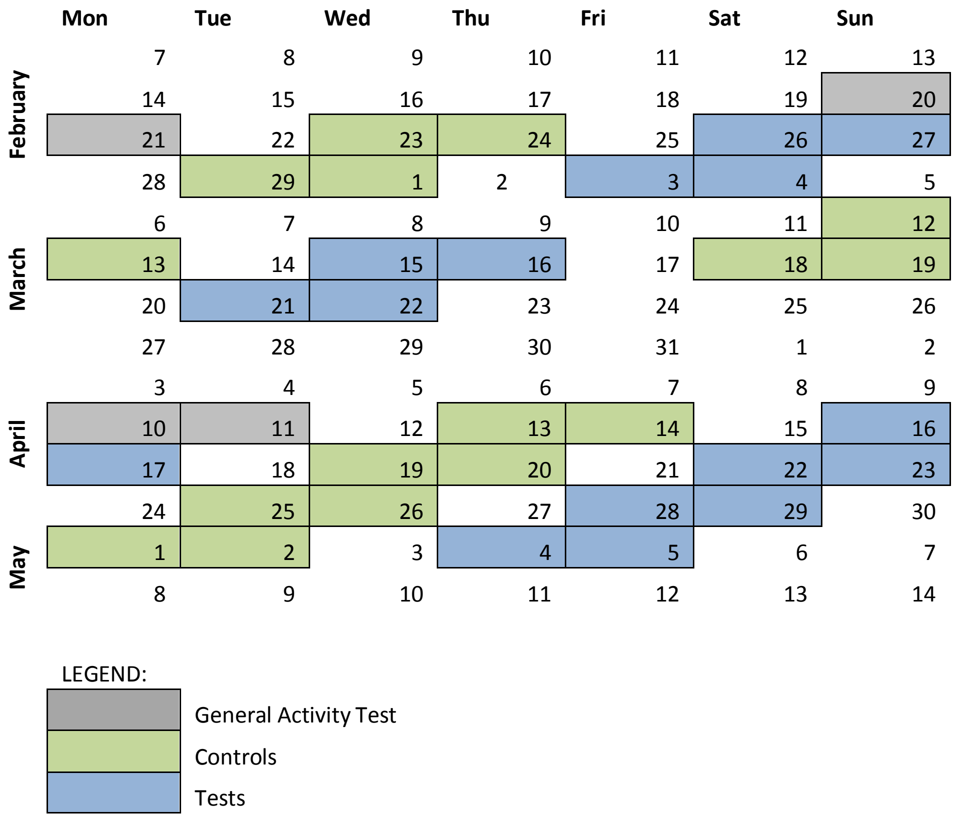
Appendix 1: All behaviours exhibited by the subjects in the experimental cage. “Categories” represent a broader division of given behaviours, “Behaviour” represents actions that the monkeys did in the experimental cage, “Description” is a thorough explanation of the given behaviours.

CATEGORY	BEHAVIOUR	DESCRIPTION
LOCOMOTION	LOCOMOTION	The actor runs, climbs, walks, jumps, or rolls over without holding/manipulating/eating, etc. any object/food.
	COMPARTMENT ALTERNATIONS	The number of compertments the actor alternated during the experiment.
LATENCY	LATENCY_ENTER	The time duration from opening the door until the actor enters the experimental cage. The actor is completely, with the whole body (without the tail) in the experimental cage.
	LATENCY_TOUCH	The time duration from opening the door until the actor touches the target (with hand/mouth/nose).
	LATENCY_BODY	The time duration from opening the door until the actor comes into one body length of the target (body length is counted without the tail).
THROW FOOD	THROW_FOOD	The moment in which the actor throws the object (food) from a height.
POSITION GROUND/MESH	GROUND	The subject is standing/moving/sitting on the ground, in the first compartment of the experimental cage.
	MESH	The subject is not on the ground, but in the first compartment of the experimental cage.
POSITION	1st COMPARTMENT	The actor is in the closest proximity to the plate/food/object/predator/mealworms, the experimental set-up is in this compartment. "Highest level of danger".
	2nd COMPARTMENT	The actor is in proximity of the plate. "Second highest level of danger".
	3rd COMPARTMENT	The actor is in the upper half of the experimental cage, directly above the experimental set-up. "Third level of danger".

	4th COMPARTMENT	The actor is in the upper half of the experimental cage, directly above the second experimental compartment. "Furthest away when still in the experimental cage".
	5th COMPARTMENT	The actor is outside of the experimental cage, in the „waiting“ compartment. Here is the monkey lured before the beginning of the experiment. After opening the opaque door, the actor can freely choose whether it will go inside the experimental cage or not. "Lowest level of danger".
TARGET-DIRECTED BEHAVIOUR	FOCUS_TARGET	The actor turns its head towards the experimental set-up.
	MANIPULATION TARGET_FOCUS LYCHEE	The actor focuses on lychee (head direction to the lychee), whilst manipulating the target (mealworms).
	MANUAL MANIPULATION_TARGET	The actor manipulates the target with its hands.
	NB EATEN_TARGET	The number of mealworms, bananas, etc. the monkey had eaten.
	SMELL_TARGET	The actor smells on the target (with nose).
	FOCUS TARGET_FOCUS LYCHEE	The actor alternates focus between the lychee & the target.
	ORAL MANIPULATION_TARGET	The actor orally manipulates the target, chews/bites/licks, but does not eat it.
	EAT_TARGET	The actor eats the target.
STRESS-RELATED BEHAVIOUR	SCENT_MARKING	The actor scent marks with genitals/nose, rubs genitals/nose on the object.
	SCRATCHING	The actor scratches himself.
	MANIPULATION_CAGE	The actor manipulates the cage (e.g. tears off the plastic).
	DEFECATION	The actor defecates.
	URINATION	The actor urinates.
	SELF-GROOMING	The actor grooms himself.
(PILO)ERECTION	PILOERECTION	The actor has a piloerected tail or a body.
	ERECTION	The actor has an erected penis.

VOCALISATIONS	TWITTER	A pleasing sound to the human ear (sounds like the trill of a small bird). Rapid series of elements, regularly and closely spaced and each rising swiftly in frequency. Mouth open.
	TSIK	Single tsik call. Very brief call; rises slightly in pitch before dropping straight down to a much lower pitch. Made when marmoset is alarmed.
	TSIK_RAPID FIRE	Rapid firing of multiple tsik calls. In the wild used as a mobbing call against conspecifics from other social groups, unfamiliar humans, and potential predators moving along the ground or in the trees. Made when marmoset is very alarmed.
	TSIK-EK	Tsik and ek straight after one another. Made in situations of some alarm.
	EK	Mouth slightly open. Low pitched call; single or several in close succession (can sound like a low squeak).
	COUGH	Low-pitched non-tonal utterance; mouth closed; situations of mild anxiety.
	CHIRP	Pleasant sound to human ears (sounds like the chirping of birds). Mouth closed or slightly open. Heard when near, or anticipating a favoured food.
	PHEE	Sounds like a soft whistle. Constant in pitch over the whole call; made singly or several in close succession. Mouth open or almost closed. Within-group contact call.
	LOUDSHRILL	Long, loud, shrill, piercing whistle-like call, of constant pitch. Long distance loud marmoset call. Mouth wide-open. An isolation call (a very long distance contact call) when made by isolated marmosets or those that have been separated from their partner. Aggressive or territorial call when made between groups by marmosets not separated from members of their own group.
	SEE	Brief call rising slightly in frequency. Made in situations of some alarm.
	GECKER	Low-pitched, harsh, staccato call. Body vibrates noticeably while making this call. Associated with intra- and intergroup aggression.
	WHIRR	Pleasant-sounding call to human ears, cyclically fluctuating frequency, various call lengths, mouth closed, body vibration.
	CALLS_SUM	Total number/duration (destinguishable with "_frequency"/"_duration") of all calls emitted during the experiment

Appendix 2.a: The schedule of experiments. Between Controls and Tests was always a one-day break. The General Activity test was always done as a first test. Between the two test sessions, there was a 14-days break.



	Mon	**Tue**	**Wed**	**Thu**	**Fri**	**Sat**	**Sun**
February	7	8	9	10	11	12	13
	14	15	16	17	18	19	▨ 20
	▨ 21	22	🟩 23	🟩 24	25	🟦 26	🟦 27
	28	🟩 29	🟩 1	2	🟦 3	🟦 4	5
March	6	7	8	9	10	11	🟩 12
	🟩 13	14	🟦 15	🟦 16	17	🟩 18	🟩 19
	20	🟦 21	🟦 22	23	24	25	26
	27	28	29	30	31	1	2
April	3	4	5	6	7	8	9
	▨ 10	▨ 11	12	🟩 13	🟩 14	15	🟦 16
	🟦 17	18	🟩 19	🟩 20	21	🟦 22	🟦 23
	24	🟩 25	🟩 26	27	🟦 28	🟦 29	30
May	🟩 1	🟩 2	3	🟦 4	🟦 5	6	7
	8	9	10	11	12	13	14

LEGEND:

▨ General Activity Test
🟩 Controls
🟦 Tests

Appendix 2.b: The monkeys were divided into two subgrups (subgroup A consisted of 11 monkeys, subgroup B consisted of 10 monkeys). The subgroup A was always tested one day before the subgroup B. The order of subjects was randomised within the subgroups.

SUBGROUP	INDIVIDUALS
A	Jack, Nemo, Clever, Veli, Smart, Kobold, Augustina, Messina, Locri, Oli, Fix
B	Yara, Sparrow, Pandu, Wichtel, Mink, Kiri, Fimo, Pooh, Foxi, Zaphod

Appendix 2.c: Apart from being divided into two subgroups, the monkeys were also divided into four groups to counterbalance the order of the tests.

GROUP	INDIVIDUALS	CONTROL 1, TEST 1	CONTROL 2, TEST 2	CONTROL 3, TEST 3	CONTROL 4, TEST 4
1	Pooh Messina Oli Zaphod Wichtel Clever	NOVEL OBJECT	NOVEL FOOD	PREDATOR	FORAGING UNDER RISK
2	Smart Yara Augustina Mink Kiri	NOVEL FOOD	PREDATOR	FORAGING UNDER RISK	NOVEL OBJECT
3	Pandu Fimo Jack Nemo Fix	PREDATOR	FORAGING UNDER RISK	NOVEL OBJECT	NOVEL FOOD
4	Locri Veli Sparrow Foxi Kobold	FORAGING UNDER RISK	NOVEL OBJECT	NOVEL FOOD	PREDATOR