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PERSONALITY ASSESSMENT IN ZOO-HOUSED SIAMANG GIBBONS AND SULAWESI MACAQUES.

By

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AUTHOR'S DECLARATION

At no time during the registration for the degree of ResM Biological Sciences has the author been registered for any other University award without prior agreement of the Doctoral College Quality Sub-Committee.

Work submitted for this research degree at the University of Plymouth has not formed part of any other degree either at the University of Plymouth or at another establishment.

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Abstract

Lewis James Rowden: Personality assessment in zoo-housed siamang gibbons and Sulawesi macaques.

Personality, differences in individual behaviour that are consistent across time and situations, have relatively recently been determined in a wide range of non-human animals. As the existence of animal personality increases within the scientific literature, the scope for practical application of knowledge increases concurrently. This study aimed to investigate ways in which personality data can be applied to the ex-situ management of threatened primate species. The first part of this research quantified personality in the European zoo population of *Symphalangus syndactylus*, including validation of trait rating techniques. Personality data were then applied to the study of reproductive success. Secondly, the ex-situ European population of *Macaca nigra* were also studied using the same Hominoid Personality Questionnaire (HPQ). With this form of trait rating previously validated for the species, personality data were here applied to investigate the temporal stability of traits within individuals. Results produced show that the HPQ produced reliable assessments of personality traits in both *S. syndactylus* and *M. nigra* (mean ICC[3,k] scores of 0.37 and 0.47 respectively). No significant effect of personality was observed on *S. syndactylus* reproductive success; however, the number of breeding transfers (males) and age (females) showed significant correlation with reproductive success scores. There were no significant correlations between the majority of trait scores when *M. nigra* were surveyed at two sample points, with an almost 10-year interval, suggesting that these traits were not temporally stable over that length of time. The reliability of personality assessment in captive primates, as well as potential applications for ex-situ species conservation, is discussed.

Key words: *Zoo, animal personality, Symphalangus syndactylus, Macaca nigra, reproductive success, temporal stability.*

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1. Introduction

1.1 The concept of personality in non-human animals

The idea of 'personality' is something that we are all aware of through common vernacular. Indeed, the concept of people having individual differences in behaviour is a commonly held and longstanding view. Origins of the idea are often attributed to scholars such as Francis Galton, who presented the idea of individual human characters and the ability to measure these (Galton 1884).

Personality was originally very much perceived as a uniquely human characteristic (Caillard 1894) and there have been disparate examples of works demonstrating personality in animals. One of the earliest comes from prominent scientist Ivan Pavlov, who was able to recognise four simple forms of personality in dogs (Weak, strong unbalanced, strong unbalanced slow and strong unbalanced mobile) featured in his neuroscience studies (Pavlov 1906). Work by Mary Crawford in 1938 made clear developments on this suggestion, by providing one of the first specified recordings of personality in animals. Her studies with laboratory chimpanzees (*Pan troglodytes*) identified that there were notable differences between individuals and involved perhaps the first tailored system to quantify these differences (Crawford 1938). Following this early work, the study of animal personality appeared to become unpopular. Studies were published infrequently and in relatively small numbers in the early 20th century (Allport & Odbert 1936; Nissen 1956; Yerkes 1939) and it is only in comparatively recent times that more evidence has been provided for personality in non-human animals. Modern opinion is that personality can be considered as a feature we share with many non-human animals (henceforth known as animals), in the same way as we share other behavioural and physiological responses (Gosling & John 1999).

A factor recognised as a potential cause of the delayed uptake of animal personality work within the scientific community, is the issue of defining ‘personality’. Even within the more established field of human personality research, there is no single definition that is universally accepted. It is commonly accepted that human personality involves characteristics that “describe and account for temporally stable patterns of affect, cognition, and behaviour” (Gosling 2008: 986); with thoughts, opinions, moods and feelings being key to this concept (Pervin *et al.* 2004). This lack of uniformity amongst definitions is also apparent when reviewing literature of animal personality (Weiss 2018). A range of terms that, on face value at least, are discussing the same phenomenon are commonly encountered. Terms such as ‘temperament’ (Curley *et al.* 2006; d’Eath *et al.* 2009; Martin & Réale 2008; McDougall *et al.* 2006), behavioural type (Sih *et al.* 2004) and more recently ‘behavioural syndrome’ (Dingemanse *et al.* 2012; Stamps & Groothuis 2010) are used by researchers in lieu of the term personality. It is accepted that this variation in terminology is inherent of any comparatively modern scientific discipline (Carter *et al.* 2013) and that it likely arises due to a desire to avoid anthropomorphisms/maintain terms used in different biological study areas (Gosling 2008); however consistent terminology will be necessary to undertake any coherent work in this field. Réale *et al.* (2007) present a comprehensive review of these interrelated terms, highlighting that definitions of animal personality typically refer to individual differences in behaviour that are consistent across time and situations. It is this definition of animal personality that will be used for this piece of work due to that fact it links coherently to the broader literature, including the similarities to terminologies used in the study of human personality.

1.2 The ecological context of personality

On face value, the concept of personality in living organisms seems to counter other ecological theorem. Theory suggests that one set of characteristics will be advantageous in a given environment, as well as the fact that behavioural plasticity by animals will make them better suited to that environment (Dall, Houston & McNamara 2004). This adaptability in behavioural expression seems to conflict with the agreed definition of personality described above, which begs the question of why individual personalities exist at all. As well as supporting this conflicting nature of personality and evolution, Briffa *et al.* (2015) highlight that personality occurs in a variety of taxa and across many contexts. Personalities manifest themselves in facets of species ecology such as foraging, territory exploration and courtship efforts; all of which have links to risk/aversion traits. Behavioural plasticity, adaptive changes in behaviour to better suit an environment, can take place in a rapid and reversible manner. Despite this however, consistent differences in behaviour are preserved over time. These reviews therefore suggest that stable personality exists alongside a more flexible set of behaviour responses, explaining how both strategies exist in nature (Briffa *et al.* 2015; Dall & Griffith 2014). Alongside this, natural evolution also involves selective changes to morphology which have a link to personality through genetic correlations in both sets of characteristics (Kern *et al.* 2016). Investigations into correlation between animal personality and physiological traits demonstrates potential adaptive value of varying personality traits. Maiti *et al.* 2018 investigate the link between variations in personality traits of three distinct genetic lines of bank voles (*Myodes glareolus*). Respective genetic lineages showed distinct personality types that would make them more or less successful in an environment, depending on selective pressure at the time. For example, some lines exhibited more explorative behaviour; which would be favoured in an environment with less resources but selected against in an environment with high predation pressure. This genetic component of personality demonstrates that the advantage of different personality types is that individuals will become better suited to the environment depending on the situation. A variety of personality types have selective advantages in the same way as variations of morphology (Dingemanse & Reale 2005).

Males and females of the same species are also known to be subject to varying selective pressures. This sexual antagonistic selection (Yli-Renko *et al.* 2018) can maintain sexual dimorphism of personality types. Where fitness has a negative correlation with one of the sexes, but a positive one with the other distinction in personality type occurs. This has been shown across taxa as well as in wild (Dingemanse *et al.* 2004; Patrick & Weimerskirch 2014; Pruitt *et al.* 2008; Thoré et al. 2017; Waters *et al.* 2017; White *et al.* 2019) and in captive settings (Dutton 2008; Yasui *et al.* 2013).

Defining personality as being consistent across time does not take into account the variation that exists in personality across ages. Age effects on personality are noted across species (Staes *et al.* 2017; Stanley *et al.* 2017; Zablocki-Thomas *et al.* 2018) and it is also acknowledged that there is development of personality (Stamps & Groothuis 2010). Knowledge of the onset of personality settlement, often at maturity, is required for each species and it should be acknowledged that there are both short- and long-term timescales that personality can be considered over (Stamps & Groothuis 2010).

1.3 Personality across taxa

A key feature of personality work in the past few decades has been to investigate the phenomenon within non-human animals, with results arising that would surprise the original theorists of personality. There has been a rapidly growing amount of literature investigating the occurrence of personality in animals e.g. Dall, Houston & McNamara (2004) and Sih *et al.* 2004; demonstrating how personality exists in a wide range of animal taxa. Considering the evolutionary context of personality, the scope of this phenomenon across taxa is perhaps not surprising. In his 2001 review of animal personality research to that time, Gosling identified 187 distinct research papers and, when grouped by taxonomy, demonstrated how the vast majority of studies have focussed upon vertebrate taxa; a substantial 96.79% (Gosling 2001). Indeed, a search of literature within Gosling's review period, as well as since this publication, reveals that there have been many studies of non-human, vertebrate personality including in bovids (Bergvall *et al.* 2011; Müller & von Keyserlingk 2006), cetaceans (Lusseau *et al.* 2006), canids (Bremner-Harrison *et al.* 2013; Svartberg *et al.* 2005) felids (Natoli *et al.* 2005), pinnipeds (Ciardelli *et al.* 2017), rodents (Günther *et al.* 2014; Le Cœur *et al.* 2015) corvids (Deventer *et al.* 2016), passerines (David *et al.* 2012; Dingemanse *et al.* 2003; Fox *et al.* 2009), reptiles (Godfrey *et al.* 2012; Waters *et al.* 2017), amphibians (Carlson & Langkilde 2013; Sih *et al.* 2003) and fish (Brown & Irving 2013; Cote *et al.* 2010).

Although the dominance of research with vertebrate taxa within the literature has continued, there is now an increased representation of invertebrate personality research. Although not an exhaustive literature review, following similar search methodologies as employed by Gosling (2001) identifies a number of invertebrate personality studies. These works both identify the need and expansion of this taxa focus (Kralj-Fišer & Schuett 2014) as well as carry out investigations into specific species and situations; including the squid *Euprymna tasmanica* (Sinn & Moltschaniwskyj 2005), hermit crab (Watanabe *et al.* 2012) and multiple species of spider (Foellmer & Khadka 2013; Holbrook *et al.* 2014; Sih & Watters 2005). Briffa and Greenaway (2011) have even identified personality in the beadlet anemone, *Actinia equine*. Increases in the amount of literature on non-human animal personality, including across previously understudied taxa, suggests that the field of study is considered increasingly relevant.

1.4 Primate personality

Perhaps because of a perceived 'relatedness' and therefore anthropomorphic affinity to the taxa, non-human primates (here on referred to as primates) have been the focus of an unparalleled quantity of animal personality research. Primatologists themselves recognise a distinction in the way that they study and interpret species of primates (Rees 2001) and within general scientific literature there is often a notable representation of primate taxa. Within zoo-specific research for example, Melfi (2009) highlights that fact that there has been a disproportionate amount of research focussing on primate species when compared to the numbers of individual animals of these species that are housed in zoos. We see a similar pattern represented in reviews of animal personality literature, with the review by Gosling in 2001 demonstrating that, of the summarised personality research, 55 (29.41%) were studying a species of primate.

In light of this taxonomic dominance within the literature, Freeman and Gosling (2010) carried out a systematic review of personality literature for primates. Several major trends within the field of primate personality research were identified. Over half of the studies assessed personality in both male and female primates, with a minority (20% and 5% respectively) of studies focussing solely on either males or females. The location of personality research for this taxon was also investigated, revealing that the majority of work took place in laboratory settings (59%) compared to the next most numerous setting of zoo-based work (14%) and only 9% of studies involving primates in the wild. This finding supports the practical logistics associated with personality assessment, principally repeatability and familiarity, which will be discussed throughout this thesis. With regards to a taxonomic perspective, although the primate order is well represented within animal personality literature there is very limited diversity in terms of species studied. The review identified that of the 394 species of primates known to science (at the time of publication), only 28 of these had been studied in relation to personality. Further to this, 40% of the studies on this order had been carried out on a single species of non-human primate, the Rhesus macaque (*Macaca mulatta*). The next most dominant in terms of number of studies is the chimpanzee (*Pan troglodytes*). This predisposition towards personality assessment in a restricted number of taxa continues to be reflected when examining the literature since 2010; with further studies on *M. mulatta* (Weiss *et al.* 2011) and great apes (Adams *et al.* 2012; Freeman *et al.* 2013; Schaefer & Steklis 2014) and only a minority on species not previously shown to be represented to such high degrees e.g. common marmosets (*Callithrix jacchus*) by Iwanicki & Lehmann (2015), Chacma baboons (*Papio ursinus*) by Carter *et al.* (2014) and Sulawesi crested black macaques (*Macaca nigra*), barbary macaques (*Macaca Sylvanus*) and squirrel monkeys (*Saimiri sciureus*) by Baker *et al.* (2015). This disproportionate representation of the Primate Order is perhaps not surprising considering the demonstrable taxonomic bias in biological research, both in the ex-situ zoo setting (Melfi 2009, Rose *et al.* 2019) but also the wider field of zoology (Bautista & Pantoja 2005). Research topics are also often directed by precedent, in that efficiencies and progression of research questions often mean studies focus on species that have already been studied in the same field. Research is often facilitated by or relies upon an existing baseline of evidence (Rose *et al.* 2019), and so this cumulative increase of work within certain species can be explained partly because of what is historically available. In addition to these points, research into primate personality is also considered to be popular because of the relevance to the study of the evolution of the phenomenon in humans and easily discernible and quantifiable relevant behaviours (Freeman & Gosling 2010) and also the opportunity to carry out comparative studies between similar species (Baker *et al.* 2015; Morton *et al.* 2013b).

Regardless of the reasoning behind this evidenced dominance in the literature, it is clear that despite the popularity of study there are still species and applications that warrant further investigation. Also, there is precedent for suitable methods of study within the taxa.

1.5 Methods for personality assessment

In a similar way to the variation in terminology related to the study of animal personality, there are also different methodologies that can be applied to the subject.

There are two distinct methods that are typically employed for the study of animal personality; trait ratings and behavioural coding. Both have been identified as methodological tools in numerous studies of primate personality (Freeman *et al.* 2011).

Trait rating involves a considered and subjective rating of defined behavioural adjectives, carried out by a person familiar with the individual animals in question. Definition of 'familiarity' is key; however, when a care-giver (often zoo keeper in zoo setting) has worked with the animal for an extended amount of time the system has been proven to be valid for various vertebrate taxa including elephants (Horback *et al.* 2013), spotted hyaena (Gosling 1998), parrots (Cussen & Mench 2014), pinnipeds (Ciardelli *et al.* 2017) and several species of primate (Freeman *et al.* 2013; Iwanicki and Lehmann 2015; Uher *et al.* 2008). There are even cases where a crosstaxa system has been shown as valid (Figueredo *et al.* 1995). Although there are several cited forms of rating tool e.g. Emotions Profile Index (Martau et al.1985), one of the most commonly applied in primate studies today is the Hominoid Personality Questionnaire (henceforth described as the HPQ). A precursor was first applied in the study of *P. troglodytes* by King & Figueredo (1997) with some of the traits taken from work listing personality 'items' (Goldberg 1990). Over time however, the HPQ has developed through further use. This tool involves familiar people rating individual animals on a designated scale for a series of adjectives or traits, allowing an average rating across observers. Potential weaknesses with trait rating are that it relies upon an appropriate list of traits being generated for use (Uher & Asendorpf 2008) and familiarity of raters is key and therefore cannot be used in all situations e.g. in-situ or with unidentifiable individuals/taxa (Vazire *et al.* 2007).

Behavioural coding typically involves collecting behavioural data through observations in natural conditions. This technique has been applied across taxa; including in primates (Fairbanks 2001; Konečná *et al.* 2008), pinnipeds (de Vere *et al.* 2017) and geese (Kralj-Fišer *et al.* 2010). This method is often employed when there is a focus on particular personality types e.g. the bold-shy continuum is Fairbanks (2001). Behavioural tests such as the open field test (Finger *et al.* 2016; Mella *et al.* 2016) or novel object tests (Baker & Pullen 2013; Blaszczyk 2017) are specific forms of behavioural coding. These involve exposure of animals to set situations with any effect observed and measured; however, there are issues here with standardisation and ambiguity as to what is being measured (Perals *et al.* 2017). Coding is often considered to be more objective as there is an assumption that accurate collection of observed behaviour is possible; however, this may lead to assumptions and lack of validation in personality work (Vazire *et al.* 2007, pg 193).

This variation in methods is sometimes cited as another limiting factor in the progression of animal personality work (Gartner & Weiss 2013); however, the diversity in available tools could also be seen as an advantage for the field. Each technique can be used in isolation, or as a combination of methods depending on the situation and requirement. When both of these techniques are used in conjunction within the same study it is possible to make more confident conclusions as to whether methods validate one another through agreement (Fox & Millam 2010; Konečná *et al.* 2008).

1.6 Applications of personality assessment

Application of reliable assessment methods mean that an understanding of animal personality can be used in a variety of animal-related fields.

Capitanios' 2011 work summarises investigations into the role of personality in non-human primate health. The link here can be behavioural and/or physiological (considering the genetic link to personality), involving a relationship between an animal's personality type and susceptibility to disease. For example, Robinson et al. (2018) showed that more confident and more anxious *M. Mulatta* experienced fewer injuries and associated infections. This sort of information can be applied when it comes to pro-active and re-active veterinary intervention in animals; for example, to identify individuals that would be at increased risk of receiving injuries or succumbing to clinical illness during management interventions such as social introductions and enclosure transfers (Gottlieb *et al.* 2018)

The welfare of animals is commonly considered for those in captivity rather than in the wild. How well an animal adapts to the captive environment has been shown to relate to individual personality type in a number of settings. Routine management and husbandry (Carlstead *et al.*1999a; O'Malley *et al.* 2019), behavioural management such as environmental enrichment (Gartner & Powell 2012), appropriate human-animal relationships (Phillips & Peck 2007) and identifying risk of abnormal behaviours (Gottlieb *et al.* 2013; Shepherdson *et al.* 2013) are all aspects of management that can be informed by personality assessment.

Personality has also been demonstrated to effect reproductive success in animals. It has been demonstrated that the personality of pair-breeding species, such as cockatiels (*Nymphicus hollandicus*) (Fox & Millam 2014), cheetah (*Acinonyx jubatus*) (Wielebnowski 1999), black rhinoceros (*Diceros bicornis*) (Carlstead *et al.*1999b) and giant pandas (*Ailuropoda melanoleuca*) (Martin-Wintle *et al.* 2017), effects reproductive success in captivity (. Application of this knowledge to improve the breeding potential of conservation populations will have a key impact on animal welfare and species conservation.

Conservation action can be facilitated through application of animal personality data. In-situ population management (Bremner-Harrison *et al.* 2018) and conservation action such as translocation and release (Baker *et al.* 2016; Germano *et al.* 2017; Haage 2016) are all noted to benefit from robust assessment of animal participants. Application of these data informs practice and ensures mitigations are as effective and viable as possible. McDougall *et al.* 2006 highlight the value of understanding personality within managed populations of conservation species to avoid issues with population change over time. This change could reduce conservation potential of species in line with adaptation to captivity.

Works by researchers such as Gartner and Weiss (2018), Powell and Gartner (2011) and Watters and Powell (2012) effectively summarise the valuable application of personality data to a range of conservation populations. These published works demonstrate how personality assessment has been applied to managed populations of animals in a range of settings, including zoos and those existing in range countries.

1.7 General aims and hypotheses

The above review of the subject area demonstrates that despite the documented increase in the number of animal personality studies over the last few decades, there continues to be value in further work. This is especially true for certain taxa and in certain settings or applications. The Freeman and Gosling review published in 2010 and also a review of the literature available since this date show that there are species of primates that have not been studied with regards to personality. At the same time, the evaluation of methods to assess personality in non-human primate species has continued. This is true both for species where assessment has already taken place (allowing for the development of related questions) as well as for species not yet studied in this regard.

As such, this study aims to carry out assessment of personality in two distinct species of non-human primates. The focus for both species will be how this information can be applied to the management of *ex-situ*, zoo-housed populations; to facilitate best-practice conservation management.

Evidence shows that behavioural ecology of species interacts with expression of personality characteristics (Eckardt *et al.* 2014); therefore we hypothesise that differences in the natural ecology of each species will translate as different personality profiles. Despite these differences though, the application of knowledge from personality assessment has potential to be applied equally in each case.

Empirical work for each species will be presented as independent chapters within this thesis, followed by an overall synthesis of conclusions.

1.8 General methodology

As part of the review process for this project, an application for support from the British and Irish Association of Zoos and Aquariums (BIAZA) was submitted. The received endorsement (Appendix 1) aimed to facilitate participation by institutions contacted for both sets of studies. Similarly, communication with EEP coordinators for both species was arranged to facilitate distribution of materials relevant to the projects.

All aspects of the study were observational and strictly non-invasive, with collection of small amounts of data from human participants. Prior to any data collection, the project received ethical approval from Plymouth University (Appendix 2).

2. Personality assessment in a zoo-housed population of siamang gibbons (*Symphalangus syndactylus*).

2.1 Introduction

2.1.1 Species biology

The siamang gibbon (*Symphalangus syndactylus*) is a Southeast Asian Hylobatidae primate, largest of the family. A strictly arboreal species classified as Endangered by the International Union for Conservation of Nature (IUCN) Red list, *S. syndactylus* have a range across Indonesia, Malaysia and Thailand (Nijman & Geissman 2008). Diet selection varies from largely folivorous to largely frugivorous across this range, which is hypothesised to reduce resource pressure on populations ((O'Brien *et al.* 2003). Original reports identify the species as purely monogamous (Chivers 1974) with greater cohesion of pair-bonds than in other Hylobate species– expressed through increased mutual grooming and physical proximity/contact (Palombit 2006). Since work by Chivers however, extra-pair copulations have been recorded by Palombit (1994) and multi-male groups have been observed in some parts of their geographic range (Lappan 2007). Most commonly though, the species is considered to exist in-situ within monogamous groups (breeding pair and dependent offspring), involving some level of parental care by both parents (Lappan 2008). Communication between individuals in close proximity often take the form of subtle facial expressions such as formal biting, grins and offering body parts (Liebal *et al.* 2004). Sexual maturity of wild *S. sndactylus* is believed to be around eight to nine years of age (Geissmann 1991), with this social factor being the key driver of dispersal from natal groups; often most frequently by male offspring (Lappan 2007). Following this dispersal, the species is stringently territorial (Nijman & Geissman

2008) with long-distance and familial communication (particularly pair duets) through vocalisation (Chivers 1976; Geissmann 1999). Palombit (1995) reports that inter-birth interval for the species may be between four and five years, with greater variance in female reproductive success than would be expected from a similar monogamous species. This increased variance is attributed to selective pressures, such as renewed mate choice and associated extra-pair copulations.

2.1.2 Zoo-housed siamang

S. syndactylus in captivity exhibit similar patterns of shared parental care (Dielentheis *et al.*1991) to wild counterparts. There is however a difference in mean age of sexual maturity, with zoo-housed males being able to breed at four years of age and females 4.3 years (Geissmann 1991).

According to the Zoological Information Management System (ZIMS) the species is held globally in 137 institutions, with a total population of 389 individuals (Species360 2019). Within the European region, the European Association of Zoos and Aquaria (EAZA) oversee the management of a population through the specialist programme known as a European Endangered Species Programme (EEP) (EAZA 2019). This studbook manages the population of a species within the region and directs management; including breeding and transfer recommendations informed by genetic and demographic analysis of the population as a whole.

In response to the species IUCN threat status and EAZA Taxon Advisory Group (TAG) priorities, the *S. syndactylus* population is managed with a breeding recommendation to maintain the current genetic variability through selective breeding of certain individuals. These individuals will have been identified as having mean kinship scores that mean their genetics are not as highly represented in the population or those of suitable age that studbook keepers consider prudent to move (based on species knowledge) (T Dobbs 2017, personal communication, 21 November; EAZA 2019). The EEP programme for the species is generally considered successful; however, there have been some issues with social management of breeding groups. Anecdotal reports from animal managers within the region suggest that young male offspring (when reaching approx. two years of age) become the focus of atypically high levels of conspecific aggression within their natal groups (Z Showell 2018, personal communication, 5 February). This is considered premature by several years, even based on the earlier onset of maturity in captivity, and results in complicated management challenges for the programme. Aggression has been cited as a management issue in other species of captive gibbon (Haarl *et al.* 2016), with personality type hypothesised as being a factor influencing onset and occurrence of this aggression.

2.1.3 Aims

Considering the paucity of general scientific work on *S. syndactylus*, the IUCN and ex-situ status of the species, as well as the fact that there have been no published works on gibbon personality; it was decided to complete an assessment of the EAZA *S. syndactylus* population in the hope of informing captive management.

Specifically, this study aimed to:

1) Validate trait rating as a method of assessing personality type in *S. syndactylus.*
2) Investigate correlation between any identifiable personality traits in the EEP population with reproductive success.

2.2 Methodology

2.2.1 Trait rating questionnaires

Following a review of existing trait rating systems for primate personality assessment, the Hominoid Personality Questionnaire (HPQ) was selected for use. This modified system (Weiss *et al.* 2009; 2011) has been used extensively in the study of primate personality; which enables future comparative analysis of data collected across multiple studies (Freeman *et al.* 2013). Review of the HPQ traits and existing literature on siamang ensured that questionnaire content reflected the natural behavioural repertoire of the species; important for use of non-specific trait rating systems (Uher & Asendorpf 2008).

In total 61 traits were selected for use in this study. Sixty of these were taken directly from previously used HPQ investigations, with 54 referring to general behaviour of siamang (interactions with conspecifics) and six referring to how animals interact with humans (human-animal interactions). Each of these 60 traits had associated definitions that explained the behavioural context of the identified trait. Upon compilation, the list of traits and associated definitions were reviewed by peers (familiar with primate behaviour) to confirm understanding of the process and proper use of the form.

The questionnaire (Appendix 3) was distributed electronically to all institutions within the EAZA EEP region holding *S. syndactylus*. Forty-eight institutions (holding a total of 171 animals) were identified as participants using the Zoological Information Management System (ZIMS) and confirmed by the species studbook keeper. Through an email contact list and with direct EEP support, the questionnaire was sent to named members of staff at each of the EEP institutions with a set of instructions for HPQ completion. Familiar members of staff; defined as people who have worked with the animals in question for one year or more (Koski *et al.* 2017; Morton *et al.* 2013a), were asked to complete the questionnaire for each animal over one year in age (Morton *et al.* 2013b) in their care. It was also requested that these ratings were completed independently from other colleagues and that ideally more than one of these familiar keepers would complete the trait rating for each animal, allowing for inter-rater reliability assessment.

Raters were asked to score each animal on a 7-point likert scale (1= animal shows a total absence or negligible amounts of the trait, 7= animal displays the trait extremely frequently) for each of the 60 featured trait adjectives. For the final question regarding physicality, potential responses to this question were either attractive, clean or scruffy; with raters only being able to select one of these options for each animal. Data relating to each individual animal were requested to provide confirmation of identification (name and studbook number), sex, age at time of survey completion and social situation. The latter information was requested to allow for investigation into whether social situation may relate to personality; as observed in other animal species (Chamove *et al.* 1972; Sih *et al.* 2015), and to assist in the identification of reproductive situation analysis.

In addition to the scoring of traits, each rater was asked to provide information on their gender, zoo of employment, date of completion and aspects of their familiarity (length of time working with the species, length of time working with the particular animals in question and frequency of contact with these animals).

2.2.2 Behavioural coding

No published work is available that lists the HPQ as a tool for personality assessment in *S. syndactylus*. Behavioural data were collected at a sample of institutions that could then be used for validation of the trait rating method. These data were collected at three zoological institutions: Fota Wildlife Park (FWP), Ireland; Thrigby Hall Wildlife Gardens (THWG), UK; and Twycross Zoo (TZ), UK. All three institutions are part of the EEP and therefore intended participants in the HPQ assessment and were selected due to a combination of accessibility and because of the numbers of animals held, as recorded in ZIMS. A total of 16 animals were observed across the institutions, with more detail outlined in Table 1.

Table 1*: Information relevant to the S. syndactylus involved in behavioural coding, including; age at time of observation, enclosure (conspecifics in shared environment) and time of year data were collected.*

Name	EAZA Studbook number	Age (years.months)	Sex	Zoo	Enclosure	Hours of data collected	Number of days data collected	Dates of data collection
Kaya	514	26.10	Female	FWP	A	10.5	9	23/8/17-2/9/17
Clyde	164	36.11	Male			10.5	7	
Homer	944	5.04	Male			10.5	8	
Rocky	896	12.03	Male		B	10.5	6	
Bart	905	10.02	Male			10.5	7	
Theo	873	14.03	Male	THWG	C	9.5	8	24/3/18-4/4/18
Hovis	953	5.07	Male			9.5	9	
Silas	2060	12.03	Male		D	10	9	
Blossom	881	12.08	Female			9	8	
Joe	956	5.02	Male			9.5	8	
Spike	830	17.00	Male	TZ	E	10	10	21/11/17-1/12/17
Tara	828	17.00	Female			10	10	
Stig	2077	8.00	Male			10	10	
Tango	292	24.00	Female		F	10	10	
Denzel	919	8.00	Male			10	10	
Darwin	951	5.04	Male			10	10	

Observations consisted of 30-minute focal follows, with state behaviours recorded using instantaneous sampling every 30 seconds and event behaviours recorded through all-occurrence sampling at any point within the focal session (Martin &

Bateson 2007). An ethogram of behaviours is shown in Appendix 4, developed from literature on species biology. As well as state behaviour at each 30 second time interval, the identity and proximity of nearest conspecific were recorded with proximity in a designated category from 1-4 (Appendix 4).

To ensure independence of data points, focal sessions were randomised and spread across enclosure within each zoo i.e. no second observation session was conducted in the same enclosure without a break of at least 15 minutes between sessions. Data collection was distributed across the duration of each research visit and time of day for each animal, with a minimum of one focal observation carried out per day per animal.

At two of the institutions (FWP and TZ), a member of husbandry staff from each zoo, familiar with the focal animals and their species behaviour, carried out a simultaneous observation using the methods described above. This allowed for assessment of inter-observer reliability by comparing results obtained by the author and the member of husbandry staff.

Behavioural data were used to generate an activity budget for each focal animal (daily mean proportion of time spent performing each state behaviour, the averaged across the observation period for each individual) as well as proportions of time in proximity categories and mean rates of event behaviours. To facilitate validation analysis and allow for meaningful interpretation, these behaviour data were consolidated into ‘behaviour categories’. The consolidation process involved grouping compatible behaviours following similar approaches as seen in other works validating trait rating data. Observed behaviours were grouped into the categories based on what would be expected to be relevant for validating calculated personality domains. Details of these consolidated categories can be found in Table 2. Daily average proportions of each of these behaviour categories were generated for individual animals to allow for statistical analyses.

Table 2: *A summary of how state and event behaviours used during behavioural coding observations were consolidated into behavioural categories for further analysis.*

Behaviour categories	**Constituent state behaviours**
Social positive	*Contact, embrace, allogroom, mutual grooming, play, reproductive, vocalisation (social).*
Locomotion	*Brachiation, locomotion*
Explorative	*Interaction with environmental enrichment, Interaction with enclosure.*
Beneficiary	*Receives grooming*
Resting	*Stationary, resting*
SDB	*Scratch, yawn, body shake.*

2.2.3 Data analyses

2.2.3.1 Inter-observer reliability of questionnaire data

To determine the reliability of trait ratings carried out across institutions, Intra-class Correlation Coefficients (ICC[3,k], ICC[3,1]) were analysed in SPSS vs. 24 (SPSS®, IBM®, Chicago, IL, USA). Across-subject reliability incorporated questionnaire data for 44 animals at 11 institutions that were rated by two or more observers. Mean trait ratings for each animal were used for further analysis, therefore average measures ICC[3,k] for all 60 traits were used to identify those that were reliable for retention in further analysis (Shrout & Fleiss 1979). The mean ICC[3,k] scores for each trait were averaged across institutions and criteria for inclusion of a particular trait for future analysis set at a positive ICC[3,k] value. Although there are cases within the literature where minimum inclusion criteria are set as ICC scores ≥.50 (Baker & Pullen 2013), there is precedent amongst primate personality work for the inclusion of any positive scores (Adams *et al.* 2015; Jin *et al.* 2013; Schaefer *et al.* 2014; Weiss *et al.* 2006; Weiss *et al.* 2015).

2.2.3.2 Principal Component Analysis of questionnaire data

Following removal of traits with negative ICC values, a Varimax rotated Principle Component Analysis (PCA) was run using animals' mean trait scores for each reliable trait. This analysis (and all subsequent) were performed using R-Statistics® (R Core team 2019), with R-script shown in Appendix 5. Outputs of this analysis in the form of parallel analysis (and associated scree plot) were consulted to determine the number of components that account for the most variability seen within the data. The results of the analysis were then reviewed, with each trait being assigned to the component that was associated with the most highly loaded (either positive or negative) value for that trait across component scores. These components, with the assigned traits encompassed within each grouping, became the personality domains for each individual animal.

Personality domain scores were formulated by averaging the mean scores of traits (with positive ICC values) assigned to respective components for each animal. Traits with negative loading had a reverse score calculated by subtracting the mean trait score of HPQ responses from 8; producing an analogous value to the scores positively loaded. This value of 8 was used as it provides a negative value for each of the trait scores from the 7-point Likert scale. These analyses produced an animal-specific score for each domain, which were incorporated in further investigation into personality validity effect.

2.2.3.3 Reliability of questionnaire data

Generalised Linear Mixed Models (GLMM) were carried out to assess the main fixed effects of Sex, Age and each personality trait identified from the PCA score on the proportion of time spent performing each behaviour category. Enclosure was also included as a random effect as behaviour is likely to differ as a result of animals being kept in different zoos/enclosure. Examination of behavioural differences between enclosures indicated that even within zoos animals exhibited differences in behaviour between enclosure therefore Enclosure rather than Zoo was included as a random effect in the model to account for these differences. GLMM models were carried out in a stepwise fashion, with the least significant fixed effect being removed from subsequent models. AIC values were compared in order to identify the most suitable model for interpretation (Appendix 6).

2.2.3.4 Personality scores and reproductive success

For all individual animals of breeding age that had completed HPQ's returned, a score for reproductive success was calculated using data obtained from the EEP studbook. This was calculated by dividing the number of offspring surviving to more than 2 years by the sum of years the animal in question was reproductively active (age-age at first reproduction). The criterion of offspring surviving to two years was selected to align with the recently updated minimum dependence age of wild infant *S. syndactylus* (Morino & Borries 2017), average inter-birth interval (Lappan 2008) as well as the longer infant maturation period in this species compared to other gibbon species e.g. *Hylobates lar* (Dal Pra & Geissmann 1994). Studbook and ZIMS data were reviewed to confirm periods of reproductive potential for all animals, including checking data on contraception and social access to a viable breeding partner. In addition to data on reproductive activity, other variables were extracted from the studbook; including origin (wild caught or captive born), rearing status (parent- or hand-reared) and details on transfers between zoos (age at first transfer and total number of transfers). A series of Generalised Linear Models (GLMs) were run to include these other factors alongside the personality domain scores and reproductive success (Appendix 7). Separate sets of models were run for males and females to eliminate a factor from the models.

2.3 Results

2.3.1 Trait rating questionnaires

Completed questionnaires were received from 24 of the contacted institutions (a response rate of 50%), providing survey data for a total of 77 animals – 44 males and 33 females. The mean age of animals in the data set was 14 years and 10 months, ranging from two to 46 years old.

Across all returned questionnaires, a total of 50 animal husbandry staff completed the HPQs. Mean time spent working with *S. syndactylus* as a species was six years and eight months and mean familiarity with the group being rated was five years and eight months. Both of these measures had a range of one to 36 years. At an institution level, the mean number of raters was two, ranging from one to five people per institution. Eight of the 24 institutions had only a single keeper carry out the HPQ rating. Fifty percent of respondents work with the animals they rated on a daily basis, with 40% working with them weekly and the remaining 10% monthly.

2.3.2 Behavioural coding

Behavioural data were compiled for each of the individual animals, and a summary of these can be found in Appendix 8. Measures of percentage agreement for simultaneous observation sessions (at two of the zoo sites) by different observers were applied as a measure of inter-observer reliability. These showed 100% agreement at each of the two zoo sites.

Average proportions of state behaviour categories (Table 3), proportions of time in proximity categories 1 and 2 (Table 4) as well as mean rate of SDB occurrence per 30 minutes (Table 5) are shown below. These variables were all incorporated into validation analysis.

Table 3: *Mean proportions of state behaviour categories for each focal animal involved in behavioural observations.*

	Behaviour (mean % of time observed)				
Animal	**Social positive**	**Locomotion**	**Explorative**	**Beneficial**	**Resting**
Kaya	15.22	6.33	4.89	1.67	54.00
Clyde	2.43	8.57	0.29	0.00	59.43
Homer	6.63	19.38	3.63	9.75	31.38
Rocky	5.67	32.83	1.33	0.67	45.17
Bart	6.57	10.71	0.14	2.29	37.71
Theo	2.75	15.88	0.00	21.38	49.25
Hovis	33.00	15.22	0.22	3.00	38.78
Silas	16.67	8.67	0.00	2.78	61.00
Blossom	13.63	5.75	0.25	28.38	36.25
Joe	20.50	20.75	5.63	3.50	32.50
Spike	3.40	9.90	0.20	2.10	70.80
Tara	17.30	5.90	0.40	2.20	58.70
Stig	10.90	23.60	4.30	6.80	31.30
Tango	1.90	8.60	0.20	0.70	56.40
Denzel	8.50	26.40	1.70	0.80	29.90
Darwin	10.80	26.20	5.90	1.20	30.20

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Table 4: *Proportion of time animals involved in behavioural coding observation spent proximity to their nearest conspecific. 1; immediate contact/ within 1 meter, 2; between 1 and 5 metres.*

	Proximity category (mean % of time observed)	
Animal	**1**	**2**
Kaya	48.16	43.26
Clyde	31.74	57.61
Homer	26.21	59.85
Rocky	17.97	51.60
Bart	23.15	47.25
Theo	25.97	63.66
Hovis	15.83	63.65
Silas	21.82	60.07
Blossom	12.53	62.29
Joe	19.71	64.84
Spike	38.15	40.64
Tara	49.56	37.44
Stig	47.31	35.58
Tango	15.44	39.89
Denzel	32.22	60.01
Darwin	58.14	29.08

Table 5: *Rate of self-directed behaviours for individuals involved in behavioural coding observations.*

	Rate of Self-Directed Behaviour (mean/30 minutes)
Animal	**SDB**
Kaya	2.09
Clyde	0.93
Homer	1.87
Rocky	1.09
Bart	0.65
Theo	1.67
Hovis	1.82
Silas	1.46
Blossom	0.60
Joe	1.54
Spike	2.02
Tara	2.59
Stig	1.53
Tango	2.14
Denzel	2.25
Darwin	3.18

2.3.3 Data analyses

2.3.3.1 Inter-observer reliability of questionnaire data

Full Intra-class Correlation Coefficient results for the 44 animals included in this analysis can be found in Appendix 9. This features both the ICC [3,1] and ICC [3,k] values for all traits included in the HPQ, regardless if they generated a negative result meaning it is not salient for this investigation.

Appendix 10 details the across-subject reliability for the institutions included in this analysis, whereby the mean overall ICC[3,k] values are salient. In total, 35 of the 60 traits were found to reach the criterion for reliability and are included in analysis for domain formation. Mean ICC[3,k] scores for salient traits was 0.37, ranging from

0.122 (depressed) to 0.81 (playful). Analysis was only performed on a sub-set of animals (44 from the 77 with HPQ data); however, traits identified as reliable here were assumed to be reliable for all animals and data from all animals rated by HPQ response were included in the PCA analysis.

2.3.3.2 Principal Component Analysis of questionnaire data

Consultation of the scree plot identifies that three components account for variance in the data and should be retained. Through assigning traits with the most highly loaded scores to respective components (as highlighted in Table 6) the following personality domains were distinguished; Excitability, Dominance and Introverted.

Table 6: *Eigen values from Principal Component Analysis showing how traits were assigned to one of three personality domains. Colour coding represents the positive loadings (green) and negative loadings (red) that assigned traits to their respective domains.*

	Personality Domain		
Traits	**Excitability**	**Dominance**	**Introverted**
Impulsive	**0.71**	0.11	0.15
Inquisitive	**0.7**	0.17	-0.15
Playful	**0.69**	-0.03	-0.28
Imitative	**0.65**	-0.14	-0.05
Active	**0.64**	-0.02	-0.22
Disorganised	**0.64**	-0.2	0.34
Defiant	**0.62**	0.11	0.23
Reckless	**0.56**	0.11	0.13
Distractible	**0.56**	-0.13	0.38
Innovative	**0.49**	0.13	-0.08
HA Social	**0.47**	0.06	-0.35
Clumsy	**0.45**	-0.37	0
Thoughtless	**0.43**	-0.17	0.05
Dependent	**0.43**	-0.42	-0.21
Dominant	-0.18	**0.79**	0.02
Stingy	0.06	**0.75**	-0.15
Bullying	0.02	**0.75**	0.2
Aggressive	0.15	**0.71**	0.21
Decisive	0.06	**0.62**	-0.11
Independent	0.16	**0.6**	0.01
Persistent	0.42	**0.46**	0.12
Protective	-0.02	**0.35**	0.04
Intelligent	-0.08	**0.32**	-0.1
Helpful	0.03	**0.16**	-0.12
Vulnerable	0.27	**-0.48**	0.32
Depressed	-0.06	-0.11	**0.81**
Unperceptive	0.12	0.1	**0.71**
Solitary	-0.07	-0.05	**0.67**
Irritable	-0.01	0.38	**0.65**
Fearful	0.12	-0.39	**0.58**
Anxious	0.1	-0.43	**0.56**
HA Oblivious	-0.19	0.12	**0.5**
Erratic	0.4	0.38	**0.45**
Autistic	0.12	0.05	**0.44**
HA Cautious	-0.27	-0.21	**0.43**

Appendix 11 shows the process of domain formation.

2.3.3.3 Reliability of questionnaire data

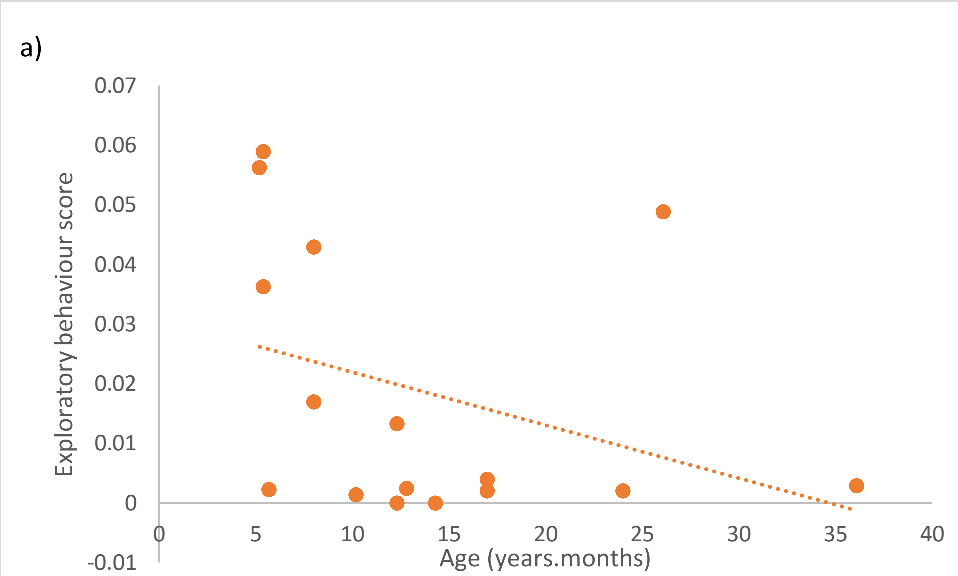
Stepwise modelling of Generalised Linear Mixed Models produced the output also displayed in Appendix 6, with significant results for each behaviour category shown in Table 7. Figures 1-6 also show the scatter plots for directionality of these significant relationships.

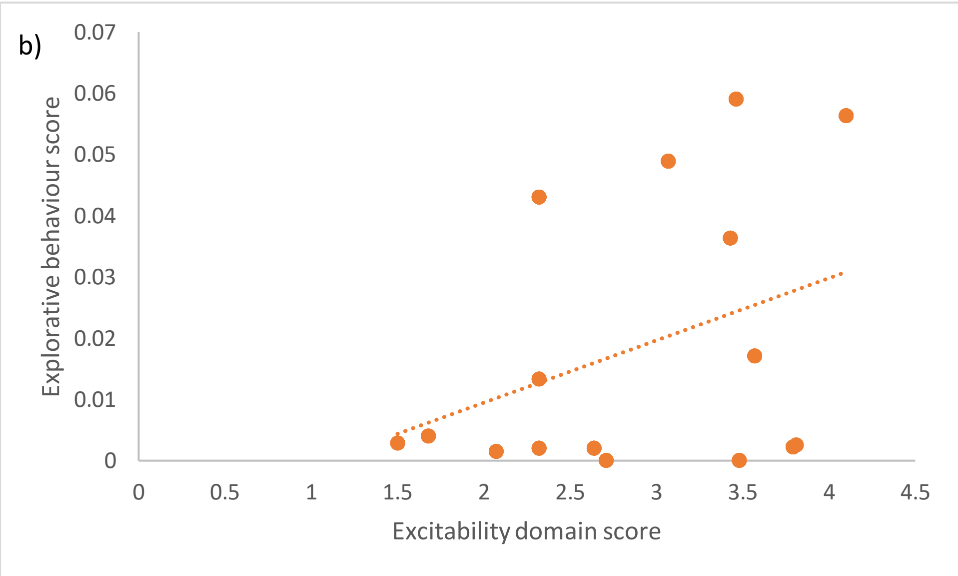
Table 7: *Presentation of significant relationships between behaviour categories and main effects. P-values to nearest 2 decimal places. All df 128*

Behaviour category	**Main effects**	**Significance?**	***P*-value**	**Direction of relationship (value)**
Social Positive	Excitability	Yes	.017	Positive
	Dominance	Yes	.025	Negative
Locomotion	Sex	Yes	<.001	-
	Excitability	Yes	.022	Positive
	Dominance	Yes	.042	Negative
	Introverted	Yes	.006	Negative
Explorative	Age	Yes	.029	Positive
	Excitability	Yes	.001	Positive
	Introverted	Yes	<.001	Negative
Beneficiary	Sex	Yes	<.001	-
	Dominance	Yes	.001	Positive
Resting	Age	Yes	.007	Positive
Proximity 1	Age	Yes	.013	Positive
	Excitability	Yes	.003	Positive
	Introverted	Yes	.002	Negative

Figure 1: *Plot for significant main effects of Excitability and Dominance personality domains on the Social positive behaviour category.*

Figure 2: *Plot for significant main effects of Excitability, Dominance and Introverted personality domains on the Locomotion behaviour category.*


a)
Exploratory behaviour score
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
-0.01
0
5
10
15
20
25
30
35
40
Age (years.months)


b)
Explorative behaviour score
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
Excitability domain score

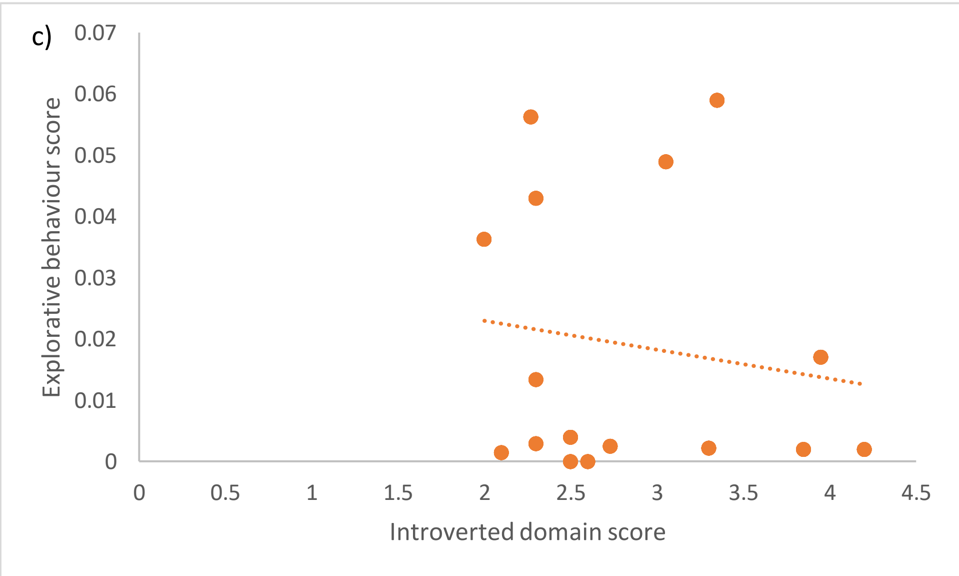

c)
Explorative behaviour score
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
Introverted domain score

Figure 3: *Plots for significant main effects of a) Age, b) Excitability personality domain and c) Introverted personality domain on the Exploratory behaviour category.*

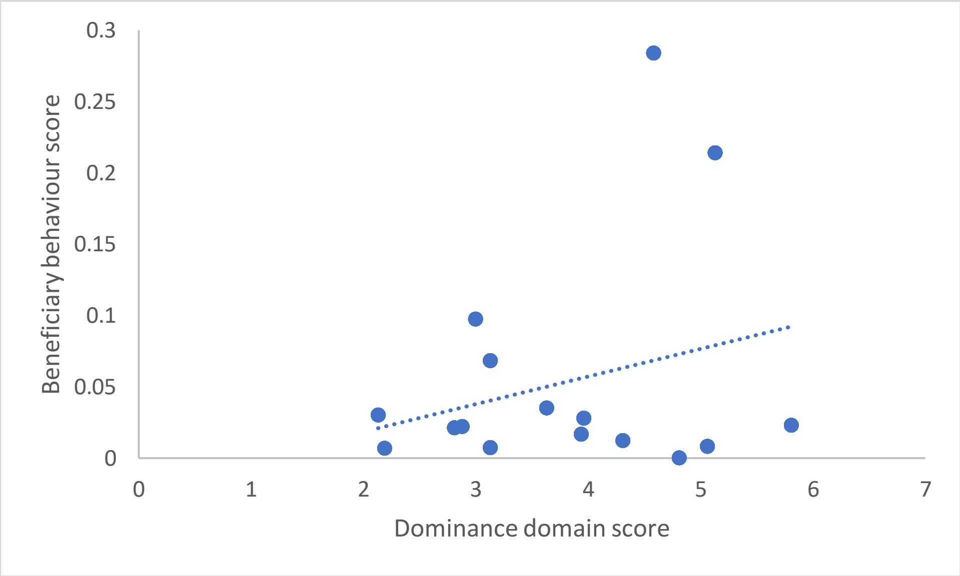


Figure 4: *Plot for the significant main effect of Dominance personality domain on the Beneficiary behaviour category.*

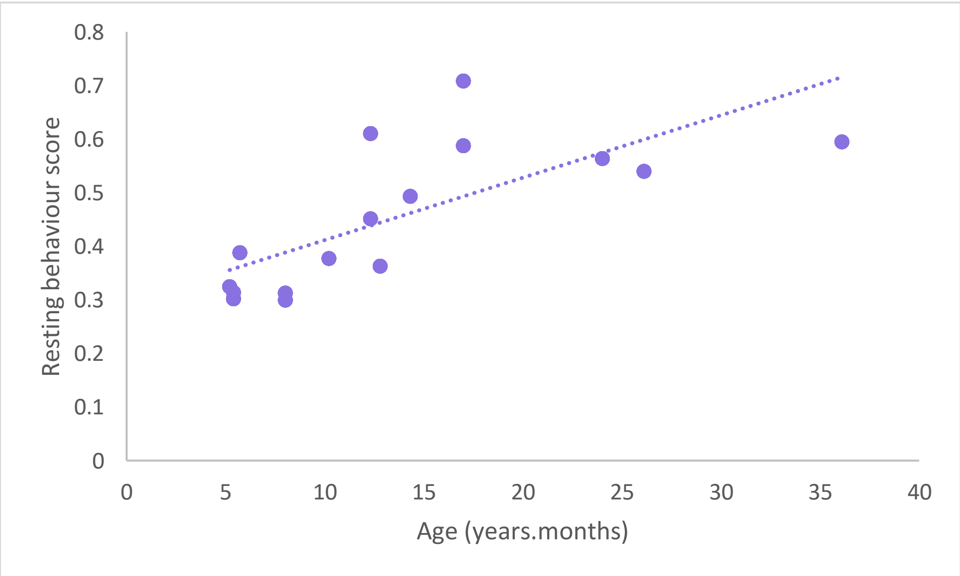
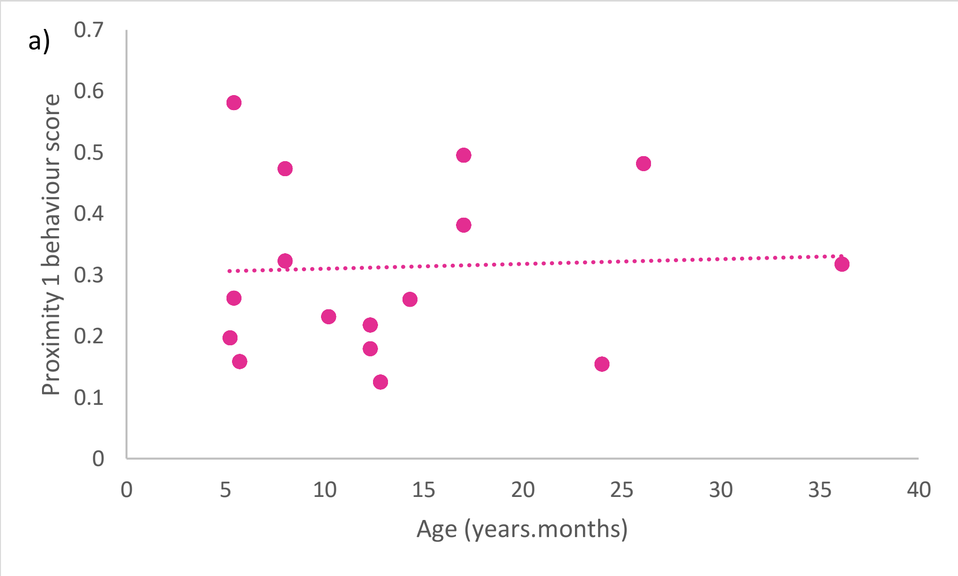
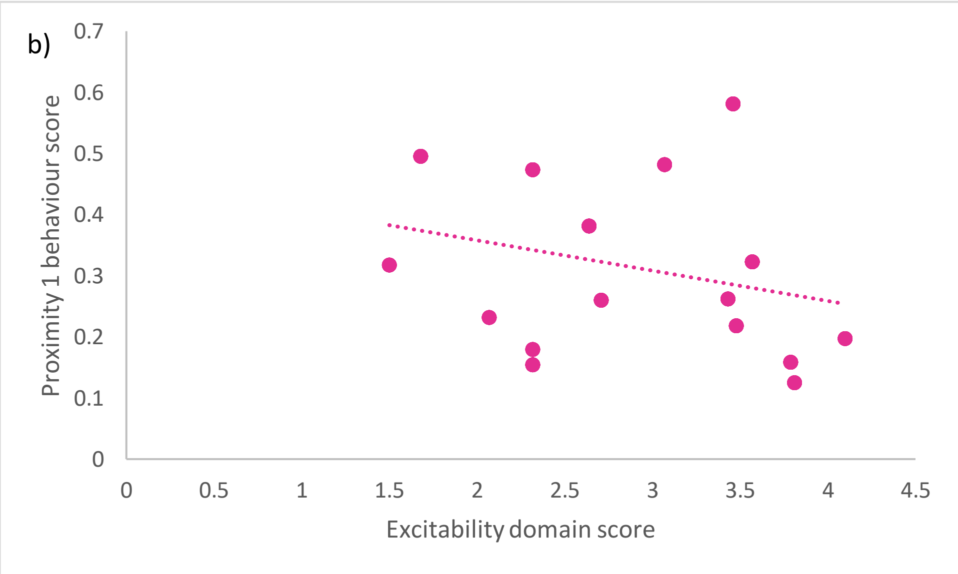


Figure 5: *Plot for the significant main effect of Age on the Resting behaviour category.*


a)
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Proximity 1 behaviour score
0 5 10 15 20 25 30 35 40
Age (years.months)


b)
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Proximity 1 behaviour score
0 0.5 1 1.5 2 2.5 3 3.5 4 4.5
Excitability domain score

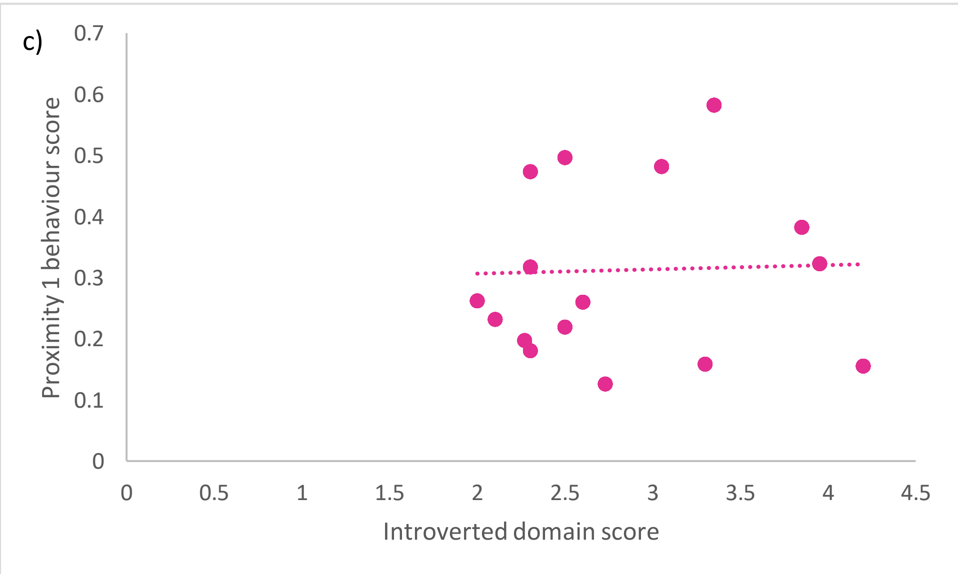

c)
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Proximity 1 behaviour score
0 0.5 1 1.5 2 2.5 3 3.5 4 4.5
Introverted domain score

Figure 6: *Plots for the significant main effects of a) Age, b) Excitability personality domain and c) Introverted personality domain on the Proximity 1 category*

Sex has a significant relationship with the categories Locomotion and Beneficiary. Males in the sample (n=12) had significant higher mean scores for both behaviour categories than females (n=4), with details shown in Figure 7 and Table 8.

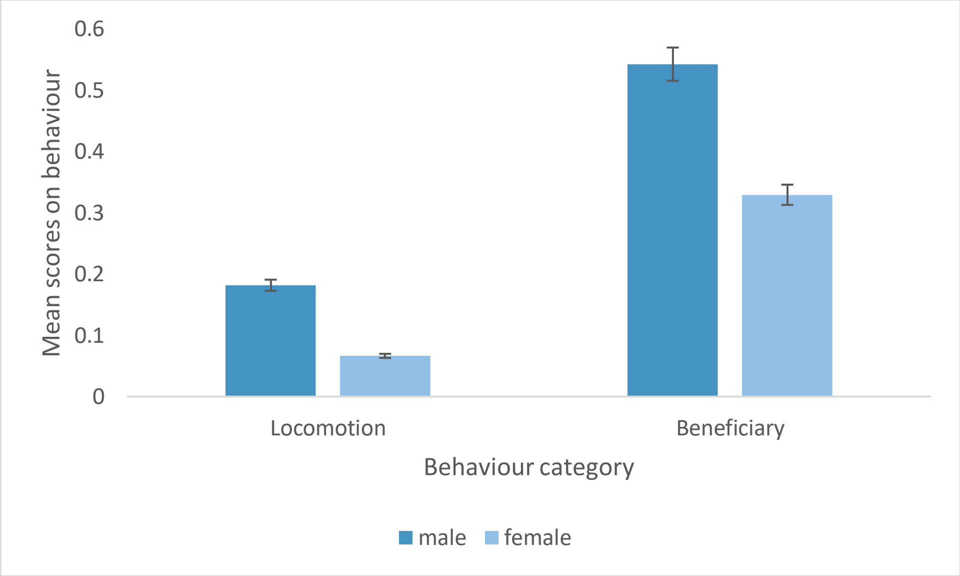


Figure 7: *mean behaviour category scores in males and females for Locomotion and Beneficiary.*

Table 8: *mean category scores for males and females.*

	Sample size (n)	Mean Locomotion score	Mean Beneficiary score	SE Locomotion	SE Beneficiary
Males	12	0.18	0.54	0.02	0.02
females	4	0.07	0.33	0.01	0.07

The categories ‘Proximity 2’ and ‘SDB’ showed no significant relationships with any of the main effects, although for Proximity 2 the domain excitability approached significance (*P*=.074).

2.3.3.4 Personality scores and reproductive success

Eighteen males and 20 females (41% and 61% respectively of total HPQ respondents) were included in this analysis after they were identified as having been in a breeding situation at some point in their lives. Studbook data for these individuals that were extracted for analysis are shown in Tables 9 and 10. Origin and rearing status were not included in the GLM analysis due to issues with the model.

Table 9: *Studbook data for male S. syndactylus used to investigate factors affecting reproductive success.*

Animal	Age (years.months)	Excitability score	Dominance score	Introverted score	Age at first transfer (years.months)	Transfer number	Reproductive Success score
Xhulu	24.04	2.285714	3.6875	1.75	7.09	1	0.531915
Guildo	19	2.571429	4.625	1.4	5.04	1	0.289436
Ricki	33	2.571429	2.5625	2.65	2.04	1	0.286738
Steve	20	2.885714	3.525	2.84	N/A	0	0.167224
Sam	31.05	4.214286	4.25	4.5	N/A	0	0.181901
Ufo	24	2.785714	3.625	2.5	5.07	1	0.390407
Niam	31	2.392857	5.125	1.5	7.11	1	0.334129
Otto	25	2.47619	2.875	1.9	5.1	1	0.211752
Josef	35	3.928571	4.75	2	3.05	2	0.194238
Clyde	36.11	1.5	4.8125	2.3	4.02	1	0.333333
Luang	32	3.02381	5	2.033333	5.03	1	0.160128
Taos	14.04	3.357143	5.125	4	5.04	1	0.28777
Patchouli	17	3.357143	3.75	1.5	6.04	2	0.337079
Ya'an	12	2.464286	3.9375	1.95	5.11	1	0.4
Spike	17	2.642857	2.8125	3.85	N/A	0	0.100402
Kiao	12.02	3.214286	6	2	3.1	1	0.607287
Theo	14.03	2.714286	5.125	2.6	N/A	0	0.168067
Silas	12.03	3.47619	3.958333	2.5	N/A	0	0.199203

Table 10: *Studbook data for female S. syndactylus used to investigate factors affecting reproductive success.*

Animal	Age (years.months)	Excitability score	Dominance score	Introverted score	Age at first transfer (years.months)	Transfer number (total)	Reproductive success score
Spindle	24.03	2.321429	4.625	1.9	7.08	1	0.502513
Konnie	14	2.857143	5	1.4	5.05	1	0.28777
Gerda	25	2.214286	2.125	1.6	N/A	0	0.42328
Lisa	14	3.814286	5.5	2.44	6.04	1	0.143885
Ella	25	4.071429	3.125	3.6	6	2	0.188679
Ebonie	29.08	2.785714	3.6875	3.9	6.07	1	0.181984
Schnudi	46	2.857143	3.25	3.1	3.03	1	0.083333
Tsao	25	1.892857	4.875	3.9	5.1	1	0.39019
Noemie	29	2.678571	4.5	1.6	5.06	1	0.333333
Niki	20	3.928571	3.125	2.2	6.09	2	0.333333
Kaya	26.1	3.071429	3.9375	3.05	4.02	1	0.367454
Simone	32	2.785714	4.125	2.033333	N/A	0	0.14301
Terkina	13	2.857143	4.375	2.1	5.06	1	0.288184
Samtra	17	3.428571	3.5	1.6	6.04	1	0.30303
Jambi	10	2.321429	3.875	2.8	4.02	1	0.404858
Sanka	15	2.547619	2.791667	3.033333	3.1	1	0.40404
Tarragon	17	1.678571	2.875	2.5	N/A	0	0.100402
Tango	24	2.321429	3.125	4.2	2.07	1	0.167411
Nina	20.05	3.142857	4.25	2.1	1.1	2	0.26738
Blossom	12.08	3.809524	4.583333	2.733333	3.1	1	0.199601

Appendix 7 shows the R-script analysis and stepwise GLM for this investigation.

Male reproductive success was found to only have a significant positive relationship with transfer number (P=.014), where individuals who had been transferred a higher number of times having increased reproductive success (Figure 8).

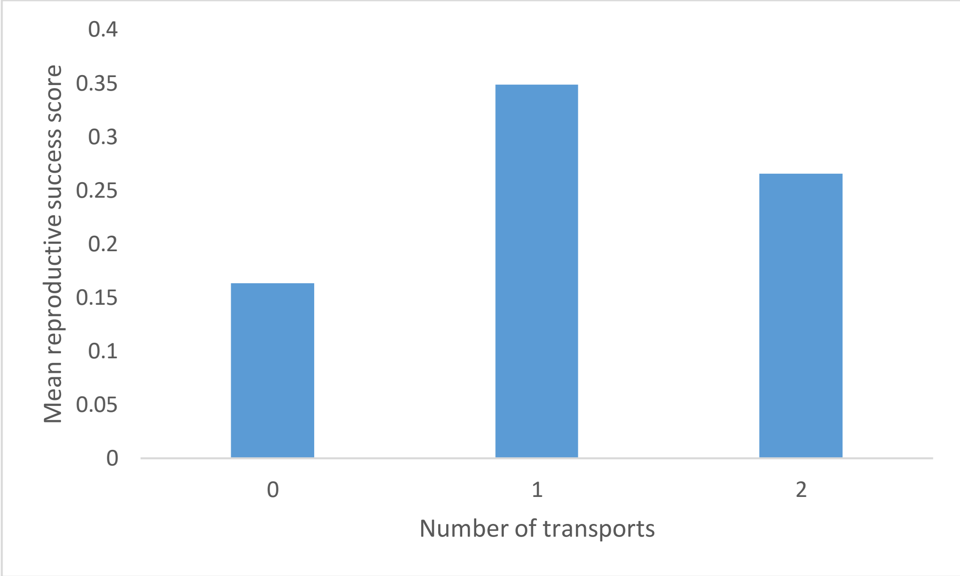


Figure 8: *Mean reproductive success for males in each category of transfer number.*

Reproductive success scores in female were shown to have a significant negative relationship with Age (*P*=.006) as depicted in Figure 9. Although not reaching statistical significance, there is negative relationship between the Excitability domain score and reproductive success that approaches significance in female *S. syndactylus* (*P*=.056), as seen in Figure10. Transfer number also approaches a significant positive relationship with reproductive success in this sex (*P*=.079).

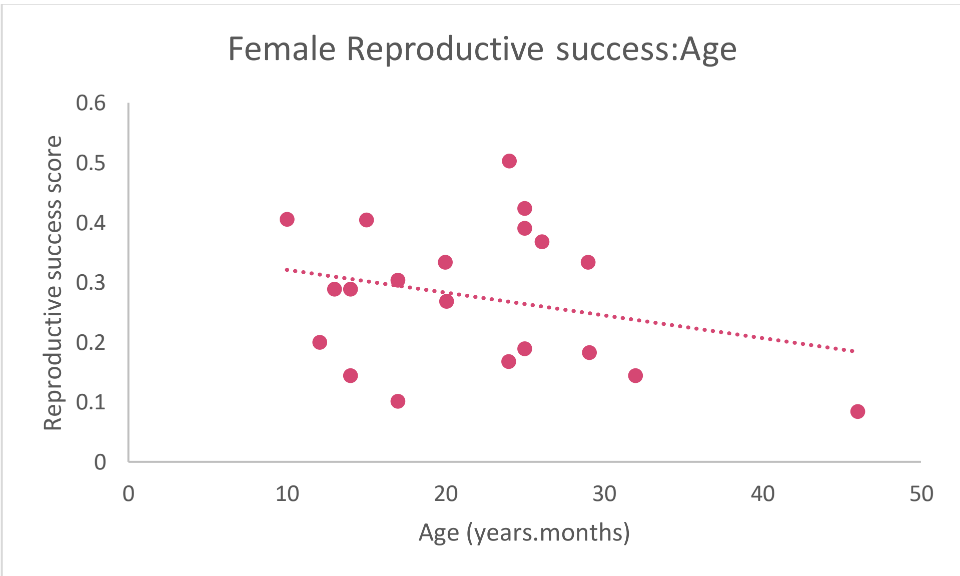


Figure 9: *Plot for the significant negative effect of age on reproductive success in females.*

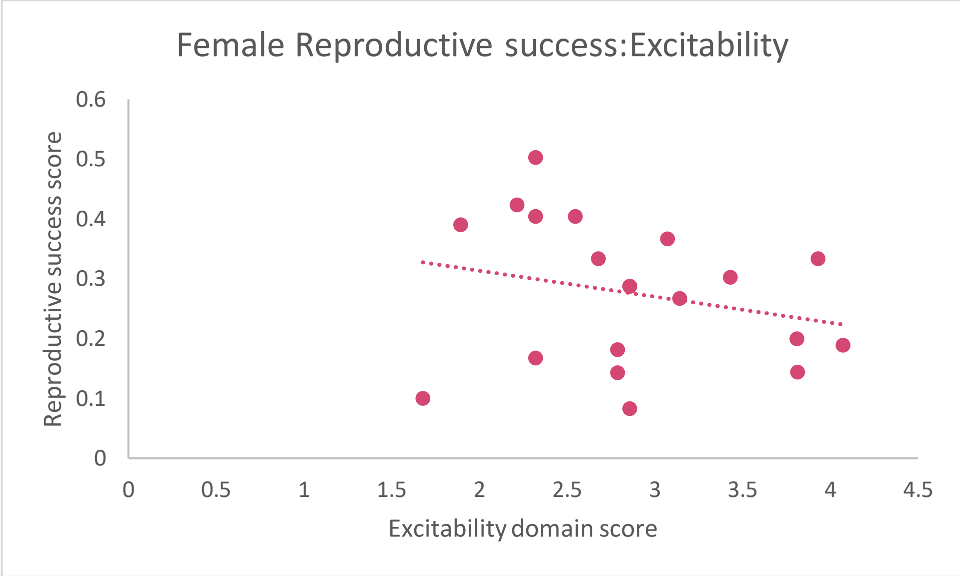


Figure 10: *Plot for the effect of Excitability domain score on reproductive success in females.*

2.4 Discussion

2.4.1 Reliability of trait ratings

Mean agreement across salient traits for this species was 0.37, which is low compared to agreement in other species. Average values taken from multiple papers in the Freeman and Gosling review of primate personality show a mean ICC[3,k] of 0.75. Mean ICC[3,k] values from studies on species of macaque (0.54 and 0.52) and great ape (0.58, 0.64) were all greater than that of the present study (Baker *et al.* 2015; Eckardt *et al.* 2015; Uher & Asendorpf 2008; Weiss *et al.* 2011). This is despite the level of keeper familiarity (both with species and individual animals) shown in this study that matches with other animal personality works (Horback *et al.* 2013). Comparative taxonomic relatedness between *S. syndactylus* and humans may suggest higher agreement, as it is noted that people have more success rating species that they share greater affinity with (Gosling 2001). There may in fact be something in the species biology of gibbons that makes rating personality less effective. Raters could be less able to reliability rate personality in this species as a result of *S. syndactylus* being kept in breeding pairs/small family groups within zoos. This would effectively limit the comparison between animals and ability for raters to score individuals on a relative scale. Macaques, gorillas, and chimpanzees referred to as having higher agreement are all kept in larger social groups within zoos - suggesting that group size and success of trait rating could be correlated. Baker (2012) discusses the effect of group size on reliability of personality measures, suggesting that this variable does have an effect and that once an optimum size is passed (in either direction) reliability can be affected. Mean ICC[3,k] values for squirrel monkeys (*Saimiri sciureus*) at 0.39 are similar to those shown in the present study (Baker *et al.* 2015). This comparatively lower reliability score is explained by the potential that raters could have difficulty scoring based on behaviour experience that doesn't involve clear animal behaviour. As an example, social behaviour in macaques are typified by apparent physical interactions such as grooming or other affiliations and are in theory therefore easier to identify. *S. syndactylus* are similar to *S. sciureus* in that their behaviours are considered to be more subtle or relying on olfactory/auditory communication (Liebal *et al*. 2004) which could be more difficult to consistently distinguish (Baker *et al.* 2015). Further work on personality of other gibbon species or even those generally kept in similar sized groups within zoos would help to investigate this theory further.

2.4.2 Identifiable personality domains

Groupings of reliable traits resulted in the formation of three personality domains for *S. syndactylus* – Excitability, Dominance and Introverted. The first two of these are identified in the Freeman & Gosling (2010) review as being domain names that feature in many primate personality studies (nine and 10 different studies respectively identified in this review). The Excitability domain is described as an animal being particularly sensitive to change, which aligns with highly loaded traits such as Impulsive (0.71) and Reckless (0.56) that the present study identifies in this domain. Similarly, with the Freeman and Gosling review citing a definition of Dominance as how an animal can threaten or displace a conspecific, highly loaded traits of Dominant (0.79), Bullying (0.75) and Aggressive (0.71) align with this terminology. Criticism exists for assigning Dominance as a personality domain due to species having different dominant traits depending on their ecology (Uher & Asendorpf 2008); however, the domain is frequently identified in primate personality literature. Although Introverted is not a domain identified by Freeman & Gosling, consideration of the associated traits means this is the best possible term the author can apply. Fearfulness is one of the most commonly identified domain names in primate literature (Freeman & Gosling 2010); however, definitions vary and despite some trait overlap Fearful was not as highly loaded as other traits including Solitary, Unperceptive and Depressed (0.58 compared to 0.67, 0.71 and 0.81 respectively). Therefore, it is considered that for the present study Fearfulness would be too specific a term for the third *S. syndactylus* domain.

The similarity of traits and their domain names for this species when compared to other primate studies reinforces the comparative applications of personality assessment (Uher 2008).

Three traits identified in this species is a lower number than cited in the majority of literature. Various works across multiple taxa (both primate and non-primate) identify between four and six domains (Gosling 1998; Horback *et al.* 2013; Martin-Wintle *et al.* 2017; Morton *et al.* 2013b; Phillips & peck 2007; Weiss *et al.* 2006; Weiss *et al.* 2009) in personality assessment. Cussen and Mench (2014) only identified two domains in their study on orange-winged Amazon parrots (*Amazona amazonica*); however, this could be explained by the fact their study animals were housed in isolation so lacked the opportunity for a Sociable domain to be determined. It could be hypothesised that perhaps as a socially monogamous species, *S. syndactylus* would also be less likely to show a fourth domain of Sociality; however, there is no literature on socially monogamous primates to compare to. It is also worth noting that the giant panda (another species that is typically housed individually or in pairs within zoos) had four domains identified in the Martin-Wintle work of 2017. Principle Component Analyses that were used to identify the traits relies on the number of reliable traits and animals involved (Baker *et al.* 2012). Therefore, the comparatively small number of salient traits included in this analysis could cause the reduced number of domains (Baker et al. 2015), which could be investigated by increasing the number of HPQ responses for various animals within the population.

2.4.3 Reliability of trait rating system

Analyses demonstrate that all three domains for this species have a significant relationship with at least one of the behaviour categories used for validation.

Increased scores for the Excitability domain correlate with increased social positive, locomotion and explorative behaviour scores. Increased social positive behaviour scores include the state behaviour play as well as other factors that would indicate an animal that frequently interacts with conspecifics and humans. Inclusion of salient traits such as Playful (0.69), Human-Animal Social (0.47) and Active (0.64) in this domain align with these behavioural observations. Similarly, positive relationship scores for behaviour categories featuring active state behaviours (interaction with enrichment and enclosure, brachiation) support validity of the Excitability domain from HPQ rating.

There is a significant positive relationship between Dominance domain scores and the behavioural category Beneficiary, which features the state behaviour of

Receiving grooming. In contrast, as scores for Dominance increase, Social positive scores decrease. Dominance theory in primates shows that directionality of primate grooming in several species of primates relates to social dominance (Cummins 2019). For example, in chimpanzee societies receipt of grooming increases as social rank increases and the reciprocal rate of grooming decreases for more dominant animals (Kaburu & Newton-Fisher 2015). The existence of this relationship in other species supports the reliability of the Dominance domain in *S. syndactylus*. A reduced occurrence of affiliative behaviours such as play and allogrooming also relate to the highly loaded traits of Bullying (0.75) and Aggressive (0.71) in this domain.

The Introverted domain has a significant negative relationship with the category Proximity 1, demonstrating that animals with increased scores in this domain spend less time in close proximity to their conspecifics. This relates to the positively loaded Solitary (0.67) trait featured within this third domain. A similar significant negative correlation with the Explorative category is reflected in the reduction in behaviours where an animal interacts with its environment (whether general or with provided enrichment). Gartner and Powell's 2012 work on personality in snow leopards demonstrated the existence of a timid/anxious personality domain (with similar traits to the Excitable domain of this study); however, found no significant correlations with any of the novel-object test variables employed. This lack of comparison could be related to species biology or the method of assessment used therefore, it would be interesting to investigate this particular domain in *S. syndactylus* using a novel object test.

The combination of these significant correlations suggests that use of the HPQ is valid for *S. syndactylus.* Continued investigation into the use of the system for other monogamous primate species should be encouraged to determine if the reliability is more widespread.

2.4.4 Personality and reproductive success

When investigating the aim of whether reproductive success was influenced personality type in this species, no significant correlation was found in either sex. There are many cases in literature where a significant relationship has been proven between personality and reproduction including Big-horn sheep (*Ovis canadensis*), blue tits (*Cyanistes caeruleus*), wild boar (*Sus scrofa*) and the zebrafish *Danio rerio* (Mutzel *et al.* 2013; Réale *et al.* 2009; Vargas *et al.* 2018; Vetter *et al.* 2016) with a review by Wolf and Weissing (2012). It is likely however, that reproductive strategy is key in this lack of relationship for *S. syndactylus*. Through analysing the domain scores of individual animals for the current study, it has not acknowledged species biology of *S. syndactylus*. Being a typically monogamous species that exhibits shared parental care of offspring, it would be prudent to assess the dyadic personality scores of a breeding pair in relation to reproductive success. Analyses on this pair level have shown significant relationships between personality and reproductive success. For example, Martin-Wintle *et al.* (2017) demonstrated that, as well as individual personality traits, the interaction of personality traits between two animals matched for breeding correlates with reproductive success. In addition to effecting reproductive success, personality has been shown to correlate with other social proxies, including social cohesion in *P. troglodytes* (Massen & Koski 2014) and latency to form social bonds in bottlenose dolphin (*Tursiops* spp.) (Moreno 2017). To investigate this further for *S. syndactylus* application of domain scores for pairs based on total difference or combined magnitude of scores could be applied. The sample size of animals in this part of the study may also have been problematic, particularly with the effect of Excitability on female reproductive success approaching significance.

Results showed a significant positive correlation between male reproductive success and transfer number, with female reproductive success significantly correlated with a decrease in age. To investigate this further, analysis of the historic studbook data for effect of age and transfer number on reproductive success in this species should be carried out. Retrospective analysis of this large data set would allow investigation as to whether these trends are observed across more than the sample of the current population.

3. Personality assessment in a zoo-housed population of Sulawesi crested black macaque (*Macaca nigra*).

3.1 Introduction

3.1.1 Species biology

The Sulawesi crested black macaque (*Macaca nigra*) is one of seven endemic species of macaque found on the Indonesian island of Sulawesi. The IUCN classification is Critically Endangered, with a decreasing population trend (Supriatna & Andayani 2008). The species exists in multi-male/multi-female groups, with female bonded relationships forming the stable core of their natal groupings (Reed *et al.* 1997). Total group sizes range between 27 and 97 animals (O'Brien & Kinnaird 1997), with males believed to disperse at sexual maturity. There is selective preference by females to associate with males at higher dominance ranks, therefore improving reproductive success (Reed *et al.*1997). *M. nigra* are often described as a 'tolerant' species (Micheletta *et al.* 2012), with balanced and appeasing behaviours being increasingly frequent amongst all females within the group (Adams *et al.* 2012). An aspect of this social living are complex and frequent social interactions and varied communication. Dixson's 1977 work summarises the wide repertoire of communication behaviours including lip smacking, grimacing, staring, presentation of ischial callosities and crest raising. The species is noted as spending approximately 40% of diurnal hours resting and socialising, in both in-situ and ex-situ environments (Melfi & Feistner 2002; O'Brien & Kinnaird 1997).

3.1.2 Zoo-housed Sulawesi macaques

According to ZIMS the species is held globally in 42 institutions, with a total of 247 individuals (Species360 2019). As with *S. syndactylus*, the Sulawesi macaque is managed via an EEP with all the same considerations and management interventions.

3.1.3 Aims

Due to IUCN threat status and EAZA TAG identification of the species as a priority for management, the EAZA population is intensively managed through an evidence-based programme. As such, data on personality type can be applied to facilitate effective management decisions.

Old-world primates are comparatively understudied in the animal personality literature (Freeman & Gosling 2010); however, there have been previous studies on personality in this species. Key pieces of work summarised in Baker *et al.* (2015) carried out the first personality assessment (data collected in 2009) in this ex-situ population and therefore provide an opportunity to compare to longitudinal data.

As such, the aim of the current study in relation to this species is to evaluate temporal stability of personality within a managed population of threatened primate species.

3.2 Methods

3.2.1 Trait rating questionnaires

To facilitate comparison between previous data, the HPQ was distributed to certain institutions within the EAZA EEP region holding *M. nigra*. Unpublished work by Hussey *et al.* in 2017 had already made contact with the EEP participants to make the same request for HPQ data. At this time, nine (36%) of the 25 EAZA member institutions replied with completed questionnaires. For the current study, the request for HPQ was redistributed electronically (with support from the EEP coordinator) to the institutions who had not yet replied. The same version of the HPQ (Appendix 3) was used, with appropriate modification to match species name. All traits and instructions to raters remained consistent with the HPQ used for *S. syndactylus* assessment.

Earlier work (Baker 2012; Hussey *et al.* 2017) had previously carried out behavioural coding observations at a total of three UK institutions, consisting of 22 animals to validate the HPQ for the species.

3.2.2 Data analyses

3.2.2.1 Inter-observer reliability and Principal Component Analysis of questionnaire data

Both sets of analyses were carried out following the same methodology and criteria for inclusion as described in sections 2.2.3.1 and 2.2.3.2.

3.2.2.2 Temporal stability of personality scores

Animals that had undergone trait rating in both 2009 data collection and 2018 data collection conditions were identified and their data pooled. Upon comparison of domain content, it was decided to select up to three traits from each domain that occurred consistently across the two temporal conditions.

Trait scores from both time points for each animal were analysed using Kendall's tau correlation in R-Statistics® (R Core team 2019) – as demonstrated in Appendix 12. All individuals, regardless of sex, age or other factor were analysed concurrently in the same set of models.

3.3 Results

3.3.1 Trait rating questionnaires

An additional six institutions responded to the HPQ request from the author of the current study, meaning total responses from 15 of the 25 institutions. This 58% institution response rate provided completed HPQ data from 100 animals (collected over the course of a year).

3.3.2 Data analyses

3.3.2.1 Inter-observer reliability and Principal Component Analysis of questionnaire data

Following the amalgamation of more recently collected HPQ responses, data from a total of 56 animals across nine institutions were included in ICC analysis. Appendix 13 presents the across-subject reliability for the institutions included in this analysis, whereby mean overall ICC[3,k] values are salient. In total 49 out of the 60 traits were found to reach the criterion for reliability and are included in analysis for domain formation. Mean ICC[3,k] scores for salient traits is 0.47, ranging from 0.05 (Individualistic) to 0.93 (Playful). Analysis was only performed on a sub-set of animals (56 from the 100 with HPQ data); however, traits identified as reliable here were assumed to be reliable for all animals and data from all animals rated by HPQ response were included in the PCA analysis.

Consultation of the scree plot identifies that three components account for variance in the data and should be retained. Traits with the most highly loaded scores were assigned to respective components, with resulting domains (Dominance, Sociability and Emotionality) displayed in Table 11.

Table 11: *Eigen values from Principal Component Analysis showing how traits were assigned to one of three personality domains. Colour coding represents the positive loadings (green) and negative loadings (red) that assigned traits to their respective domains.*

	Personality Domain		
	Dominance	**Sociability**	**Emotionality**
Dominant	**0.86**	-0.04	-0.02
Bullying	**0.84**	-0.15	0.17
Decisive	**0.78**	0.22	-0.25
Aggressive	**0.77**	-0.14	0.38
Independent	**0.75**	0.11	-0.28
Persistent	**0.69**	0.29	0.09
Stingy	**0.69**	0.13	0.15
Irritable	**0.61**	-0.38	0.15
Intelligent	**0.58**	0.21	-0.1
HA Aggressive	**0.56**	-0.31	0.1
Manipulative	**0.52**	0.32	0.45
Individualistic	**0.51**	0.29	0
Jealous	**0.45**	0.17	0.29
Protective	**0.38**	-0.05	-0.13
Anxious	**-0.37**	-0.32	0.01
Dependent	**-0.48**	0.43	0.2
Timid	**-0.6**	0.12	0.11
Vulnerable	**-0.67**	-0.09	0.07
Submissive	**-0.73**	0.18	0.13
Imitative	-0.05	**0.74**	0.32
Sociable	0.14	**0.73**	0.05
Friendly	-0.15	**0.72**	-0.05
Active	0.02	**0.71**	0.33
Affectionate	0.01	**0.71**	-0.14
Innovative	0.45	**0.69**	0.09
Inquisitive	0.13	**0.66**	0.4
Playful	-0.15	**0.63**	0.4
Inventive	0.53	**0.56**	0.1
HA Social	0.25	**0.56**	-0.21
Curious	0.51	**0.55**	0.07
Distractible	-0.13	**0.53**	0.37
Reckless	0.39	**0.45**	0.38
HA Cooperative	0.38	**0.4**	-0.15
HA Cautious	0.09	**-0.19**	-0.15
HA Oblivious	0.02	**-0.27**	0.03

Depressed	-0.1	**-0.35**	-0.03
Lazy	0.41	**-0.53**	-0.36
Defiant	0.29	0.21	**0.66**
Impulsive	-0.01	0.56	**0.57**
Thoughtless	0.1	-0.02	**0.43**
Erratic	-0.13	0.17	**0.37**
Unperceptive	-0.2	0.1	**0.33**
Autistic	0.06	0	**0.19**
Conventional	0.03	-0.27	**-0.27**
Gentle	-0.48	0.43	**-0.49**
Predictable	0.39	0.18	**-0.49**
Cool	0.53	0.17	**-0.55**
Unemotional	0.14	-0.09	**-0.56**
Sensitive	0	-0.03	**-0.58**

3.3.2.2 Temporal stability of personality scores

A total of 26 animals were identified as being surveyed in both time conditions, with their domain score data shown in Appendix 14. Dominant, Playful, Active and Lazy were the individual traits that occurred consistently across the conditions. Table 12 show the traits and the respective values associated with analyses. (4 traits) values that are being compared, with scores for each animal.

Table 12: *Four personality traits, with associated Eigen values (from PCA analysis) as well as P- and tau values from Kendall's tau correlation tests.*

Trait	Eigen value	Loading	*P*-value	Tau
Dominant	0.83	Positive	.018	0.345
Playful	0.88	Positive	.488	0.108
Active	0.88	Positive	.672	0.066
Lazy	-0.77	Negative	.322	0.151

Of the four traits, only Dominant showed a significant (but weak) positive correlation between the scores taken at each time point (Figure 11). There were no significant correlations between time points in the other three traits.

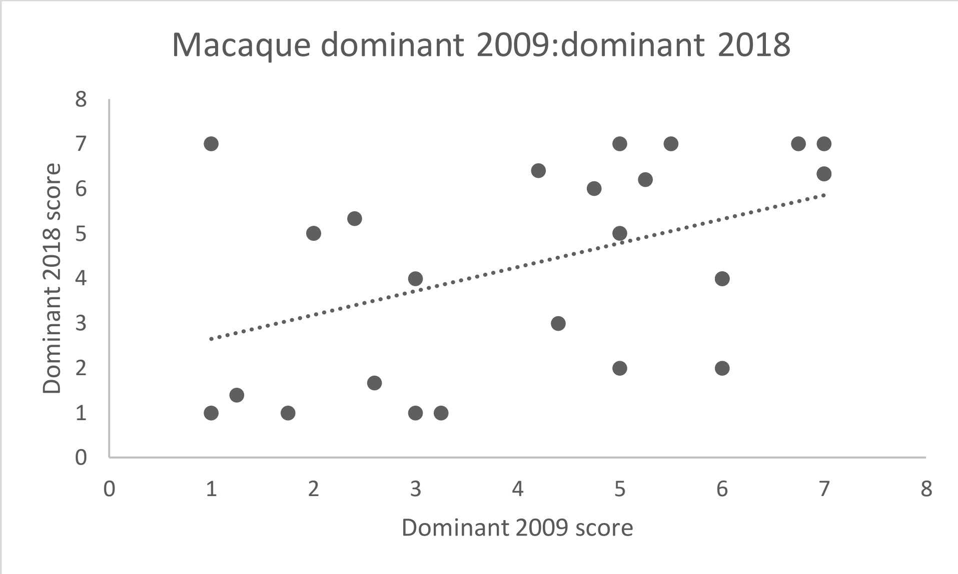


Figure 11: *Plot visualising the relationship between trait scores for Dominant made in 2009 and 2018 sampling periods (total of 26 animals).*

3.4 Discussion

3.4.1 Temporal stability of personality

Having a majority of the selected traits show no significant correlation across time appears to contradict personality theory; however further inspection of the literature suggests otherwise. In their review, Stamps & Groothuis (2010) highlight the fact that although between individual variation is stable, there are various timescales that relate to personality development and plasticity. This point is demonstrated by several examples from animal personality work. Boulton *et al.* 2014 ran assessments to determine if population- and individual-level personality distinction was stable over time in a species of tropical fish (*Xiphophorus birchmanni*). Multivariate analysis revealed that the variation in broader personality domains remains limited over both short- (4 days) and long-term (56 days) time periods. When investigating specific traits and their stability though the statistical support is much more mixed; demonstrating time-scale and behaviour level differences in stability. Similarly, David *et al.* (2012) investigated stability of two personality measures in zebra finch

(*Taeniopygia guttata*) across two distinct time intervals. Short term intervals showed stability in both personality factors, whereas only Exploratory personality tendencies remained stable over the longer-term tests. It may be that this behaviour trait is more fixed and less subject to change because of the ecological significance of personality (David *et al.* 2012). Inter-individual variation in stability was also noted in this study, suggesting that sample size is key to gain a comprehensive understanding of this phenomenon. Both of these studies also highlight the importance of acknowledging species biology in assessment of personality stability. The same length of time will have different implications for species depending on their longevity. For instance, a seven-month interval in a study on *T. guttata* accounts for approx. ¼ of species mean longevity and so consideration over this timescale would be more relevant than for a species that lived 10x that amount. The almost 10-year gap between assessment of *M. nigra* personality accounts for close to the mean age of individuals rated by the HPQ (mean age of population sampled being 10 years seven months). This is a significant proportion of the lifespan of many of these animals and therefore they will likely have been exposed to many perturbations. It is not known what environmental variables will have changed for the animals involved i.e. some are at different institutions, many will have undergone husbandry changes etc., and these perturbations could have resulted in adaptive plasticity of personality.

The singular significant correlation observed in the Dominant domain could potentially be explained by species biology of *M. nigra*. Maternal rank inheritance is a feature of sociality common to many species of primate and other mammals (Holekamp & Smale 1991) including macaque species (Adams *et al.* 2012). With individuals tending to inherit their social rank from their dam, their social dominance and therefore human perception of Dominant could remain stable over their lifespan., whereas other traits (such as Playful and Active) could be perceived differently especially as animals age.

This variation in personality timescale has implications for application of personality data to captive management. For certain traits, individual animals and shorter timescales the data can be applied to inform management decisions; however perhaps longer-term application and at the population level should be investigated further.

4. Conclusion

Data from the two studies presented here demonstrate that personality assessment tools can identify personality profiles for individual animals of two threatened primate species. Despite this success though it is important to ensure that robust methodological assessment takes place. Sample size is always likely to be a limiting factor with small population sizes typical of zoo conservation programmes; however, personality data has continued potential to contribute to effective animal management and conservation. With further work, potentially increasing the number of animals or similar species involved, gibbon personality could be shown to have valuable applications to ex-situ management. Further exploration of macaque personality data is also likely to yield more significant results, particularly as it becomes more practical to apply the standardised, longitudinal data sets to applied situations.

<u>**References**</u>

Adams M.J., King J.E. and Weiss A. 2012. The majority of genetic variation in orangutan personality and subjective well-being is nonadditive. *Behavior genetics*, 42 (4); 675-686.

Adams M.J., Majolo B., Ostner J., Schülke O., De Marco A., Thierry B., Engelhardt A., Widdig A., Gerald M.S. and Weiss A. 2015. Personality structure and social style in macaques. *Journal of Personality and Social Psychology*, 109 (2); 338..

Allport G.W. and Odbert H.S. 1936. Trait-names: A psycho-lexical study. *Psychological monographs*, 47 (1); 1-171.

Baker K.R 2012. Personality assessment of three species of captive monkey *Macaca nigra*, *Macaca sylvanus*, and *Saimiri sciureus*: Cross-species comparisons of personality and implications for captive management. (Unpublished doctoral dissertation). University of Exeter, Exeter, United Kingdom.

Baker L., Lawrence M.S., Toews M., Kuling S. and Fraser D. 2016. Personality differences in a translocated population of endangered kangaroo rats (*Dipodomys stephensi*) and implications for conservation success. *Behaviour*, 153 (13-14); 1795-1816.

Baker K.R., Lea S.E. and Melfi V.A. 2015. Comparative personality assessment of three captive primate species: *Macaca nigra*, *Macaca sylvanus*, and *Saimiri sciureus*. *International Journal of Primatology*, 36 (3); 625-646.

Baker K.R. and Pullen K. 2013. The impact of housing and husbandry on the personality of cheetah (*Acinonyx jubatus*). *Journal of Zoo and Aquarium Research*, 1 (1); 35-40.

Bautista LM and Pantoja JC. 2005. What animal species should we study next? *Bulletin of the British Ecological Society*, 36 (4); 27–28

Bergvall U.A., Schäpers A., Kjellander P. and Weiss A. 2011. Personality and foraging decisions in fallow deer, *Dama dama*. *Animal Behaviour*, 81 (1); 101-112.

Blaszczyk M.B. 2017. Boldness towards novel objects predicts predator inspection in wild vervet monkeys. *Animal Behaviour*, *123*; 91-100.

Boulton K., Grimmer A.J., Rosenthal G.G., Walling C.A. and Wilson A.J. 2014. How stable are personalities? A multivariate view of behavioural variation over long and short timescales in the sheepshead swordtail, *Xiphophorus birchmanni*. *Behavioral Ecology and Sociobiology*, 68 (5); 791-803.

Bremner-Harrison S., Cypher B.L., Job C.V.H. and Harrison S.W. 2018. Assessing personality in San Joaquin kit fox in situ: efficacy of field-based experimental methods and implications for conservation management. *Journal of ethology*, 36 (1); 23-33.

Briffa M. and Greenaway J. 2011. High in situ repeatability of behaviour indicates animal personality in the beadlet anemone *Actinia equina* (Cnidaria). *PLoS One*, 6 (7); 21963.

Briffa M., Sneddon L.U. and Wilson A.J. 2015. Animal personality as a cause and consequence of contest behaviour. *Biology letters*, 11 (3); 20141007.

Brown C. and Irving E. 2013. Individual personality traits influence group exploration in a feral guppy population. *Behavioral Ecology*, 25 (1); 95-101.

Caillard E.M. 1894. Personality as the outcome of evolution. *The Contemporary review, 1866-1900*, 65; 713-721.

Capitanio J.P. 2011. Nonhuman primate personality and immunity: Mechanisms of health and disease. In *Personality and temperament in nonhuman primates* (pp. 233-255). Springer, New York, NY.

Carlson B.E. and Langkilde T. 2013. Personality traits are expressed in bullfrog tadpoles during open-field trials. *Journal of Herpetology*, 47 (2); 378-383.

Carlstead K., Fraser J., Bennett C. and Kleiman D.G. 1999a. Black rhinoceros (*Diceros bicornis*) in US zoos: II. Behavior, breeding success, and mortality in relation to housing facilities. *Zoo biology*, 18 (1); 35-52.

Carlstead K., Mellen J. and Kleiman D.G. 1999b. Black rhinoceros (*Diceros bicornis*) in US zoos: I. Individual behavior profiles and their relationship to breeding success. *Zoo Biology*, 18 (1); 17-34.

Carter A.J., Feeney W.E., Marshall H.H., Cowlishaw G. and Heinsohn R. 2013. Animal personality: what are behavioural ecologists measuring? *Biological Reviews*, 88 (2); 465-475.

Carter A.J., Marshall H.H., Heinsohn R. and Cowlishaw G., 2014. Personality predicts the propensity for social learning in a wild primate. *PeerJ*, *2*; 283.

Chamove A.S., Eysenck H.J. and Harlow H.F. 1972. Personality in monkeys: Factor analyses of rhesus social behaviour. *Quarterly Journal of Experimental Psychology, 24 (4); 496-504.*

Chivers D. 1974. The siamang in Malaya: a field study of a primate in tropical rain forest. *Contributions to Primatology*, 4; 1-335.

Chivers, D.J., 1976. Communication within and between family groups of siamang (Symphalangus syndactylus). *Behaviour*, *57*(1-2), pp.116-135.

Ciardelli L.E., Weiss A., Powell D.M. and Reiss D. 2017. Personality dimensions of the captive California sea lion (*Zalophus californianus*). *Journal of Comparative Psychology*, 131 (1); p.50.

Cote J., Fogarty S., Weinersmith K., Brodin T. and Sih A. 2010. Personality traits and dispersal tendency in the invasive mosquitofish (*Gambusia affinis*). *Proceedings of the Royal Society B: Biological Sciences*, 277 (1687); 1571-1579.

Crawford M.P. 1938. A behavior rating scale for young chimpanzees. *Journal of Comparative Psychology*, 26 (1); 79.

Cummins D.D. 2019. Dominance Theory, IN: Shackleford T., Weekes-Shackleford V. (Eds). Encyclopaedia of Evolutionary Psychological Science. Springer.

Curley Jr K.O., Paschal J.C., Welsh Jr T.H. and Randel R.D. 2006. Exit velocity as a measure of cattle temperament is repeatable and associated with serum concentration of cortisol in Brahman bulls. *Journal of animal science*, 84 (11); 3100-3103.

Cussen V.A. and Mench J.A. 2014. Personality predicts cognitive bias in captive psittacines, *Amazona amazonica*. *Animal behaviour*, 89; 123-130.

Dall S.R. and Griffith S.C. 2014. An empiricist guide to animal personality variation in ecology and evolution. *Frontiers in Ecology and Evolution*, 2 (3).

Dall S.R.X., Houston A.I. and McNamara J.M. 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters*, 7; 734-739.

Dal Pra G. and Geissmann T. 1994. Behavioural development of twin siamangs (*Hylobates syndactylus*). *Primates*, 35 (3); 325-342.

David M., Auclair Y. and Cézilly F. 2012. Assessing short-and long-term repeatability and stability of personality in captive zebra finches using longitudinal data. *Ethology*, 118 (10); 932-942.

d'Eath R.B., Roehe R., Turner S.P., Ison S.H., Farish M., Jack M.C. and Lawrence A.B. 2009. Genetics of animal temperament: aggressive behaviour at mixing is genetically associated with the response to handling in pigs. *Animal*, 3 (11); 1544-1554.

Dixson A.F. 1977. Observations on the displays, menstrual cycles and sexual behaviour of the "Black ape" of Celebes (*Macaca nigra*). *Journal of Zoology*, 182 (1); 63-84.

de Vere A.J., Lilley M.K. and Highfill L. 2017. Do pinnipeds have personality? Broad dimensions and contextual consistency of behavior in harbor seals (*Phoca vitulina*) and California sea lions (*Zalophus californianus*). *International Journal of Comparative Psychology*, *30*.

Deventer S.A., Uhl F., Bugnyar T., Miller R., Fitch W.T., Schiestl M., Ringler M. and Schwab C. 2016. Behavioural type affects space use in a wild population of crows (*Corvus corone*). *Ethology*, 122 (11); 881-891.

Dielentheis T.F., Zaiss E. and Geissmann T. 1991. Infant care in a family of siamangs (*Hylobates syndactylus*) with twin offspring at Berlin Zoo. *Zoo Biology*, 10 (4); 309-317.

Dingemanse N.J., Both C., Drent P.J. and Tinbergen J.M. 2004. Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 271 (1541); 847-852.

Dingemanse N.J., Both C., Van Noordwijk A.J., Rutten A.L. and Drent P.J. 2003. Natal dispersal and personalities in great tits (*Parus major*). *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270 (1516); 741-747.

Dingemanse N.J., Dochtermann N.A. and Nakagawa S. 2012. Defining behavioural syndromes and the role of 'syndrome deviation' in understanding their evolution. *Behavioral Ecology and Sociobiology*, 66 (11); 543-1548.

Dingemanse N.J. and Reale D. 2005. Natural selection and animal personality. *Behaviour*, 142 (9-10); 1159-1184.

Dutton D.M. 2008. Subjective assessment of chimpanzee (*Pan troglodytes*) personality: Reliability and stability of trait ratings. *Primates*, 49 (4); 253-259.

Eckardt W, Steklis D.H., Steklis N.G., Fletcher A.W.,Stoinski T.S. and Weiss A. 2015. Personality dimensions and their behavioral correlates in wild Virunga mountain gorillas (*Gorilla beringei beringei*). *Journal of Comparative Psychology,* 129 (1); 26-41.

European Association of Zoos and Aquaria (EAZA). 2019. [online] Available at https://www.eaza.net/conservation/programmes/ [Accessed 8th January 2020].

Fairbanks L.A. 2001. Individual differences in response to a stranger: social impulsivity as a dimension of temperament in vervet monkeys (*Cercopithecus aethiops sabaeus*). *Journal of Comparative Psychology*, 115 (1); 22.

Figueredo A.J., Cox R.L. and Rhine R.J. 1995. A generalizability analysis of subjective personality assessments in the stumptail macaque and the zebra finch. *Multivariate Behavioral Research*, 30 (2); 167-197.

Finger J.S., Dhellemmes F., Guttridge T.L., Kurvers R.H., Gruber S.H. and Krause J. 2016. Rate of movement of juvenile lemon sharks in a novel open field, are we measuring activity or reaction to novelty? *Animal Behaviour*, 116; 75-82.

Foellmer M.W. and Khadka K.K. 2013. Does personality explain variation in the probability of sexual cannibalism in the orb-web spider *Argiope aurantia*? *Behaviour*, 150 (14); 1731-1746.

Fox R.A., Ladage L.D., Roth II T.C. and Pravosudov V.V. 2009. Behavioural profile predicts dominance status in mountain chickadees, *Poecile gambeli*. *Animal Behaviour*, 77 (6);1441-1448.

Fox R.A. and Millam J.R. 2010. The use of ratings and direct behavioural observation to measure temperament traits in cockatiels (*Nymphicus hollandicus*). *Ethology*, 116 (1); 59-75.

Fox R.A. and Millam J.R. 2014. Personality traits of pair members predict pair compatibility and reproductive success in a socially monogamous parrot breeding in captivity. *Zoo Biology*, 33 (3); 166-172.

Freeman H.D., Brosnan S.F., Hopper L.M., Lambeth S.P., Schapiro S.J. and Gosling S.D., 2013. Developing a comprehensive and comparative questionnaire for measuring personality in chimpanzees using a simultaneous top-down/bottom-up design. *American Journal of Primatology*, 75 (10); 1042-1053.

Freeman H.D. and Gosling S.D. 2010. Personality in nonhuman primates: a review and evaluation of past research. *American journal of primatology*, 72 (8); 653-671.

Freeman H., Gosling S.D. and Schapiro S.J. 2011. Comparison of methods for assessing personality in nonhuman primates. In *Personality and temperament in nonhuman primates* (pp. 17-40). Springer, New York, NY.

Galton F. 1884. Measurement of character. *Fortnightly*, 36 (212); 179-185.

Gartner M.C. and Powell D. 2012. Personality assessment in snow leopards (*Uncia uncia*). *Zoo Biology*, 31 (2); 151-165.

Gartner M.C. and Weiss A. 2013. Personality in felids: A review. *Applied Animal Behaviour Science*, 144 (1-2); 1-13.

Gartner M.C. and Weiss A. 2018. Studying primate personality in zoos: Implications for the management, welfare and conservation of great apes. *International Zoo Yearbook*, 52 (1); 79-91.

Geissmann T. 1991. Reassessment of age of sexual maturity in gibbons (Hylobates spp.). *American Journal of Primatology*, 23 (1); 11-22.

Geissmann T. 1999. Duet songs of the siamang, Hylobates syndactylus: II. Testing the pair-bonding hypothesis during a partner exchange. *Behaviour*, 136 (8); 1005-1039.

Germano J.M., Nafus M.G., Perry J.A., Hall D.B. and Swaisgood R.R. 2017. Predicting translocation outcomes with personality for desert tortoises. *Behavioral Ecology*, 28 (4); 1075-1084.

Godfrey S.S., Bradley J.K., Sih A. and Bull C.M. 2012. Lovers and fighters in sleepy lizard land: where do aggressive males fit in a social network? *Animal Behaviour*, 83 (1); 209-215.

Goldberg L.R. 1990. An alternative" description of personality": the big-five factor structure. *Journal of personality and social psychology*, 59 (6); 1216.

Gosling S.D. 1998. Personality dimensions in spotted hyenas (*Crocuta crocuta*). *Journal of Comparative Psychology*, 112 (2); 107.

Gosling S.D. 2001. From mice to men: what can we learn about personality from animal research? *Psychological Bulletin*, 127 (1); 45.

Gosling S.D. 2008. Personality in non-human animals. *Social and Personality Psychology Compass*, *2* (2); 985-1001.

Gosling S.D. and John O.P. 1999. Personality dimensions in nonhuman animals: A cross-species review. *Current directions in psychological science*, 8 (3); 69-75.

Gottlieb D.H., Capitanio J.P. and McCowan B. 2013. Risk factors for stereotypic behavior and self-biting in rhesus macaques (*Macaca mulatta*): animal's history, current environment, and personality. *American Journal of Primatology*, 75 (10); 995-1008.

Gottlieb D.H., Del Rosso L., Sheikhi F., Gottlieb A., McCowan B., Capitanio J.P. 2018. Personality, environmental stressors, and diarrhea in rhesus macaques: an interactionist perspective. *American Journal of Primatology*, 80 (12).

Günther A., Finkemeier M.A. and Trillmich F. 2014. The ontogeny of personality in the wild guinea pig. *Animal Behaviour*, 90; 131-139.

Haage M. 2016. *Conservation, personality and ecology of the European mink (Mustela lutreola)* (Doctoral dissertation, Department of Zoology, Stockholm University).

Harl H., Stevens L., Margulis S.W. and Petersen J. 2016. Gibbon Aggression During Introductions: An International Survey. *Journal of Applied Animal Welfare Science,* 19 (3); 260-270.

Holbrook C.T., Wright C.M. and Pruitt J.N. 2014. Individual differences in personality and behavioural plasticity facilitate division of labour in social spider colonies. *Animal Behaviour*, 97; 177-183.

Holekamp K.E. and Smale L. 1991. Dominance acquisition during mammalian social development: the "inheritance" of maternal rank. *American Zoologist*, 31 (2); 306-317.

Horback K.M., Miller L.J. and Kuczaj II S.A. 2013. Personality assessment in African elephants (*Loxodonta africana*): Comparing the temporal stability of ethological coding versus trait rating. *Applied Animal Behaviour Science*, 149 (1-4); 55-62.

Hussey G., Newbolt J. and Baker K.R. 2017. Personality assessment in the Sulawesi crested black macaque (Macaca nigra). (Unpublished Undergraduate thesis), University of Bath, United Kingdom.

Iwanicki S. and Lehmann J. 2015. Behavioral and trait rating assessments of personality in common marmosets (*Callithrix jacchus*). *Journal of Comparative Psychology*, 129 (3); 205.

Jin J., Su Y., Tao Y., Guo S. and Yu Z. 2013. Personality as a predictor of general health in captive golden snub-nosed monkeys (*Rhinopithecus roxellana*). *American journal of primatology*, 75 (6); 524-533.

Kaburu S.S.K. and Newton-Fisher N.E. 2015. Egalitarian despots: Hierarchy steepness, reciprocity and the grooming-trade model in wild chimpanzees, *Pan troglodytes*. *Animal Behavior*, 99; 1–154.

Kern E.M., Robinson D., Gass E., Godwin J. and Langerhans R.B. 2016. Correlated evolution of personality, morphology and performance. *Animal behaviour*, 117; 79-86.

King J.E. and Figueredo A.J. 1997. The five-factor model plus dominance in chimpanzee personality. *Journal of research in personality*, 31 (2); 257-271.

Kralj-Fišer S. and Schuett W. 2014. Studying personality variation in invertebrates: why bother? *Animal Behaviour*, 91; 41-52.

Konečná M., Lhota S., Weiss A., Urbánek T., Adamová T. and Pluháček J. 2008. Personality in free-ranging Hanuman langur (*Semnopithecus entellus*) males: subjective ratings and recorded behavior. *Journal of Comparative Psychology, 122 (4); 379-389.*

Koski S.E., Buchanan-Smith H.M., Ash H., Burkart J.M., Bugnyar T. and Weiss A. 2017. Common marmoset (*Callithrix jacchus*) personality. *Journal of Comparative Psychology*, 131 (4); 326.

Kralj-Fišer S., Weiß B.M. and Kotrschal K. 2010. Behavioural and physiological correlates of personality in greylag geese (*Anser anser*). *Journal of Ethology*, 28 (2); 363-370.

Lappan S. 2007. Patterns of dispersal in Sumatran siamangs (*Symphalangus syndactylus*): Preliminary mtDNA evidence suggests more frequent male than female dispersal to adjacent groups. *American Journal of Primatology* 69; 692–698.

Lappan S. 2008. Male care of infants in a siamang (*Symphalangus syndactylus*) population including socially monogamous and polyandrous groups. *Behavioral Ecology and Sociobiology*, 62 (8); 1307-1317.

Liebal K., Pika S. and Tomasello M. 2004. Social communication in siamangs (*Symphalangus syndactylus*): use of gestures and facial expressions. *Primates*, 45 (1); 41-57.

Le Cœur C., Thibault M., Pisanu B., Thibault S., Chapuis J.L. and Baudry E. 2015. Temporally fluctuating selection on a personality trait in a wild rodent population. *Behavioral Ecology*, 26 (5); 1285-1291.

Lusseau D., Wilson B.E.N., Hammond P.S., Grellier K., Durban J.W., Parsons K.M., Barton T.R. and Thompson P.M. 2006. Quantifying the influence of sociality on population structure in bottlenose dolphins. *Journal of Animal Ecology*, 75 (1); 14-24.

Maiti U., Sadowska E.T., ChrzĄścik K.M. and Koteja P. 2018. Experimental evolution of personality traits: open-field exploration in bank voles from a multidirectional selection experiment. *Current Zoology*, 65 (4);375-384.

Martau P.A., Caine N.G. and Candland D.K. 1985. Reliability of the emotions profile index, primate form, with *Papio hamadryas*, *Macaca fuscata*, and two *Saimiri* species. *Primates*, 26 (4); 501-505.

Martin P. and Bateson P. 2007. *Measuring behaviour: An introductory guide* (3rd Edition). Cambridge: Cambridge University Press.

Martin J.G. and Réale D. 2008. Animal temperament and human disturbance: implications for the response of wildlife to tourism. *Behavioural Processes*, 77 (1); 66-72.

Martin-Wintle M.S., Shepherdson D., Zhang G., Huang Y., Luo B. and Swaisgood R.R. 2017. Do opposites attract? Effects of personality matching in breeding pairs of captive giant pandas on reproductive success. *Biological Conservation*, *207*, pp.27-37.

Massen J.J. and Koski S.E. 2014. Chimps of a feather sit together: chimpanzee friendships are based on homophily in personality. *Evolution and Human Behavior*, 35 (1);1-8.

McDougall P.T., Réale D., Sol D. and Reader S.M. 2006. Wildlife conservation and animal temperament: causes and consequences of evolutionary change for captive, reintroduced, and wild populations. *Animal Conservation*, 9 (1); 39-48.

Melfi V.A. 2009. There are big gaps in our knowledge, and thus approach, to zoo animal welfare: a case for evidence-based zoo animal management. *Zoo Biology,* 28 (6); 574-588.

Melfi V.A. and Feistner A.T.C. 2002. A comparison of the activity budgets of wild and captive Sulawesi crested black macaques (*Macaca nigra*). *ANIMAL WELFARE*, 11 (2); 213-222.

Mella V.S., Krucler J., Sunderasan L., Hawkins J., Herath A.P., Johnstone K.C., Troxell-Smith S.M., Banks P.B. and McArthur C. 2016. Effective field-based methods to quantify personality in brushtail possums (*Trichosurus vulpecula*). *Wildlife research*, 43 (4); 332-340.

Micheletta J., Waller B.M., Panggur M.R., Neumann C., Duboscq J., Agil M. and Engelhardt A. 2012. Social bonds affect anti-predator behaviour in a tolerant species of macaque, *Macaca nigra*. *Proceedings of the Royal Society B: Biological Sciences*, 279 (1744); 4042-4050.

Moreno K.R. 2017. Does personality similarity in bottlenose dolphin pairs influence dyadic bond characteristics? (Unpublished Master's these). 274. The University of Southern Mississippi, United States of America. https://aquila.usm.edu/masters_theses/274

Morino L. and Borries C. 2017. Offspring loss after male change in wild siamangs: the importance of abrupt weaning and male care. *American journal of physical anthropology*, 162 (1); 180-185.

Morton F.B., Lee P.C. and Buchanan-Smith H.M. 2013a. Taking personality selection bias seriously in animal cognition research: a case study in capuchin monkeys (*Sapajus apella*). *Animal cognition*, 16 (4); 677-684.

Morton F.B., Lee P.C., Buchanan-Smith H.M., Brosnan S.F., Thierry B., Paukner A., de Waal F., Widness J., Essler J.L. and Weiss A. 2013b. Personality structure in brown capuchin monkeys (*Sapajus apella*): Comparisons with chimpanzees (*Pan troglodytes*), orangutans (*Pongo* spp.), and rhesus macaques (*Macaca mulatta*). *Journal of Comparative Psychology*, 127 (3); 282.

Müller R. and von Keyserlingk M.A. 2006. Consistency of flight speed and its correlation to productivity and to personality in *Bos taurus* beef cattle. *Applied Animal Behaviour Science*, 99 (3-4); 193-204.

Mutzel A., Dingemanse N.J., Araya-Ajoy Y.G. and Kempenaers B. 2013. Parental provisioning behaviour plays a key role in linking personality with reproductive success. *Proceedings of the Royal Society B: Biological Sciences*, 280 (1764); 20131019.

Natoli E., Say L., Cafazzo S., Bonanni R., Schmid M. and Pontier D. 2005. Bold attitude makes male urban feral domestic cats more vulnerable to Feline Immunodeficiency Virus. *Neuroscience & Biobehavioral Reviews*, 29 (1); 151-157.

Nijman V. & Geissman T. 2008. *Symphalangus syndactylus*. *The IUCN Red List of Threatened Species* 2008: e.T39779A10266335. http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T39779A10266335.en.

Nissen H.W. 1956. Individuality in the behavior of chimpanzees. *American Anthropologist*, 58 (3); 407-413.

O'brien T.G. and Kinnaird M.F. 1997. Behavior, diet, and movements of the Sulawesi crested black macaque (*Macaca nigra*). *International Journal of Primatology*, 18 (3); 321-351.

O'Brien T.G., Kinnaird M.F., Nurcahyo A., Prasetyaningrum M. and Iqbal M. 2003. Fire, demography and the persistence of siamang (*Symphalangus syndactylus*: Hylobatidae) in a Sumatran rainforest. *Animal Conservation*, 6 (2); 15-121.

O'Malley C.I., Turner S.P., D'Eath R.B., Steibel J.P., Bates R.O., Ernst C.W. and Siegford J.M. 2019. Animal personality in the management and welfare of pigs. *Applied Animal Behaviour Science*. 104821. https://doi.org/10.1016/j.applanim.2019.06.002

Palombit R. 1994. Extra-pair copulations in a monogamous ape. *Animal Behaviour* 47; 721 - 723.

Palombit R.1995. Longitudinal patterns of reproduction in wild female siamang (*Hylobates syndactylus*) and white-handed gibbons (*Hylobates lar*). *International Journal of Primatology*, 16 (5); 739-760.

Palombit R.1996. Pair bonds in monogamous apes: a comparison of the siamang *Hylobates syndactylus* and the white-handed gibbon *Hylobates lar*. *Behaviour*, 133 (5-6); 321-356.

Patrick S.C. and Weimerskirch H. 2014. Personality, foraging and fitness consequences in a long lived seabird. *PloS one*, 9 (2); 87269.

Pavlov I. P. (1906). The scientific investigation of the psychical faculties or processes in the higher animals. *Science*, 24; 613–619.

Perals D., Griffin A.S., Bartomeus I. and Sol D. 2017. Revisiting the open-field test: what does it really tell us about animal personality? *Animal Behaviour*, *123*; 69-79.

Pervin L.A., Cervone D. and John O.P. 2004. *Personality: Theory and Research* (9th Edition). John Wiley and Sons.

Phillips C. and Peck D. 2007. The effects of personality of keepers and tigers (*Panthera tigris tigris*) on their behaviour in an interactive zoo exhibit. *Applied Animal Behaviour Science*, 106 (4); 244-258.

Powell D.M. and Gartner M.C. 2011. Applications of personality to the management and conservation of nonhuman animals. In *From genes to animal behavior* (pp. 185-199). Springer, Tokyo.

Pruitt J.N., Riechert S.E. and Jones T.C. 2008. Behavioural syndromes and their fitness consequences in a socially polymorphic spider, *Anelosimus studiosus*. *Animal Behaviour*, 76 (3); 871-879.

R Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org

Réale D., Martin J., Coltman D.W., Poissant J. and Festa-Bianchet M., 2009. Male personality, life-history strategies and reproductive success in a promiscuous mammal. *Journal of evolutionary biology*, 22 (8); 1599-1607.

Réale D., Reader S.M., Sol D., McDougall P.T. and Dingemanse N.J. 2007. Integrating animal temperament within ecology and evolution. *Biological reviews*, 82 (2); 291-318.

Reed C., O'brien T.G. and Kinnaird M.F. 1997. Male social behavior and dominance hierarchy in the Sulawesi crested black macaque (*Macaca nigra*). *International Journal of Primatology*, 18 (2); 247-260.

Rees A. 2001. Anthropomorphism, anthropocentrism, and anecdote: Primatologists on primatology. *Science, Technology, & Human Values*, 26 (2); 227-247.

Robinson L.M., Coleman K., Capitanio J.P., Gottlieb D.H., Handel I.G., Adams M.J., Leach M.C., Waran N.K. and Weiss A., 2018. Rhesus macaque personality, dominance, behavior, and health. *American journal of primatology*, 80 (2); p.e22739.

Rose P.E., Brereton J.E., Rowden L.J., de Figueiredo R.L. and Riley L.M. 2019. What's new from the zoo? An analysis of ten years of zoo-themed research output. *Palgrave Communications*, *5* (1); 1-10.

Schaefer S.A. and Steklis H.D. 2014. Personality and subjective well-being in captive male western lowland gorillas living in bachelor groups. *American Journal of Primatology*, 76 (9); 879-889.

Shepherdson D., Lewis K.D., Carlstead K., Bauman J. and Perrin N. 2013. Individual and environmental factors associated with stereotypic behavior and fecal glucocorticoid metabolite levels in zoo housed polar bears. *Applied Animal Behaviour Science*, 147 (3-4); 268-277.

Shrout P. E. and Fleiss J. L. 1979. Intraclass correlations: Uses in assessing rater reliability. *Psychological Bulletin*, 86 (2); 420-428.

Sih A., Kats L.B. and Maurer E.F. 2003. Behavioural correlations across situations and the evolution of antipredator behaviour in a sunfish–salamander system. *Animal Behaviour*, 65 (1); 29-44.

Sih A., Bell A. and Johnson J.C. 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends in ecology & evolution*, 19 (7); 372-378.

Sih A., Mathot K.J., Moirón M., Montiglio P.O., Wolf M. and Dingemanse N.J. 2015. Animal personality and state–behaviour feedbacks: a review and guide for empiricists. *Trends in Ecology & Evolution*, 30 (1); 50-60.

Sih A. and Watters J.V. 2005. The mix matters: behavioural types and group dynamics in water striders. *Behaviour*, 142 (9); 1423.

Sinn D.L. and Moltschaniwskyj N.A. 2005. Personality traits in dumpling squid (*Euprymna tasmanica*): context-specific traits and their correlation with biological characteristics. *Journal of Comparative Psychology*, 119 (1); 99.

Species360 Zoological Information Management System (ZIMS). 2019. https://zims.species360.org/Main.aspx

Staes N., Eens M., Weiss A. and Stevens J.M. 2017. Bonobo personality: age and sex effects and links with behavior and dominance in. *Bonobos: unique in mind brain and behavior*. Oxford University Press; 183-198.

Stamps J. and Groothuis T.G. 2010. The development of animal personality: relevance, concepts and perspectives. *Biological Reviews*, 85 (2); 301-325.

Stanley C.R., Mettke-Hofmann C. and Preziosi R.F. 2017. Personality in the cockroach *Diploptera punctata*: Evidence for stability across developmental stages despite age effects on boldness. *PloS one*, 12 (5); e0176564.

Supriatna J. and Andayani N. 2008. *Macaca nigra* . *The IUCN Red List of Threatened Species* 2008: e.T12556A3357272. http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T12556A3357272.en. Downloaded on 08 January 2020.

Svartberg K., Tapper I., Temrin H., Radesäter T. and Thorman S. 2005. Consistency of personality traits in dogs. *Animal Behaviour*, 69 (2); 283-291.

Thoré E., Grégoir A., Philippe C., Brendonck L. and Pinceel T. 2017. Different strokes for different folks-personality divergence in a short-lived killifish. In *Behaviour 2017, Location: Estoril, Portugal*.

Uher J. 2008. Comparative personality research: methodological approaches. *European Journal of Personality*, 22 (5); 427-455.

Uher J. and Asendorpf J.B. 2008. Personality assessment in the Great Apes: Comparing ecologically valid behavior measures, behavior ratings, and adjective ratings. *Journal of Research in Personality*, 42 (4); 821-838.

Uher J., Asendorpf J.B. and Call J. 2008. Personality in the behaviour of great apes: temporal stability, cross-situational consistency and coherence in response. *Animal Behaviour*, 75 (1); 99-112.

Vargas R., Mackenzie S. and Rey S. 2018. 'Love at first sight': The effect of personality and colouration patterns in the reproductive success of zebrafish (*Danio rerio*). *PloS one*, 13 (9); p.e0203320.

Vazire S., Gosling S.D., Dickey A.S. and Schapiro S.J. 2007. Measuring personality in nonhuman animals. *Handbook of research methods in personality psychology;* 190-206.

Vetter S.G., Brandstätter C., Macheiner M., Suchentrunk F., Gerritsmann H. and Bieber C. 2016. Shy is sometimes better: personality and juvenile body mass affect adult reproductive success in wild boars, *Sus scrofa*. *Animal Behaviour*, 115; 193-205.

Watanabe N.M., Stahlman W.D., Blaisdell A.P., Garlick D., Fast C.D. and Blumstein D.T. 2012. Quantifying personality in the terrestrial hermit crab: different measures, different inferences. *Behavioural Processes*, 91 (2); 133-140.

Waters R.M., Bowers B.B. and Burghardt G.M. 2017. Personality and individuality in reptile behavior. In *Personality in Nonhuman Animals* (pp. 153-184). Springer, Cham.

Watters J.V. and Powell D.M. 2012. Measuring animal personality for use in population management in zoos: suggested methods and rationale. *Zoo Biology*, 31 (1); 1-12.

Wielebnowski N.C. 1999. Behavioral differences as predictors of breeding status in captive cheetahs. *Zoo Biology,* 18 (4); 335-349.

Weiss A. 2018. Personality traits: a view from the animal kingdom. *Journal of Personality*, 86 (1); 12-22.

Weiss A., Adams M.J., Widdig A. and Gerald M.S. 2011. Rhesus macaques (*Macaca mulatta*) as living fossils of hominoid personality and subjective well-being. *Journal of Comparative Psychology*, *125* (1); 72.

Weiss A., Inoue-Murayama M., Hong K.W., Inoue E., Udono T., Ochiai T., Matsuzawa T., Hirata S. and King J.E. 2009. Assessing chimpanzee personality and subjective well-being in Japan. *American Journal of Primatology,* 71 (4); 283-292.

Weiss A., King J.E. and Perkins L. 2006. Personality and subjective well-being in orangutans (*Pongo pygmaeus* and *Pongo abelii*). *Journal of Personality and Social Psychology*, 90 (3); 501.

Weiss A., Staes N., Pereboom J.J., Inoue-Murayama M., Stevens J.M. and Eens M. 2015. Personality in bonobos. *Psychological Science*, 26 (9); 1430-1439.

White S.J., Houslay T.M. and Wilson A.J. 2019. Evolutionary genetics of personality in the Trinidadian guppy II: sexual dimorphism and genotype-by-sex interactions. *Heredity*, *122* (1); 15-28.

Wolf M. and Weissing F.J. 2012. Animal personalities: consequences for ecology and evolution. *Trends in Ecology & Evolution*, 27 (8); 452-461.

Yasui S., Konno A., Tanaka M., Idani G.I., Ludwig A., Lieckfeldt D. and Inoue-Murayama M. 2013. Personality assessment and its association with genetic factors in captive Asian and African elephants. *Zoo Biology*, 32 (1); 70-78.

Yerkes R.M. 1939. The life history and personality of the chimpanzee. *The American Naturalist*, 73 (745); 97-112.

Yli-Renko M., Pettay J.E. and Vesakoski O. 2018. Sex and size matters: Selection on personality in natural prey-predator interactions. *Behavioural Processes*, 148; 20-26.

Zablocki-Thomas P.B., Herrel A., Hardy I., Rabardel L., Perret M., Aujard F. and Pouydebat E. 2018. Personality and performance are affected by age and early life parameters in a small primate. *Ecology and Evolution*, 8 (9); 4598-4605.

Appendix 1: BIAZA RC support letter

BIAZA
BRITISH & IRISH ASSOCIATION OF ZOOS & AQUARIUMS

BIAZA Research Committee

Letter of Support for Research Project

The BIAZA Research Committee promotes good quality basic and applied research by and within BIAZA's member collections.

Following critical consideration of the research proposal and subsequent satisfactory responses by the researcher, the committee has agreed to give a letter of support for this study by Lewis Rowden of the Plymouth University/Zoological Society of London.

In the opinion of the BIAZA Research Committee the outcomes of the project are likely to be relevant and useful to zoos and aquariums

The BIAZA Research Committee realises that involvement in this project is likely to require significant levels of staff time and effort, which will not be feasible for many collections. However, in the opinion of the committee this is a very worthwhile project and we encourage members to take part if at all possible.

Yours faithfully,

Jessica Harley
Chair, BIAZA Research Committee
7 July 2017

Appendix 2: Plymouth University ethical approval

RESEARCH WITH PLYMOUTH UNIVERSITY

11 April 2017

CONFIDENTIAL
Lewis Rowden
School of Biological and Marine Sciences

Dear Lewis

Ethical Approval Application

Thank you for submitting the ethical approval form and details concerning your project:

Application of personality assessment to inform the management of captive primate populations

I am pleased to inform you that this has been approved subject to the following condition:

- Written confirmation of agreement with your project is received from BIAZA (or individual zoos from which keepers will be recruited).

Kind regards

Paula Simson
Secretary to Faculty Research Ethics Committee

Cc. Dr Mark Farnworth

Faculty of Science and Engineering
Plymouth University
Drake Circus
PL4 8AA

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W www.plymouth.ac.uk

Mrs Jayne Brenen
Head of Faculty Operations

Appendix 3: Hominoid Personality Questionnaire

Personality Trait Assessment – Siamang (*Symphalangus syndactylus*)

Information:

Animal personality assessment is increasingly becoming recognised as an important tool for the management of wild animals in captivity.

This study aims to collect information on the personality of animals under captive care by looking at the scores for various personality traits they are assigned by keeping staff. These results will then be applied to studbook data to investigate a range of management aspects including reproduction and social group management.

Your response to this study is entirely voluntary (and at the discretion of your line manager); however, participation will be greatly appreciated as the results of this study will inform management within the EEP.

Instructions and consent:

- This Hominoid personality questionnaire (based on the modified version by Weiss *et al.* 2011) is presented in a way to allow scorers to assess the personality traits of multiple primates by assigning one of the predetermined numerical scores for each personality trait in the tables below.
- Please make your own judgments, **independently from any colleagues**, based purely on your interpretation of each trait and its associated definition.
- Decisions on ratings should be based purely on your experience of working with the animal over time and not on any imposed interactions as part of this study.
- Please do not discuss your ratings with anyone else.
- Rating should take between 5 and 10 minutes per animal.
- Please provide a rating for all of the described traits, even if you are unsure.
- Ratings can be provided using the drop down menus within the tables or alternatively by printing the form and writing in values by hand.
- Ratings are based on the following 7 point scale.

1	2	3	4	5	6	7
Total absence or negligible amounts			Displays an average amount			Displays the trait extremely

- This presentation of the questionnaire allows up to 6 individual animals to be scored on a single sheet (with animal identification information to be completed in table 1 below). If your collection houses more than 6 animals that meet the criteria, please use additional sheets.
- Please only carry out this trait rating if you have worked with the animals in question for over 1 year.
- Please only carry out trait rating for animals that are over 1 year of age at time of completion.
- You have the right to withdraw any data provided as part of this study within 2 weeks of submission by contacting the author at lewis.rowden@zsl.org After this time, data will be anonymised and therefore will not be available to withdraw but will be confidential in nature.
- The same author email address can be used to contact for a debrief of results anytime from January 2019.

I have read and understood the above information and am happy for data I provide to be used as part of this study. ☐

Questions about You:

Name of Zoo: Name of Rater: Gender: Choose an item. Date:

How long have you worked with siamang as a species? Years and Months

How long have you worked with this group of siamang? Years and Months

How regularly do you work with these animals? Choose an item.

Table 1: Animal ID information

	Animal					
	1.	2.	3.	4.	5.	6.
Name						
Sex						
Age						
Studbook Number						
Social situation	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.

Section One: Interactions with conspecifics

	Individual Trait Ratings from 1 to 7 (1=absence of trait, 7= frequently displays trait) 1.	2.	3.	4.	5.	6.
FEARFUL: Subject reacts excessively to real or imagined threats by displaying behaviours such as screaming, grimacing, running away or other signs of anxiety or distress.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
DOMINANT: Subject is able to displace, threaten, or take food from conspecifics. Or subject may express high status by decisively intervening in social interactions.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
PERSISTENT: Subject tends to continue in a course of action, task, or strategy for a long time or continues despite opposition conspecifics.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
CAUTIOUS: Subject often seems attentive to possible harm or danger from its actions. Subject avoids risky behaviours.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
STABLE: Subject reacts to its environment including the behaviour of conspecifics in a calm, equable, way. Subject is not easily upset by the behaviours of conspecifics.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
AUTISTIC: Subject often displays repeated, continuous, and stereotyped behaviours such as rocking or self-clasping.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
CURIOUS: Subject has a desire to see or know about objects, devices, or conspecifics. This includes a desire to know about the affairs of conspecifics that do not directly concern the subject.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
THOUGHTLESS: Subject often behaves in a way that seems imprudent or forgetful.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
STINGY/GREEDY: Subject is excessively desirous or covetous of food, favoured locations, or other resources. Subject is unwilling to share these resources with others.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
JEALOUS: Subject is often troubled by others who are in a desirable or advantageous situation such as having food, a choice location, or access to social groups. Subject may attempt to disrupt activities of advantaged conspecifics.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
INDIVIDUALISTIC: Subject's behaviour stands out compared to that of the other individuals in the group. This does not mean that it does not fit or is incompatible with the group.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.

	Individual Trait Ratings from 1 to 7 (1=absence of trait, 7= frequently displays trait)					
	1.	2.	3.	4.	5.	6.
RECKLESS: Subject is rash or unconcerned about the consequences of its behaviours.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.

SOCIABLE: Subject seeks and enjoys the company of conspecifics and engages in amicable, affable, interactions with them.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
DISTRACTIBLE: Subject is easily distracted and has a short attention span.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
TIMID: Subject lacks self-confidence, is easily alarmed and is hesitant to venture into new social or non-social situations.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
SYMPATHETIC: Subject seems to be considerate and kind towards conspecifics as if sharing their feelings or trying to provide reassurance.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
PLAYFUL: Subject is eager to engage in lively, vigorous, sportive, or acrobatic behaviours with or without conspecifics.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
SOLITARY: Subject prefers to spend considerable time alone not seeking or avoiding contact with conspecifics.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
VULNERABLE: Subject is prone to be physically or emotionally hurt as a result of dominance displays, highly assertive behaviour, aggression, or attack by a conspecific.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
INNOVATIVE: Subject engages in new or different behaviours that may involve the use of objects or materials or ways of interacting with others.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
ACTIVE: Subject spends little time idle and seems motivated to spend considerable time either moving around or engaging in some overt, energetic behaviour.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
HELPFUL: Subject is willing to assist, accommodate, or cooperate with conspecifics.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
BULLYING: Subject is overbearing and intimidating towards younger or lower ranking conspecifics.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
AGGRESSIVE: Subject often initiates fights or other menacing and agonistic encounters with conspecifics.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
MANIPULATIVE: Subject is adept at forming social relationships for its own advantage, especially using alliances and friendships to increase its social standing. Seems able and willing to use others.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
GENTLE: Subject responds to others in an easy-going, kind, and considerate manner. Subject is not rough or threatening.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.

	Individual Trait Ratings from 1 to 7 (1=absence of trait, 7= frequently displays trait) 1.	2.	3.	4.	5.	6.
AFFECTIONATE: Subject seems to have a warm attachment or closeness with conspecifics. This may entail frequently grooming, touching, embracing, or lying next to others.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
EXCITABLE: Subject is easily aroused to an emotional state. Subject becomes highly aroused by situations that would cause less arousal in most individuals.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
IMPULSIVE: Subject often displays some spontaneous or sudden behaviour that could not have been anticipated. There often seems to be some emotional reason behind the sudden behaviour.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
INQUISITIVE: Subject seems drawn to new situations, objects, or animals. Subject behaves as if it wishes to learn more about conspecifics, objects, or persons within its view.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
SUBMISSIVE: Subject often gives in or yields to a conspecific. Subject acts as if it is subordinate or of lower rank than others.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
COOL: Subject seems unaffected by emotions and is usually undisturbed, assured, and calm.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
DEPENDENT/FOLLOWER: Subject often relies on conspecifics for leadership, reassurance, touching, embracing and other forms of social support.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
IRRITABLE: Subject often seems in a bad mood or is impatient and easily provoked to anger exasperation and consequent agonistic behaviour.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
UNPERCEPTIVE: Subject is slow to respond or understand moods, dispositions, or behaviours of conspecifics.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
PREDICTABLE: Subject's behaviour is consistent and steady over extended periods of time. Subject does little that is unexpected or deviates from its usual behavioural routine.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
DECISIVE: Subject is deliberate, determined, and purposeful in its activities.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
DEPRESSED: Subject does not seek out social interactions with others and often fails to respond to social interactions of conspecifics. Subject often appears isolated, withdrawn, sullen, brooding, and has reduced activity.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
CONVENTIONAL: Subject seems to lack spontaneity or originality. Subject behaves in a consistent manner from day to day and stays well within the social rules of the group.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.

	Individual Trait Ratings from 1 to 7 (1=absence of trait, 7= frequently displays trait) 1.	2.	3.	4.	5.	6.
SENSITIVE: Subject is able to understand or read the mood, disposition, feelings, or intentions of conspecifics often on the basis of subtle, minimal cues.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
DEFIANT: Subject is assertive or contentious in a way inconsistent with the usual dominance order. Subject maintains these actions despite unfavourable consequences or threats from others.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
INTELLIGENT: Subject is quick and accurate in judging and comprehending both social and non-social situations. Subject is perceptive and discerning about social relationships.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
PROTECTIVE: Subject shows concern for conspecifics and often intervenes to prevent harm or annoyance from coming to them.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
QUITTING: Subject readily stops or gives up activities that have recently been started.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
INVENTIVE: Subject is more likely than others to do new things including novel social or non-social behaviours. Novel behaviour may also include new ways of using devices or materials.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
CLUMSY: Subject is relatively awkward or uncoordinated during movements including but not limited to walking, acrobatics, and play.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
ERRATIC: Subject is inconsistent, indefinite, and widely varying in its behaviour and moods.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
FRIENDLY: Subject often seeks out contact with conspecifics for amiable, genial activities. Subject infrequently initiates hostile behaviours towards conspecifics.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
ANXIOUS: Subject often seems distressed, troubled, or is in a state of uncertainty.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
LAZY: Subject is relatively inactive, indolent, or slow moving and avoids energetic activities.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
DISORGANIZED: Subject is scatter-brained, sloppy, or haphazard in its behaviour as if not following a consistent goal.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
UNEMOTIONAL: Subject is relatively placid and unlikely to become aroused, upset, happy, or sad.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
IMITATIVE: Subject often mimics, or copies behaviours that it has observed in conspecifics.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
INDEPENDENT: Subject is individualistic and determines its own course of action without control or interference from conspecifics.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.

Section 2: Human-Animal Interactions

	Individual Trait Ratings from 1 to 7 (1=absence of trait, 7= frequently displays trait)					
	1.	2.	3.	4.	5.	6.
SOCIAL: Initiates interaction with people.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
CAUTIOUS: Spends a long time assessing the environment before taking action.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
COOPERATIVE: Responds positively to human cues/commands.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
NERVOUS: Cowers and is reluctant to respond to cues/commands. If responses are made they tend to be quick and erratic.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
AGGRESSIVE: Threatens and tries to attack	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.
OBLIVIOUS: Doesn't respond to human presence.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.

PHYSICALITY The physical appearance of individual animal (based on the opinion of the rater).	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.	Choose an item.

References

Weiss, A., Adams, M. J., Widdig, A., Gerald, M.S., 2011. Rhesus Macaques (*Macaca mulatta*) as Living Fossils of Hominoid Personality and Subjective Well-Being. *Journal of Comparative Psychology*, 125(1), pp. 72-83.

Contact details

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NW1 4RY

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Appendix 4: Behavioural coding ethogram *S. syndactylus*

ACTIVE BEHAVIOURS	**CODE**	**DESCRIPTION**
Brachiation	B	Arboreal locomotion whereby animal locomotes using fore limbs only, in a hand-over-hand action.
Locomotion	Lo	Any form of locomotion excluding brachiation e.g. bipedal or quadrupedal. Can be terrestrial or arboreal.
Feeding/foraging	F	Animal actively gathers and/or consumes food or water.
SOCIAL BEHAVIOURS	**CODE**	**DESCRIPTION**
Contact	C	Relaxed stationary contact where animals sit in physical contact with each other i.e. huddle. Can involve more than 2 animals
Embrace	E	Stationary ventral-ventral contact between 2 animals, during which at least one animal puts its arms around another
Allogroom	Al	Animal deliberately and intently picks through the fur of a conspecific with fingers.
Receives grooming	RG	Animal remains stationary whilst having fur being picked through deliberately and intently by a conspecific.
Mutual grooming	MG	Animal deliberately and intently picks through the fur of a conspecific with fingers, whilst the same conspecific simultaneously picks through the fur of the focal animal.
Play	P	Animal involved in play behaviours with conspecific e.g. wrestling, slapping.
Reproductive	Rep	Animal presents genitals or is involved in copulation with conspecific.
Aggression	A	Animal exhibits threat postures (staring, shaking enclosure fittings, agonistic chasing) or physical aggression (full force biting, grabbing, pulling) towards a conspecific. Animal may be instigator or receiver of aggression.
Vocalisation (social)	VS	Any vocalisation carried out by an individual at the same time as another conspecific (whether in the same enclosure or not).
GENERAL BEHAVIOURS	**CODE**	**DESCRIPTION**
Vocalisation (individual)	VI	Any vocalisation carried out by an individual independently from another conspecific.
Autogroom	Au	Animal deliberately and intently picks through own fur with fingers.
Interaction with environmental enrichment	IEE	Animal interacts in any way (touching, biting carrying etc.) with environmental enrichment devices that have been put into the enclosure.
Interaction with enclosure	IEn	Animal interacts in any way (touching, biting, carrying etc.) with enclosure features that are not food or enrichment related.
Stationary	S	Animal is stationary but with eyes open and seemingly alert to surroundings.
Resting	R	Animal is stationary with eyes closed and does not respond quickly to surrounding stimuli.
Excretion	Ex	Animal defecates/urinates
Out of sight	OOS	Animal is not visible to the observer.
EVENT BEHAVIOURS		**DESCRIPTION**
Scratch	Sc	Repetitive raking of the animals own skin using fingers or feet.

Yawn	Y	Gaping movement of the mouth, whereby mouth is fully opened and teeth fully exposed.
Formal bite	FB	Animal touches conspecific on any part of its body with an open mouth, low intensity/tactile bite.
Grin	G	Animals mouth is slightly opened and the corners of the mouth are withdrawn with teeth barely visible between lips.
Lipsmack	LS	Animals mouth moves from slightly open to slightly closed several times consecutively in rapid succession.
Body shake	BS	Animal actively shakes the whole of its body, often particularly the shoulder region.

Proximity categories for nearest neighbour:

1	In physical contact or within 1m
2	Between 1 and 5m
3	Between 5 and 10m
4	>10m

Appendix 5: R-script for *S. syndactylus* PCA analysis

```
dframe1 <- read.csv(file.choose(),header = T)

summary(dframe1)

cor(dframe1[1:61])



pairs (dframe1[1:61], panel = panel.smooth)

PRCOMP1 <- prcomp(~ FEARFUL + DOMINANT + PERSISTENT + AUTISTIC + THOUGHTLESS +
        STINGY +RECKLESS +DISTRACTIBLE + PLAYFUL + SOLITARY + VULNERABLE +
INNOVATIVE+ ACTIVE + HELPFUL + BULLYING + AGGRESSIVE + IMPULSIVE + INQUISITIVE +
DEPENDENT + IRRITABLE + UNPERCEPTIVE + DECISIVE + DEPRESSED + DEFIANT +
INTELLIGENT + PROTECTIVE + CLUMSY + ERRATIC + ANXIOUS + DISORGANIZED + IMITATIVE +
INDEPENDENT + SOCIAL + CAUTIOUS + OBLIVIOUS , data = dframe1, na.action = na.omit)

summary(PRCOMP1)

summary(PRCOMP1)

plot(PRCOMP1, type = "lines")

PRCOMP1$sdev^2

PRCOMP1$rotation

install.packages("paran")

library(relimp, pos = 4)

library(paran)
```

```
dframe2 <- read.csv('C:/Users/rowden.l/Desktop/siamang ICC/Trait Scores siamang
PCA.csv',header = T)

summary(dframe2)

cor(dframe2[1:35])

paran(dframe2[c(1:35)], iterations=5000, centile=0, quietly=FALSE,
    status=TRUE, all=TRUE, cfa=TRUE, graph=TRUE,
    color=TRUE, col=c("black","red","blue"), lty = c(1,2,3), lwd=1, legend=TRUE, file="",
width=640, height=640, grdevice="png", seed=0)

library(psych)

fit <- principal(dframe2, nfactors=3, rotate="varimax")
```

Appendix 6: GLMM validation script *S. syndactylus*

```
> GIBBON<-read.csv(file.choose())
> names(GIBBON)
 [1] "Zoo"            "Animal"          "Enclosure"       "Sex"            "
Age"             "RC1"             "RC2"             "RC3"             "Social
positive"
[10] "Locomotion"     "Explorative"     "Beneficiary"     "Resting"        "
X1"              "X2"              "SDB"
> summary(GIBBON)
      Zoo              Animal      Enclosure            Sex              Age
RC1              RC2              RC3            Socialpositive      Locomotion
 Min.   :1.000   Darwin :10   Min.   :1.000   Min.   :1.000   Min.   : 5.2
0   Min.   :1.500   Min.   :2.130   Min.   :2.000   Min.   :0.000   Min.
:0.0000
 1st Qu.:1.000   Denzel :10   1st Qu.:2.000   1st Qu.:1.000   1st Qu.: 6.8
5   1st Qu.:2.320   1st Qu.:2.940   1st Qu.:2.300   1st Qu.:0.020   1st Qu
.:0.0700
 Median :2.000   Spike  :10   Median :4.000   Median :1.000   Median :12.3
0   Median :3.070   Median :3.630   Median :2.600   Median :0.070   Median
:0.1300
 Mean   :2.165   Stig   :10   Mean   :3.504   Mean   :1.266   Mean   :13.6
0   Mean   :2.908   Mean   :3.753   Mean   :2.896   Mean   :0.112   Mean
:0.1514
 3rd Qu.:3.000   Tango  :10   3rd Qu.:5.000   3rd Qu.:2.000   3rd Qu.:17.0
0   3rd Qu.:3.525   3rd Qu.:4.580   3rd Qu.:3.350   3rd Qu.:0.170   3rd Qu
.:0.2100
 Max.   :3.000   Tara   :10   Max.   :6.000   Max.   :2.000   Max.   :36.1
1   Max.   :4.100   Max.   :5.810   Max.   :4.200   Max.   :0.700   Max.
:1.1000
                 (Other):79
  Explorative       Beneficiary          Resting             X1
X2               SDB
 Min.   :0.00000   Min.   :0.00000   Min.   :0.0700   Min.   :0.0000   Min
.   :0.0000   Min.   :0.00000
 1st Qu.:0.00000   1st Qu.:0.00000   1st Qu.:0.3150   1st Qu.:0.1333   1st
Qu.:0.3625   1st Qu.:0.09444
 Median :0.00000   Median :0.01000   Median :0.4300   Median :0.2633   Med
ian :0.5000   Median :0.16667
 Mean   :0.01871   Mean   :0.05245   Mean   :0.4535   Mean   :0.3128   Mea
n   :0.5020   Mean   :0.17873
 3rd Qu.:0.02000   3rd Qu.:0.05500   3rd Qu.:0.5400   3rd Qu.:0.4500   3rd
Qu.:0.6361   3rd Qu.:0.23333
 Max.   :0.27000   Max.   :0.75000   Max.   :1.4300   Max.   :1.0000   Max
.   :0.9833   Max.   :0.86667

> GIBBON$Zoo<-factor(GIBBON$Zoo)
> GIBBON$Animal<-factor(GIBBON$Animal)
> GIBBON$Enclosure<-factor(GIBBON$Enclosure)
> GIBBON$Sex<-factor(GIBBON$Sex)

> summary(GIBBON)
 Zoo         Animal    Enclosure Sex           Age             RC1
RC2              RC3          Socialpositive    Locomotion        Explorative
 1:37   Darwin :10   1:24       1:102   Min.   : 5.20   Min.   :1.500   Min
.   :2.130   Min.   :2.000   Min.   :0.000   Min.   :0.0000   Min.   :0.00
000
 2:42   Denzel :10   2:13       2: 37   1st Qu.: 6.85   1st Qu.:2.320   1st
Qu.:2.940   1st Qu.:2.300   1st Qu.:0.020   1st Qu.:0.0700   1st Qu.:0.000
00
 3:60   Spike  :10   3:30               Median :12.30   Median :3.070   Med
ian :3.630   Median :2.600   Median :0.070   Median :0.1300   Median :0.00
000
        Stig   :10   4:30               Mean   :13.60   Mean   :2.908   Mea
n   :3.753   Mean   :2.896   Mean   :0.112   Mean   :0.1514   Mean   :0.01
871
        Tango  :10   5:25               3rd Qu.:17.00   3rd Qu.:3.525   3rd
Qu.:4.580   3rd Qu.:3.350   3rd Qu.:0.170   3rd Qu.:0.2100   3rd Qu.:0.020
00
```

```
         Tara    :10    6:17              Max.    :36.11    Max.    :4.100    Max
.    :5.810    Max.    :4.200    Max.    :0.700    Max.    :1.1000    Max.    :0.27
000
         (Other):79
  Beneficiary         Resting            X1                X2              
SDB
 Min.    :0.00000   Min.    :0.0700   Min.    :0.0000   Min.    :0.0000   Min.   
:0.00000
 1st Qu.:0.00000   1st Qu.:0.3150   1st Qu.:0.1333   1st Qu.:0.3625   1st 
Qu.:0.09444
 Median :0.01000   Median :0.4300   Median :0.2633   Median :0.5000   Medi
an :0.16667
 Mean    :0.05245   Mean    :0.4535   Mean    :0.3128   Mean    :0.5020   Mean   
:0.17873
 3rd Qu.:0.05500   3rd Qu.:0.5400   3rd Qu.:0.4500   3rd Qu.:0.6361   3rd 
Qu.:0.23333
 Max.    :0.75000   Max.    :1.4300   Max.    :1.0000   Max.    :0.9833   Max.   
:0.86667
```

SOCIAL POSIITVE

```
library(nlme)
> model1<-lme(Socialpositive~Sex+Age+RC1+RC2+RC3, random=~1|Enclosure, met
hod="REML", data=GIBBON)
> summary(model1)
Linear mixed-effects model fit by REML
 Data: GIBBON 
        AIC       BIC   logLik
  -141.0105 -117.8877 78.50523

Random effects:
 Formula: ~1 | Enclosure
        (Intercept)  Residual
StdDev:  0.02440945 0.1188918

Fixed effects: Socialpositive ~ Sex + Age + RC1 + RC2 + RC3 
                  Value  Std.Error  DF    t-value p-value
(Intercept)  0.12821514 0.09171598 128  1.3979586  0.1645
Sex2         0.04479469 0.02756354 128  1.6251425  0.1066
Age         -0.00072385 0.00224690 128 -0.3221536  0.7479
RC1          0.05705336 0.02362617 128  2.4148374  0.0172
RC2         -0.02485049 0.01091442 128 -2.2768485  0.0245
RC3         -0.03100342 0.02094194 128 -1.4804466  0.1412
 Correlation: 
     (Intr) Sex2   Age    RC1    RC2   
Sex2  0.074                            
Age  -0.445 -0.399                     
RC1  -0.638 -0.091  0.715              
RC2  -0.448  0.184 -0.221 -0.085       
RC3  -0.239 -0.048 -0.448 -0.462  0.188

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max 
-1.5206640 -0.5859146 -0.1688278  0.3018642  4.8597080 

Number of Observations: 139
Number of Groups: 6 
> model2<-lme(Socialpositive~Sex+RC1+RC2+RC3, random=~1|Enclosure, method=
"REML", data=GIBBON)
> summary(model2)
Linear mixed-effects model fit by REML
 Data: GIBBON 
        AIC       BIC   logLik
  -153.2876 -133.0027 83.64378

Random effects:
 Formula: ~1 | Enclosure
        (Intercept)  Residual
StdDev:  0.02162704 0.1186676

Fixed effects: Socialpositive ~ Sex + RC1 + RC2 + RC3 
```

```
                  Value  Std.Error  DF   t-value p-value
(Intercept)  0.11672194 0.07980685 129  1.462555  0.1460
Sex2         0.04028822 0.02505763 129  1.607823  0.1103
RC1          0.06234812 0.01605725 129  3.882864  0.0002
RC2         -0.02605697 0.01052441 129 -2.475861  0.0146
RC3         -0.03384418 0.01817948 129 -1.861669  0.0649
 Correlation: 
     (Intr) Sex2   RC1    RC2   
Sex2 -0.125                     
RC1  -0.506  0.294              
RC2  -0.621  0.103  0.089       
RC3  -0.548 -0.272 -0.225  0.099

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max 
-1.5171966 -0.5917335 -0.1726533  0.2444979  4.9063203 

Number of Observations: 139
Number of Groups: 6 
> model3<-lme(Socialpositive~RC1+RC2+RC3, random=~1|Enclosure, method="REM
L", data=GIBBON)
> summary(model3)
Linear mixed-effects model fit by REML
 Data: GIBBON 
        AIC       BIC   logLik
  -158.4241 -140.9924 85.21203

Random effects:
 Formula: ~1 | Enclosure
        (Intercept)  Residual
StdDev:  0.01234854 0.1198566

Fixed effects: Socialpositive ~ RC1 + RC2 + RC3 
                  Value  Std.Error  DF   t-value p-value
(Intercept)  0.13658967 0.07249279 130  1.884183  0.0618
RC1          0.05612328 0.01426938 130  3.933127  0.0001
RC2         -0.02905299 0.01021964 130 -2.842859  0.0052
RC3         -0.02709967 0.01601691 130 -1.691941  0.0931
 Correlation: 
    (Intr) RC1    RC2   
RC1 -0.473              
RC2 -0.602  0.003       
RC3 -0.605 -0.158  0.111

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max 
-1.5261870 -0.5653494 -0.1729853  0.1882261  5.0776860 

Number of Observations: 139
Number of Groups: 6 
> model4<-lme(Socialpositive~RC1+RC2, random=~1|Enclosure, method="REML",
data=GIBBON)
> summary(model4)
Linear mixed-effects model fit by REML
 Data: GIBBON 
        AIC       BIC   logLik
  -164.3285 -149.7652 87.16426

Random effects:
 Formula: ~1 | Enclosure
        (Intercept)  Residual
StdDev:   0.0221411 0.1198501

Fixed effects: Socialpositive ~ RC1 + RC2 
                  Value  Std.Error  DF   t-value p-value
(Intercept)  0.06127716 0.06358618 131  0.963687  0.3370
RC1          0.05113992 0.01534661 131  3.332326  0.0011
RC2         -0.02570509 0.01048945 131 -2.450566  0.0156
 Correlation: 
    (Intr) RC1   
RC1 -0.755       
RC2 -0.682  0.087
```

```
Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max 
-1.2750767 -0.6358279 -0.1547802  0.2820293  5.1195696 

Number of Observations: 139
Number of Groups: 6 
> anova(model1,model2,model3,model4)
       Model df       AIC       BIC   logLik   Test   L.Ratio p-value
model1     1  8 -141.0104 -117.8877 78.50523                         
model2     2  7 -153.2876 -133.0027 83.64378 1 vs 2 10.277100  0.0013
model3     3  6 -158.4240 -140.9924 85.21203 2 vs 3  3.136498  0.0766
model4     4  5 -164.3285 -149.7652 87.16426 3 vs 4  3.904462  0.0482
```

LOCOMOTION

```
> library(nlme)
> model1<-lme(Locomotion~Sex+Age+RC1+RC2+RC3, random = ~1|Enclosure, metho
d = "REML", data = GIBBON)
> summary(model1)
Linear mixed-effects model fit by REML
 Data: GIBBON 
        AIC       BIC   logLik
  -162.5361 -139.4133 89.26805

Random effects:
 Formula: ~1 | Enclosure
        (Intercept)  Residual
StdDev:   0.1302255 0.1050495

Fixed effects: Locomotion ~ Sex + Age + RC1 + RC2 + RC3 
                 Value  Std.Error  DF   t-value p-value
(Intercept)  0.15474577 0.14126133 128  1.095457  0.2754
Sex2        -0.08876779 0.02511597 128 -3.534316  0.0006
Age          0.00691290 0.00467261 128  1.479452  0.1415
RC1          0.13067906 0.05632028 128  2.320285  0.0219
RC2         -0.02190182 0.01066863 128 -2.052917  0.0421
RC3         -0.13013683 0.04606377 128 -2.825145  0.0055
 Correlation: 
     (Intr) Sex2   Age    RC1    RC2   
Sex2  0.055                            
Age  -0.638 -0.258                     
RC1  -0.734 -0.103  0.938              
RC2  -0.293  0.215 -0.226 -0.120       
RC3   0.385  0.082 -0.879 -0.862  0.257

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max 
-1.80954041 -0.49042834 -0.06774211  0.35124689  7.99535695 

Number of Observations: 139
Number of Groups: 6 
```

```
> model2<-lme(Locomotion~Sex+RC1+RC2+RC3, random = ~1|Enclosure, method = 
"REML", data = GIBBON)
> summary(model2)
Linear mixed-effects model fit by REML
 Data: GIBBON 
        AIC       BIC   logLik
  -173.4683 -153.1834 93.73416

Random effects:
 Formula: ~1 | Enclosure
        (Intercept)  Residual
StdDev:  0.07040605 0.1069103
```

```
Fixed effects: Locomotion ~ Sex + RC1 + RC2 + RC3
                  Value  Std.Error  DF   t-value p-value
(Intercept)  0.27680794 0.09650465 129  2.868338  0.0048
Sex2        -0.08437447 0.02431331 129 -3.470300  0.0007
RC1          0.04665440 0.01888424 129  2.470546  0.0148
RC2         -0.01798368 0.01039916 129 -1.729339  0.0861
RC3         -0.06022664 0.02133334 129 -2.823123  0.0055
 Correlation:
     (Intr) Sex2   RC1    RC2
Sex2 -0.152
RC1  -0.545  0.396
RC2  -0.632  0.154  0.246
RC3  -0.524 -0.310 -0.231  0.123

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-1.83204750 -0.43698121 -0.06001252  0.33819823  8.05802219

Number of Observations: 139
Number of Groups: 6
```

```
> model3<-lme(Locomotion~Sex+RC1+RC3, random = ~1|Enclosure, method = "REM
L", data = GIBBON)
> summary(model3)
Linear mixed-effects model fit by REML
 Data: GIBBON
        AIC       BIC   logLik
  -179.7903 -162.3586 95.89514

Random effects:
 Formula: ~1 | Enclosure
        (Intercept)  Residual
StdDev:  0.06923387 0.1077788

Fixed effects: Locomotion ~ Sex + RC1 + RC3
                  Value  Std.Error  DF   t-value p-value
(Intercept)  0.17095397 0.07493397 130  2.281395  0.0242
Sex2        -0.07823615 0.02419671 130 -3.233338  0.0016
RC1          0.05425818 0.01840193 130  2.948506  0.0038
RC3         -0.05511036 0.02128299 130 -2.589409  0.0107
 Correlation:
     (Intr) Sex2   RC1
Sex2 -0.071
RC1  -0.520  0.373
RC3  -0.583 -0.335 -0.272

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-1.67667166 -0.45430716 -0.07213228  0.33154334  8.31116371

Number of Observations: 139
Number of Groups: 6
```

```
> anova(model1,model2,model3)
       Model df       AIC       BIC   logLik   Test  L.Ratio p-value
model1     1  8 -162.5361 -139.4133 89.26805
model2     2  7 -173.4683 -153.1834 93.73416 1 vs 2 8.932209  0.0028
model3     3  6 -179.7903 -162.3586 95.89514 2 vs 3 4.321959  0.0376
```

EXPLORATIVE

```
> model4<-lme(Explorative~Sex+Age+RC1+RC2+RC3, random = ~1|Enclosure, meth
od = "REML", data = GIBBON)
> summary(model4)
Linear mixed-effects model fit by REML
 Data: GIBBON
        AIC       BIC   logLik
  -459.6677 -436.5449 237.8338

Random effects:
 Formula: ~1 | Enclosure
        (Intercept)   Residual
StdDev:  0.04455581 0.03432506

Fixed effects: Explorative ~ Sex + Age + RC1 + RC2 + RC3
                  Value  Std.Error  DF   t-value p-value
(Intercept) -0.04960803 0.04685912 128 -1.058663  0.2917
Sex2        -0.00186176 0.00820937 128 -0.226785  0.8210
Age          0.00342121 0.00155318 128  2.202721  0.0294
RC1          0.06308299 0.01873658 128  3.366836  0.0010
RC2         -0.00283966 0.00348947 128 -0.813780  0.4173
RC3         -0.05333065 0.01530664 128 -3.484151  0.0007
 Correlation:
     (Intr) Sex2   Age    RC1    RC2
Sex2  0.056
Age  -0.640 -0.257
RC1  -0.734 -0.104  0.940
RC2  -0.286  0.216 -0.227 -0.123
RC3   0.394  0.084 -0.883 -0.867  0.258

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-1.4111920 -0.3766063 -0.1906699  0.1133821  6.8440364

Number of Observations: 139
Number of Groups: 6
```

```
> model5<-lme(Explorative~Age+RC1+RC2+RC3, random = ~1|Enclosure, method =
"REML", data = GIBBON)
> summary(model5)
Linear mixed-effects model fit by REML
 Data: GIBBON
       AIC       BIC   logLik
  -469.387 -449.1021 241.6935

Random effects:
 Formula: ~1 | Enclosure
        (Intercept)   Residual
StdDev:  0.04396336 0.03421477

Fixed effects: Explorative ~ Age + RC1 + RC2 + RC3
                  Value  Std.Error  DF   t-value p-value
(Intercept) -0.04831261 0.04648185 129 -1.039387  0.3006
Age          0.00329569 0.00149047 129  2.211167  0.0288
RC1          0.06219672 0.01850283 129  3.361470  0.0010
RC2         -0.00265730 0.00339554 129 -0.782584  0.4353
RC3         -0.05268428 0.01514852 129 -3.477849  0.0007
 Correlation:
    (Intr) Age    RC1    RC2
Age -0.648
RC1 -0.733  0.950
RC2 -0.308 -0.182 -0.102
RC3  0.390 -0.894 -0.865  0.247

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-1.4061390 -0.3688000 -0.1918068  0.1001033  6.8446988

Number of Observations: 139
Number of Groups: 6
```

```
> model6<-lme(Explorative~Age+RC1+RC3, random = ~1|Enclosure, method = "RE
ML", data = GIBBON)
> summary(model6)
Linear mixed-effects model fit by REML
 Data: GIBBON 
        AIC       BIC   logLik
  -480.3294 -462.8977 246.1647

Random effects:
 Formula: ~1 | Enclosure
        (Intercept)   Residual
StdDev:  0.04039337 0.03425864

Fixed effects: Explorative ~ Age + RC1 + RC3 
                  Value  Std.Error  DF   t-value p-value
(Intercept) -0.05322546 0.04286198 130 -1.241787  0.2166
Age          0.00280193 0.00141979 130  1.973477  0.0506
RC1          0.05708807 0.01781536 130  3.204429  0.0017
RC3         -0.04693221 0.01424106 130 -3.295557  0.0013
 Correlation: 
    (Intr) Age    RC1   
Age -0.753              
RC1 -0.811  0.949       
RC3  0.490 -0.884 -0.863

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max 
-1.3835991 -0.3564653 -0.1236806  0.1453677  6.8450924 

Number of Observations: 139
Number of Groups: 6 



> model7<-lme(Explorative~RC1+RC3, random = ~1|Enclosure, method = "REML",
data = GIBBON)
> summary(model7)
Linear mixed-effects model fit by REML
 Data: GIBBON 
        AIC       BIC   logLik
  -492.7308 -478.1675 251.3654

Random effects:
 Formula: ~1 | Enclosure
        (Intercept)   Residual
StdDev:  0.01926198 0.03511785

Fixed effects: Explorative ~ RC1 + RC3 
                   Value   Std.Error  DF   t-value p-value
(Intercept)  0.009059438 0.023501624 131  0.385481  0.7005
RC1          0.021493537 0.005474488 131  3.926127  0.0001
RC3         -0.019184807 0.006410097 131 -2.992905  0.0033
 Correlation: 
    (Intr) RC1   
RC1 -0.543       
RC3 -0.656 -0.170

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max 
-1.54157032 -0.42824187 -0.21781815  0.01872756  6.94077465 

Number of Observations: 139
Number of Groups: 6 



> anova(model4,model5,model6,model7)
```

```
        Model df       AIC       BIC   logLik   Test   L.Ratio p-value
model4      1  8 -459.6677 -436.5449 237.8338
model5      2  7 -469.3870 -449.1021 241.6935 1 vs 2  7.719345  0.0055
model6      3  6 -480.3294 -462.8977 246.1647 2 vs 3  8.942395  0.0028
model7      4  5 -492.7308 -478.1675 251.3654 3 vs 4 10.401386  0.0013
W
```

BENEFICIARY

```
> model8<-lme(Beneficiary~Sex+Age+RC1+RC2+RC3, random = ~1|Enclosure, meth
od = "REML", data = GIBBON)
> summary(model8)
Linear mixed-effects model fit by REML
 Data: GIBBON
       AIC       BIC   logLik
  -197.408 -174.2852 106.704

Random effects:
 Formula: ~1 | Enclosure
        (Intercept)   Residual
StdDev:  0.04560897 0.09470462

Fixed effects: Beneficiary ~ Sex + Age + RC1 + RC2 + RC3
                  Value  Std.Error  DF   t-value p-value
(Intercept) -0.04429816 0.09346158 128 -0.473972  0.6363
Sex2         0.07666371 0.02238740 128  3.424413  0.0008
Age         -0.00170298 0.00260485 128 -0.653773  0.5144
RC1          0.02090788 0.03005619 128  0.695626  0.4879
RC2          0.03045233 0.00927020 128  3.284970  0.0013
RC3         -0.02545929 0.02569151 128 -0.990961  0.3236
 Correlation:
     (Intr) Sex2   Age    RC1    RC2
Sex2  0.043
Age  -0.513 -0.317
RC1  -0.683 -0.079  0.848
RC2  -0.429  0.199 -0.209 -0.063
RC3   0.041  0.022 -0.711 -0.689  0.231

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-1.4668828 -0.6363922 -0.1482965  0.2257278  6.1357029

Number of Observations: 139
Number of Groups: 6
```

```
> model9<-lme(Beneficiary~Sex+RC1+RC2+RC3, random = ~1|Enclosure, method =
"REML", data = GIBBON)
> summary(model9)
Linear mixed-effects model fit by REML
 Data: GIBBON
        AIC       BIC   logLik
  -209.0996 -188.8147 111.5498

Random effects:
 Formula: ~1 | Enclosure
        (Intercept)  Residual
StdDev:  0.04131653 0.0947399

Fixed effects: Beneficiary ~ Sex + RC1 + RC2 + RC3
                  Value  Std.Error  DF   t-value p-value
(Intercept) -0.07411131 0.07854074 129 -0.943603  0.3471
Sex2         0.07150467 0.02112532 129  3.384786  0.0009
RC1          0.03758086 0.01565651 129  2.400334  0.0178
RC2          0.02879326 0.00901205 129  3.194974  0.0018
RC3         -0.03739768 0.01776683 129 -2.104916  0.0372
```

```
 Correlation: 
     (Intr) Sex2   RC1    RC2   
Sex2 -0.144                     
RC1  -0.542  0.369              
RC2  -0.639  0.139  0.209       
RC3  -0.537 -0.302 -0.234  0.118

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max 
-1.4624950 -0.6647304 -0.1626573  0.2347935  6.1372598 

Number of Observations: 139
Number of Groups: 6 



> anova(model8,model9)
       Model df       AIC       BIC   logLik   Test  L.Ratio p-value
model8     1  8 -197.4080 -174.2852 106.7040                        
model9     2  7 -209.0996 -188.8147 111.5498 1 vs 2 9.691568  0.0019
```

RESTING

```
> model10<-lme(Resting~Sex+Age+RC1+RC2+RC3, random = ~1|Enclosure, method
= "REML", data = GIBBON)
> summary(model10)
Linear mixed-effects model fit by REML
 Data: GIBBON 
        AIC      BIC   logLik
  -20.04474 3.078052 18.02237

Random effects:
 Formula: ~1 | Enclosure
        (Intercept)  Residual
StdDev:  0.06702432 0.1856665

Fixed effects: Resting ~ Sex + Age + RC1 + RC2 + RC3 
                  Value  Std.Error  DF    t-value p-value
(Intercept)  0.29582144 0.16752820 128  1.7658009  0.0798
Sex2        -0.04801191 0.04363571 128 -1.1002895  0.2733
Age          0.01210859 0.00439056 128  2.7578720  0.0067
RC1         -0.02632907 0.04927744 128 -0.5343028  0.5941
RC2         -0.02603962 0.01782462 128 -1.4608790  0.1465
RC3          0.06294922 0.04283075 128  1.4697201  0.1441
 Correlation: 
     (Intr) Sex2   Age    RC1    RC2   
Sex2  0.050                            
Age  -0.476 -0.347                     
RC1  -0.663 -0.079  0.801              
RC2  -0.448  0.193 -0.211 -0.060       
RC3  -0.075 -0.001 -0.623 -0.609  0.220

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max 
-2.0807745 -0.6184645 -0.1151486  0.4856842  5.1364662 

Number of Observations: 139
Number of Groups: 6 


> model11<-lme(Resting~Sex+Age+RC2+RC3, random = ~1|Enclosure, method = "REML", data =
> summary(model11)
Linear mixed-effects model fit by REML
 Data: GIBBON 
        AIC       BIC   logLik
```

```
   -26.08244 -5.797559 20.04122

 Random effects:
  Formula: ~1 | Enclosure
         (Intercept)  Residual
 StdDev:   0.0554619 0.1858865

 Fixed effects: Resting ~ Sex + Age + RC2 + RC3
                   Value  Std.Error  DF   t-value p-value
 (Intercept)  0.25649093 0.12003450 129  2.136810  0.0345
 Sex2        -0.04910540 0.04334720 129 -1.132839  0.2594
 Age          0.01392606 0.00256945 129  5.419865  0.0000
 RC2         -0.02812167 0.01754884 129 -1.602481  0.1115
 RC3          0.04411209 0.03226240 129  1.367291  0.1739
  Correlation:
     (Intr) Sex2   Age    RC2
 Sex2  0.005
 Age   0.090 -0.477
 RC2  -0.654  0.185 -0.258
 RC3  -0.800 -0.076 -0.253  0.210

 Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
 -2.0870380 -0.6124216 -0.1268973  0.4898131  5.1216622

 Number of Observations: 139
 Number of Groups: 6


> model12<-lme(Resting~Age+RC2+RC3, random = ~1|Enclosure, method = "REML"
, data = GIBBON)
> summary(model12)
Linear mixed-effects model fit by REML
 Data: GIBBON
        AIC       BIC   logLik
  -31.24267 -13.81102 21.62134

Random effects:
 Formula: ~1 | Enclosure
        (Intercept)  Residual
StdDev:  0.05365507 0.1862154

Fixed effects: Resting ~ Age + RC2 + RC3
                  Value  Std.Error  DF   t-value p-value
(Intercept)  0.26113864 0.11927083 130  2.189459  0.0303
Age          0.01253207 0.00225270 130  5.563136  0.0000
RC2         -0.02475948 0.01722808 130 -1.437158  0.1531
RC3          0.04038400 0.03189924 130  1.265986  0.2078
 Correlation:
    (Intr) Age    RC2
Age  0.098
RC2 -0.667 -0.193
RC3 -0.801 -0.324  0.225

Standardized Within-Group Residuals:
       Min          Q1         Med          Q3         Max
-2.0223696 -0.5810878 -0.1507006  0.4980243  5.1735977

Number of Observations: 139
Number of Groups: 6



> model13<-lme(Resting~Age+RC3, random = ~1|Enclosure, method = "REML", da
ta = GIBBON)
> summary(model13)
Linear mixed-effects model fit by REML
 Data: GIBBON
       AIC       BIC   logLik
  -37.6277 -23.06443 23.81385
```

```
Random effects:
 Formula: ~1 | Enclosure
        (Intercept)  Residual
StdDev:  0.06483465 0.1860243

Fixed effects: Resting ~ Age + RC3
                 Value  Std.Error  DF  t-value p-value
(Intercept) 0.13051516 0.09305279 131 1.402593  0.1631
Age         0.01192177 0.00225493 131 5.286982  0.0000
RC3         0.05647182 0.03263201 131 1.730565  0.0859
 Correlation:
    (Intr) Age
Age -0.007
RC3 -0.891 -0.319

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-1.7834820 -0.5934388 -0.1814877  0.4302238  5.4198770

Number of Observations: 139
Number of Groups: 6
```

```
> model14<-lme(Resting~Age, random = ~1|Enclosure, method = "REML", data =
GIBBON)
> summary(model14)
Linear mixed-effects model fit by REML
 Data: GIBBON
        AIC       BIC   logLik
  -41.95925 -30.27933 24.97962

Random effects:
 Formula: ~1 | Enclosure
        (Intercept)  Residual
StdDev:  0.04981247 0.1884008

Fixed effects: Resting ~ Age
                 Value  Std.Error  DF  t-value p-value
(Intercept) 0.27800385 0.03870178 132 7.183231       0
Age         0.01286972 0.00212451 132 6.057744       0
 Correlation:
    (Intr)
Age -0.738

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-1.8123075 -0.5939565 -0.1434648  0.4600736  5.3001874

Number of Observations: 139
Number of Groups: 6
```

```
> anova(model10,model11,model12,model13,model14)
        Model df       AIC        BIC   logLik   Test  L.Ratio p-value
model10     1  8 -20.04474   3.078052 18.02237
model11     2  7 -26.08244  -5.797559 20.04122 1 vs 2 4.037697  0.0445
model12     3  6 -31.24267 -13.811024 21.62134 2 vs 3 3.160236  0.0755
model13     4  5 -37.62770 -23.064426 23.81385 3 vs 4 4.385027  0.0363
model14     5  4 -41.95925 -30.279325 24.97962 4 vs 5 2.331549  0.1268
```

PROXIMITY 1

```
> model15<-lme(ONE~Sex+Age+RC1+RC2+RC3, random = ~1|Enclosure, method = "R
EML", data = GIBBON)
```

```
> summary(model15)
Linear mixed-effects model fit by REML
 Data: GIBBON
       AIC      BIC   logLik
  -7.335543 15.78725 11.66777

Random effects:
 Formula: ~1 | Enclosure
        (Intercept)  Residual
StdDev:   0.3204857 0.1861942

Fixed effects: ONE ~ Sex + Age + RC1 + RC2 + RC3
                 Value  Std.Error  DF   t-value p-value
(Intercept) -0.2743793 0.27917608 128 -0.982818  0.3276
Sex2        -0.0011365 0.04460611 128 -0.025478  0.9797
Age          0.0231145 0.00919567 128  2.513628  0.0132
RC1          0.3364911 0.11135589 128  3.021763  0.0030
RC2          0.0277168 0.01902348 128  1.456979  0.1476
RC3         -0.2899597 0.09047170 128 -3.204976  0.0017
 Correlation:
     (Intr) Sex2   Age    RC1    RC2
Sex2  0.060
Age  -0.640 -0.253
RC1  -0.720 -0.112  0.949
RC2  -0.246  0.219 -0.235 -0.138
RC3   0.431  0.095 -0.901 -0.886  0.266

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-2.1078374 -0.6834508 -0.1824486  0.6750995  2.9744115

Number of Observations: 139
Number of Groups: 6



> model16<-lme(ONE~Age+RC1+RC2+RC3, random = ~1|Enclosure, method = "REML"
, data = GIBBON)
> summary(model16)
Linear mixed-effects model fit by REML
 Data: GIBBON
       AIC      BIC   logLik
  -13.72065 6.564233 13.86032

Random effects:
 Formula: ~1 | Enclosure
        (Intercept)  Residual
StdDev:   0.3207609 0.1854681

Fixed effects: ONE ~ Age + RC1 + RC2 + RC3
                 Value  Std.Error  DF   t-value p-value
(Intercept) -0.2757052 0.27803157 129 -0.991633  0.3232
Age          0.0231392 0.00887314 129  2.607775  0.0102
RC1          0.3372387 0.11036010 129  3.055803  0.0027
RC2          0.0278017 0.01849003 129  1.503603  0.1351
RC3         -0.2905796 0.08981717 129 -3.235234  0.0015
 Correlation:
    (Intr) Age    RC1    RC2
Age -0.647
RC1 -0.718  0.958
RC2 -0.265 -0.191 -0.117
RC3  0.429 -0.911 -0.885  0.252

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-2.1159185 -0.6874701 -0.1821569  0.6757353  2.9858330

Number of Observations: 139
Number of Groups: 6
```

```
> model17<-lme(ONE~Age+RC1+RC3, random = ~1|Enclosure, method = "REML", da
ta = GIBBON)
> summary(model17)
Linear mixed-effects model fit by REML
 Data: GIBBON
       AIC       BIC   logLik
  -19.6297 -2.198056 15.81485

Random effects:
 Formula: ~1 | Enclosure
        (Intercept)  Residual
StdDev:   0.3422961 0.1859168

Fixed effects: ONE ~ Age + RC1 + RC3
                 Value  Std.Error  DF   t-value p-value
(Intercept) -0.1893485 0.27518996 130 -0.688065  0.4926
Age          0.0267886 0.00886506 130  3.021814  0.0030
RC1          0.3708148 0.11157971 130  3.323317  0.0012
RC3         -0.3355866 0.08841226 130 -3.795702  0.0002
 Correlation:
    (Intr) Age    RC1
Age -0.730
RC1 -0.775  0.961
RC3  0.532 -0.911 -0.893

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-2.1279570 -0.7328850 -0.2145226  0.7376953  2.9604981

Number of Observations: 139
Number of Groups: 6
```

```
> anova(model15,model16,model17)
        Model df        AIC       BIC   logLik   Test  L.Ratio p-value
model15     1  8  -7.335543 15.787250 11.66777
model16     2  7 -13.720646  6.564233 13.86032 1 vs 2 4.385103  0.0363
model17     3  6 -19.629705 -2.198056 15.81485 2 vs 3 3.909059  0.0480
```

PROXIMITY 2

```
> model18<-lme(TWO~Sex+Age+RC1+RC2+RC3, random = ~1|Enclosure, method = "R
EML", data = GIBBON)
> summary(model18)
Linear mixed-effects model fit by REML
 Data: GIBBON
        AIC       BIC   logLik
  -28.17078 -5.047988 22.08539

Random effects:
 Formula: ~1 | Enclosure
        (Intercept)  Residual
StdDev:  0.06481404 0.1800914

Fixed effects: TWO ~ Sex + Age + RC1 + RC2 + RC3
                  Value  Std.Error  DF    t-value p-value
(Intercept)  0.28356701 0.16234772 128  1.7466645  0.0831
Sex2        -0.05918417 0.04232258 128 -1.3984065  0.1644
Age          0.00574314 0.00425237 128  1.3505743  0.1792
RC1          0.08587398 0.04771089 128  1.7998824  0.0742
RC2          0.00667109 0.01728550 128  0.3859356  0.7002
RC3         -0.03816802 0.04147581 128 -0.9202476  0.3592
 Correlation:
```

```
     (Intr) Sex2   Age    RC1    RC2   
Sex2  0.050                            
Age  -0.476 -0.347                     
RC1  -0.663 -0.079  0.801              
RC2  -0.448  0.193 -0.211 -0.060       
RC3  -0.077 -0.002 -0.622 -0.608  0.219

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max 
-2.60513001 -0.58013094  0.06167969  0.61687496  2.24743870 

Number of Observations: 139
Number of Groups: 6 
```

```
> model19<-lme(TWO~Sex+Age+RC1+RC3, random = ~1|Enclosure, method = "REML"
, data = GIBBON)
> summary(model19)
Linear mixed-effects model fit by REML
 Data: GIBBON 
        AIC       BIC   logLik
  -36.30349 -16.01861 25.15174

Random effects:
 Formula: ~1 | Enclosure
        (Intercept)  Residual
StdDev:  0.06335057 0.1795916

Fixed effects: TWO ~ Sex + Age + RC1 + RC3 
                  Value  Std.Error  DF   t-value p-value
(Intercept)  0.30962632 0.14381246 129  2.152987  0.0332
Sex2        -0.06251787 0.04139367 129 -1.510325  0.1334
Age          0.00616034 0.00410452 129  1.500866  0.1358
RC1          0.08811497 0.04692864 129  1.877637  0.0627
RC3         -0.04248383 0.03992388 129 -1.064121  0.2893
 Correlation: 
     (Intr) Sex2   Age    RC1   
Sex2  0.157                     
Age  -0.651 -0.322              
RC1  -0.772 -0.069  0.804       
RC3   0.016 -0.047 -0.597 -0.605

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max 
-2.60625855 -0.58475678  0.04228196  0.67173917  2.22599075 

Number of Observations: 139
Number of Groups: 6 
```

```
> model20<-lme(TWO~Sex+Age+RC1, random = ~1|Enclosure, method = "REML", da
ta = GIBBON)
> summary(model20)
Linear mixed-effects model fit by REML
 Data: GIBBON 
        AIC      BIC   logLik
  -42.03085 -24.5992 27.01543

Random effects:
 Formula: ~1 | Enclosure
        (Intercept) Residual
StdDev:  0.07891149 0.178468

Fixed effects: TWO ~ Sex + Age + RC1 
                 Value  Std.Error  DF   t-value p-value
(Intercept)  0.3487660 0.15317707 130  2.276882  0.0244
Sex2        -0.0615341 0.04127133 130 -1.490966  0.1384
Age          0.0030100 0.00340043 130  0.885183  0.3777
RC1          0.0478528 0.03971848 130  1.204799  0.2305
```

```
 Correlation: 
     (Intr) Sex2   Age   
Sex2  0.153              
Age  -0.804 -0.428       
RC1  -0.954 -0.120  0.713

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max 
-2.56628897 -0.57041899  0.04308745  0.64646439  2.21651274 

Number of Observations: 139
Number of Groups: 6 



> model21<-lme(TWO~Sex+RC1, random = ~1|Enclosure, method = "REML", data = 
GIBBON)
> summary(model21)
Linear mixed-effects model fit by REML
 Data: GIBBON 
        AIC       BIC   logLik
  -52.83548 -38.27221 31.41774

Random effects:
 Formula: ~1 | Enclosure
        (Intercept)  Residual
StdDev:  0.08674078 0.1777806

Fixed effects: TWO ~ Sex + RC1 
                 Value  Std.Error  DF   t-value p-value
(Intercept)  0.4664383 0.09303217 131  5.013731  0.0000
Sex2        -0.0463104 0.03729465 131 -1.241744  0.2165
RC1          0.0199603 0.02819255 131  0.708000  0.4802
 Correlation: 
     (Intr) Sex2  
Sex2 -0.355       
RC1  -0.905  0.297

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max 
-2.60135003 -0.58658640  0.04017852  0.66330892  2.26122129 

Number of Observations: 139
Number of Groups: 6 



> model22<-lme(TWO~Sex, random = ~1|Enclosure, method = "REML", data = GIB
BON)
> summary(model22)
Linear mixed-effects model fit by REML
 Data: GIBBON 
        AIC      BIC   logLik
  -59.68833 -48.0084 33.84416

Random effects:
 Formula: ~1 | Enclosure
        (Intercept)  Residual
StdDev:  0.09398013 0.1769593

Fixed effects: TWO ~ Sex 
                 Value  Std.Error  DF   t-value p-value
(Intercept)  0.5261176 0.04223952 132 12.455577  0.0000
Sex2        -0.0536662 0.03549247 132 -1.512046  0.1329
 Correlation: 
     (Intr)
Sex2 -0.196

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max 
-2.57751683 -0.61912176  0.03906262  0.66255597  2.32003221 
```

```
Number of Observations: 139
Number of Groups: 6


> anova(model18,model19,model20,model21,model22)
        Model df       AIC       BIC   logLik   Test  L.Ratio p-value
model18     1  8 -28.17078  -5.04799 22.08539
model19     2  7 -36.30349 -16.01861 25.15174 1 vs 2 6.132708  0.0133
model20     3  6 -42.03085 -24.59920 27.01543 2 vs 3 3.727362  0.0535
model21     4  5 -52.83548 -38.27221 31.41774 3 vs 4 8.804633  0.0030
model22     5  4 -59.68833 -48.00840 33.84416 4 vs 5 4.852844  0.0276
```

SDB

```
> model23<-lme(SDB~Sex+Age+RC1+RC2+RC3, random = ~1|Enclosure, method = "R
EML", data = GIBBON)
> summary(model23)
Linear mixed-effects model fit by REML
 Data: GIBBON
        AIC       BIC   logLik
  -128.1459 -105.0232 72.07297

Random effects:
 Formula: ~1 | Enclosure
        (Intercept)  Residual
StdDev:  0.04933208 0.1233983

Fixed effects: SDB ~ Sex + Age + RC1 + RC2 + RC3
                  Value  Std.Error  DF    t-value p-value
(Intercept)  0.19908220 0.11487828 128  1.7329838  0.0855
Sex2         0.02094990 0.02906506 128  0.7207934  0.4724
Age         -0.00318290 0.00307204 128 -1.0360844  0.3021
RC1         -0.00825698 0.03484601 128 -0.2369562  0.8131
RC2         -0.00859046 0.01193372 128 -0.7198477  0.4729
RC3          0.02309692 0.03011731 128  0.7668985  0.4446
 Correlation: 
     (Intr) Sex2   Age    RC1    RC2   
Sex2  0.047                            
Age  -0.488 -0.336                     
RC1  -0.670 -0.079  0.818              
RC2  -0.443  0.195 -0.210 -0.060       
RC3  -0.036  0.007 -0.655 -0.638  0.224

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max 
-1.7013737 -0.6089442 -0.1931657  0.4427959  5.0593615 

Number of Observations: 139
Number of Groups: 6


> model24<-lme(SDB~Sex+Age+RC2+RC3, random = ~1|Enclosure, method = "REML"
, data = GIBBON)
> summary(model24)
Linear mixed-effects model fit by REML
 Data: GIBBON
        AIC       BIC   logLik
  -135.0197 -114.7348 74.50986

Random effects:
 Formula: ~1 | Enclosure
        (Intercept)  Residual
StdDev:  0.04369559 0.1233139
```

```
Fixed effects: SDB ~ Sex + Age + RC2 + RC3
                  Value  Std.Error  DF    t-value p-value
(Intercept)  0.17189069 0.08290028 129  2.0734633  0.0401
Sex2         0.02043516 0.02887753 129  0.7076493  0.4804
Age         -0.00259966 0.00174053 129 -1.4936088  0.1377
RC2         -0.00863190 0.01180075 129 -0.7314709  0.4658
RC3          0.02174935 0.02245789 129  0.9684503  0.3346
 Correlation:
     (Intr) Sex2   Age    RC2
Sex2 -0.002
Age   0.121 -0.475
RC2  -0.653  0.189 -0.271
RC3  -0.807 -0.064 -0.282  0.229

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-1.6800670 -0.6060468 -0.1900216  0.4493153  5.0838711

Number of Observations: 139
Number of Groups: 6



> summary(model25)
Linear mixed-effects model fit by REML
 Data: GIBBON
        AIC       BIC   logLik
  -141.7714 -124.3397 76.8857

Random effects:
 Formula: ~1 | Enclosure
        (Intercept)  Residual
StdDev:  0.04361766 0.1230854

Fixed effects: SDB ~ Age + RC2 + RC3
                  Value  Std.Error  DF    t-value p-value
(Intercept)  0.17202949 0.08274784 130  2.0789605  0.0396
Age         -0.00201458 0.00152879 130 -1.3177596  0.1899
RC2         -0.01021162 0.01156629 130 -0.8828779  0.3789
RC3          0.02276564 0.02237066 130  1.0176563  0.3107
 Correlation:
    (Intr) Age    RC2
Age  0.136
RC2 -0.665 -0.210
RC3 -0.808 -0.356  0.246

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-1.6401494 -0.6064253 -0.2337919  0.4316973  5.0808948

Number of Observations: 139
Number of Groups: 6



> model26<-lme(SDB~Age+RC3, random = ~1|Enclosure, method = "REML", data =
GIBBON)
> summary(model26)
Linear mixed-effects model fit by REML
 Data: GIBBON
        AIC       BIC    logLik
  -150.0764 -135.5131 80.03821

Random effects:
 Formula: ~1 | Enclosure
        (Intercept) Residual
StdDev:  0.04235472 0.123072

Fixed effects: SDB ~ Age + RC3
                  Value  Std.Error  DF   t-value p-value
(Intercept)  0.12158059 0.06136600 131  1.981237  0.0497
```

```
Age         -0.00229635 0.00148982 131 -1.541364  0.1256
RC3          0.02832951 0.02151990 131  1.316433  0.1903
 Correlation:
    (Intr) Age
Age -0.010
RC3 -0.891 -0.317

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-1.6334021 -0.6399202 -0.2303848  0.4454818  5.0623939

Number of Observations: 139
Number of Groups: 6
```

```
> model27<-lme(SDB~Age, random = ~1|Enclosure, method = "REML", data = GIB
BON)
> summary(model27)
Linear mixed-effects model fit by REML
 Data: GIBBON
       AIC      BIC   logLik
  -156.611 -144.931 82.30548

Random effects:
 Formula: ~1 | Enclosure
        (Intercept)  Residual
StdDev:  0.05468017 0.1223231

Fixed effects: SDB ~ Age
                  Value   Std.Error  DF   t-value p-value
(Intercept)  0.19384787 0.031248565 132  6.203416  0.0000
Age         -0.00177955 0.001424667 132 -1.249101  0.2138
 Correlation:
    (Intr)
Age -0.609

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-1.5956116 -0.6304316 -0.2163170  0.3588580  5.0144760

Number of Observations: 139
Number of Groups: 6
```

```
> anova(model23,model24,model25,model26,model27)
        Model df       AIC       BIC   logLik   Test  L.Ratio p-value
model23     1  8 -128.1459 -105.0232 72.07297
model24     2  7 -135.0197 -114.7348 74.50986 1 vs 2 4.873780  0.0273
model25     3  6 -141.7714 -124.3397 76.88570 2 vs 3 4.751664  0.0293
model26     4  5 -150.0764 -135.5131 80.03821 3 vs 4 6.305029  0.0120
model27     5  4 -156.6110 -144.9310 82.30548 4 vs 5 4.534542  0.0332
```

Behaviour term	Main effects	Significance?	P-value	d.f.	Direction of relationship (value)
Social positive	Sex	No	0.1066	128	-
	Age	No	0.7479	128	Negative
	Excitability	Yes	0.0172	128	Positive
	Dominance	Yes	0.0245	128	Negative
	Fearfulness	No	0.1412	128	Negative
Locomotion	Sex	Yes	0.0006	128	-
	Age	No	0.1415	128	Positive
	Excitability	Yes	0.0219	128	Positive
	Dominance	Yes	0.0421	128	Negative
	Fearfulness	Yes	0.0055	128	Negative
Explorative	Sex	No	0.8210	128	-
	Age	Yes	0.0294	128	Positive
	Excitability	Yes	0.0010	128	Positive
	Dominance	No	0.4173	128	Negative
	Fearfulness	Yes	0.0007	128	Negative
Beneficiary	Sex	Yes	0.0008	128	-
	Age	No	0.5144	128	Negative
	Excitability	No	0.4879	128	Positive
	Dominance	Yes	0.0013	128	Positive
	Fearfulness	No	0.3236	128	Negative
Resting	Sex	No	0.2733	128	-
	Age	Yes	0.0067	128	Positive
	Excitability	No	0.5941	128	Negative
	Dominance	No	0.1465	128	Negative
	Fearfulness	No	0.1441	128	Positive
Proximity1	Sex	No	0.9797	128	-
	Age	Yes	0.0132	128	Positive
	Excitability	Yes	0.0030	128	Positive
	Dominance	No	0.1476	128	Positive
	Fearfulness	Yes	0.0017	128	Negative
Proximity2	Sex	No	0.1644	128	-
	Age	No	0.1792	128	Positive
	Excitability	No	0.0742	128	Positive
	Dominance	No	0.7002	128	Positive
	Fearfulness	No	0.3592	128	Negative
SDB	Sex	No	0.4724	128	-
	Age	No	0.3021	128	Negative
	Excitability	No	0.8131	128	Negative
	Dominance	No	0.4729	128	Negative
	Fearfulness	no	0.4446	128	Positive

Appendix 7: GLM reproductive success script *S. syndactylus*

```
> MALEGIBBON<-read.csv(file.choose())
> names(MALEGIBBON)
 [1] "NAME"                 "INST"                 "SEX"
"AGE"                  "RC1"                  "RC2"                  "RC3"
 [8] "ORIGIN"               "REARING"              "REPRODUCTIVE.SUCCESS"
"TRANSFERAGE"          "TRANSFERNUMBER"
> summary(MALEGIBBON)
      NAME            INST           SEX          AGE             RC1
RC2              RC3            ORIGIN      REARING       REPRODUCTIVE.SUCCES
S
 Clyde  : 1   Thrigby  : 2   Min.   :1   Min.   :12.00   Min.   :1.500   M
in.   :2.562   Min.   :1.400   Min.   :1   Min.   :1.000   Min.   :0.1004
 Guildo : 1   Attica   : 1   1st Qu.:1   1st Qu.:14.78   1st Qu.:2.500   1
st Qu.:3.641   1st Qu.:1.913   1st Qu.:1   1st Qu.:1.000   1st Qu.:0.1850
 Josef  : 1   Banham   : 1   Median :1   Median :22.00   Median :2.750   M
edian :4.104   Median :2.167   Median :1   Median :1.000   Median :0.2873
 Kiao   : 1   Besancon : 1   Mean   :1   Mean   :22.68   Mean   :2.881   M
ean   :4.197   Mean   :2.432   Mean   :1   Mean   :1.222   Mean   :0.2878
 Luang  : 1   Boissiere: 1   3rd Qu.:1   3rd Qu.:31.04   3rd Qu.:3.321   3
rd Qu.:4.953   3rd Qu.:2.638   3rd Qu.:1   3rd Qu.:1.000   3rd Qu.:0.3363
 Niam   : 1   Burgers  : 1   Max.   :1   Max.   :36.11   Max.   :4.214   M
ax.   :6.000   Max.   :4.500   Max.   :1   Max.   :3.000   Max.   :0.6073
 (Other):12   (Other)  :11
  TRANSFERAGE TRANSFERNUMBER
 N/A     :5   Min.   :0.0000
 5.04    :2   1st Qu.:0.2500
 2.04    :1   Median :1.0000
 3.05    :1   Mean   :0.8333
 3.1     :1   3rd Qu.:1.0000
 4.02    :1   Max.   :2.0000
 (Other):7
> MALEGIBBON$SEX<-as.factor(MALEGIBBON$SEX)
> MALEGIBBON$ORIGIN<-as.factor(MALEGIBBON$ORIGIN)
> MALEGIBBON$REARING<-as.factor(MALEGIBBON$REARING)
> MALEGIBBON$TRANSFERNUMBER<-as.factor(MALEGIBBON$TRANSFERNUMBER)
> MALEGIBBON$TRANSFERAGE<-as.numeric(MALEGIBBON$TRANSFERAGE)
> summary(MALEGIBBON)
      NAME            INST     SEX          AGE             RC1             R
C2             RC3          ORIGIN REARING REPRODUCTIVE.SUCCESS  TRANSFERAGE
 Clyde  : 1   Thrigby  : 2    1:18    Min.   :12.00   Min.   :1.500   Min.
:2.562   Min.   :1.400   1:18   1:15    Min.   :0.1004        Min.   : 1.00
0
 Guildo : 1   Attica   : 1           1st Qu.:14.78   1st Qu.:2.500   1st Qu
.:3.641   1st Qu.:1.913          2: 2    1st Qu.:0.1850        1st Qu.: 5.2
50
 Josef  : 1   Banham   : 1           Median :22.00   Median :2.750   Median
:4.104   Median :2.167          3: 1    Median :0.2873        Median : 8.50
0
 Kiao   : 1   Besancon : 1           Mean   :22.68   Mean   :2.881   Mean
:4.197   Mean   :2.432                  Mean   :0.2878        Mean   : 8.27
8
 Luang  : 1   Boissiere: 1           3rd Qu.:31.04   3rd Qu.:3.321   3rd Qu
.:4.953   3rd Qu.:2.638                  3rd Qu.:0.3363        3rd Qu.:12.7
50
 Niam   : 1   Burgers  : 1           Max.   :36.11   Max.   :4.214   Max.
:6.000   Max.   :4.500                  Max.   :0.6073        Max.   :13.00
0
 (Other):12   (Other)  :11
 TRANSFERNUMBER
 0: 5
 1:11
 2: 2

> model1<-glm(REPRODUCTIVE.SUCCESS~RC1+RC2+RC3+AGE+TRANSFERAGE+TRANSFERNUM
BER, family=inverse.gaussian(link=identity),na.action=na.exclude, data=MAL
EGIBBON)
> summary(model1)
Call:
```

```
glm(formula = REPRODUCTIVE.SUCCESS ~ RC1 + RC2 + RC3 + AGE +
    TRANSFERAGE + TRANSFERNUMBER, family = inverse.gaussian(link = identit
y),
    data = MALEGIBBON, na.action = na.exclude)

Deviance Residuals:
     Min        1Q    Median        3Q       Max
-1.41310  -0.33533   0.01692   0.23792   0.69490

Coefficients:
                 Estimate Std. Error t value Pr(>|t|)
(Intercept)     -0.056369   0.172915  -0.326   0.7511
RC1              0.044914   0.033702   1.333   0.2122
RC2              0.015541   0.021041   0.739   0.4771
RC3             -0.026769   0.027438  -0.976   0.3523
AGE             -0.000938   0.002851  -0.329   0.7489
TRANSFERAGE      0.009143   0.009145   1.000   0.3410
TRANSFERNUMBER  0.250091   0.083768   2.986    0.0137 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for inverse.gaussian family taken to be 0.3397841)

    Null deviance: 13.9524  on 17  degrees of freedom
Residual deviance:  4.4932  on 10  degrees of freedom
AIC: -28.543

Number of Fisher Scoring iterations: 14



> model2<-glm(REPRODUCTIVE.SUCCESS~RC1+RC2+RC3+TRANSFERAGE+TRANSFERNUMBER,
family=inverse.gaussian(link=identity),na.action=na.exclude, data=MALEGIBB
ON)
> summary(model2)

Call:
glm(formula = REPRODUCTIVE.SUCCESS ~ RC1 + RC2 + RC3 + TRANSFERAGE +
    TRANSFERNUMBER, family = inverse.gaussian(link = identity),
    data = MALEGIBBON, na.action = na.exclude)

Deviance Residuals:
     Min        1Q    Median        3Q       Max
-1.42910  -0.28912   0.05229   0.19842   0.77978

Coefficients:
                Estimate Std. Error t value Pr(>|t|)
(Intercept)     -0.06362    0.16584  -0.384   0.7086
RC1              0.04287    0.03132   1.369   0.1983
RC2              0.01481    0.02017   0.734   0.4781
RC3             -0.03105    0.02463  -1.260   0.2336
TRANSFERAGE      0.01014    0.00827   1.227   0.2456
TRANSFERNUMBER1  0.24634    0.08007   3.076   0.0105 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for inverse.gaussian family taken to be 0.3143346)

    Null deviance: 13.9524  on 17  degrees of freedom
Residual deviance:  4.5367  on 11  degrees of freedom
AIC: -30.369

Number of Fisher Scoring iterations: 14

> model3<-glm(REPRODUCTIVE.SUCCESS~RC1+RC3+TRANSFERAGE+TRANSFERNUMBER, fam
ily=inverse.gaussian(link=identity),na.action=na.exclude, data=MALEGIBBON)
> summary(model3)

Call:
glm(formula = REPRODUCTIVE.SUCCESS ~ RC1 + RC3 + TRANSFERAGE +
    TRANSFERNUMBER, family = inverse.gaussian(link = identity),
```

```
    data = MALEGIBBON, na.action = na.exclude)

Deviance Residuals:
     Min        1Q    Median        3Q       Max
-1.43220  -0.24163   0.03324   0.18772   0.83215

Coefficients:
                 Estimate Std. Error t value Pr(>|t|)
(Intercept)     -0.003974   0.146231  -0.027  0.97877
RC1              0.056291   0.024463   2.301  0.04012 *
RC3             -0.041888   0.020132  -2.081  0.05956 .
TRANSFERAGE      0.009415   0.008352   1.127  0.28164
TRANSFERNUMBER1  0.246961   0.078624   3.141  0.00852 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for inverse.gaussian family taken to be 0.3014951)

    Null deviance: 13.9524  on 17  degrees of freedom
Residual deviance:  4.7136  on 12  degrees of freedom
AIC: -31.681

Number of Fisher Scoring iterations: 12

> model4<-glm(REPRODUCTIVE.SUCCESS~RC1+RC3+TRANSFERNUMBER, family=inverse.
gaussian(link=identity),na.action=na.exclude, data=MALEGIBBON)
> summary(model4)

Call:
glm(formula = REPRODUCTIVE.SUCCESS ~ RC1 + RC3 + TRANSFERNUMBER,
    family = inverse.gaussian(link = identity), data = MALEGIBBON,
    na.action = na.exclude)

Deviance Residuals:
     Min        1Q    Median        3Q       Max
-1.45283  -0.22473  -0.04568   0.23784   0.69117

Coefficients:
                Estimate Std. Error t value Pr(>|t|)
(Intercept)      0.12853    0.08297   1.549  0.14536
RC1              0.05620    0.02457   2.287  0.03959 *
RC3             -0.04467    0.02011  -2.221  0.04474 *
TRANSFERNUMBER1  0.17485    0.04339   4.030  0.00143 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for inverse.gaussian family taken to be 0.304142)

    Null deviance: 13.9524  on 17  degrees of freedom
Residual deviance:  5.1098  on 13  degrees of freedom
AIC: -32.228

Number of Fisher Scoring iterations: 9
```

FEMALE REPRO SUCCESS

```
> FEMALEGIBBON<-read.csv(file.choose())
> names(FEMALEGIBBON)
 [1] "NAME"                   "INST"                   "SEX"
"AGE"                    "RC1"                    "RC2"                    "RC3"
 [8] "ORIGIN"               "REARING"              "REPRODUCTIVE.SUCCESS"
"TRANSFERAGE"          "TRANSFERNUMBER"
> summary(FEMALEGIBBON)
      NAME              INST          SEX          AGE              RC1
RC2               RC3             ORIGIN        REARING      REPRODUCTIVE.SUCCE
SS
 Blossom: 1    Twycross   : 2   Min.   :2   Min.   :10.00   Min.   :1.679
Min.   :2.125   Min.   :1.400   Min.   :1.0   Min.   :1.00   Min.   :0.083
33
 Ebonie : 1    Amersfoort: 1   1st Qu.:2   1st Qu.:14.75   1st Qu.:2.321
1st Qu.:3.125   1st Qu.:2.000   1st Qu.:1.0   1st Qu.:1.00   1st Qu.:0.178
34
 Ella   : 1    Attica     : 1   Median :2   Median :22.02   Median :2.821
Median :3.906   Median :2.470   Median :1.0   Median :1.00   Median :0.287
98
 Gerda  : 1    Besancon   : 1   Mean   :2   Mean   :21.87   Mean   :2.869
Mean   :3.862   Mean   :2.590   Mean   :1.1   Mean   :1.15   Mean   :0.275
68
 Jambi  : 1    Boissiere : 1   3rd Qu.:2   3rd Qu.:25.27   3rd Qu.:3.214
3rd Qu.:4.521   3rd Qu.:3.062   3rd Qu.:1.0   3rd Qu.:1.00   3rd Qu.:0.373
14
 Kaya   : 1    Burgers    : 1   Max.   :2   Max.   :46.00   Max.   :4.071
Max.   :5.500   Max.   :4.200   Max.   :3.0   Max.   :3.00   Max.   :0.502
51
 (Other):14    (Other)    :13
  TRANSFERAGE  TRANSFERNUMBER
 N/A      :3    Min.    :0
 3.1      :2    1st Qu.:1
 4.02     :2    Median :1
 5.06     :2    Mean    :1
 6.04     :2    3rd Qu.:1
 1.1      :1    Max.    :2
 (Other):8


> FEMALEGIBBON$SEX<-as.factor(FEMALEGIBBON$SEX)
> FEMALEGIBBON$ORIGIN<-as.factor(FEMALEGIBBON$ORIGIN)
> FEMALEGIBBON$REARING<-as.factor(FEMALEGIBBON$REARING)
> FEMALEGIBBON$TRANSFERNUMBER<-as.factor(FEMALEGIBBON$TRANSFERNUMBER)
> FEMALEGIBBON$TRANSFERAGE<-as.numeric(FEMALEGIBBON$TRANSFERAGE)
> summary(FEMALEGIBBON)
      NAME              INST       SEX          AGE              RC1
RC2               RC3          ORIGIN  REARING REPRODUCTIVE.SUCCESS   TRANSFERAG
E
 Blossom: 1    Twycross   : 2   2:20    Min.   :10.00   Min.   :1.679   Min.
:2.125    Min.   :1.400    1:19    1:18    Min.   :0.08333       Min.   : 1.00
 Ebonie : 1    Amersfoort: 1            1st Qu.:14.75   1st Qu.:2.321   1st Q
u.:3.125    1st Qu.:2.000    3: 1    2: 1    1st Qu.:0.17834       1st Qu.: 4.
75
 Ella   : 1    Attica     : 1            Median :22.02   Median :2.821   Media
n :3.906    Median :2.470            3: 1    Median :0.28798       Median : 7.
50
 Gerda  : 1    Besancon   : 1            Mean   :21.87   Mean   :2.869   Mean
:3.862    Mean    :2.590                    Mean   :0.27568       Mean   : 7.95
 Jambi  : 1    Boissiere : 1            3rd Qu.:25.27   3rd Qu.:3.214   3rd Q
u.:4.521    3rd Qu.:3.062                    3rd Qu.:0.37314       3rd Qu.:11.
25
 Kaya   : 1    Burgers    : 1            Max.   :46.00   Max.   :4.071   Max.
:5.500    Max.    :4.200                    Max.   :0.50251       Max.   :14.00
```

```
 (Other):14   (Other)   :13
 TRANSFERNUMBER
 0: 3
 1:14
 2: 3
```

FEMALE

```
> model1<-glm(REPRODUCTIVE.SUCCESS~RC1+RC2+RC3+AGE+TRANSFERAGE+TRANSFERNUM
BER, family=inverse.gaussian(link=identity),na.action=na.exclude, data=FEM
ALEGIBBON)
> summary(model1)

Call:
glm(formula = REPRODUCTIVE.SUCCESS ~ RC1 + RC2 + RC3 + AGE +
    TRANSFERAGE + TRANSFERNUMBER, family = inverse.gaussian(link = identit
y),
    data = FEMALEGIBBON, na.action = na.exclude)

Deviance Residuals:
     Min        1Q    Median        3Q       Max
-2.25802  -0.39722  -0.02122   0.16240   1.40655

Coefficients:
                 Estimate Std. Error t value Pr(>|t|)
(Intercept)      0.727879   0.253187   2.875  0.01396 *
RC1             -0.108235   0.051108  -2.118  0.05576 .
RC2             -0.021905   0.039221  -0.559  0.58677
RC3             -0.057731   0.037117  -1.555  0.14582
AGE             -0.006341   0.001910  -3.319  0.00612 **
TRANSFERAGE      0.008699   0.007968   1.092  0.29643
TRANSFERNUMBER1  0.187231   0.097655   1.917  0.07932 .

---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for inverse.gaussian family taken to be 0.6396063)

    Null deviance: 19.701  on 19  degrees of freedom
Residual deviance: 10.033  on 12  degrees of freedom
AIC: -22.853

Number of Fisher Scoring iterations: 21
```

```
> model2<-glm(REPRODUCTIVE.SUCCESS~RC1+RC3+AGE+TRANSFERAGE+TRANSFERNUMBER,
family=inverse.gaussian(link=identity),na.action=na.exclude, data=FEMALEGI
BBON)
> summary(model2)

Call:
glm(formula = REPRODUCTIVE.SUCCESS ~ RC1 + RC3 + AGE + TRANSFERAGE +
    TRANSFERNUMBER, family = inverse.gaussian(link = identity),
    data = FEMALEGIBBON, na.action = na.exclude)

Deviance Residuals:
     Min        1Q    Median        3Q       Max
-2.19556  -0.42794  -0.06997   0.16364   1.38550

Coefficients:
                 Estimate Std. Error t value Pr(>|t|)
(Intercept)      0.668681   0.213963   3.125  0.00805 **
RC1             -0.113530   0.050338  -2.255  0.04199 *
RC3             -0.060842   0.035567  -1.711  0.11089
AGE             -0.005873   0.001623  -3.620  0.00311 **
TRANSFERAGE      0.007412   0.007737   0.958  0.35558
```

```
TRANSFERNUMBER1  0.181530   0.096997   1.872  0.08395 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for inverse.gaussian family taken to be 0.6258623)

    Null deviance: 19.701  on 19  degrees of freedom
Residual deviance: 10.268  on 13  degrees of freedom
AIC: -24.391

Number of Fisher Scoring iterations: 19
```

```
> model3<-glm(REPRODUCTIVE.SUCCESS~RC1+RC3+AGE+TRANSFERNUMBER, family=inve
rse.gaussian(link=identity),na.action=na.exclude, data=FEMALEGIBBON)
> summary(model3)

Call:
glm(formula = REPRODUCTIVE.SUCCESS ~ RC1 + RC3 + AGE + TRANSFERNUMBER,
    family = inverse.gaussian(link = identity), data = FEMALEGIBBON,
    na.action = na.exclude)

Deviance Residuals:
     Min        1Q    Median        3Q       Max
-2.30029  -0.45929   0.01984   0.15501   1.35064

Coefficients:
                 Estimate Std. Error t value Pr(>|t|)
(Intercept)      0.855605   0.181668   4.710 0.000335 ***
RC1             -0.135777   0.049182  -2.761 0.015319 *
RC3             -0.056041   0.032871  -1.705 0.110298
AGE             -0.006899   0.001393  -4.952 0.000213 ***
TRANSFERNUMBER1  0.114443   0.057928   1.976 0.068251 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for inverse.gaussian family taken to be 0.5519762)

    Null deviance: 19.701  on 19  degrees of freedom
Residual deviance: 10.631  on 14  degrees of freedom
AIC: -25.695

Number of Fisher Scoring iterations: 15
```

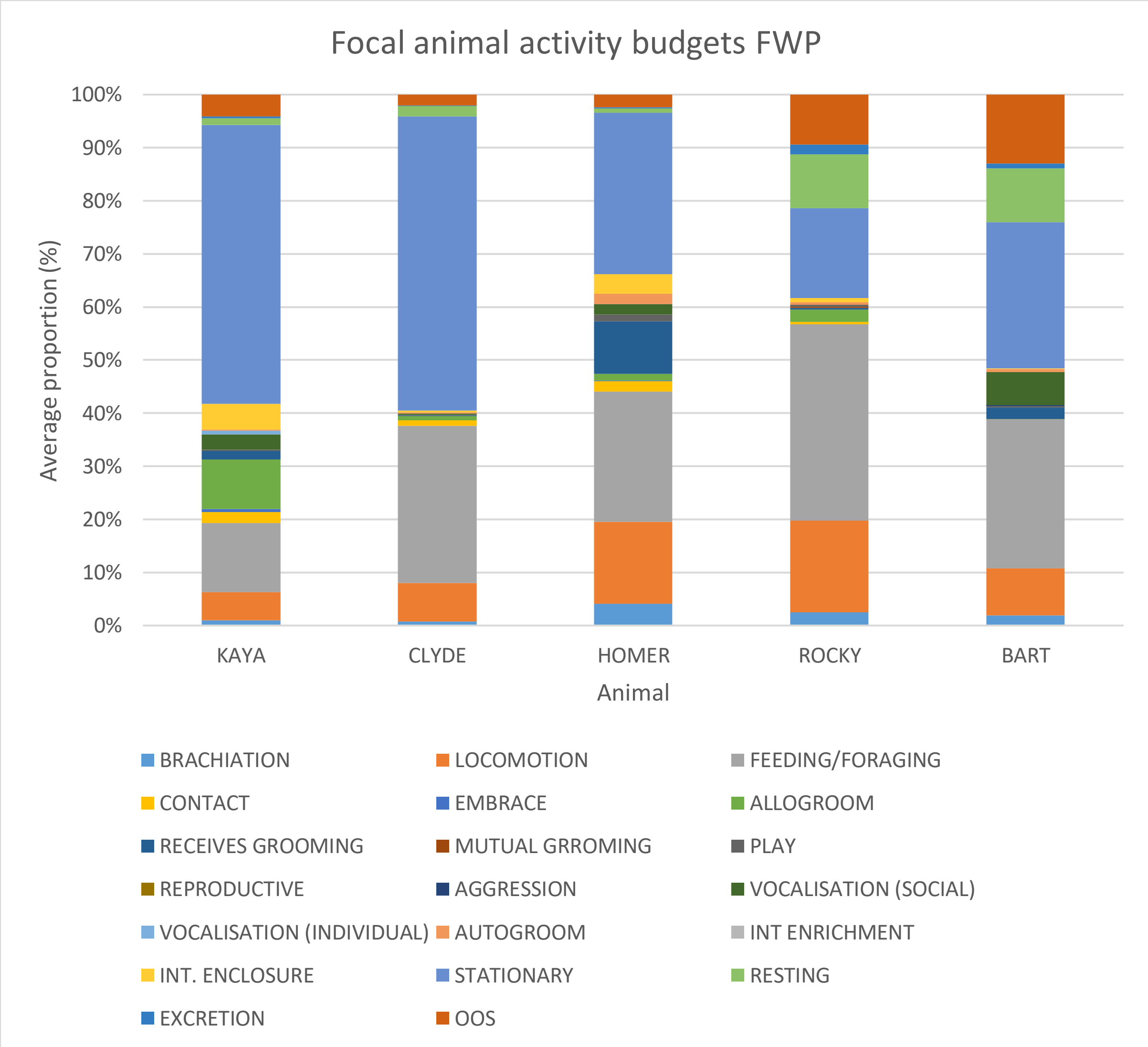
```
> model4<-glm(REPRODUCTIVE.SUCCESS~RC1+AGE+TRANSFERNUMBER, family=inverse.
gaussian(link=identity),na.action=na.exclude, data=FEMALEGIBBON)
> summary(model4)

Call:
glm(formula = REPRODUCTIVE.SUCCESS ~ RC1 + AGE + TRANSFERNUMBER,
    family = inverse.gaussian(link = identity), data = FEMALEGIBBON,
    na.action = na.exclude)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-2.4299  -0.4061  -0.1668   0.4594   1.1291

Coefficients:
                 Estimate Std. Error t value Pr(>|t|)
(Intercept)      0.827660   0.164025   5.046 0.000145 ***
RC1             -0.150381   0.049892  -3.014 0.008718 **
AGE             -0.008167   0.001410  -5.791 3.56e-05 ***
TRANSFERNUMBER1  0.065524   0.045493   1.440 0.170330
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for inverse.gaussian family taken to be 0.516816)
```

```
    Null deviance: 19.701  on 19  degrees of freedom
Residual deviance: 12.063  on 15  degrees of freedom
AIC: -25.168

Number of Fisher Scoring iterations: 13
```

```
> model5<-glm(REPRODUCTIVE.SUCCESS~RC1+AGE, family=inverse.gaussian(link=i
dentity),na.action=na.exclude, data=FEMALEGIBBON)
> summary(model5)

Call:
glm(formula = REPRODUCTIVE.SUCCESS ~ RC1 + AGE, family = inverse.gaussian(
link = identity), 
    data = FEMALEGIBBON, na.action = na.exclude)

Deviance Residuals: 
     Min        1Q    Median        3Q       Max  
-2.36310  -0.57305  -0.08143   0.41976   0.93831  

Coefficients:
             Estimate Std. Error t value Pr(>|t|)    
(Intercept)  0.643962   0.131287   4.905 0.000134 ***
RC1         -0.061686   0.035503  -1.737 0.100381    
AGE         -0.008280   0.001343  -6.164 1.04e-05 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for inverse.gaussian family taken to be 0.5337323)

    Null deviance: 19.701  on 19  degrees of freedom
Residual deviance: 13.622  on 17  degrees of freedom
AIC: -26.737

Number of Fisher Scoring iterations: 8
```

Appendix 8: Behavioural coding data summaries

<u>Fota Wildlife park</u>



		Animal name				
		KAYA	CLYDE	HOMER	ROCKY	BART
Behaviour (mean % of time observed)	Brachiation	0.94	0.74	4.08	4.18	1.87
	Locomotion	5.32	7.61	15.45	28.75	8.87
	Feeding/foraging	13.06	30.61	24.50	61.55	28.08
	Contact	2.02	1.04	1.99	0.83	0.08
	Embrace	0.56	0.00	0.13	0.00	0.00
	Allogroom	9.35	0.83	1.28	3.87	0.00
	Receives grooming	1.59	0.11	9.85	0.61	2.17

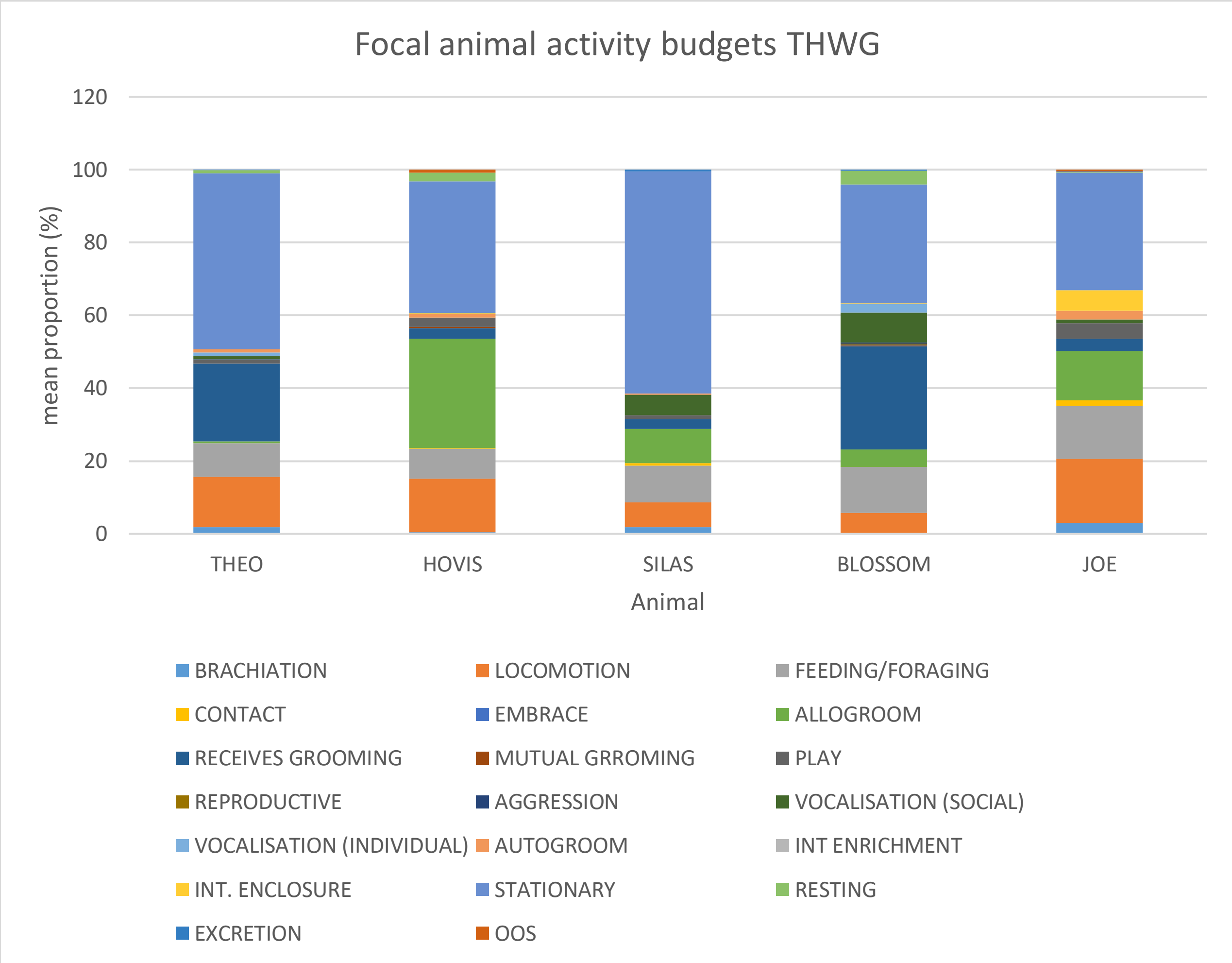
	Mutual grooming	0.11	0.00	0.00	0.28	0.00
	Play	0.23	0.12	1.31	0.65	0.29
	Reproductive	0.00	0.00	0.00	0.00	0.00
	Aggression	0.00	0.00	0.00	0.00	0.17
	Vocalisation (social)	2.87	0.29	1.89	0.00	6.19
	Vocalisation (individual)	0.69	0.00	0.04	0.00	0.00
	Autogroom	0.22	0.31	2.01	0.73	0.56
	Interaction with enrichment	0.00	0.00	0.00	0.00	0.00
	Interaction with enclosure	4.81	0.29	3.62	1.34	0.14
	Stationary	52.48	57.36	30.39	28.28	27.59
	Resting	1.34	2.04	0.81	16.94	10.14
	Excretion	0.34	0.11	0.29	2.90	0.87
	Out of Sight	4.06	2.14	2.36	15.76	12.97

		Behaviour (mean rate/30 minutes)					
		Scratch	Yawn	Formal bite	Grin	Lipsmack	Body shake
Animal name	KAYA	0.20	0.01	0.00	0.00	0.00	0.00
	CLYDE	0.09	0.00	0.00	0.00	0.00	0.00
	HOMER	0.17	0.02	0.00	0.00	0.00	0.00
	ROCKY	0.11	0.00	0.00	0.00	0.00	0.00
	BART	0.06	0.01	0.00	0.00	0.00	0.00

2 decimal places

		Proximity category (mean % of time observed)				
		1	2	3	4	Out of Sight
Animal name	KAYA	48.16	43.26	4.66	0.00	3.92
	CLYDE	31.74	57.61	7.91	1.00	1.74
	HOMER	26.21	59.85	8.60	3.36	1.97
	ROCKY	17.97	51.60	17.88	2.69	9.88
	BART	23.15	47.25	15.17	3.82	10.61

Thrigby Hall Wildlife Gardens



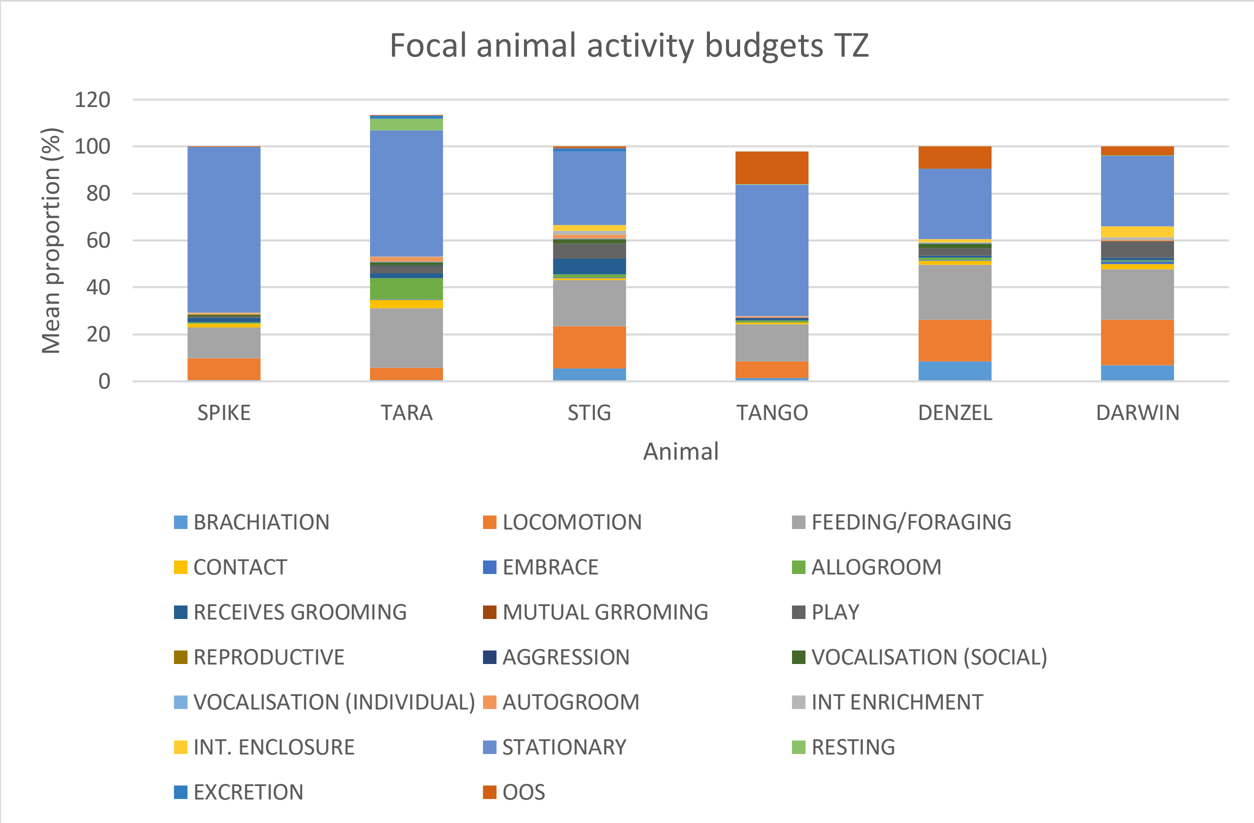
		Animal name				
		THEO	HOVIS	SILAS	BLOSSOM	JOE
Behaviour (mean % of time observed)	Brachiation	1.75	0.49	1.74	0.05	2.99
	Locomotion	13.85	14.72	6.98	5.73	17.57
	Feeding/foraging	9.18	8.07	9.97	12.57	14.51
	Contact	0.00	0.19	0.68	0.10	1.60
	Embrace	0.00	0.00	0.00	0.00	0.00
	Allogroom	0.63	30.02	9.41	4.72	13.51
	Receives grooming	21.37	3.01	2.75	28.39	3.33
	Mutual grooming	0.00	0.29	0.00	0.17	0.00
	Play	1.04	2.42	1.02	0.28	4.31
	Reproductive	0.00	0.00	0.00	0.21	0.00
	Aggression	0.10	0.00	0.00	0.31	0.00
	Vocalisation (social)	0.89	0.12	5.60	8.23	1.01
	Vocalisation (individual)	1.01	0.00	0.00	2.41	0.00
	Autogroom	0.83	0.99	0.40	0.00	2.50
	Interaction with enrichment	0.00	0.00	0.00	0.00	0.00
	Interaction with enclosure	0.00	0.25	0.00	0.17	5.63

	Stationary	48.26	36.27	60.94	32.59	32.26
	Resting	0.90	2.41	0.00	3.78	0.21
	Excretion	0.17	0.00	0.51	0.28	0.17
	Out of Sight	0.00	0.76	0.00	0.00	0.42

		Behaviour (mean rate/30 minutes)					
		Scratch	Yawn	Formal bite	Grin	Lipsmack	Body shake
Animal name	THEO	0.16	0.02	0.00	0.00	0.00	0.01
	HOVIS	0.15	0.01	0.00	0.00	0.00	0.00
	SILAS	0.31	0.02	0.00	0.00	0.00	0.01
	BLOSSOM	0.18	0.02	0.00	0.00	0.00	0.00
	JOE	0.24	0.02	0.00	0.00	0.00	0.02

		Proximity category (mean % of time observed)				
		1	2	3	4	Out of Sight
Animal name	THEO	32.86	39.83	26.16	1.15	0.00
	HOVIS	49.97	35.00	13.86	1.17	0.00
	SILAS	35.19	42.38	18.47	3.97	0.00
	BLOSSOM	72.12	23.47	4.41	0.00	0.00
	JOE	56.42	36.04	7.05	0.49	0.00

Twycross Zoo



		Animal name					
		SPIKE	TARA	STIG	TANGO	DENZEL	DARWIN
Behaviour (mean % of time observed)	Brachiation	0.64	0.58	5.36	1.53	8.53	6.81
	Locomotion	9.19	5.28	18.17	6.93	17.72	19.33
	Feeding/foraging	13.19	25.31	19.49	15.84	23.31	21.75
	Contact	1.42	3.53	0.93	0.75	1.72	2.14
	Embrace	0.00	0.17	0.29	0.17	0.17	1.00
	Allogroom	0.56	9.08	1.25	0.83	1.17	0.47
	Receives grooming	2.00	2.17	6.78	0.68	0.75	1.14
	Mutual grooming	0.00	0.08	0.08	0.00	0.00	0.00
	Play	0.53	2.92	6.40	0.17	3.28	7.08
	Reproductive	0.00	0.00	0.00	0.00	0.00	0.00
	Aggression	0.00	0.25	0.00	0.17	0.08	0.00
	Vocalisation (social)	0.83	1.50	1.83	0.00	1.92	0.00
	Vocalisation (individual)	0.00	0.08	0.22	0.00	0.25	0.00
	Autogroom	0.58	2.06	1.63	0.64	0.14	0.53
	Interaction with enrichment	0.00	0.08	1.76	0.08	0.08	1.17
	Interaction with enclosure	0.17	0.25	2.47	0.08	1.47	4.72
	Stationary	70.81	53.47	31.19	55.97	29.86	29.94
	Resting	0.00	5.11	0.00	0.28	0.00	0.17
	Excretion	0.00	1.17	1.31	0.00	0.08	0.08

	Out of Sight	0.08	0.33	0.83	13.89	9.47	3.67

		Behaviour (mean rate/30 minutes)					
		Scratch	Yawn	Formal bite	Grin	Lipsmack	Body shake
Animal name	SPIKE	0.13	0.06	0.00	0.00	0.00	0.04
	TARA	0.16	0.01	0.00	0.00	0.00	0.01
	STIG	0.18	0.03	0.01	0.00	0.00	0.01
	TANGO	0.06	0.01	0.00	0.00	0.00	0.01
	DENZEL	0.11	0.00	0.00	0.00	0.00	0.02
	DARWIN	0.15	0.01	0.00	0.00	0.01	0.02

		Proximity category (mean % of time observed)				
		1	2	3	4	Out of Sight
Animal name	SPIKE	13.69	33.23	36.03	17.05	0.00
	TARA	23.50	65.39	10.03	1.08	0.00
	STIG	23.44	68.04	8.21	0.31	0.00
	TANGO	15.53	60.89	14.75	3.14	5.69
	DENZEL	20.47	62.01	10.86	1.81	4.86
	DARWIN	18.88	67.97	9.75	1.00	2.41

Appendix 9: Total ICC values *S. syndactylus*

	Besancon		Boissiere		Burgers		Cotswolds		Fota		Manor House	
	ICC[3,1]	ICC[3,K]	ICC[3,1]	ICC[3,K]	ICC[3,1]	ICC[3,K]	ICC[3,1]	ICC[3,K]	ICC[3,1]	ICC[3,K]	ICC[3,1]	ICC[3,K]
FEARFUL	0.9	0.947	0	0	1	1	0.5	0.667	0.786	0.88	0.684	0.915
DOMINANT	0.978	0.989	0.375	0.545	0.677	0.808	0.276	0.432	0.896	0.945	0.953	0.99
PERSISTENT	-0.3	-0.857	0.545	0.706	0.4	0.571	-0.125	-0.286	0.545	0.706	0.849	0.966
CAUTIOUS	0	0	-0.133	-0.308	0.421	0.593	.	.	0.226	0.369	0.744	0.936
STABLE	-0.75	-6	0	0	0.771	0.871	-0.192	-0.476	-0.789	-7.467	0.476	0.82
AUTISTIC	.	.	0	0	0.977	0.988	.	.	0.923	0.96	.	.
CURIOUS	-0.75	-6	0	0	0.129	0.229	0.625	0.769	-0.044	-0.93	0.476	0.82
THOUGHTLESS	0	0	0.686	0.814	NC	NC	.	.	1	1	0	0
STINGY/GREEDY	0.529	0.692	0.222	0.364	0.667	0.8	0	0	-0.051	-0.107	0.786	0.948
JEALOUS	0	0	0.158	0.273	0.979	0.989	-0.632	-3.429	0.13	0.23	0.87	0.971
INDIV.	-0.632	-3.429	-0.4	-1.333	0.8	0.889	0	0	0	0	0	0
RECKLESS	NC	NC	0.615	0.762	0.8	0.889	0.471	0.64	0.216	0.355	0.572	0.87
SOCIABLE	0.462	0.632	0	0	0	0	.	.	-0.6	-3	-0.083	-0.625
DISTRACTIBLE	0.462	0.632	NC	NC	0.814	0.897	.	.	0.167	0.286	0.2	0.556
TIMID	-0.462	-1.714	-0.541	-2.353	0.267	0.421	.	.	-0.019	-0.038	0.675	0.912
SYMPATHETIC	0.947	0.973	-0.645	-3.636	NC	NC	0.3	0.462	0	0	0.8	0.952
PLAYFUL	0.75	0.857	0.655	0.791	0.945	9.72	1	1	0.789	0.882	0.921	0.983
SOLITARY	0.857	0.923	-0.043	-0.091	0.889	0.941	.	.	-0.14	-0.326	0.646	0.901
VULNERABLE	0.581	0.735	0.163	0.281	0.75	0.857	0	0	0.296	0.457	0.778	0.946
INNOVATIVE	0.581	0.735	NC	NC	1	1	0	0	0	0	0.031	0.139
ACTIVE	0.632	0.774	0.296	0.457	0.789	0.882	0.938	0.968	0.761	0.864	0.467	0.814
HELFPUL	0.966	0.982	0.053	0.1	0.968	0.984	0	0	0.067	0.125	0.227	0.595
BULLYING	0	0	0.348	0.516	1	1	0	0	0.98	0.99	0.808	0.955
AGGRESSIVE	0	0	0.714	0.833	.	.	0	0	0.493	0.661	0.754	0.939
MANIPULATIVE	0	0	-0.253	-0.678	.	.	.	.	0	0	0	0
GENTLE	0.885	0.939	-0.655	-3.789	.	.	-0.625	-3.333	-0.029	-0.059	0.797	0.951
AFFECTIONATE	0.5	0.667	-0.372	-1.185	.	.	0	0	-0.533	-2.286	0	0
EXCITABLE	0.609	0.757	0	0	0.543	0.704	0.563	0.72	0.46	0.63	0.217	0.581
IMPULSIVE	0.588	0.741	-0.571	-2.667	0.4	0.571	1	1	0.906	0.95	0.396	0.766
INQUISITIVE	0.698	0.822	NC	NC	0.8	0.889	1	1	0.622	0.767	0.356	0.734
SUBMISSIVE	0.909	0.952	0.831	0.907	1	1	-0.696	-4.571	0.892	0.943	0.863	0.969

COOL	0.914	0.955	0.842	0.914	1	1	0	0	0.639	0.779	0.147	0.463
DEPENDENT/FOLLOWER	0.927	0.962	NC	NC	0.971	0.986	0	0	0.1	0.182	0.214	0.577
IRRITABLE	-0.192	-0.476	0	0	0.778	0.875	0	0	0.457	0.627	0.158	0.485
UNPERCEPTIVE	0	0	.	.	0.897	0.946	0	0	0	0	0.2	0.556
PREDICTABLE	0.914	0.955	0.429	0.6	1	1	0.4	0.571	0.426	0.597	0.393	0.764
DECISIVE	0	0	0.174	0.296	0.739	0.85	-0.4	-1.333	0	0	0.174	0.513
DEPRESSED	0.857	0.923	0	0	0.871	0.931	0	0	-0.2	-0.5	-0.125	-1.25
CONVENTIONAL	0	0	0.714	0.833	NC	NC	0	0	0	0	0.225	0.592
SENSITIVE	0.182	0.308	0	0	0.789	0.882	.	.	0	0	-0.1	-0.833
DEFIANT	0.75	0.857	-0.255	-0.686	0.933	0.966	0	0	0	0	0.158	0.484
INTELLIGENT	0.696	0.821	0	0	1	1	.	.	0.432	0.603	-0.125	-1.25
PROTECTIVE	0.069	0.129	0.593	0.744	0.975	0.987	0	0	0.238	0.385	0.53	0.85
QUITTING	0	0	NC	NC	0.966	0.982	0	0	0.514	0.679	-0.125	-1.25
INVENTIVE	0	0	-0.143	-0.333	0.2	0.333	NC	NC	0.2	0.333	-0.157	-1.185
CLUMSY	0	0	0	0	.	.	0	0	-0.2	-0.5	0.396	0.766
ERRATIC	.	.	.	.	1	1	0	0	0.343	0.511	0.41	0.777
FRIENDLY	0.441	0.612	NC	NC	0.889	0.941	0	0	0	0	0.125	0.417
ANXIOUS	-0.344	-1.048	1	1	0.714	0.833	-0.4	-1.333	0.886	0.94	0.5	0.833
LAZY	0	0	0	0	0.938	0.968	0.947	0.973	0.703	0.826	0.636	0.897
DISORGANIZED	1	1	0	0	0.958	0.978	0	0	0	0	0	0
UNEMOTIONAL	0.825	0.904	0	0	0	0	0.4	0.571	-0.706	-4.8	-0.208	-6.25
IMITATIVE	0	0	0	0	1	1	0	0	.	.	0.422	0.785
INDEPENDENT	1	1	0.478	0.647	0.973	0.986	-0.4	-1.333	0.909	0.952	0.458	0.772
HA SOCIAL	0.488	0.656	0.593	0.744	0.889	0.941	0.5	0.667	0.374	0.544	0.809	0.955
HA CAUTIOUS	0.923	0.96	0.522	0.686	0.908	0.952	0	0	-0.24	-0.632	0.923	0.983
HA COOPERATIVE	0	0	0	0	0.229	0.372	-0.5	-2	0.431	0.602	0.146	0.461
HA NERVOUS	0.316	0.48	.	.	0.632	0.774	.	.	0	0	0.125	0.417
HA AGGRESSIVE	-0.923	-24	.	.	0.324	0.49	.	.	0.565	0.722	0	0
HA OBLIVIOUS	0.537	0.698	0	0	1	1	.	.	0.433	0.605	0.231	0.6

Marwell		Ramat Gan		Terra Natura		Thrigby		Twycross CEN		Twycross GF		Mean	
ICC[3,1]	ICC[3,K]	ICC[3,1]	ICC[3,K]	ICC[3,1]	ICC[3,K]	ICC[3,1]	ICC[3,K]	ICC[3,1]	ICC[3,K]	ICC[3,1]	ICC[3,K]	ICC[3,1]	ICC[3,K]
0.387	0.558	0	0	-0.263	-1.661	0.798	0.922	0.923	0.96	.	.	0.47625	0.432333
0.873	0.954	0.471	0.64	0.551	0.786	0.739	0.895	0.5	0.667	0.85	0.919	0.67825	0.7975
0	0	0	0	0.3	0.563	0	0	0.9	0.947	0	0	0.2595	0.276333
0.5	0.75	0	0	0.122	0.294	-0.038	-0.125	0	0	-0.8	-8	0.086833	-0.45758
0	0	-0.4	-1.333	0	0	-0.325	-2.795	-0.909	-20	-0.5	-2	-0.21817	-3.19833
.	.	.	.	0.374	0.642	0.1	0.25	0.909	0.952	0.8	0.889	0.34025	0.390083
0.64	0.842	0.857	0.923	-0.154	-0.667	0.326	0.592	0	0	.	.	0.175417	-0.28517
0.286	0.545	0	0	0.52	0.765	0	0	.	.	.	.	0.207667	0.260333
0.765	0.907	.	.	0.335	0.602	0.142	0.332	0.727	0.842	0	0	0.3435	0.448333
0.318	0.583	-0.75	-6	0.52	0.765	0.244	0.492	0.857	0.923	0	0	0.2245	-0.35025
0	0	-0.8	-8	0.383	0.65	0.333	0.6	0.947	0.973	0.471	0.64	0.091833	-0.75083
0.357	0.635	.	.	0.613	0.826	0.414	0.679	0.699	0.816	0.96	0.98	0.476417	0.621
0	0	0.75	0.857	0	0	0.756	0.903	0	0	0.6	0.75	0.157083	-0.04025
0	0	0	0	0.918	0.971	-0.053	-0.179	-0.4	-1.333	0.75	0.857	0.238167	0.223917
0.768	0.908	0	0	0	0	0.413	0.678	0.857	0.923	0	0	0.163167	-0.02192
0.25	0.5	0.75	0.857	0.13	0.31	-0.152	-0.652	0	0	0	0	0.198333	-0.0195
0.483	0.737	0.5	0.667	0.343	0.61	0.314	0.578	0.857	0.923	0.6	0.75	0.67975	0.8125
0	0	0.824	0.903	0.255	0.506	0.425	0.689	0.4	0.571	0.923	0.96	0.419667	0.498083
0.5	0.75	0	0	0.539	0.778	0.697	0.874	0	0	0	0	0.358667	0.473167
0	0	0	0	-0.278	-1.875	0.375	0.643	0	0	.	.	0.142417	0.0535
0.3	0.563	0.625	0.769	0.552	0.787	0.289	0.55	-0.4	-1.333	0	0	0.437417	0.507917
0.5	0.75	0	0	-0.093	-0.343	-0.06	-0.205	.	.	0	0	0.219	0.249
0.373	0.641	0	0	0.649	0.847	0.547	0.784	.	.	0.846	0.917	0.462583	0.554167
0.213	0.448	0	0	0.351	0.618	0.053	0.144	0	0	0.909	0.952	0.290583	0.382917
.	.	.	.	0	0	0.465	0.723	0	0	-0.125	-0.286	0.00725	-0.02008
0.421	0.686	0	0	-0.177	-0.824	0.367	0.635	-0.5	-2	-0.462	-1.714	0.001833	-0.709
0	0	0.4	0.571	0.014	0.042	0.503	0.752	0.625	0.769	0.5	0.667	0.136417	-0.00025
0	0	-0.182	-0.444	0.127	0.305	-0.24	-1.385	0	0	-0.5	-2	0.133083	-0.011
0	0	0	0	0.471	0.727	0.432	0.695	0.75	0.857	0	0	0.364333	0.303333
0.286	0.545	-0.682	-4.286	0.447	0.708	0.111	0.273	0	0	0.8	0.889	0.369833	0.195083
0.73	0.89	-0.857	-12	0.092	0.233	0.837	0.939	0	0	0	0	0.383417	-0.8115

0.786	0.917	0	0	-0.177	-0.824	0.548	0.784	-0.72	-5.143	0	0	0.331583	-0.01292
0.261	0.514	0.923	0.96	0.395	0.662	-0.041	-0.132	.	.	.	.	0.3125	0.392583
0.326	0.592	0	0	0.383	0.651	0.857	0.947	0.8	0.889	0	0	0.29725	0.3825
0	0	.	.	0.296	0.558	0.333	0.6	0.6	0.75	.	.	0.193833	0.284167
0	0	0	0	0	0	0	0	-0.857	-12	0	0	0.225417	-0.62608
0.581	0.806	0.857	0.923	0.068	0.179	-0.063	-0.214	0	0	0	0	0.1775	0.168333
0.071	0.188	0	0	0.452	0.712	0.222	0.462	0	0	.	.	0.179	0.122167
-0.087	-0.316	-0.8	-8	-0.284	-1.969	0	0	0	0	0	0	-0.01933	-0.73833
-0.286	-2	0	0	0.385	0.652	0.139	0.326	0	0	0	0	0.092417	-0.05542
0.343	0.61	0.96	0.98	0.144	0.335	-0.293	-2.118	0.3	0.462	0.143	0.25	0.26525	0.178333
0	0	0	0	0.611	0.825	0	0	0	0	0	0	0.217833	0.166583
0.465	0.723	0.923	0.96	0.211	0.444	0.093	0.234	0	0	0	0	0.341417	0.454667
0	0	.	.	-0.444	-12	0	0	0	0	0	0	0.075917	-0.96575
0.364	0.632	1	1	-0.397	-5.75	0.117	0.284	0.75	0.857	0	0	0.161167	-0.31908
0	0	0.8	0.889	0.488	0.741	0.865	0.95	.	.	.	.	0.19575	0.237167
0.065	0.171	0	0	0.239	0.485	0	0	0.824	0.903	0	0	0.240083	0.320583
-0.194	-0.947	0.625	0.769	-0.299	-2.229	-0.091	-0.333	0.5	0.667	.	.	0.166333	-0.00858
0.632	0.837	0.5	0.667	-0.357	-3.75	0.291	0.551	0.75	0.857	0.4	0.571	0.381	0.079833
0.184	0.407	0.357	0.526	-0.065	-0.225	0.378	0.646	0.5	0.667	-0.75	-6	0.319	-0.02625
0.071	0.188	0	0	0.719	0.885	0.674	0.861	0	0	0	0	0.285167	0.326
0	0	-0.5	-2	-0.214	-1.119	-0.182	-0.857	-0.75	-6	.	.	-0.11125	-1.62925
0.133	0.316	0.947	0.973	0.025	0.072	0.448	0.709	.	.	.	.	0.247917	0.32125
0.036	0.102	0.781	0.877	0.252	0.502	0.537	0.777	.	.	0.125	0.222	0.429083	0.458667
0.133	0.316	-0.5	-2	0.36	0.628	0.071	0.188	0.186	0.316	0.462	0.632	0.36375	0.38225
0.4	0.667	0	0	0.177	0.393	0	0	0.6	0.75	0	0	0.351083	0.396583
0.444	0.706	-0.786	-7.33	0.478	0.733	0.326	0.592	0.75	0.857	0.5	0.667	0.168167	-0.36167
0	0	0.5	0.667	-0.048	-0.161	0	0	-0.9	-18	0.4	0.571	0.085417	-1.271
0	0	0	0	0.239	0.485	0.16	0.363	0.96	0.98	0.5	0.667	0.152083	-1.69108
0	0	0	0	0.476	0.732	0.071	0.188	0.9	0.947	0	0	0.304	0.3975

Appendix 10: Salient ICC[3,k] values *S. syndactylus*

	Besancon	Boissiere	Burgers	Cotswolds	Fota	Manor House	Marwell	Ramat Gan	Terra Natura	Thrigby	Twycross CEN	Twycross GF	Mean
							ICC[3,k]						
FEARFUL	0.947	0	1	0.667	0.88	0.915	0.558	0	-1.661	0.922	0.96		**0.432333**
DOMINANT	0.989	0.545	0.808	0.432	0.945	0.99	0.954	0.64	0.786	0.895	0.667	0.919	**0.7975**
PERSISTENT	-0.857	0.706	0.571	-0.286	0.706	0.966	0	0	0.563	0	0.947	0	**0.276333**
AUTISTIC		0	0.988		0.96				0.642	0.25	0.952	0.889	**0.390083**
THOUGHTLESS	0	0.814			1	0	0.545	0	0.765	0			**0.260333**
STINGY/GREEDY	0.692	0.364	0.8	0	-0.107	0.948	0.907		0.602	0.332	0.842	0	**0.448333**
RECKLESS		0.762	0.889	0.64	0.355	0.87	0.635		0.826	0.679	0.816	0.98	**0.621**
DISTRACTIBLE	0.632		0.897		0.286	0.556	0	0	0.971	-0.179	-1.333	0.857	**0.223917**
PLAYFUL	0.857	0.791	0.972	1	0.882	0.983	0.737	0.667	0.61	0.578	0.923	0.75	**0.8125**
SOLITARY	0.923	-0.091	0.941		-0.326	0.901	0	0.903	0.506	0.689	0.571	0.96	**0.498083**
VULNERABLE	0.735	0.281	0.857	0	0.457	0.946	0.75	0	0.778	0.874	0	0	**0.473167**
INNOVATIVE	0.735		1	0	0	0.139	0	0	-1.875	0.643	0		**0.0535**
ACTIVE	0.774	0.457	0.882	0.968	0.864	0.814	0.563	0.769	0.787	0.55	-1.333	0	**0.507917**
HELFPUL	0.982	0.1	0.984	0	0.125	0.595	0.75	0	-0.343	-0.205		0	**0.249**
BULLYING	0	0.516	1	0	0.99	0.955	0.641	0	0.847	0.784		0.917	**0.554167**
AGGRESSIVE	0	0.833		0	0.661	0.939	0.448	0	0.618	0.144	0	0.952	**0.382917**
IMPULSIVE	0.741	-2.667	0.571	1	0.95	0.766	0	0	0.727	0.695	0.857	0	**0.303333**
INQUISITIVE	0.822		0.889	1	0.767	0.734	0.545	-4.286	0.708	0.273	0	0.889	**0.195083**
DEPENDENT/FOLLOWE	0.962		0.986	0	0.182	0.577	0.514	0.96	0.662	-0.132			**0.392583**
IRRITABLE	-0.476	0	0.875	0	0.627	0.485	0.592	0	0.651	0.947	0.889	0	**0.3825**
UNPERCEPTIVE	0		0.946	0	0	0.556	0		0.558	0.6	0.75		**0.284167**
DECISIVE	0	0.296	0.85	-1.333	0	0.513	0.806	0.923	0.179	-0.214	0	0	**0.168333**
DEPRESSED	0.923	0	0.931	0	-0.5	-1.25	0.188	0	0.712	0.462	0		**0.122167**
DEFIANT	0.857	-0.686	0.966	0	0	0.484	0.61	0.98	0.335	-2.118	0.462	0.25	**0.178333**
INTELLIGENT	0.821	0	1		0.603	-1.25	0	0	0.825	0	0	0	**0.166583**
PROTECTIVE	0.129	0.744	0.987	0	0.385	0.85	0.723	0.96	0.444	0.234	0	0	**0.454667**
CLUMSY	0	0		0	-0.5	0.766	0	0.889	0.741	0.95			**0.237167**
ERRATIC			1	0	0.511	0.777	0.171	0	0.485	0	0.903	0	**0.320583**
ANXIOUS	-1.048	1	0.833	-1.333	0.94	0.833	0.837	0.667	-3.75	0.551	0.857	0.571	**0.079833**
DISORGANIZED	1	0	0.978	0	0	0	0.188	0	0.885	0.861	0	0	**0.326**
IMITATIVE	0	0	1	0		0.785	0.316	0.973	0.072	0.709			**0.32125**
INDEPENDENT	1	0.647	0.986	-1.333	0.952	0.772	0.102	0.877	0.502	0.777		0.222	**0.458667**
HA SOCIAL	0.656	0.744	0.941	0.667	0.544	0.955	0.316	-2	0.628	0.188	0.316	0.632	**0.38225**
HA CAUTIOUS	0.96	0.686	0.952	0	-0.632	0.983	0.667	0	0.393	0	0.75	0	**0.396583**
HA OBLIVIOUS	0.698	0	1		0.605	0.6	0	0	0.732	0.188	0.947	0	**0.3975**

Appendix 11: Domain formation *S. syndactylus*

EXCITABILITY

	Thoughtle	Reckless	Distractibl	Playful	Innovative	Active	Impulsive	Inquisitive	Depender	Defiant	Clumsy	Disorganis	Imitative	HASocial	SCORE
Xhulu	1	2.5	2.5	2	2	3	2	3	4	1.5	1.5	1	1.5	4.5	2.285714
Spindle	1	2.5	2.5	2	2	2.5	2	3	4	1.5	1.5	1	1.5	5.5	2.321429
Manny	1	5	2.5	7	2.5	5.5	4	5	5	2	3.5	1.5	2	6.5	3.785714
Guildo	1	1	4	5	2	3	2	4	2	1	2	1	2	6	2.571429
Konnie	1	1	4	6	3	3	2	5	2	1	2	1	2	7	2.857143
Bloem	3	5	6	7	5	6	5	7	6	3	4	3	6	7	5.214286
Gicko	1	4	6	7	2	4	5	7	2	1	4	2	2	7	3.857143
William	2.5	5	4.5	7	5.5	5	3.5	5	2	1	1.5	2	3.5	5	3.785714
Ricki	2.5	1.5	2.5	1.5	5	2.5	1	4.5	2.5	1.5	2	1.5	4	3.5	2.571429
Raja	1	3	4	4	1	6	2	1	1	1	1	1	1	4	2.214286
Gerda	2	3	4	2	1	6	2	1	1	1	1	1	1	5	2.214286
Steve	2.4	2	2.8	3.4	4.4	3.6	2.4	4	4.4	2.4	1.8	1.8	1.8	3.2	2.885714
Lisa	2.2	5	3.4	5	5	4.8	4.6	5.8	2.8	3.4	2	1.6	2	5.8	3.814286
Bryn	2.2	3.2	3.4	6.6	4.4	5	3.2	5.2	4	2.2	3	1.8	3.2	6.2	3.828571
Luca	1	5	5	4	5	6	4	5	4	5	3	3	4	3	4.071429
Ella	6	2	5	3	5	2	4	6	3	5	3	3	4	6	4.071429
Sam	2	3.5	6	5	3	4.5	5.5	5.5	1	6	1.5	6	4	5.5	4.214286
Ebonie	2	1.5	2.5	3.5	3	4	3	4	1.5	3	1.5	4.5	1	4	2.785714
Anak	2	4.5	4.5	7	6	6.5	6	7	4.5	6.5	1.5	2.5	3	6	4.821429
Titus	2	1.5	3.5	6	3	6	4.5	5.5	6	5.5	1.5	2.5	3	4	3.892857
Cayaha	6	1	2	7	1	6	1	5	4	4	1	1	3	4	3.285714
Schnudi	2	1	5	2	2	3	1	2	4	6	1	3	2	6	2.857143
Rokan	2	3	5	4	3	5	3	6	4	2	1	2	2	5	3.357143
Tiku	3	3	3	4.333333	3.666667	3.666667	2.333333	6	1.666667	5.333333	1.333333	1	2.333333	6	3.333333
Kali	2	2.333333	3.666667	3.666667	4	3	2	5.666667	4.333333	1.666667	1	1	2.333333	5.333333	3
Tsao	1	0.5	4.5	1	2	1.5	3.5	2.5	2	1.5	1	1	2.5	2	1.892857
Ufo	1.5	0.5	1.5	5	4.5	3.5	2	3	5.5	3	1	1	3	4	2.785714
Pimprenelle	3	0.5	6.5	7	6	7	5	7	7	5.5	1.5	5	4	6.5	5.107143
Laosso	2.333333	0.666667	3	6.666667	3.666667	5	3.333333	5.333333	3	3.666667	1.333333	2.333333	3.333333	6	3.547619
Niam	1	3	1	3.5	2	3.5	3	2.5	1	2	1.5	1.5	3	5	2.392857
Noemie	1.5	4.5	1.5	3	2	2.5	3	2.5	2.5	2.5	1.5	2	3	5.5	2.678571
Tahan	2.5	2	2.5	5	2.5	4	3	3	1.5	3	1.5	2	3.5	3.5	2.821429
Ewa	3.5	6	3	6	2.5	4.5	4	3	3.5	4	2.5	2.5	3.5	5.5	3.857143
Otto	1	2	3.333333	5	2.666667	4	2	2	1.666667	1.666667	1.666667	1.666667	2.333333	3.666667	2.47619
Pygmy	1.333333	2	4	3.333333	2.666667	3.666667	2.333333	2.333333	2.666667	2	1.666667	1.666667	2.333333	3	2.5
Josef	2	4	3	6	6	6	5	5	3	4	2	2	3	4	3.928571
Niki	5	4	5	3	4	3	4	4	5	2	5	4	3	4	3.928571
Kaya	1	4	4.5	3.5	1	4.5	6.5	5.5	2.5	1	1	1	1	6	3.071429
Clyde	3	1	2.5	1	1	1.5	1	1.5	2.5	1	2	1	1	1	1.5
Homer	1	2.5	3.5	7	4	6	2.5	5.5	6	1.5	1.5	1.5	1	4.5	3.428571
Rocky	1	1	2.5	3.5	1.5	2.5	1.5	5.5	4.5	3	1	1	1	3	2.321429
Bart	1	2	3.5	2.5	1.5	3	1.5	4.5	3.5	1	1	1	1	2	2.071429
Maggie	1	1	2	7	7	6	2	7	6	2	1	1	1	7	3.642857
Luang	3.333333	2.666667	3	4.666667	5	2	2	3.666667	2	2	1	2.333333	2	6.666667	3.02381
Simone	2	2.333333	2.333333	5	5	2	2	3	2.333333	2.666667	1	1.666667	1.666667	6	2.785714
Hale-bop	2.666667	1.666667	2.666667	7	4.666667	3.333333	2	3.333333	3.333333	1.666667	1.333333	1.666667	2	5.666667	3.071429
Rosh	2	3.333333	3.333333	7	5	3.333333	2.666667	3.666667	2.666667	3.333333	1	2.333333	2.666667	6	3.452381
Taos	3	3	4	5	3	4	4	4	1	3	2	2	4	5	3.357143
Terkina	6	1	3	1	1	7	4	7	2	3	1	2	1	1	2.857143
Patchouli	2	2	3	5	3	5	3	3	4	2	2	3	4	6	3.357143
Samtra	2	2	3	5	3	5	3	4	4	2	2	3	4	6	3.428571
Sianouk	3	2	4	7	4	7	5	6	5	2	2	3	6	7	4.5
Ya'an	1	1	1.5	6	4	5	1	4.5	1.5	1	1	1	1.5	4.5	2.464286
Jumby	2	1	1.5	5	3.5	4.5	1	3.5	1.5	1	1	1	2	4	2.321429
Gor	1	1	3	7	4.5	6.5	2.5	5	6.5	4.5	4	1.5	7	3.5	4.107143
Tilus	4.666667	4.333333	4	5.666667	3.333333	6	5	5	2.333333	4.333333	1.666667	2.333333	2.333333	5.666667	4.047619
Sanka	1.666667	1.666667	2.666667	3.666667	2.333333	2.666667	2	3.333333	4.333333	2	1.666667	1.666667	2.333333	3.666667	2.547619
Tolo	5	5	6.333333	6.333333	3.333333	5.666667	5	3.333333	2.333333	3.666667	4.666667	5.666667	3.666667	3.333333	4.52381
Oscarina	4.333333	3	3.333333	6.333333	3	5	2.666667	4.333333	5	1.666667	1.666667	2.666667	4	5.333333	3.738095
Spike	1	4.5	4	3	3.5	3	4	1.5	1.5	2	1	2.5	1	4.5	2.642857
Tarragon	1	1	3.5	1.5	4	2.5	1	1.5	1.5	1.5	0.5	1	1	2	1.678571
Stig	1	1	3	3.5	4.5	3.5	2	2.5	1.5	3.5	0.5	1.5	1	3.5	2.321429
Tango	1	1	3.5	3	3	4.5	1.5	3	3.5	2	1	1	3	1.5	2.321429
Denzel	1	5	5	7	3	5.5	3	4.5	3.5	4	1	1.5	3	3	3.571429
Darwin	1	3.5	4.5	7	3	5.5	3	4.5	3.5	4	1	1	3	4	3.464286
Maliwan ting-ton	1	1	3.5	3	2	2.5	1.5	1.5	3.5	1	4	1	2	3.5	2.214286
Malacca	1.5	1.5	6	7	5	6.5	5.5	4.5	3	3	1	2.5	3	7	4.071429
Kiao	1	2	2	4	5	5	2	6	1	5	2	2	3	5	3.214286
Nina	1	2	2	3	5	3	2	6	4	3	2	2	5	4	3.142857
Bali	6	6	5	7	4	7	5	7	6	6	4	5	6	3	5.5
Samu	2	2	3	5	5	6	3	6	2	5	2	2	3	3	3.5
Bianca	5	2	4	5	4	6	2	6	5	4	2	2	4	7	4.142857
Theo	2.666667	2.666667	3.666667	3	2.666667	3.666667	1	3.666667	2.666667	2.333333	1.666667	2.666667	2	3.666667	2.714286
Hovis	3.666667	3	5.333333	4	2.333333	3.666667	1	3.333333	3.333333	2.666667	6.666667	5.666667	3.333333	5	3.785714
Silas	2.666667	3.333333	3.666667	5.333333	3	3.666667	1.666667	4	4.666667	2.333333	2.666667	2.666667	4	5	3.47619
Blossom	3.333333	4.333333	4.333333	5.333333	3	4	3	4	4.666667	3.333333	2.333333	2.666667	4	5	3.809524
Joe	3.333333	4.333333	4.333333	6.333333	4	5	3.333333	4.666667	3.666667	3	2.333333	3	5	5	4.095238

DOMINANCE

	Dominant	Persistent	Stingy	Bullying	Aggressiv	Decisive	Independer	TOTAL +VE		Vulnerable	SCORE
Xhulu	2.5	2	5	2.5	1.5	6	4	23.5	2	6	3.6875
Spindle	4.5	3.5	6	4.5	3.5	5.5	3.5	31	2	6	4.625
Manny	1	3	5	1.5	1.5	5	4.5	21.5	4	4	3.1875
Guildo	5	3	6	3	2	6	5	30	1	7	4.625
Konnie	5	5	7	3	2	6	5	33	1	7	5
Bloem	3	6	7	1	2	5	5	29	2	6	4.375
Gicko	1	5	5	1	1	5	6	24	6	2	3.25
William	6	4	5	5.5	5.5	4.5	5	35.5	1.5	6.5	5.25
Ricki	1	2.5	2.5	1	1	4	5	17	4.5	3.5	2.5625
Raja	6	4	6	1	3	1	2	23	5	3	3.25
Gerda	3	4	2	1	1	1	2	14	5	3	2.125
Steve	3.8	2.8	3.2	3	1.8	4.6	3.8	23	2.8	5.2	3.525
Lisa	6.4	5.2	6.6	5.6	5.2	5	4.4	38.4	2.4	5.6	5.5
Bryn	1.6	2.2	2	1.6	2	3.6	3.4	16.4	6	2	2.3
Luca	5	4	3	4	5	3	6	30	5	3	4.125
Ella	3	4	3	2	2	3	5	22	5	3	3.125
Sam	5	6	6.5	4	2	6	3	32.5	6.5	1.5	4.25
Ebonie	4.5	3.5	5	4	2	5	1.5	25.5	4	4	3.6875
Anak	2.5	4	3	5	2	3	4.5	24	4.5	3.5	3.4375
Titus	2	4.5	4.5	4	2	4	6.5	27.5	5	3	3.8125
Cayaha	4	4	3	2	2	3	1	19	3	5	3
Schnudi	3	6	5	1	1	4	4	24	6	2	3.25
Rokan	4	4	5	4	2	6	4	29	2	6	4.375
Tiku	6	4.333333	6	5.333333	4	5	4.66666667	35.33333	1.333333	6.66666667	5.25
Kali	2	3.666667	2.666667	1	1.333333	5	3.66666667	19.33333	4.333333	3.66666667	2.875
Tsao	6.5	3.5	6	4	3.5	4	5	32.5	1.5	6.5	4.875
Ufo	4	4	3	3	2	4	4	24	3	5	3.625
Pimprenelle	1	2.5	2	2.5	2.5	5.5	1	17	5.5	2.5	2.4375
Laosso	3.333333	4.333333	5.333333	4	3	6.333333	3.33333333	29.66667	2.666667	5.33333333	4.375
Niam	5.5	4	5.5	6	2.5	5.5	5.5	34.5	1.5	6.5	5.125
Noemie	5.5	4.5	5	4	1	4.5	5	29.5	1.5	6.5	4.5
Tahan	1.5	2	2.5	2	1	4.5	3	16.5	4.5	3.5	2.5
Ewa	3.5	4.5	5	2.5	1.5	6	3.5	26.5	5	3	3.6875
Otto	3	2	1.666667	1	1	4.666667	3.66666667	17	2	6	2.875
Pygmy	5.333333	2	3.666667	1.333333	1.666667	5	3	22	2	6	3.5
Josef	6	5	5	2	4	5	5	32	2	6	4.75
Niki	4	4	3	1	2	3	3	20	3	5	3.125
Kaya	3	4.5	4	2.5	1.5	5	6	26.5	3	5	3.9375
Clyde	5	4.5	5	6	2	5.5	4.5	32.5	2	6	4.8125
Homer	2.5	2.5	5.5	1.5	1	3.5	3	19.5	3.5	4.5	3
Rocky	1	1.5	3.5	1	1	3.5	3	14.5	5	3	2.1875
Bart	7	3.5	7	7	5	5.5	4.5	39.5	1	7	5.8125
Maggie	2	7	7	1	1	6	7	31	6	2	4.125
Luang	6.333333	4.666667	4.666667	3.333333	3	5.333333	6	33.33333	1.333333	6.66666667	5
Simone	4	3.666667	4.333333	2	2.333333	4.666667	5.33333333	26.33333	1.333333	6.66666667	4.125
Hale-bop	1.333333	3.666667	3.333333	1.333333	1.333333	3.666667	4.66666667	19.33333	3.666667	4.33333333	2.958333
Rosh	4.333333	3.666667	4.666667	3.666667	3	5.333333	6.33333333	31	2.333333	5.66666667	4.583333
Taos	5	5	4	4	4	6	6	34	1	7	5.125
Terkina	5	1	4	2	3	6	7	28	1	7	4.375
Patchouli	5	3	4	2	2	5	3	24	2	6	3.75
Samtra	6	3	3	1	2	4	3	22	2	6	3.5
Sianouk	4	4	3	1	1	3	3	19	2	6	3.125
Ya'an	3.5	4	3	2	2	5	5.5	25	1.5	6.5	3.9375
Jumby	3.5	3	3	2.5	2	4.5	6	24.5	1.5	6.5	3.875
Gor	1	3	3	1	1	3	2	14	1	7	2.625
Tilus	5	4	5.666667	5	4.333333	5	3.66666667	32.66667	2.666667	5.33333333	4.75
Sanka	2.333333	2	3	3	1.333333	4.666667	4	20.33333	6	2	2.791667
Tolo	1	4	2	2	1.666667	4	5.33333333	20	3.666667	4.33333333	3.041667
Oscarina	1.666667	2	2.333333	2	1.333333	3	2	14.33333	4.333333	3.66666667	2.25
Spike	1.5	4.5	1.5	1	1.5	3.5	2.5	16	1.5	6.5	2.8125
Tarragon	2.5	2	3	1	1	4	2.5	16	1	7	2.875
Stig	2	3.5	4	1	1	4	2.5	18	1	7	3.125
Tango	2.5	5	4.5	1.5	1	3.5	4	22	5	3	3.125
Denzel	6	5.5	5	5.5	5.5	5	5.5	38	5.5	2.5	5.0625
Darwin	4.5	5.5	5	3.5	4	4	5.5	32	5.5	2.5	4.3125
Maliwan ting-ton	2	1.5	2	1.5	1	2	3	13	4	4	2.125
Malacca	6.5	4.5	5.5	5.5	1.5	5	6	34.5	1.5	6.5	5.125
Kiao	5	4	7	6	5	7	7	41	1	7	6
Nina	4	4	5	3	2	6	6	30	4	4	4.25
Bali	1	5	4	1	1	4	5	21	3	5	3.25
Samu	5	4	7	6	5	6	7	40	1	7	5.875
Bianca	2	4	4	2	2	6	5	25	4	4	3.625
Theo	6.333333	3.666667	5	4.666667	3.666667	4.666667	6.33333333	34.33333	1.333333	6.66666667	5.125
Hovis	1.333333	3	2	1	1.666667	3.333333	3	15.33333	6.333333	1.66666667	2.125
Silas	2.666667	3.666667	4	4	3	3.666667	5.33333333	26.33333	2.666667	5.33333333	3.958333
Blossom	4.333333	3.666667	4.333333	4.666667	3.333333	4	6.33333333	30.66667	2	6	4.583333
Joe	2.333333	3.666667	3.666667	2.666667	3	3.333333	5	23.66667	2.666667	5.33333333	3.625

INTROVERTED

	Fearful	Autistic	Solitary	Irritable	Unpercep	Depresse	Erratic	Anxious	HACautiou	HAObliviou	SCORE
Xhulu	1.5	1	1.5	2	1.5	1.5	1.5	1.5	4.5	1	1.75
Spindle	2	1	1.5	3	1.5	1	1.5	2	4.5	1	1.9
Manny	2.5	1	1.5	1	2	1	2	2.5	3.5	1	1.8
Guildo	2	1	2	1	1	1	1	1	2	2	1.4
Konnie	2	1	2	1	1	1	1	1	2	2	1.4
Bloem	3	1	2	1	1	1	2	2	2	1	1.6
Gicko	2	1	4	1	1	2	2	2	2	1	1.8
William	2	1	4	4.5	4	1.5	3	2	3	2	2.7
Ricki	5	1	4.5	1.5	2	3	1	3	3.5	2	2.65
Raja	1	1	1	2	1	1	1	1	2	1	1.2
Gerda	1	4	1	2	1	1	1	1	3	1	1.6
Steve	3.2	1.2	2.6	2	2.4	2.8	2.2	2.6	6.4	3	2.84
Lisa	2	1.2	2.8	3.4	2.4	2.4	4.4	1.6	2.2	2	2.44
Bryn	4.6	1.2	4	2	3	2.4	4	3.6	4	2	3.08
Luca	2	2	4	5	3	2	3	3	5	1	3
Ella	3	2	4	3	3	6	4	5	5	1	3.6
Sam	4	6.5	3	5.5	5.5	2.5	7	3	1	7	4.5
Ebonie	4	1	5.5	2.5	5	5	5	4	5	2	3.9
Anak	4	1.5	4	3.5	2	2	2	2.5	4.5	2	2.8
Titus	5	1	4	2.5	2.5	1.5	2	2.5	6	2	2.9
Cayaha	2	1	1	1	1	1	1	1	4	1	1.4
Schnudi	2	1	4	6	2	4	1	2	4	5	3.1
Rokan	2	1	4	5	6	3	1	2	4	2	3
Tiku	1	4.333333	1.333333	1.666667	1	1	2	1	2	1.3333333	1.666667
Kali	3.333333	1.333333	1.333333	1	1.666667	1	1.333333	3	2.3333333	1.3333333	1.766667
Tsao	4.5	1	5	4	3.5	4	1	3.5	6.5	6	3.9
Ufo	2	1	2	1.5	4.5	2	1	4	4	3	2.5
Pimprenelle	3.5	1	1	2	2.5	2.5	1	6	4	1.5	2.5
Laosso	2	1	3	1.666667	1.666667	1	1	2.666667	4.6666667	1.3333333	2
Niam	1.5	1	1.5	1	1	1	1	2	3	2	1.5
Noemie	1.5	1	1.5	1	1	2	1	2	3.5	1.5	1.6
Tahan	2	2	3.5	1.5	1	2.5	1	5	4	1	2.35
Ewa	2	1	2.5	1	1	1	1	2	5	1	1.75
Otto	1.666667	2.666667	2.333333	1.333333	1.333333	1.333333	1.666667	1.666667	1.6666667	3.3333333	1.9
Pygmy	1.333333	1.333333	2.333333	1.666667	1.666667	1.333333	1.666667	1.666667	2.6666667	3.3333333	1.9
Josef	1	1	3	2	2	2	2	1	2	4	2
Niki	1	1	3	2	2	2	2	2	4	3	2.2
Kaya	2	6	3.5	6.5	1	2.5	3.5	2	2.5	1	3.05
Clyde	1.5	1	2	3.5	4	1.5	1	1	4	3.5	2.3
Homer	3	1	1.5	2	3	1.5	1.5	2.5	2.5	1.5	2
Rocky	5	1	1	2	1	2	1	4.5	2.5	3	2.3
Bart	1	1	1	5	3	1.5	1	1	4.5	2	2.1
Maggie	1	1	1	2	1	2	1	1	2	1	1.3
Luang	1.333333	1	1.666667	2.666667	2.666667	2	3	2	2	2	2.033333
Simone	1.333333	1	2.333333	2.666667	2.333333	2	2.333333	2.333333	2.3333333	1.6666667	2.033333
Hale-bop	2.666667	1	2.666667	1.333333	2.333333	2.666667	2.666667	3.333333	3.3333333	1.6666667	2.366667
Rosh	1.666667	1	2	3.333333	2.666667	2.666667	3.666667	2	2.3333333	2.3333333	2.366667
Taos	2	4	2	4	4	4	6	4	7	3	4
Terkina	4	1	2	1	4	2	2	1	3	1	2.1
Patchouli	1	1	2	1	1	1	1	2	2	3	1.5
Samtra	1	1	2	1	1	1	1	3	2	3	1.6
Sianouk	2	1	1	1	1	1	1	4	2	2	1.6
Ya'an	2.5	1	1.5	2	1	1	1.5	1	5	3	1.95
Jumby	3	1	4	3	1	2	2.5	2	6	3.5	2.8
Gor	3	1	1	1.5	1	1	1	1.5	6	3	2
Tilus	2.666667	2.333333	2.333333	3.333333	2	2.333333	3	3	3	1	2.5
Sanka	4.333333	1.666667	4.333333	1.666667	1.666667	3.666667	2	3.333333	4.6666667	3	3.033333
Tolo	3.666667	5	3.666667	1.333333	3	2	4	2.333333	3.6666667	3	3.166667
Oscarina	4	1	1.666667	2	1.666667	2.333333	2	2.666667	2.6666667	1.3333333	2.133333
Spike	4	6	4	5	3	3	5	5.5	2	1	3.85
Tarragon	1.5	1.5	4.5	2	1	3	2	2	4	3.5	2.5
Stig	1.5	3	3	2	1	2	2.5	2	4	2	2.3
Tango	4.5	4	5	3.5	3.5	3.5	3.5	5	5.5	4	4.2
Denzel	4.5	1	2.5	5	3.5	3.5	5	4.5	4.5	5.5	3.95
Darwin	4.5	1	2.5	3	3.5	3.5	3.5	3.5	3.5	5	3.35
Maliwan ting-ton	1	1	2.5	1	1.5	1	1	3	5	1	1.8
Malacca	1	1	1	1.5	2	1	2.5	1.5	2.5	1	1.5
Kiao	1	2	3	2	1	1	6	1	2	1	2
Nina	1	2	4	2	1	1	6	1	2	1	2.1
Bali	2	1	1	1	2	1	5	1	2	1	1.7
Samu	1	2	3	3	1	1	6	1	2	1	2.1
Bianca	1	2	3	1	1	1	4	3	1	1	1.8
Theo	2.333333	1.666667	5.666667	1.333333	1.666667	4	1.666667	2	4	1.6666667	2.6
Hovis	5	2.666667	5.333333	1.333333	4	4	1.666667	3.666667	4	1.3333333	3.3
Silas	2	2	3	2	2.666667	3.333333	2.333333	2	4	1.6666667	2.5
Blossom	2.333333	2	2.666667	5	3	2.666667	2.666667	2	3.3333333	1.6666667	2.733333
Joe	3.333333	2	1.333333	1.333333	3.666667	2.333333	3	1.333333	3.3333333	1	2.266667

Appendix 12: Kendall's tau correlation script *M. nigra*

```
> MACAQUESTAB<-read.csv(file.choose())
> names(MACAQUESTAB)
[1] "Animal"        "Dominant2009" "Dominant2018" "Playful2009"  "Playful20
18"  "Active2009"   "Active2018"   "NegLazy2009"
[9] "NegLazy2018"
> summary(MACAQUESTAB)
       Animal     Dominant2009     Dominant2018     Playful2009      Playful20
18       Active2009       Active2018     NegLazy2009      NegLazy2018
 Anneke    : 1   Min.   :1.000   Min.   :1.000   Min.   :1.750   Min.   :1.
000   Min.   :4.000   Min.   :2.00   Min.   :3.250   Min.   :1.000
 Bella     : 1   1st Qu.:2.450   1st Qu.:2.000   1st Qu.:3.000   1st Qu.:1.
000   1st Qu.:5.050   1st Qu.:3.00   1st Qu.:5.213   1st Qu.:3.750
 Cheeketo : 1   Median :4.575   Median :5.000   Median :5.600   Median :2.
000   Median :6.100   Median :3.00   Median :6.000   Median :5.000
 Cinta     : 1   Mean   :4.158   Mean   :4.333   Mean   :4.869   Mean   :2.
296   Mean   :5.971   Mean   :3.55   Mean   :5.883   Mean   :4.536
 Douglas   : 1   3rd Qu.:5.875   3rd Qu.:6.333   3rd Qu.:6.900   3rd Qu.:3.
000   3rd Qu.:7.000   3rd Qu.:4.30   3rd Qu.:6.950   3rd Qu.:5.000
 Drusilla : 1   Max.   :7.000   Max.   :7.000   Max.   :7.000   Max.   :4.
800   Max.   :7.000   Max.   :7.00   Max.   :7.000   Max.   :7.000
 (Other)   :20

> cor.test(MACAQUESTAB$Dominant2009, MACAQUESTAB$Dominant2018, method="ken
dall")

        Kendall's rank correlation tau

data:  MACAQUESTAB$Dominant2009 and MACAQUESTAB$Dominant2018
z = 2.364, p-value = 0.01808
alternative hypothesis: true tau is not equal to 0
sample estimates:
      tau
0.3453428



> cor.test(MACAQUESTAB$Playful2009, MACAQUESTAB$Playful2018, method="kenda
ll")

        Kendall's rank correlation tau

data:  MACAQUESTAB$Playful2009 and MACAQUESTAB$Playful2018
z = 0.69371, p-value = 0.4879
alternative hypothesis: true tau is not equal to 0
sample estimates:
      tau
0.1080711



> cor.test(MACAQUESTAB$Active2009, MACAQUESTAB$Active2018,

method="kendall")


Kendall's rank correlation tau

data:  MACAQUESTAB$Active2009 and MACAQUESTAB$Active2018
z = 0.42383, p-value = 0.6717
alternative hypothesis: true tau is not equal to 0
sample estimates:
       tau
0.06606405
```

```
> cor.test(MACAQUESTAB$NegLazy2009, MACAQUESTAB$NegLazy2018, method="kenda
ll")

	Kendall's rank correlation tau

data:  MACAQUESTAB$NegLazy2009 and MACAQUESTAB$NegLazy2018
z = 0.98847, p-value = 0.3229
alternative hypothesis: true tau is not equal to 0
sample estimates:
      tau 
0.1514545 
```

Appendix 13: Salient ICC[3,k] scores *M. nigra*

	Boras	Drusillas	Dublin	London	Marwell	Newquay	Paignton	Ramat Gan	Rotterdam	
	6,2	4,2	6,2	8,2	4,5	9,2	10,3	6,2	3,2	
	Average	Average	Average	Average	Average	Average	Average	Average	Average	
FEARFUL	-0.304	0.923	1.000	1.000	-1.607	0.988	0.918	0.113	-4.444	**-0.157**
DOMINANT	0.695	0.963	0.990	1.000	0.976	0.940	0.870	0.075	-6.000	**0.056556**
PERSISTENT	0.625	0.686	0.977	1.000	0.666	0.994	0.990	-0.464	0.571	**0.671667**
CAUTIOUS	0.542	0.878	1.000	0.873	0.625	0.996	0.983	-2.143	-6.000	**-0.24956**
STABLE	-1.038	0.167	0.868	1.000	-6.250	1.000	0.955	0.422	0.000	**-0.31956**
AUTISTIC		0.000		1.000	0.835	0.000				**0.203889**
CURIOUS	0.384	-0.119	0.919	0.762	0.913	0.946	0.993	-0.706	0.000	**0.454667**
THOUGHTLESS	0.000	0.500	1.000	1.000	0.381	0.993	0.937	-0.128	0.750	**0.603667**
STINGY/GREEDY	-0.238	0.944		1.000	0.939	0.988	0.971	-1.088	0.571	**0.454111**
JEALOUS	-0.778	0.828	0.984	1.000	0.833	0.986	0.970	-2.000	0.640	**0.384778**
INDIV.	0.809	0.855	1.000	0.922	0.762	0.955	0.989	0.220	-6.000	**0.056889**
RECKLESS	0.914	0.784	0.978	0.727	0.898	0.966	0.965	0.000	0.632	**0.762667**
SOCIABLE	0.000	0.000		0.851	0.278	0.971	0.957	-0.906	-1.333	**0.090889**
DISTRACTIBLE	0.792	-0.375		0.886	0.735	1.000	0.921	0.000	-2.571	**0.154222**
TIMID	0.388	0.982	0.988	0.977	0.871	0.986	0.989	-0.259	-1.053	**0.541**
SYMPATHETIC	-5.854	0.000	0.979	0.901	0.400	0.982	0.962	0.429	-0.333	**-0.17044**
PLAYFUL	0.909	0.929	0.988	1.000	0.943	0.935	0.990	0.694	0.968	**0.928444**
SOLITARY	0.912	0.706		0.926	0.757	1.000	0.856	-1.391	-6.000	**-0.24822**
VULNERABLE	0.619	0.970	0.989	0.948	0.893	0.933	0.971	0.199	-2.000	**0.502444**
INNOVATIVE	0.565	0.000	1.000	1.000	0.706	0.956	0.988	0.755	0.923	**0.765889**
ACTIVE	0.926	0.853	1.000	1.000	-3.000	0.984	1.000	0.923	0.889	**0.508333**
HELFPUL	0.000	0.747	1.000	1.000	0.361	0.985	0.953	0.000	-6.000	**-0.106**
BULLYING	0.571	0.965	0.992	1.000	0.980	1.000	0.985	-0.119	0.000	**0.708222**
AGGRESSIVE	0.000	0.917	1.000	0.975	0.944	1.000	0.975	0.326	0.000	**0.681889**
MANIPULATIVE	0.832	0.457	0.986	1.000	0.759	0.992	0.980	0.000	0.000	**0.667333**
GENTLE	0.410	-0.186	0.992	0.889	0.918	1.000	0.933	0.000	-2.000	**0.328444**
AFFECTIONATE	0.000	0.842	0.113	0.000	-0.446	0.988	0.721	0.686	0.000	**0.322667**
EXCITABLE	0.742	0.000		1.000	0.214	0.942	0.859	-4.966	0.667	**-0.06022**
IMPULSIVE	0.273	0.533	-1.846	0.889	0.827	1.000	0.943	0.000	0.000	**0.291**
INQUISITIVE	1.000	-0.889		0.000	0.788	0.939	0.981	0.759	0.571	**0.461**
SUBMISSIVE	0.048	0.913	-0.916	1.000	0.929	1.000	0.987	-0.857	-0.714	**0.265556**
COOL	-1.108	0.000	0.000	1.000	0.313	0.988	0.939	0.000	0.000	**0.236889**
DEPENDENT/FOLLOWE	0.850	0.936	-1.027	0.954	0.901	0.990	0.989	0.236	-0.750	**0.453222**
IRRITABLE	0.000	0.904	-0.400	0.962	0.874	1.000	0.974	-1.404	0.000	**0.323333**
UNPERCEPTIVE	0.000	0.000		0.948	0.556	1.000	0.943	0.000	0.000	**0.383**
PREDICTABLE	0.970	0.000	0.434	0.945	0.333	0.917	0.984	0.000	0.000	**0.509222**
DECISIVE	0.104	0.800	-0.400	1.000	0.775	0.966	0.931	0.000	-2.000	**0.241778**
DEPRESSED	0.750	0.948		0.511	0.633	1.000	0.582	-0.828	-0.857	**0.304333**
CONVENTIONAL	0.658	0.748	0.645	0.932	-0.185	0.983	0.989	0.000	0.526	**0.588444**
SENSITIVE	0.000	0.703		1.000	0.610	1.000	0.928	0.000	0.000	**0.471222**
DEFIANT	0.930	0.929	1.000	1.000	0.460	0.916	0.988	0.000	-1.333	**0.543333**
INTELLIGENT	0.000	0.800	1.000	1.000	0.682	0.981	0.989	-1.412	0.889	**0.547667**
PROTECTIVE	0.689	0.722		1.000	0.728	0.772	0.980	0.593	-0.333	**0.572333**
QUITTING	0.333	-1.750	1.000	0.948	-3.333	1.000	0.990	0.000	-2.000	**-0.31244**
INVENTIVE	0.403	0.814	1.000	1.000	0.786	1.000	0.987	0.000	0.952	**0.771333**
CLUMSY	0.622	0.000		0.681	-4.167	0.750	0.879	0.000	-6.000	**-0.80389**
ERRATIC	0.702	0.747		1.000	0.811	0.000	0.888	0.000		**0.460889**
FRIENDLY	0.713	1.000	1.000	1.000	0.489	0.967	0.916	0.000	0.462	**0.727444**
ANXIOUS	0.828	0.974	1.000	1.000	0.382	0.993	0.888	-0.812	0.968	**0.691222**
LAZY	0.841	0.000		1.000	0.526	1.000	0.833	0.000	-1.333	**0.318556**
DISORGANIZED	0.675	0.000		1.000	0.556	1.000	0.896		-6.000	**-0.20811**
UNEMOTIONAL	0.000	0.000		1.000	0.196	1.000	0.895	1.000		**0.454556**
IMITATIVE	0.713	0.000	1.000	1.000	0.709	1.000	0.978	0.000	0.000	**0.6**
INDEPENDENT	-1.655	0.000	1.000	1.000	0.845	0.841	0.976	0.432	0.095	**0.392667**
SOCIAL	0.573	0.952	1.000	0.788	0.760	0.994	0.991	-1.660	0.308	**0.522889**
CAUTIOUS	0.639	0.905	0.848	0.388	0.392	0.960	0.960	-0.214	-3.111	**0.196333**
COOPERATIVE	-0.406	0.941	0.955	1.000	-0.030	0.978	0.950	0.000	0.000	**0.487556**
NERVOUS	0.000	0.983	0.960	1.000	0.446	0.994	0.683	-1.333	-6.000	**-0.25189**
AGGRESSIVE	0.640	0.964		1.000	0.915	0.983	0.936	0.400	0.000	**0.648667**
OBLIVIOUS	0.828	0.000	1.000	1.000		1.000	0.789	0.000	0.000	**0.513**

Appendix 14: Domain and trait scores for temporal stability *M. nigra*

				2009 DATA			2018 DATA		
ANIMAL	**INSTITUTION**	**SB#**	**SEX**	**DOMINANCE**	**SOCIABILITY**	**EMOTIONALITY**	**DOMINANCE**	**SOCIABILITY**	**EMOTIONALITY**
Wanita	Paignton	394	2	5.075	4.48	5.12	6.070175439	3.851851852	2.777777778
Tyrone	Paignton	395	1	5.425	4.54	5.64	5.192982456	5.055555556	1.583333333
Anneke	Paignton	428	2	4.35	4.1	4.04	3.315789474	3.462962963	1.805555556
Sara	Paignton	468	2	3.475	3.78	2.12	2.964912281	2.685185185	2.472222222
Douglas	Paignton	588	1	5.075	5.84	2.96	5.778947368	5.211111111	3.95
Jasmine	Paignton	633	2	4.125	5.04	2.4	5.157894737	4.444444444	4.166666667
Hickory	Paignton	690	1	4.175	4.86	1.68	4.50877193	5.555555556	2.472222222
Cheeketo	Newquay	399	1	5.70833333	4.7166667	4.8	5.263157895	3.444444444	3.333333333
Maggie	Newquay	510	2	3.84375	5.0916667	2.5	2.394736842	3.222222222	2.916666667
Solina	Newquay	529	2	4.69791667	5.3416667	3.45	6.631578947	2.972222222	4.625
Theo	Newquay	706	2	3.82291667	5.9916667	2.85	2.473684211	2.75	2.625
Melfi	Newquay	707	2	4.375	5.4	2.2	3.894736842	4.277777778	3
Ramol	Wroclaw	564	1	5.3125	5.25	3.9	4.552631579	4.138888889	3.916666667
Maya	Artis	478	2	5.375	5.2	1.4	3.526315789	3.833333333	3.333333333
Cinta	Artis	575	2	5.5	6.2	3.2	3.052631579	3.888888889	3.333333333
Toraya	Artis	704	2	4.125	5.7	4	3.105263158	3.888888889	3.25
Drusilla	Marwell	479	2	6.3125	6.6	3.25	5.147368421	4.433333333	4.1
Satan	Marwell	608	2	2.3125	3	1.75	2.978947368	4.333333333	3.116666667
Magic	Howletts	423	2	6	6.3	2.2	4.842105263	3.555555556	2.5
Tonks	Howletts	574	2	3.75	5.6	3.2	4	3.444444444	2.5
Raven	Howletts	722	2	3.375	5.5	4.2	3.105263158	3.388888889	2.583333333
Loki	Howletts	724	1	2.5	6.1	3.2	5.473684211	3.333333333	2.666666667
Natasha	Jersey	416	2	5.1875	4.05	3	4.315789474	2.888888889	3
Kato	Jersey	616	1	6	6.35	2	5.368421053	4.722222222	2.333333333
Bella	Jersey	687	2	2.75	3.15	1	2.736842105	2.444444444	4.166666667
Maria	Rotterdam	425	2	3.75	5.4	1.8	3.131578947	3.916666667	3.625