

RESEARCH ARTICLE

A Behavioral View on Chimpanzee Personality: Exploration Tendency, Persistence, Boldness, and Tool-Orientation Measured With Group Experiments

JORG J.M. MASSEN^{1,2*}, ALEXANDRA ANTONIDES², ANNE-MARIE K. ARNOLD², THOMAS BIONDA², AND SONJA E. KOSKI^{3*}

¹Department of Cognitive Biology, University of Vienna, Vienna, Austria

²Department of Behavioural Biology, Utrecht University, Utrecht, The Netherlands

³Anthropological Institute and Museum, University of Zürich, Zürich, Switzerland

Human and nonhuman animals show personality: temporal and contextual consistency in behavior patterns that vary among individuals. In contrast to most other species, personality of chimpanzees, *Pan troglodytes*, has mainly been studied with non-behavioral methods. We examined boldness, exploration tendency, persistence and tool-orientation in 29 captive chimpanzees using repeated experiments conducted in an ecologically valid social setting. High temporal repeatability and contextual consistency in all these traits indicated they reflected personality. In addition, Principal Component Analysis revealed two independent syndromes, labeled exploration-persistence and boldness. We found no sex or rank differences in the trait scores, but the scores declined with age. Nonetheless, there was considerable inter-individual variation within age-classes, suggesting that behavior was not merely determined by age but also by dispositional effects. In conclusion, our study complements earlier rating studies and adds new traits to the chimpanzee personality, thereby supporting the existence of multiple personality traits among chimpanzees. We stress the importance of ecologically valid behavioral research to assess multiple personality traits and their association, as it allows inclusion of ape studies in the comparison of personality structures across species studied behaviorally, and furthers our attempts to unravel the causes and consequences of animal personality. Am. J. Primatol. 75:947–958, 2013.

© 2013 Wiley Periodicals, Inc.

Key words: chimpanzee; boldness; exploration; persistence; tool-orientation; group-experiment

INTRODUCTION

The realization that behavior is constrained within the limits of individual dispositions has challenged classical assumptions about individual behavioral plasticity [Dingemanse et al., 2010; Sih & Bell, 2008]. Similarly, traditionally evolutionary mechanisms were thought to favor a single adaptive trait, although evolution can favor multiple evolutionary stable strategies (ESSs). Indeed, extensive population-level variation in individually stable behavioral traits is actively maintained by selection [Dingemanse & Wolf, 2010; Wolf & Weissing, 2010]. Consequently, research on animal personality is booming, and a diverse range of taxa show personality, defined as inter-individual differences in behavior that are consistent over time and contexts [Réale et al., 2007].

Invertebrates and vertebrates in all classes express personality in boldness, exploration tendency, aggressiveness, or activity [Bell et al., 2009; Conrad et al., 2011; Réale et al., 2010; Sih & Bell, 2008]. In addition, personality in basic sociability, described as

approach tendency or tolerance to proximity is described for example in domestic cats, *Felis catus* [Feaver et al., 1986], common lizards, *Lacerta vivipara* [Cote & Clobert, 2007], and guppies, *Poecilia reticulata* [Budaev, 1997]. Having such a wide distribution among taxa, these traits are proposed to be universal personality traits [Réale et al., 2007].

Contract grant sponsor: Lucie Burgers Foundation; Contract grant sponsor: Austrian Science Foundation FWF; contract grant number: M 1351-B17; contract grant sponsor: Academy of Finland; contract grant number: 126094; contract grant sponsor: Ella and Georg Ernrooth Foundation.

*Correspondence to: Jorg J.M. Massen, Department of Cognitive Biology, University of Vienna, Althanstrasse 14, Wien A-1090, Austria. E-mail: jorg.massen@univie.ac.at or

*Correspondence to: Sonja E. Koski, Anthropological Institute and Museum, University of Zürich, Winterthurerstrasse 190, Zürich CH-8057, Switzerland. E-mail: sonjaelena.koski@uzh.ch

Received 2 November 2012; revised 25 March 2013; revision accepted 7 April 2013

DOI: 10.1002/ajp.22159

Published online 3 May 2013 in Wiley Online Library (wileyonlinelibrary.com).

However, some species that live in stable social groups with individualized relationships exhibit a broader range of social personality traits. For example, meerkats, *Suricata suricatta* [English et al., 2010], and cichlids, *Neolamprologus pulcher* [Bergmüller & Taborsky, 2007], also show personality in their cooperative behavior.

Social personality traits may form syndromes, that is, consistent covariation among traits [Sih et al., 2004], with non-social traits or be expressed independently [Bergmüller & Taborsky, 2007; Budaev, 1997; Conrad et al., 2011; Schuerch & Heg, 2010]. In lion-tailed macaques, *Macaca silenus* [Rouff et al., 2005], wild Hanuman langurs, *Semnopithecus entellus* [Konecná et al., 2008], and chacma baboons, *Papio hamadryas ursinus* [Seyfarth et al., 2012], three syndromes are identified, including several traits of social behavior. Thus, personality in the social realm includes a range of behaviors beyond what is usually described for non-gregarious species, and they structure in multiple dimensions.

Chimpanzees (*Pan troglodytes*) have also been intensively studied in personality research [Freeman & Gosling, 2010]. However, in contrast to personality research in the aforementioned species, the majority of chimpanzee personality research has used a subjective rating method, which involves humans assessing chimpanzee characteristics described by behavioral or adjective descriptors. The rating studies have found chimpanzee personality to consist of a broad chimpanzee-specific construct labeled Dominance and five constructs similar, though not identical, to the human five-factor model [Digman, 1990]: extraversion, agreeableness, conscientiousness, neuroticism, and openness [King et al., 2005, 2008; Weiss et al., 2007; 2009]. Several of these constructs describe individuals' social behavior and attitude, and suggest that chimpanzee personality contains several social and non-social traits, forming six broad syndromes.

Behavioral measures of personality are needed to complement the subjective assessment, but only a few studies have assessed the correspondence of rated items with their direct behavioral counterparts [review: Murray, 2011]. Behavioral assessment of personality is crucial for direct comparisons with non-primate species, predominantly studied with behavioral methods. However, behavioral work on chimpanzee personality has been limited in comparison. In an early study, Hebb [1949] exposed captive chimpanzees to keepers exhibiting particular behaviors, novel objects such as a stuffed spider monkey and an infant chimpanzee cadaver, and a manipulation board. The results showed repeatable individual differences in friendly, aggressive, avoidant, and mechanical manipulation behavior. Since then, behavioral chimpanzee personality studies have involved only young [Anestis, 2005] or a small number of individuals [Uher et al., 2008], or have

not assessed the basic criterion of personality, that is, temporal repeatability or contextual consistency [Anestis, 2005; 2011; Murray, 2011; Pederson et al., 2005]. For example, Herrmann et al. [2007, 2011] tested boldness–shyness in 106 chimpanzees using several novel objects, stranger and familiar humans, and differently preferred food items as stimuli. However, the battery was not repeated without modifications, and the authors do not report formal repeatability or consistency measures for the species.

The first broad-scale behavioral study employing formal personality criteria assessment on 75 chimpanzees found 15 highly repeatable behavioral variables suggestive of personality traits [Koski, 2011a]. The traits consisted mainly of social behavior, and structured into five independent syndromes: sociability, positive affect, anxiety, grooming equitability, and activity. However, this study did not assess the universal traits of boldness and exploration tendency.

In the present study, we assessed boldness and exploration tendency, as well as two less commonly measured behaviors as potential personality traits, namely persistence and tool-orientation, with experiments in 29 captive chimpanzees. Persistence may influence individual innovation and problem solving ability [Cole & Quinn, 2012; Gajdon et al., 2006; Overington et al., 2011]. Tool-orientation was assessed as a general proxy for an individual's tendency to involve tools in problem solving. Individuals may vary in their proneness and prowess to use tools [van Schaik et al., 2003], which in turn may be associated with exploration tendency or intelligence. Persistence and tool-orientation thus have ecological relevance for chimpanzees, and they may shed light on factors that influence innovation and technology [Morand-Ferron et al., 2011; Reader, 2003].

We defined boldness as a non-fearful response to a threat, and exploration tendency as a neophilic response to novel stimuli [Réale et al., 2007]. However, the distinction between exploration tendency and boldness is unclear in the literature [Carter et al., 2012; Conrad et al., 2011; Toms et al., 2010], so we used multiple paradigms to target these traits and assessed the association among the responses. Similarly, exploration tendency and persistence may underlie some similar outcome behaviors. Therefore, we recorded the same variables across all experiments (in so far as it was possible) and assessed their cross-experiment associations. This approach allowed us to assess the contextual consistency of singular behaviors bottom-up, across multiple experiments [Burns, 2008]. Similarly, we assessed the temporal consistency of behaviors at the singular behavior level between the repeated sets of experiments.

We conducted the experiments in a group setting. Individuals of social species express their personality

in a social environment. Therefore, the standard practice of isolating subjects in a solitary space to measure their response to a test stimulus [e.g., classic novel environment test: Verbeek et al., 1994] may yield results that are not identical to how an individual expresses its personality in everyday life. Moreover, the experimental paradigms were chosen by their ecological validity, representing natural predators, natural kinds of novel food or objects, and extractive foraging tasks. Thus, our study is novel in two ways: we assessed chimpanzee personality with behavioral methods comparable to many other species, allowing thus a comparison to the rich ecological personality literature, and we sampled individuals of both sexes with an emphasis on ecological validity. Such a fundamental study is crucial to establish the behavioral personality variation in chimpanzees, which in turn allows research on the functions, mechanisms and evolutionary history of personality traits and syndromes.

METHODS

Subjects and Housing

Data were collected at two zoos in the Netherlands: Burgers' Zoo in Arnhem ($N = 16$ chimpanzees: 3 adult males, 12 adult females, 1 immature) and Dierenpark Amersfoort ($N = 15$ chimpanzees: 3 adult or adolescent males, 11 adult females, 1 immature). In both groups a juvenile (age < 6 years) was excluded from the analyses, leading to a sample size of 29 individuals (15 and 14, respectively). All but the oldest subjects (three in Arnhem, six in Amersfoort) were born in captivity and reared by their mothers. The wild born individuals have resided in these groups for decades. The Arnhem group is housed in an indoor enclosure (368 m^2) with access to a large outdoor compound (ca. 0.7 ha). Similarly, the Amersfoort group is housed in an indoor enclosure (96 m^2) with access to an outdoor compound (475 m^2). Both facilities are enriched with plenty of climbing structures. All chimpanzees had ad lib access to water and were fed an alternating diet of fruit, vegetables, seeds and commercially available monkey chow.

Ethical Statement

Both zoos are members of the European Association of Zoo and Aquaria and thus fulfill the legal and ethical regulations on captive animal welfare. Due to the non-invasive character of the study, our study did not meet the definition of an animal experiment as mentioned in Article 1 of the Dutch "Experiments on Animals Act." Consequently, the ethics committee of Utrecht University waived the need for approval, and thus the experiments comply with the Dutch law and with the American Society of Primatologists

principles for the ethical treatment of nonhuman primates.

Experimental Design and Set-Up

We confronted each group with a battery of 10 experiments. The experiments formed three categories: predator models, novel foods or objects, and puzzles. The experiments were based on established personality test paradigms [Réale et al., 2007; Wilson et al., 1993] or earlier studies [e.g., Uher et al., 2008]. To test individual consistency in responses over time (i.e., repeatability), we exposed the groups twice to the battery: the Arnhem group in Feb.–Mar. 2011 (1st set) and in Jun.–Jul. 2011 (2nd set; 3 months after the first); the Amersfoort group in Feb.–Mar. 2010 (1st set) and in Apr.–May 2011 (2nd set; 14 months after the first). To test for consistency over contexts, we had at least two different experiments per category (see Table I for the test battery).

We confronted the groups with real-size models of a predator: a stuffed leopard ("Leopard"; real size in an up-right sitting position) and a rubber "snake" ("Snake"; approximately 4 m long with the pattern of African rock python). These predator models were placed in sight, yet out of reach of the chimpanzees and their behavior towards these models was recorded. The novel food items were multiple items of durian ("Durian") and cups of fly maggots ("Maggots"). These novel foods were spread throughout the chimpanzees' enclosures and their behavior towards these foods was recorded. The novel object was a large (1 m diameter) water-filled bucket dug into the ground ("Bucket"). Either chimpanzee group had no previous experience with such a pond in their enclosure. In the puzzle category we had five different foraging devices: a seed-filled barrel ("Barrel"), a large horizontal maze ("Maze") filled with oranges, a large vertical finger-hole puzzle box ("Puzzle") filled with tangerines, the same water-filled bucket dug in ground but filled with pieces of pear (that sink to the bottom of the pond) and covered with mesh too small to allow a chimpanzee hand through ("Bucket-mesh"), and a large dipping cube filled with honey ("Honey cube"). All these puzzles required different techniques to get to the reward and consequently we could also measure the attempts of tool-use. For a full description of the experiments and the measures we recorded, please see the Electronic Supplemental Materials (ESM). The experiments were conducted in quasi-randomized order so that the predator models were separated by at least one other type of experiment, and Bucket was always conducted before Bucket-mesh. We conducted one experiment a day, maximum four per week. All experiments were done in the presence of all group members, who accessed the stimuli at the same time. The stimuli were presented to the chimpanzees for 30 min (predator models) or 2 hr (all other experiments).

TABLE I. The Experiments, the Targeted Traits, Measured Variables and Their Test-Retest Consistency as Intra-Class Correlation (ICC 3,1) With 95% Confidence Intervals

Type of experiment	Experiment (code)	Measure	ICC (3,1)	95% CI lower, upper	F, P-value
Predator model	Leopard	Latency approach	0.20	-0.17, 0.53	1.508, 0.141
		Time in proximity	0.02	-0.35, 0.37	1.031, 0.468
		No. approaches	0.32	-0.04, 0.61	1.960, 0.040
Predator model	Snake	Time in proximity	0.39	0.04, 0.66	2.289, 0.016
		No. approaches	0.45	0.11, 0.70	2.664, 0.006
		Latency approach	0.28	-0.09, 0.58	1.762, 0.070
Novel object	Bucket	Time in proximity	0.44	0.09, 0.69	2.567, 0.008
		No. approaches	0.49	0.16, 0.72	2.935, 0.003
		Latency approach	-0.01	-0.37, 0.35	0.972, 0.530
Novel food	Maggots	Latency approach	0.09	-0.24, 0.44	1.191, 0.323
Puzzle	Durian	Latency approach	-0.11	-0.56, 0.43	0.807, 0.648
		Time in proximity	0.47	0.13, 0.71	2.737, 0.005
		No. approaches	0.22	-0.15, 0.54	1.578, 0.117
Puzzle	Barrel	Time manipulating	0.62	0.36, 0.80	4.279, <0.001
		Latency approach	-0.03	-0.39, 0.33	0.935, 0.569
		Time in proximity	0.76	0.55, 0.88	7.413, <0.001
Puzzle	Maze	No. approaches	0.62	0.33, 0.80	4.264, <0.001
		Time manipulating	0.79	0.61, 0.90	8.657, <0.001
		Success obtaining rewards	0.66	0.39, 0.82	4.851, <0.001
Puzzle	Bucket-mesh	Latency approach	0.16	-0.21, 0.50	1.392, 0.193
		Time in proximity	0.74	0.51, 0.87	6.562, <0.001
		No. approaches	0.72	0.49, 0.86	6.194, <0.001
Puzzle	Puzzle	Time manipulating	0.73	0.50, 0.86	6.344, <0.001
		No. tools	0.63	0.35, 0.81	4.442, <0.001
		Tool modification	0.82	0.66, 0.91	10.326, <0.001
Puzzle	Honey cube	Success obtaining rewards	0.64	0.36, 0.81	4.494, <0.001
		Latency approach	0.68	0.42, 0.83	5.197, <0.001
		Time in proximity	0.63	0.35, 0.81	4.440, <0.001
Puzzle	Honey cube	No. approaches	0.61	0.32, 0.80	4.121, <0.001
		Time manipulating	0.67	0.41, 0.83	5.093, <0.001
		No. tools	0.43	0.08, 0.69	2.519, 0.009
Puzzle	Honey cube	Tool modification	0.02	-0.35, 0.38	1.035, 0.464
		Latency approach	0.47	0.14, 0.71	2.805, 0.004
		Time in proximity	0.66	0.39, 0.82	4.879, <0.001
Puzzle	Honey cube	No. approaches	0.69	0.44, 0.84	5.404, <0.001
		Time manipulating	0.62	0.34, 0.80	4.320, <0.001
		No. tools	0.64	0.36, 0.81	4.522, <0.001

ICC values significantly different from zero are indicated with bold typeface; only those variables were retained for further analyses.

Measures and Data Analyses

We recorded all experiments from two angles using camcorders (JVC, Everio S, GZ-MS215). We coded all behaviors from the videos in a frame-by-frame manner using VLC Media Player 1.1.11.

Data were coded by AA, AMKA, and TB. Inter-observer reliability was tested with two people scoring 15% of videos. Since we scored data not in discrete categories but as durations and occasions in continuously recorded behavior, we used Spearman's rank correlations to calculate inter-observer reliability [Martin & Bateson, 1993]. All measures were scored almost identically ($\rho > 0.89$, $P < 0.01$). From each experiment, we scored several variables per individual, depending on the trait the experiment targeted (see Tables I and II). The individual data

were collected continuously from the instant of entering the enclosure. Each individual was scored for every measure (see Tables I and II), and there were no missing data. Importantly, we measured the same variables across all experiments, as far as it was possible, to allow bottom-up testing of behavioral consistency across experiments (Table I and ESM). The variables measuring time (latency, time in proximity, time spent manipulating) were coded to the nearest second; number of approaches was considered per occasion an individual was in touching distance; the number of tools and successfully obtained items were calculated per individual tool/reward; and tool modifications were operationalized by the number of distinct breaks, twists, and mouth manipulations of the tool. We standardized the raw data into z-scores (per zoo) before pooling the data of the two zoos.

TABLE II. The Contextual Consistency of Measures Across the Experiments

Trait	Variable	Experiments	Cronbach's alpha
Boldness	No. of approaches	Leopard and Snake	0.740
Exploration	Latency of approach	Puzzle and Honey Cube	0.333
Exploration	No. of approaches	Bucket, Puzzle, Maze, Honey Cube, and Bucket-mesh	0.856
Persistence and/or exploration ^a	Time in proximity	Barrel, Bucket, Puzzle, Maze, Honey Cube, and Bucket-mesh	0.841
Persistence	Time manipulating	Barrel, Puzzle, Maze, Honey Cube and Bucket-mesh	0.791
Tool-orientation	No. of tools used	Puzzle, Honey Cube and Bucket-mesh	0.795
Tool-orientation	No. of successfully obtained rewards	Maze and Bucket-mesh	0.665

Significantly consistent variables are indicated with a bold typeface.^aWe assigned these responses into the trait category “persistence,” but additionally they may reflect exploration tendency.

Repeatability across the two sets of experiments was tested with intra-class correlation coefficient (ICC). We tested each behavioral measure separately, because testing repeatability at the most fundamental level of behavior is more rigorous than assessing the consistency of broader trait categories. ICC is mathematically equivalent to the standard repeatability test [Lessells & Boag, 1987], and crucial to assure that a behavior agrees with the definition of personality. It assesses the proportion of variation in behavior that is due to inter-individual variation compared to that of intra-individual variation. We used a two-way mixed-model ICC (3,1) with the experiment as fixed and individual as the random factor [McGraw & Wong, 1996; Shrout & Fleiss, 1979].

We calculated an individual mean of the two repeated experiments of those variables that had high repeatability. These were subjected to an assessment of contextual consistency with Cronbach's alpha, again separately for each measure across all experiments in which it was recorded (see Table II). Contextual consistency assesses a similarity of behavior in two or more different situations; high contextual consistency gives thus support for dispositionalism of behavior (i.e., that the behavior is more strongly determined by individual's behavioral disposition than the particular contextual circumstances). As a coefficient of reliability, Cronbach's alpha is used to assess internal consistency of measures reflecting a latent variable. A Cronbach's alpha ≥ 0.7 was considered consistent [Bland & Altman, 1997]. Approach latency may reflect either boldness or exploration tendency, depending on the context. Therefore we tested its consistency first in all situations and then separately in approaching the predator models (presumably reflecting boldness) and in approaching the puzzles, novel food and novel objects (presumably reflecting exploration tendency) [cf. Carter et al., 2012; Réale et al., 2007]. We calculated an individual mean across the experiments of the consistent measures to yield an individual trait value. If Cronbach's alpha was <0.7 , we used the original scores (i.e., standardized and averaged over the two repeated experiments, but

not over the different experiments) for further analyses.

To assess the trait structure, we entered the individual trait values, obtained as detailed above, in a principle component analyses (PCA). We used parallel analysis [Horn, 1965] and a scree-plot to decide the number of components to extract. The PCA-solution was varimax rotated and variable leadings $>\pm 0.5$ were considered salient [Budaev, 2010]. We repeated the analysis with an oblique (direct oblimin) rotation to address the independency of the components [Tabachnik & Fidell, 2007].

We obtained individual component scores for the PCA-components with the regression method, which produces scores that have a mean of zero and a variance equal to the squared multiple correlation between the estimated and the true component values. We used linear mixed models (LMM) to assess the influence of sex ($N_{\text{males}} = 6, N_{\text{females}} = 23$), age (continuous variable, range 8–56 years), and rank on the component scores, while controlling for the different locations ($N_{\text{Af}} = 14, N_{\text{Arn}} = 15$).

Rank was treated as a categorical, yet ordinal variable for which we estimated rank positions in a group as “very high” ($N = 3$), “high” ($N = 8$), “middle” ($N = 10$), and “low” ($N = 8$). Unfortunately, we could not use rank positions based on a matrix analysis, as formal indicators of dominance were rare or absent especially among females. The estimated categories were based on a composite measure of the number of submissions given (to males and females), number of submissions received (from males and females), and the ratio of displacing to being displaced. The estimated rank category was confirmed with observation notes on dominance displays and submissions that were observed opportunistically (i.e., not within subject's own focal observation). Most adult males had a higher rank score than adult females, but there were also high-ranking females and low-ranking males.

Sex and categorical rank were entered as fixed factors and age as a fixed covariate into the linear mixed model (LMM), while location (zoo) was entered as a random effect. In the full model, we included all

two-way interactions. All interactions were non-significant and therefore, we proceeded the analyses with main effects only.

RESULTS

We found that 27 standardized variables were significantly repeatable, indicating temporal (i.e., test-re-test) consistency and inter-individual variation. The ICC repeatability values ranged from 0.32 to 0.82 (Table I). We also tested the zoos separately, and their ICC values did not differ significantly from each other (independent samples *t*-test, $t = -1.77$, $df = 73$, $P = 0.08$).

Only the significantly repeatable variables were retained for analyses on cross-experimental consistency. Most of these variables were sufficiently consistent (Table II). The *number of approaches* was consistent across predatory and non-predatory contexts, that is, in Leopard-, Snake-, Bucket-, Bucket-mesh-, Puzzle-, Maze- and Honey cube-experiments ($\alpha = 0.86$). Number of approaches was also consistent when tested separately in Leopard- and Snake-experiments ($\alpha = 0.74$), presumably reflecting boldness, and in Bucket-, Bucket-mesh-, Puzzle-, Maze- and Honey cube-experiments ($\alpha = 0.86$), presumably reflecting exploration tendency. Exploration measured by *latency to approach* in FPB and HC was not consistent ($\alpha = 0.33$). Persistence was consistent as measured by the *time spent in proximity* of the stimuli in Barrel-, Bucket-, Bucket-mesh-, Puzzle-, Maze-, and Honey cube-experiments ($\alpha = 0.84$), and by *time spent manipulating* in Barrel-, Bucket-mesh-, Puzzle-, Maze-, and Honey cube-experiments ($\alpha = 0.79$). Tool-orientation was consistent as measured by the *number of tools used* in Puzzle-, Honey cube-, and Bucket-mesh-experiments ($\alpha = 0.80$) but not by the *number of successfully obtained rewards* in Maze- and Bucket-mesh-experiments ($\alpha = 0.67$).

The variables that showed significant cross-experiment consistency were averaged across experiments to give a single trait score for each individual:

number of approaches to experimental devices (representing exploration tendency), number of approaches to predator models (representing boldness), time in proximity and time spent manipulating objects (both representing persistence), and number of tools used (representing tool orientation). The variables that did not show cross-experiment consistency were kept in the further analyses as uncombined scores: latency measures in Puzzle and Honey cube (representing exploration) and success in obtaining rewards in Maze and Bucket-mesh (representing tool-orientation). The same was done with the measures that were the only repeatable measures of its kind: time in proximity of the Snake (representing boldness), and number of tool modifications in Bucket-mesh (representing tool orientation).

These 11 mean or singular individual scores were analyzed with PCA. In the first run, the two latency scores showed poor communality estimates, indicating that their variance was poorly covered by the solution and consequently they were excluded. In the final analysis we thus had nine variables ($N = 29$ individuals; Table III). The analysis indicated appropriate sampling adequacy (Kaiser-Meyer-Olkin measure KMO = 0.65). We extracted and Varimax-rotated two components explaining 70.9% of the variance. The first component explained 51.6% of the variance and had high ($>\pm 0.5$) loadings of time in proximity of devices, time spent manipulating objects, number of approaches to the novel object and the puzzles, # of tools used, number of tool modifications, and number of successfully retrieved items. The variables represented exploration tendency, persistence, tool-orientation, and possibly problem-solving abilities, so we labeled the component “exploration-persistence.” The second component explained 19.3% of variance with high loadings of number of approaches to predator models and time in proximity of the snake model. In addition, number of approaches to the novel object and puzzles nearly reached the cut-off criterion on this component. We labeled the component “boldness.”

TABLE III. Variable Loadings in Principal Component Analysis

	Exploration-persistence	Boldness	Communality h^2
Time in proximity	0.91	0.11	0.84
Time manipulating	0.90	0.11	0.82
No. approaches (all but predators)	0.70	0.47	0.70
Number of tools used	0.80	0.36	0.77
Tool modification	0.88	0.07	0.78
Success in obtaining rewards (maze)	0.55	-0.32	0.41
Success in obt. rewards (Bucket-mesh)	0.62	0.11	0.39
No. approaches (snake and leopard)	0.22	0.91	0.88
Proximity (snake)	0.02	0.90	0.81
Eigen value	4.65	1.74	
% of variance explained	51.63	19.30	

Loadings >0.5 are shown with bold typeface. Analysis on correlation matrix, $N = 29$.

With only two components and high communalities (Table III), based on nine original variables and a sample size of 29 a good recovery is achieved in exploratory PCA [Preacher & MacCallum, 2002]. Moreover, we re-ran the analysis with a direct Oblimin rotation to address the independency of the components [Tabachnick & Fidell, 2007]. The solution was almost identical to the Varimax rotated one regarding the variable loadings. The components did not correlate strongly with each other (factor intercorrelation $r = 0.15$).

We found no sex differences in component scores (exploration-persistence: $F = 0.310$, $df = 23$, $P = 0.583$; boldness: $F = 0.276$, $df = 23$, $P = 0.605$), and also no effect of categorical rank on the component scores (exploration-persistence: $F = 0.440$, $df = 23$, $P = 0.727$; boldness: $F = 1.203$, $df = 23$, $P = 0.331$). In contrast, age significantly predicted boldness scores ($F = 7.877$, $df = 23$, $P = 0.010$), and showed a similar effect, albeit not significant, on exploration-persistence scores ($F = 4.192$, $df = 23$, $P = 0.052$). Negative coefficient estimates (exploration-persistence: $\beta = -0.029$; boldness: $\beta = -0.035$) indicate that both exploration-persistence and boldness decreased in older adults (Figs. 1 and 2). However, these results are to be treated with some caution due to the limited power of this analysis.

DISCUSSION

We tested behavioral consistency in 29 captive chimpanzees. Using group-based experiments we measured several variables that showed inter-indi-

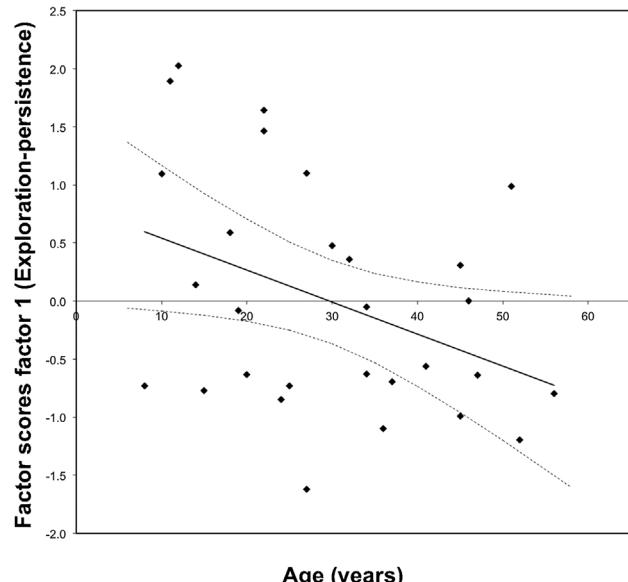


Fig. 1. Component scores of factor 1 of all individuals and its relation to the age of all these individuals. The solid line is a trend-line and the dashed lines indicate the 95% confidence interval.

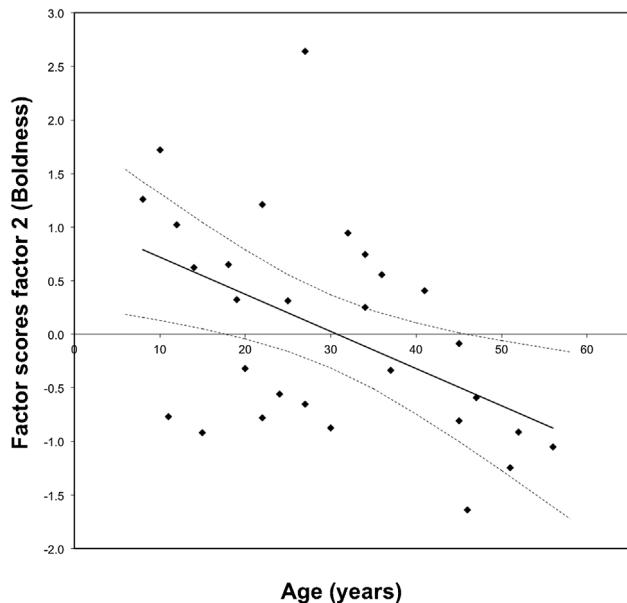


Fig. 2. Component scores of factor 2 of all individuals and its relation to the age of all these individuals. The solid line is a trend-line and the dashed lines indicate the 95% confidence interval.

vidual differences, which were consistent over time and context. Using Principal Component Analyses, we extracted from these variables two independent behavioral syndromes: exploration-persistence and boldness.

We assessed two common personality traits, boldness and exploration tendency, and two less frequently sampled ones, persistence and tool-orientation. Each trait was assessed with several behavioral variables in several experiments. Most variables were temporally repeatable, indicating that individuals' responses were consistent between temporally separated experiments and that individuals differed from each other. The repeatability was within the range found for personality traits in many species [Bell et al., 2009], and often remarkably high (ICC = 0.6–0.8). A few variables, most notably latency to approach the test stimuli, failed to show repeatability in seven out of nine experiments. Low repeatability suggests that individuals may have perceived the situation differently over time, for example so that some individuals might have habituated to the threatening stimulus more than others. Alternatively, these measures may have been influenced by the varying social conditions more than other measures, or the measures did not reflect the targeted traits. The time lag between the first and the second round of experiments differed between the two locations, which might also confound analyses on temporal consistency. However, there was no significant difference between the repeatability values of the zoos, suggesting that temporally consistent behaviors remain consistent over shorter

and longer time span. Congruent with this, social personality traits of chimpanzees were found to be similarly consistent across a few months and 3 years [Koski, 2011a].

Most of the repeatable variables were also consistent across different experiments. Approaches to the two predator models, indicating boldness, were consistent, as were the exploratory responses to a novel object and several puzzle-type stimuli. Similarly, two measures of persistence were highly consistent across six experiments, and tool-orientation was consistent in the number of tools used by an individual, although not in success in obtaining rewards. In contrast, latency to approach test stimuli (in the only two experiments in which it was temporally repeatable) was contextually inconsistent, indicating further that latency is not an informative measure of personality in these chimpanzees or in our experimental setting. In sum, individuals showed remarkable temporal and contextual consistency in many, but not all, behaviors reflecting boldness, exploration tendency, persistence, and tool-orientation. We thus conclude that we found chimpanzee personality in these traits.

Assessment of the covariance among the variables revealed two independent principal components representing syndromes. The exploration-persistence was the predominant syndrome explaining more than half of the variance in the data. Besides measures of exploratory tendency and persistence, it included tool-orientation measures, and measures of success in solving the puzzles, one of which (Bucket-mesh) required the use of tools. Thus, the chimpanzees that showed a high exploratory tendency were also more likely to persist at a task and use tools to solve them. Boldness in the vicinity of predator models was independent from the exploration-persistence syndrome. Thus, in these chimpanzees exploration tendency and boldness did not appear to associate as a tight syndrome, supporting the view that neophobia and neophilia may be independent aspects [Carter et al., 2012; Greenberg, 2003].

We used a social experimental environment to increase the ecological validity of the tests. In obligate social species, a social environment is an ecologically valid starting point to assess individuals' behavioral tendencies. While such an approach yields a behavioral measure of both dispositional and situational effects, it shows how individuals express their outcome behavior and thus, the level where personality has both immediate and evolutionary consequences. Arguably, a social setting may not allow all individuals the same possibilities to interact with the stimuli, due to crowding or monopolization of the test device. However, we did not find any effect of dominance rank on the component scores, suggesting no rank-driven monopolization of the test devices. In addition, nearly all experiments allowed simulta-

neous presence of and handling of the devices by many individuals. The only truly monopolizable device was the Barrel, all other experiments involved either multiple items (Durian, Maggots), large or out of reach items (Bucket, Leopard, Snake, Bucket-mesh), or items with a fairly large size and more than one exit hole (Honey cube, Puzzle, Maze). They therefore allowed multiple individuals simultaneous access to the stimuli (see also ESM). Indeed, in all test situations the subjects approaching or handling the stimuli were in close proximity of many group members. Nonetheless, a social environment may have more subtle effects on the individual behavior, and individuals may vary in how they are influenced by others. Therefore, while we maintain that we have tested chimpanzees as they exhibit their behavior in the daily life, testing individuals in solitary and social settings will help partition the dispositional and situational effects. Ideally, the effect of the social audience on individual behavior should be analyzed regarding the relationship quality of near neighbors. It is conceivable that individuals are keener to approach and manipulate an object if they are near kin or a close affiliate than if they are with non-kin or non-friends. Unfortunately, we could not analyze such effects, because the spatial and temporal distribution of individuals with various relationship qualities (regarding both kinship and friendship) was highly varied throughout each experiment.

Personality always interacts with external and other internal allowances as a reaction norm [Dingemanse et al., 2010]. Age had a significant, negative effect on boldness, and showed a trend in the same direction with exploration-persistence. While we cannot draw too stringent conclusions from these analyses because of limited statistical power due to our relatively small sample size, we note the considerable variation within age-classes that remained in the component scores of both syndromes (see Figs. 1 and 2). This indicates that the chimpanzees' behavior was also strongly influenced by dispositional effects. Declining mean trait levels of exploration-persistence and boldness may reflect a genuine decrease of boldness and exploration-persistence with age, or a decreased interest in interacting with human-provided objects with increased exposure to them. Support for the age-related decline in trait levels is given by the same pattern in humans [Roberts et al., 2006] and in chimpanzees studied with the rating approach [King et al., 2008]. High levels of exploration, boldness and persistence in young may be beneficial in chimpanzees and humans, who, like many other primates, strongly rely on learning to acquire the necessary survival skills.

Our results are consistent with earlier behavioral personality studies in chimpanzees. Uher et al. [2008] assessed behavior of five captive chimpanzees with experiments and observations, and found consistency in several behaviors, including persistence and

curiosity. Anestis [2005] identified six social behavioral syndromes, possibly reflecting personality (albeit repeatability was not tested) in a group of young captive chimpanzees. Finally, Herrmann et al. [2007, 2011] showed that chimpanzees, bonobos, orangutans, and human children differ in their responses to novel objects and humans, although data on repeatability or contextual consistency were not provided.

Our results also agree with rating studies in that chimpanzee personality encompasses several lower-level traits organized in multiple broader constructs [cf. Koski, 2011a; Weiss et al., 2007]. Moreover, the behaviors that are personality traits in chimpanzees are largely captured by both methods. However, there are also differences in the contents of the behaviorally measured syndromes and the rating-derived constructs. For example, the rated construct Openness includes aspects of inquisitiveness and curiosity, which is consistent with the behavioral exploration tendency. However, in rating studies persistence associates with dominance (as a descriptor of assertiveness, not the social rank), bullying and independence, while in our study persistence was associated with exploration. We found no association between exploration-persistence and the estimated social rank. Such differences may reflect jinglefallacy, that is, the same term is used to describe different traits. For example, the item descriptor “persistent” in the Hominoid Personality Questionnaire (HPQ) [King & Figueiredo, 1997] and its revision [Weiss et al., 2009] emphasizes persistence in the opposition from others, while we measured persistence at a task per se. It seems that instead, the HPQ term “quitting,” found in the Conscientiousness construct, corresponds better with persistence in our study. To assess such aspects in detail, it is necessary to test item descriptors’ construct validity with a priori defined behavioral counterparts at the trait level (i.e., individuals’ scores of each item should correspond to their scores of behaviors that are conceptually and ecologically similar to the meaning of the descriptors). Thus far validation efforts of chimpanzee personality have produced inconsistent results. Typically, a few descriptors show the predicted correspondence with behavior, while other predicted relationships are weak or absent and many unpredicted relationships are observed [reviewed in Murray, 2011].

Beyond comparisons within a species, however, we feel that comparisons should be made on a broader scale to understand the evolutionary history of personality. Boldness and exploration tendency are a natural starting point in such comparisons, as they show remarkable conservation in the animal kingdom [Beaton and Schmidt, 2008; Réale et al., 2007]. Generally, animals respond with more or less neophobia, and more or less neophilia to novel and/or threatening situations [reviews in Carere et al., 2010;

Conrad et al., 2011]. Boldness or exploration is often associated with anxiety and aggression, forming a boldness-exploration-aggressiveness-anxiety-syndrome [review in Carere et al., 2010]. However, not all species express such a syndrome. In redshanks, *Tringa tetanus*, exploration and aggression do not correlate [Couchoux & Cresswell, 2012], and in vervet monkeys, *Chlorocebus aethiops sabaeus*, boldness and aggression do not correlate with each other [Fairbanks et al., 2004]. Our results suggested the dissociation of exploration and boldness. Pleiotropic effects and correlational selection pressures are proposed as the mechanisms that maintain syndromes [Dingemanse & Réale, 2005; Sih & Bell, 2008]. Dissociation of traits that have been expressed as syndromes suggests either a mechanistic decoupling or a change in selection pressures. Fundamental research on the similarities and differences in syndrome structures and on the proximate mechanisms of syndromes is necessary to unravel the evolutionary history of personality.

Persistence as a personality trait is rarely studied in animals. It is conceivable that persistence in various activities may offer fitness benefits. On the other hand, persistence may waste valuable time or energy that could be spent gaining rest or resources. Such trade-offs are one of the mechanisms proposed to maintain personality variation [Dingemanse & Wolf, 2010], so persistence as a personality trait should occur in species where the benefits are considerable, yet the costs of extreme trait levels maintain inter-individual variability in the trait. Persistence in our study was associated with exploration tendency and tool-orientation, indicating that subjects that approach objects readily also stay persistent and use tools in a task. Chimpanzees are extractive foragers and tool-users, and rely heavily on learnt skills to survive [McGrew, 1992]. We hypothesize that persistence may be a personality trait especially in extractive foragers, as it may increase payoffs in foraging of extractable food items. Moreover, persistence may increase learning, both individually by persisting with the task and trying repeatedly after errors, and socially by paying close attention and restricting impulses to leave or monopolize the target [Cole & Quinn, 2012]. A persistence-exploration-tool-orientation syndrome may thus influence individuals’ tendency to approach objects, pay attention to their properties and correct use, manipulate them, and persist in doing so. Supporting this hypothesis, in keas (*Nestor notabilis*) and Carib grackles (*Quiscalus lugubris*), persistence influences learning novel foraging techniques [Gajdon et al., 2006; Overington et al., 2011]. Both species are known for their innovativeness and explorative tendencies [e.g., Lefebvre & Sol, 2008], and keas are extractive foragers with great manipulation skills [Auersberg et al., 2011]. Therefore, we hypothesize that a persistence-exploration-tool-orientation

syndrome may have been selected for in extractive foragers, in species that rely on learning and, especially, in “technological” taxa, including *Homo*, *Pan*, *Pongo*, *Cebus*, and *Corvidae* [Hunt, 2000; McGrew, 2010; van Schaik & Burkart, 2011; Visalberghi et al., 2009].

GLOSSARY

Animal Personality (Aka Temperament)

Consistent differences between individuals in their behavior across time and contexts [Dingemanse et al., 2010; Réale et al., 2007].

Behavioral Syndrome

Consistent correlation of two or more behavioral traits (note, that we use the term “syndrome” only in this meaning, not in the meaning of single-trait consistency across time or contexts [Dochtermann and Dingemanse, 2013; Sih & Bell, 2008; cf. Uher, 2011]).

Disposition

Individual’s core tendency of its personality that, together with non-dispositional internal factors incl. age and sex, result in the outcome behavior at a given time point. Disposition is close to the concept of intercept in a behavioral reaction norm [Dingemanse et al., 2010].

Trait

In biological research, a trait is any quantifiable phenotypic characteristic; thus, a behavioral trait is a behavioral characteristic. Phenotypic traits can associate with other traits. We do not take a stand on the traits’ determinants (incl. genetic, epigenetic, developmental, or situational effects) [Koski, 2011b; Réale et al., 2007].

Repeatability

A measure of consistency in behavior within- and across-individuals. Calculated as the proportion of variance explained by differences between individuals.

Temporal Consistency

Similarity in individual’s behavior over time. Often assessed over relatively short time in two or more repeated experiments (thus known as test–retest reliability).

In conclusion, we found that captive chimpanzees express personality in exploration tendency, boldness, persistence and tool-orientation. These traits formed two syndromes, exploration-persistence and boldness, that have equivalents in many other vertebrate species. However, examining the personality structure in chimpanzees and non-primate vertebrates we find also intriguing differences. Structural differences in trait organization suggest changes in selection pressures or mechanisms coupling traits. Understanding the causes of syndrome structures can help illuminate the complex consequences of trait consistency and covariance in different species. Future studies should explore multiple personality traits in other species and aim at delineating personality structures across taxa. To do so, we emphasize the use of behavioral tests in ecologically valid environments that make comparisons between species possible.

ACKNOWLEDGMENTS

We thank Arnhem and Amersfoort Zoo for supporting our research, especially Tom de Jong, Wineke Schoo, Raymond van der Meer, and all the keepers for enthusiasm and cooperation during the study. We thank Athena Vervloet for help in Amersfoort, Thomas Bugnyar, Carel van Schaik, and Liesbeth Sterck for inspirational discussions, and Alexander Weiss, William Hopkins, and anonymous reviewers for constructive comments on the manuscript. We gratefully acknowledge our funding bodies: the Lucie Burgers Foundation (to J.J.M.M.), the Austrian Science Foundation FWF (grant no. M 1351-B17 to J.J.M.M.), the Academy of Finland (grant no. 126094 to S.E.K.), and the Ella and Georg Ernrooth Foundation (to S.E.K.).

REFERENCES

- Anestis S. 2005. Behavioral style, dominance rank, and urinary cortisol in young chimpanzees (*Pan troglodytes*). *Behaviour* 142:1245–1268.
- Auersberg AMI, Bayern von AMP, Gajdon GK, Huber L, Kacelnik A. 2011. Flexibility in problem solving and tool use of kea and New Caledonian crows in a multi access box paradigm. *PLoS ONE* 6:e20231.
- Beaton EA, Schmidt LA, Schulkin J, et al. 2008. Different neural responses to stranger and personally familiar faces in shy and bold adults. *Behav Neurosci* 122:704–709.
- Bell AM, Hankison SJ, Laskowski KL. 2009. The repeatability of behaviour: a meta-analysis. *Anim Behav* 77:771–783.
- Bergmüller R, Taborsky M. 2007. Adaptive behavioural syndromes due to strategic niche specialization. *BMC Eco* 17:12.
- Bland JM, Altman DG. 1997. Statistics notes: Cronbach’s alpha. *Brit Med J* 314:572.
- Budaev SV. 1997. “Personality” in the guppy (*Poecilia reticulata*): a correlational study of exploratory behavior and social tendency. *J Comp Psychol* 111:399–411.
- Budaev SV. 2010. Using principal components and factor analysis in animal behaviour research: caveats and guidelines. *Ethology* 116:472–480.

- Burns JG. 2008. The validity of three tests of temperament in guppies (*Poecilia reticulata*). *J Comp Psychol* 122:344–356.
- Carere C, Caramaschi D, Fawcett TW. 2010. Covariation between personalities and individual differences in coping with stress: converging evidence and hypotheses. *Curr Zool* 56:728–740.
- Carter AJ, Marshall HH, Heinsohn R, Cowlishaw G. 2012. How not to measure boldness: novel object and antipredator responses are not the same in wild baboons. *Anim Behav* 84:603–609.
- Cole EF, Quinn JL. 2012. Personality and problem-solving performance explain competitive ability in the wild. *Proc R Soc B* 279:1168–1175.
- Conrad JL, Weinersmith KL, Brodin T, Saltz JB, Sih A. 2011. Behavioural syndromes in fishes: a review with implications for ecology and fisheries management. *J Fish Biol* 78:395–435.
- Cote J, Clobert J. 2007. Social personalities influence natal dispersal in a lizard. *Proc R Soc B* 274:383–390.
- Couchoux C, Cresswell W. 2012. Personality constraints versus flexible antipredation behaviors: how important is boldness in risk management of redshanks (*Tringa totanus*) foraging in a natural system? *Behav Ecol* 23:290–301.
- Digman JM. 1990. Personality structure: emergence of the five-factor model. *Annu Rev Psychol* 41:417–440.
- Dingemanse N, Réale D. 2005. Natural selection and animal personality. *Behaviour* 142:1159–1184.
- Dingemanse NJ, Wolf M. 2010. Recent models for adaptive personality differences: a review. *Philos T R Soc B* 365:3947–3958.
- Dingemanse NJ, Kazem AJN, Réale D, Wright J. 2010. Behavioural reaction norms: animal personality meets individual plasticity. *Trends Ecol Evol* 25:81–89.
- Dochtermann NA, Dingemanse NJ. 2013. Behavioral syndromes as evolutionary constraints. *Behav Ecol Online* advance print; DOI: 10.1093/beheco/art002
- English S, Nakagawa S, Clutton-Brock TH. 2010. Consistent individual differences in cooperative behaviour in meerkats (*Suricata suricatta*). *J Evol Biol* 23:1597–1604.
- Fairbanks LA, Newman TK, Bailey JN, et al. 2004. Genetic contributions to social impulsivity and aggressiveness in vervet monkeys. *Biol Psychiat* 55:642–647.
- Feaver J, Mendl M, Bateson P. 1986. A method for rating the individual distinctiveness of domestic cats. *Anim Behav* 34:1016–1025.
- Freeman HD, Gosling SD. 2010. Personality in nonhuman primates: a review and evaluation of past research. *Am J Primatol* 72:653–671.
- Gajdon GK, Fijn N, Huber L. 2006. Limited spread of innovation in a wild parrot, the kea (*Nestor notabilis*). *Anim Cogn* 9:173–181.
- Greenberg R. 2003. The role of neophobia and neophilia in the development of innovative behaviour of birds. In: Reader SM, Lal KN, editors. *Animal innovation*. Cambridge (UK): Cambridge University Press. p 175–196.
- Hebb D. 1949. Temperament in chimpanzees. *J Comp Physiol Psychol* 42:192–206.
- Herrmann E, Call J, Hernández-Lloreda MV, Hare B, Tomasello M. 2007. Humans have evolved specialized skills of social cognition: the cultural intelligence hypothesis. *Science* 317:1360–1366.
- Herrmann E, Hare B, Cissewski J, Tomasello M. 2011. A comparison of temperament in nonhuman apes and human infants. *Dev Sci* 14:1393–1405.
- Horn JL. 1965. A rationale and test for the number of factors in factor analysis. *Psychometrika* 30:179–185.
- Hunt GR. 2000. Human-like, population-level specialization in the manufacture of pandanus tools by New Caledonian crows *Corvus monedulaoides*. *Proc R Soc B* 267:403–413.
- King JE, Figueredo AJ. 1997. The five-factor model plus dominance in chimpanzee personality. *J Res Pers* 31:257–271.
- King JE, Weiss A, Farmer KH. 2005. A chimpanzee (*Pan troglodytes*) analogue of cross-national generalization of personality structure: zoological parks and an African sanctuary. *J Pers* 73:389–410.
- King JE, Weiss A, Sisco MM. 2008. Aping humans: age and sex effects in chimpanzee (*Pan troglodytes*) and human (*Homo sapiens*) personality. *J Comp Psychol* 122:418–427.
- Konecná M, Lhota S, Weiss A, et al. 2008. Personality in free-ranging Hanuman langur (*Semnopithecus entellus*) males: subjective ratings and recorded behavior. *J Comp Psychol* 122:379–389.
- Koski SE. 2011a. Social personality traits in chimpanzees: temporal stability and structure of behaviourally assessed personality traits in three captive populations. *Behav Ecol Sociobiol* 65:2161–2174.
- Koski SE. 2011b. How to measure animal personality and why does it matter? Integrating the psychological and biological approaches to animal personality. In: Inoue-Murayama M, Kawamura S, Weiss A, editors. *From genes to animal behavior. Social structures, personalities, communication by color*. New York: Springer. p 115–136.
- Lefebvre L, Sol D. 2008. Brains, lifestyles and cognition: are there general trends? *Brain Behav Evol* 72:135–144.
- Lessells CM, Boag PT. 1987. Unrepeatable repeatabilities: a common mistake. *AUK* 104:116–121.
- Martin P, Bateson P. 1993. *Measuring behaviour: an introductory guide*. 2nd ed. Cambridge (UK): Cambridge University Press.
- McGraw KO, Wong SP. 1996. Forming inferences about some intraclass correlation coefficients. *Psychol Methods* 1:30–46.
- McGrew WC. 1992. Chimpanzee material culture: implications for human evolution. Cambridge (UK): Cambridge University Press.
- McGrew WC. 2010. Chimpanzee technology. *Science* 328:579–580.
- Morand-Ferron J, Cole EF, Rawles JEC, Quinn JL. 2011. Who are the innovators? A field experiment with 2 passerine species. *Behav Ecol* 22:1241–1248.
- Murray L. 2011. Predicting primate behavior from personality ratings. In: Weiss A, King JE, Murray L, editors. *Personality and temperament in nonhuman primates*. New York: Springer. p 129–168.
- Overington SE, Cauchard L, Côté K-A, Lefebvre L. 2011. Innovative foraging behaviour in birds: what characterizes an innovator? *Behav Process* 87:274–285.
- Pederson AK, King JE, Landau VI. 2005. Chimpanzee (*Pan troglodytes*) personality predicts behavior. *J Res Pers* 39:534–549.
- Preacher KJ, MacCallum RC. 2002. Exploratory factor analysis in behavior genetics research: factor recovery with small sample sizes. *Behav Gen* 32:153–161.
- Reader SM. 2003. Innovation and social learning: individual variation and brain evolution. *Anim Biol* 53:147–158.
- Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ. 2007. Integrating animal temperament within ecology and evolution. *Biol Rev* 82:291–318.
- Réale D, Dingemanse NJ, Kazem AJN, Wright J. 2010. Evolutionary and ecological approaches to the study of personality. *Philos T R Soc B* 365:3937–3946.
- Roberts BW, Walton KE, Viechtbauer W. 2006. Patterns of mean-level change in personality traits across the life-course: a meta-analysis of longitudinal studies. *Psychol Bull* 132:1–125.
- Rouff JH, Sussman RW, Strube MJ. 2005. Personality traits in captive lion-tailed macaques (*Macaca silenus*). *Am J Primatol* 67:177–198.

- Schuerch R, Heg D. 2010. Life history and behavioral type in the highly social cichlid *Neolamprologus pulcher*. *Behav Ecol* 21:588–598.
- Seyfarth RM, Silk JB, Cheney DL. 2012. Variation in personality and fitness in wild female baboons. *PNAS* 109:16980–16985.
- Shrout PE, Fleiss JL. 1979. Intraclass correlations: uses in assessing rater reliability. *Psychol Bull* 86:420–428.
- Sih A, Bell AM. 2008. Insights for behavioral ecology from behavioral syndromes. *Adv Stud Behav* 38:227–281.
- Sih A, Bell AM, Johnson JC, Ziembra RE. 2004. Behavioural syndromes: an integrative overview. *Q J Biol* 79:241–277.
- Tabachnik BG, Fidell LS. 2007. Using multivariate statistics. 3rd ed. Boston: Pearson/Ally & Bacon.
- Toms C, Echevarria D, Jouandot DJ. 2010. A methodological review of personality-related studies in fish: focus on the shy-bold axis of behavior. *Int J Comp Psychol* 23:1–25.
- Uher J. 2011. Individual behavioral phenotypes: an integrative meta-theoretical framework. Why “behavioral syndromes” are not analogs of “personality.” *Devel Psychobiol* 53:521–548.
- Uher J, Asendorpf JB, Call J. 2008. Personality in the behaviour of great apes: temporal stability, cross-situational consistency and coherence in response. *Anim Behav* 75:99–112.
- van Schaik CP, Burkart JM. 2011. Social learning and evolution: the cultural intelligence hypothesis. *Philos T R Soc B* 366:1008–1016.
- van Schaik CP, Fox E, Fechtman L. 2003. Individual variation in the rate of use of tree-hole tools among wild orang-utans: implications for hominin evolution. *J Hum Evol* 44:11–23.
- Verbeek MEM, Drent PJ, Wiepkema PR. 1994. Consistent individual differences in early exploratory behaviour of male great tits. *Anim Behav* 48:1113–1121.
- Visalberghi E, Addessi E, Truppa V, et al. 2009. Selection of effective stone tools by wild bearded capuchin monkeys. *Curr Biol* 19:213–217.
- Weiss A, King JE, Hopkins WD. 2007. A cross-setting study of chimpanzee (*Pan troglodytes*) personality structure and development: zoological parks and Yerkes National Primate Research Center. *Am J Primatol* 69:1264–1277.
- Weiss A, Inoue-Murayama M, Hong K-W, et al. 2009. Assessing chimpanzee personality and subjective well-being in Japan. *Am J Primatol* 71:283–292.
- Wilson DS, Coleman K, Clark AB, Biederman L. 1993. The shy-bold continuum: an ecological study of a psycho-logical trait. *J Comp Psychol* 107:250–260.
- Wolf M, Weissling FJ. 2010. An explanatory framework for adaptive personality differences. *Philos T R Soc B* 365:3959–3968.