Influence of personality, age, sex, and estrous state on chimpanzee problem-solving success

Lydia M Hopper[1,2*], Sara A Price[2,3,4], Hani D Freeman[1], Susan P Lambeth[2], Steven J Schapiro[2,5] and Rachel L Kendal[4]

1. Lester E. Fisher Center for the Study and Conservation of Apes, Lincoln Park Zoo, Chicago, IL, USA

2. Michale E Keeling Center for Comparative Medicine and Research, UT MD Anderson Cancer Center, Bastrop, TX, USA

3. Language Research Center, Georgia State University, Atlanta, GA, USA

4. Centre for Coevolution of Biology & Culture, Department of Anthropology, Durham University, Durham, UK

5. Department of Experimental Medicine, University of Copenhagen, Copenhagen, Denmark

* LM Hopper correspondence: lhopper@lpzoo.org

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Abstract

Despite the importance of individual problem-solvers for group- and individual-level fitness, the correlates of individual problem-solving success is still an open topic of investigation. In addition to demographic factors, such as age or sex, certain personality dimensions have also been revealed as reliable correlates of problem solving by animals. Such correlates, however, have been little-studied in chimpanzees. To empirically test the influence of different personality factors on chimpanzee problem-solving, we individually tested 36 captive chimpanzees with two novel foraging puzzles. We included both female (N = 24) and male (N = 12) adult chimpanzees (aged 14-47 years) in our sample. We also took care to control for the females' estrous state – a potential influence on cognitive reasoning – by testing cycling females both when their sexual swelling was maximally tumescent (associated with the luteinizing hormone surge of a female's estrous cycle) and again when it was flaccid. Although we found no correlation between the chimpanzees' success with either puzzle and their age or sex, the males' personality ratings did correlate with their problem-solving success. Specifically, those male chimpanzees that were rated highly in the factors Methodical and Dominance spent longer interacting with the novel puzzles and obtained more food rewards. No significant correlations were found for the female chimpanzees' personality factors, but we report tentative evidence for increased problem-solving success by the females when their estrous swelling was most flaccid.

Keywords: *Pan troglodytes*; chimpanzees; personality; problem solving; enrichment; sexual swelling; estrous state

Introduction

At the group level, innovation has been defined as 'a new or modified learned behavior not previously found in the population' (Reader and Laland 2003) but such innovation cannot arise without individual problem-solvers (Ramsey et al. 2007). The importance of such problem-solvers is undisputed as they enable the emergence of new behavior patterns, and potentially cultures, fuelling investigations of animal innovation both in captivity (e.g., Kendal et al. 2005) and the wild (e.g., Lefebvre et al. 2004; Sol et al. 2005). Empirical research suggests that those animals that cannot outcompete others are more likely to develop novel solutions to problems (e.g., Laland and Reader 1999b, but see Boogert et al. 2006), although innovation may also arise from environmental pressures, like food scarcity (e.g., Laland and Reader 1999a, but see Kummer and Goodall 1985) or 'spare time' (e.g., in captivity or during juvenile dependency). In addition to such environmental correlates of novel problem-solving, individual characteristics, such as neophobia, have also been shown to influence an animal's problem-solving abilities and successes (e.g., Webster and Lefebvre 2001; Cole and Quinn 2011).

Despite the importance of individual problem-solvers for group- and individual-level fitness, the correlates of individual problem-solving ability is still an open topic of investigation. In addition to physiological correlates of problem-solving success (Boogert et al. 2010; Morand-Ferron et al. 2011), specific 'personality' traits (Dall et al. 2004; or 'behavioral syndromes', Sih et al. 2004), have also been revealed as reliable correlates of problem-solving (but see Cole et al., 2011). Indeed, from their field experiment with meerkats (*Suricata suricata*), Thornton and Samson (2012) concluded that "certain intrinsic individual characteristics may make some individuals particularly likely to innovate" (p. 1464). Following this, we wished to elucidate whether the problem-solving abilities of chimpanzees (*Pan troglodytes*) – a species whose problem-solving skills have been long-studied – correlated with specific personality ratings.

Chimpanzee personality ratings are robust over time (Uher et al. 2008), predict species-typical behaviors (Pederson et al. 2005), and can reflect an individual's well-being (Weiss et al. 2012b), but do they also correlate with a chimpanzee's problem-solving ability? Personality traits and factors are robust for a number of species (for reviews see Gosling 2001; Weiss et al. 2011; Carere and Maestripieri 2013) and certain personality traits or factors are correlated with both increased individual (Dall et al. 2004; Dingemanse et al. 2010; Cole and Quinn 2011) and group-level (Réale et al. 2010) fitness. Specifically, certain personality traits have been shown to correlate with life-history success (Biro and Stamps 2008), digestive health (Jin et al. 2013), longevity (Weiss et al. 2013), metabolic rate (Careau et al. 2008), immunity measures (Koolhaas 2008), and self-injurious behavior (Gottlieb et al. 2013). However, despite one recent study that presented chimpanzees with tool-use tasks in a group setting (Massen et al. 2013), and which reported two 'behavioral syndromes' ('exploration-persistence' and 'boldness') to be descriptive of their problem-solving abilities, there are limited data available to answer whether specific personality factors are predictive of an individual chimpanzee's problem-solving ability. This lack of data is surprising, not only given the wealth of research that has focused on chimpanzee problem-solving and cognition (e.g., Boakes 1984; Tomasello and Call 1997; Hanus and Call 2011), but also because the relationship between personality traits and problem-solving or foraging skill has been studied in a broad array of species, including humans (Goldsmith 1984), birds (e.g., *Parus major*, Titulaer et al. 2012; *Taeniopygia guttata*, Brust et al. 2013), ungulates (e.g., *Dama dama*, Bergvall et al. 2011), hyenas (Benson-Amram and Holekamp 2012) and other nonhuman primates (e.g., *Microcebus murinus*, Dammhahn and Almeling 2012; *Otolemur garnettii*, Watson and Ward 1996).

In addition to the impact of chimpanzee personality factors on their problem-solving, we also tested the importance of demographic characteristics (e.g., age) and state-dependent factors (e.g., estrous state). While both age (Bard et al. 1995) and sex (Lonsdorf et al. 2004) may predict a chimpanzee's tool-use skills (but see Massen et al. 2013), a meta-analysis of studies of chimpanzees in the wild revealed that these factors also correlate with chimpanzees' proclivity to innovate novel foraging strategies (Reader and Laland 2001). Furthermore, there is also tentative evidence that a female chimpanzee's estrous state may mediate her ability with cognitive tasks (Inoue and Matsuzawa 2011, but see Wagner and Ross in press), potentially relating to changes in problem-solving success. Although the evidence for the impact of a female's estrous state is limited for chimpanzees (N=1, Inoue and Matsuzawa 2011), estrous state and sex hormone levels have been shown to influence cognitive abilities and behavioral strategies for a number of species (e.g., *Rattus norvegicus*, Korol et al. 2004; *Macaca mulatta*, Rapp et al. 2003; *Homo sapiens*, Kimura and Hampson 1994). Accordingly, we controlled for a female chimpanzee's estrous state in the present study by testing cycling female chimpanzees in a counter-balanced manner across their estrous cycles.

Through this study, our aim was to assess chimpanzees at the level of the individual (e.g., Herrmann and Call 2012), rather than looking for species-level correlates of problem-solving (e.g., Reader and Laland 2001). In order to ensure that we were testing each chimpanzee's individual problem-solving skills – as opposed to their ability to learn via social influences – we presented individual chimpanzees with novel foraging puzzles, out-of-sight of the rest of their social group. Additionally, to reduce the chance of experimenter 'cueing' (regarding end-states or reward locations) we baited the puzzles with food rewards prior to entering the testing area. As we tested chimpanzees individually, we do not address whether these newly-learned behaviors would be adopted by naïve group-members and transmitted throughout their home-group – a requirement in some definitions of innovation (Reader and Laland 2003; see also Kendal et al. 2007). Given the current data available for both wild (Reader and Laland 2001) and captive (Massen et al. 2013) chimpanzees, we predicted that the chimpanzees' problem-solving abilities would vary according to age, sex and estrous state. Furthermore, we also expected to find inter-individual variation but intra-individual consistency, indicative of differences in skill according to specific personality factors.

Methods

Subjects

Thirty-six chimpanzees, socially-housed in highly enriched and spacious indoor/outdoor enclosures at the Michale E. Keeling Center for Comparative Medicine and Research, UT MD Anderson Cancer Center, USA ('UT MD Anderson' hereafter), were the subjects in this study. The chimpanzee subjects comprised of 24 females (average age: 26.8 years, age range: 14-47 years), on a variety of contraceptive plans, and 12 reproductively intact males (average age: 26.7 years, age range: 17-39 years). Full demographic information is provided in the Electronic Supplementary Materials (Table S1). In addition to their daily allowance of commercial chimpanzee pellets, the chimpanzees were fed three fresh produce meals a day and had continual access to water. Chimpanzees were not food or water deprived at any time.

Apparatus

The two novel foraging puzzles were modified 'dog activity toys' (the DogCasino – renamed 'Pin-Release Puzzle' – and the DogDomino – renamed 'Slide-Release Puzzle' – from Nina

Ottoson, http://www.nina-ottosson.com/). Both foraging toys were novel to the chimpanzees and had not been presented to any of the chimpanzees prior to the commencement of this study. However, we note that these chimpanzees live in a highly enriched environment and are regularly provided with enrichment devices that encourage their natural foraging behaviors (e.g., "termite" fishing tasks, Hopper et al., 2007) and so they are familiar with manipulating devices to retrieve food rewards.

The first task, the Pin-Release Puzzle, was a 5cm deep board (20x36cm) that had four trays protruding from each of the longer sides (eight trays total). These trays could be pulled out by the chimpanzees to reveal a food reward hidden in a well of each tray. Food rewards could be retrieved from the Pin-Release Puzzle according to two levels of complexity. The first, Phase A, is as described; the chimpanzee had to pull out each of the eight trays in order to get all eight rewards. In the second level, Phase B, eight pins were inserted into holes on the front of the Pin-Release Puzzle, each holding its corresponding tray in place. In this Phase B, to pull out a tray, the chimpanzee first had to remove the corresponding pin to release the tray (Figure 1). The second task, the Slide-Release Puzzle, was also a 5cm deep board (20x38cm), on which were five inverted cups. Each cup contained a food reward and slotted into its own socket. For the chimpanzee to remove a cup to get the food reward, it had to first slide one or more of the four sliding panels that ran along the center line on the front of the Slide-Release Puzzle. Sliding these panels along their tracks allowed each cup to be released from its socket in turn (Figure 1).

FIGURE 1 ABOUT HERE

For use with the chimpanzees, both tasks were (i) structurally reinforced with a plastic fascia, (ii) modified to include larger pins (Pin-Release Puzzle) or cups (Slide-Release Puzzle), which could be more easily manipulated by the chimpanzees, and (iii) mounted on a plastic frame which allowed each puzzle to be hung on the chimpanzees' cage mesh in such a way that the chimpanzees had sufficient room to reach through the mesh and manipulate the task.

Personality Ratings

Personality ratings were collected for each of the 36 chimpanzees as part of a wider assessment of the personalities of the chimpanzees housed at UT MD Anderson (Freeman et al. 2013). Full details of the procedures used to generate the personality rating scale are described in Freeman et al. (2013, also see the Electronic Supplementary Material: ESM1). Briefly, a questionnaire created by Freeman et al. (2013), requiring staff members to rate chimpanzees against a list of 41 traits, was given to 17 staff members, all of whom had at least six months experience with the chimpanzees at UT MD Anderson. Ratings were completed at weekly meetings from 2006 to 2008 and raters were instructed not to speak to each other about the ratings during or outside of the meetings. From the responses to the personality questionnaire, factor analysis of the 41 traits revealed six dimensions of chimpanzee personality: Methodical, Extroversion, Agreeableness, Openness (to experience), Reactivity/Undependability, and Dominance (Freeman et al. 2013, Table 1 lists which traits loaded on to each of the six factors). These factors were correlated against various measures of success recorded for the chimpanzees when exposed to the two novel foraging tasks.

TABLE 1 ABOUT HERE

Procedure

For testing, each chimpanzee was called into their inside enclosure by the experimenter, enabling entirely voluntary participation in the study. Given this choice, and the stimulation provided by the foraging test itself (e.g., Clark and Smith, 2013), these sessions created environmental variety and cognitive stimulation for these chimpanzees. Because participation was voluntary, and the chimpanzees had a positive/familiar relationship with the researcher, all subjects were calm when individually housed for these brief (≤15 minutes) tests. Once inside, the researcher rewarded the chimpanzee with a small food reward (e.g., a slice of apple) for coming inside and the puzzle was presented to the chimpanzee by hanging it on the outside of the enclosure. To avoid cueing, the chimpanzees were not explicitly encouraged to interact with the puzzle, and the experimenter made no contact with it nor did she draw the chimpanzee's attention to it verbally.

The Pin-Release Puzzle was first presented in the easier state (Phase A). Each chimpanzee was given five minutes in which to interact with the puzzle, beginning from the time it was hung on their cage. At the end of the five-minute period, if a subject had not retrieved any of the food rewards (by sliding out one or more of the eight trays), the puzzle was removed, and the session terminated, at which time the chimpanzee returned to its social group. If the chimpanzee was able to obtain one or more of the eight food rewards from the Pin-Release Puzzle, the session continued for an additional five minutes. Thus, each session that contained the successful attainment of at least one reward ended when 10 minutes had elapsed or when the chimpanzee had successfully removed all eight food rewards from the Pin-Release Puzzle, whichever occurred first. Unsuccessful chimpanzees were only given five minutes to interact with the task because, a pilot study, and our own previous research (e.g., Hopper et al. 2007, 2008), indicated that chimpanzees do not persist in exploring the task if unrewarded for five minutes.

For those chimpanzees that were able to retrieve one or more of the eight rewards from the Pin-Release Puzzle in Phase A, the puzzle was removed, the eight pins were added, out-of-sight of the chimpanzee, and the re-baited puzzle was re-presented to the chimpanzee for Phase B. Phase B for the Pin-Release Puzzle followed the same parameters as Phase A, such that if the chimpanzees were successful within the first five minutes, the session continued for 10 minutes or until all rewards had been retrieved. At the end of their test session, the chimpanzee immediately returned to its social group.

The Slide-Release Puzzle was presented following the same protocol as that for Phase A of the Pin-Release Puzzle.

Although the majority of the female chimpanzees were on some form of contraceptive (Electronic Supplementary Materials: Table S1), nine of the 24 females exhibited a regular estrous cycle, as measured by the size of their sexual swelling. In the Electronic Supplementary Materials (ESM2) we provide details of how we recorded the females' sexual swelling cycles and information about the impact of birth control on the females' cycling. The presentation of the two tasks was counterbalanced across the cycling females such that four were tested with the Pin-release task when their sexual swelling was maximally tumescent (rated as '4') and with the Slide-release task when their sexual swelling was flaccid (rated as '0', Electronic Supplementary Materials: Table S1). The remaining five cycling females received the tasks in the opposite order.

The time period between the presentation of the two tasks was dictated by each female's estrous cycle: across the nine females who exhibited a regular cycle, the average delay between presentations of each novel puzzle was 15.7 days. In order to allow comparisons between the cycling females and both the non-cycling females and the males, the remaining 15 females and 12 males were presented with the two tasks in a counterbalanced order with a two-week period between task presentations. For non-cycling females, the order of presentation of each task was also counterbalanced within the birth control method that they were prescribed (Electronic Supplementary Materials: Table S1).

Coding and analysis

All test sessions were videotaped with a Canon ZR900 camcorder (Canon U.S.A., Inc.) and the footage coded using EthoLog 2.2 (Ottoni 2000). We recorded the number of defenses (trays, pins and cups) that each chimpanzee removed (Figure 1). For the Pin-Release Puzzle in Phase A the maximum number of defenses and rewards that could be removed was eight: the eight trays, each of which held a food reward. For the Pin-Release Puzzle in Phase B the maximum number of defenses was 16: the eight trays, as described for Phase A, plus the eight pins which corresponded with each of the trays. In Phase B, to remove any tray, the chimpanzee had to first remove the associated pin and so the minimum number of defense removals required to gain a food reward was two. For the Slide-Release Puzzle the maximum number of defenses that could be removed was five: the five food cups, each of which contained a food reward.

We also coded the latency for each chimpanzee to begin interacting with the task (defined as first contact with either a hand or mouth), the latency for the chimpanzee to successfully remove the first defense and get the food reward, and the length of time they spent actively interacting with the task (using their hands or mouth to manipulate any part of the task, not exclusive to the defenses, and thus in contact with the task, rather than just in proximity to it).

All data were tested for normality and due to small sample sizes, nonparametric statistics were used throughout. All analyses reported were two-tailed unless otherwise stated. To account for familywise errors arising from multiple comparisons, we applied a Holm's sequential Bonferroni method (Holm 1979). For example, for comparisons across the six personality factors, $\alpha^*= 0.05/1\text{-}6$ personality factors.

Results

Personality factors as correlates of success

A chimpanzee's success (i.e. proportion of possible defenses removed) with one task was significantly positively correlated with their success with the other. Specifically, a chimpanzees' success with the Pin-Release Puzzle (Phase A) significantly positively correlated with their success with the Slide-Release Puzzle (Related Samples Wilcoxon, $T+ = 292.0$, N = 36, P = 0.003) and their success on both phases of the Pin-Release Puzzle combined significantly positively correlated with their success with the Slide-Release Puzzle ($T+ = 49.5$, N = 36, P = 0.001). Such consistency by individual chimpanzees suggested that their success may be indicative of individual traits, or personality factors. To assess this, we correlated the chimpanzees' personality factor ratings with their success on the two tasks. Given that it has been shown that male and female chimpanzees are typified by different personality factors (King et al. 2008, see also Titulaer et al. 2012; Sussman et al., 2013), we analyzed each sex individually.

For males, the proportion of defenses removed from the Pin-Release Puzzle in Phase A and B (r = 0.762, N = 12, P = 0.006) was significantly positively correlated with the trait 'Methodical' (Figure 2). Given the Holm's sequential Bonferroni method ($\alpha^*=$ [0.05/1-6 personality factors]), no such correlations for the Slide-Release Puzzle were found, although success with this task showed a pattern of positive correlation with Methodical (r = 0.640, N = 12, P = 0.034), Openness (to experience) (r = 0.640, N = 12, P = 0.034) and Dominance (r = 0.744, N = 12, P = 0.009). However, when the males' success with the Slide-Release Puzzle and Pin-Release Puzzle (Phase A) were combined, success rates were significantly correlated with Methodical (r = 0.756, N = 12, P = 0.007) and Dominance (r = 0.725, N = 12, P = 0.01).

FIGURE 2 ABOUT HERE

The males' latency to interact with the Pin-Release Puzzle (Phase A) was significantly correlated with Methodical (r = 0.778, PN = 12, = 0.005). No significant correlations were found between personality factors and the males' latency to interact with the Pin-Release Puzzle Phase B (all P > 0.1, most likely because of the small sample size for males tested with Pin-Release Puzzle in Phase B (N=3)) or the Slide-Release Puzzle (all P > 0.1). Overall, the time males spent interacting with the Pin-Release Puzzle was only significantly correlated with Methodical (r = 0.778, N = 12, P = 0.005 for both Phase A and B). In contrast, three personality factors were significantly correlated with the time the males spent interacting with the Slide-Release Puzzle: Dominance (r = 0.809, N = 12, P = 0.003), Openness (r = 0.755, N = 12, P = 0.007), and Methodical (r = 0.798, N = 12, P = 0.003).

For the females, no correlations between personality factor and success (as measured by the proportion of possible defenses removed) were found for either of the two puzzles. The same was true when we analyzed the latency to begin interacting with the foraging puzzles and the duration of time spent interacting with them. There were also no correlations found, for either males or females, between their personality rating and the number of ‘paired defenses’ (i.e. a pin and its associated tray) removed from the Pin-Release Puzzle in Phase B. For male chimpanzees, Methodical correlated with the number of paired defenses removed (r = 0.998, N = 3, P = 0.038), but this was not significant when the Holm’s sequential Bonferroni correction was applied (but given the strength of this correlation, r = 0.998, perhaps with a larger sample size, and thus greater power, this might be significant). No other correlations were significant (for all, P > 0.05).

Estrous state, age, and sex as correlates of success

We also analyzed the impact of a chimpanzee’s age, sex, and estrous state (for females) on their ability to retrieve the food rewards from either of the two tasks. Although we found tentative evidence for differing success across some of the females related to their estrous state, no impact of a chimpanzee’s age or sex was found (i.e. males were not able to retrieve any more food rewards than females). We present the key findings here, but see the Electronic Supplementary Materials (ESM3) for complete details.

Regardless of what form of birth control a female was prescribed, for the Slide-Release Puzzle, observably cycling females removed a greater proportion of defenses when their swelling flaccid and rated 0 than females whose swellings were fully tumescent and rated 4 (U = 1.50, N_0 = 4, N_4 = 5, P = 0.034). This was not true, however, for the Pin-Release Puzzle in Phase A (U = 10.0, N_0 = 4, N_4 = 5, P = 1.00), or Phase B (U = 10.0, N_0 = 4, N_4 = 5, P = 1.00).

There was no significant sex difference in the chimpanzees’ latency to begin interacting with the tasks (Pin-Release Puzzle Phase A: Mann Whitney U, U = 98.0, $N_{females}$ = 24, N_{males} = 12, P = 0.818; Pin-Release Puzzle Phase B U = 22.0, $N_{females}$ = 24, N_{males} = 12, P = 0.900 and

Slide-Release Puzzle U = 97.0, $N_{females}$ = 24, N_{males} = 12, P = 0.785) or the time they spent actively interacting with each task: Pin-Release Puzzle Phase A (U = 97.5, $N_{females}$ = 24, N_{males} = 12, P = 0.118), Pin-Release Puzzle Phase B (U = 27.0, $N_{females}$ = 24, N_{males} = 12, P = 0.450), or the Slide-Release Puzzle (U = 143.5, $N_{females}$ = 24, N_{males} = 12, P = 0.987). There was no significant difference in the number of food rewards that female, compared to male, chimpanzees removed from the Slide-Release Puzzle (14/24 *versus* 7/12, two-tailed Fisher's Exact Test, P = 1.000) or the Pin-Release Puzzle in Phase A or B (14/24 *versus* 3/12, P = 0.083 for both).

There was no correlation in the proportion of successful responses and the chimpanzee's age for either the Pin-Release Puzzle Phase A (Pearson's correlation, r = 0.187, N = 36, P = 0.274) or Slide-Release Puzzle (r = -0.020, N = 36, P = 0.908). Nor was there a significant correlation between a chimpanzee's age and its latency to begin interacting with either the Pin-Release Puzzle, Phase A (r = -0.238, N = 36, P = 0.189), or Slide-Release Puzzle (r = -0.217, N = 36, P = 0.233).

Comparing the complexity of the two puzzles

The chimpanzees showed differing success across the two puzzles (Table 2). Of the 36 (24 female, 12 male) chimpanzees, 17 (14 females, 3 males) were able to remove one or more defenses from the Pin-Release Puzzle (Phase A) to get a food reward and 21 chimpanzees (14 females, 7 males) were able to remove one or more of the five food cups from the Slide-Release Puzzle to get a food reward. Of those chimpanzees that were able to remove a defense with the Pin-Release Puzzle, all but one removed more than one defense (mode=8) while only 15 of the 21 chimpanzees that were successful with the Slide-Release Puzzle removed more than one defense. Ten chimpanzees (8 females, 2 males) were able to remove all eight defenses from the

Pin-Release Puzzle (Phase A) but none showed 100% success for the Pin-Release Puzzle in Phase B or for the Slide-Release Puzzle.

TABLE 2 ABOUT HERE

Of the 17 chimpanzees that were able to remove one or more of the eight defenses (trays) from the Pin-Release Puzzle in Phase A, all were also able to remove one or more of the 16 defenses in Phase B (necessitating removal of at least one pin that they had not seen in Phase A, Figure 1, Table 2). For the Pin-Release Puzzle in Phase B, there were eight pairs of defenses (8 pins associated with 8 trays) and the chimpanzees had to remove a pin before they could open the associated tray. Fourteen of the 17 successful chimpanzees removed at least one pair of defenses (average of 3.5/8 pairs removed, range: 1–6). Eleven of these 14 chimpanzees opened every tray for each associated pin successfully removed (Table 3). Considering the pattern of responses shown by these 14 chimpanzees, six removed a pin and its associated tray with their first two defense removals, while the remaining eight removed two pins sequentially (Table 3).

TABLE 3 ABOUT HERE

In contrast to the pattern revealed by the number of the defenses that the chimpanzees removed from each task, the chimpanzees' latency to first success (i.e. retrieval of a food reward) revealed that the chimpanzees were quicker with the Slide-Release Puzzle (average latency to food retrieval: 68.8 seconds) than the Pin-Release Puzzle (average latency: 86.3 seconds). However, for those 10 chimpanzees that retrieved one or more food rewards with both of the puzzles, there was no difference in their latency to gain a reward across the two puzzles (Wilcoxon signed rank test, $T = 26.0$, $N = 10$, $P = 0.534$). The quicker that chimpanzees first interacted with the task, the greater the proportion of defenses removed from the Slide-Release Puzzle (Pearson's correlation, $r = -0.398$, $N = 21$, $P = 0.024$), but not for the Pin-Release Puzzle in either Phase A ($r = -0.305$, $N = 18$, $P = 0.090$) or Phase B ($r = -0.034$, $N = 18$, $P = 0.897$). For both tasks, however, there was a strong positive correlation between the overall amount of time individuals spent actively interacting with the task and their overall success (Pin-Release Puzzle in Phase A ($r = 0.865$, $N = 18$, $P < 0.001$) and Phase B ($r = 0.865$, $N = 18$, $P < 0.001$); Slide-Release Puzzle ($r = 0.789$, $N = 21$, $P < 0.001$)).

Discussion

The problem-solving abilities of the male chimpanzees correlated with the personality factor Methodical; those chimpanzees that rated as highly Methodical removed more defenses from both novel foraging puzzles and spent more time actively interacting with them (i.e. foraging). We also found evidence for a significant positive correlation between the latency for males to interact with one of the puzzles (Pin-Release Puzzle) and the factor Methodical. We also report tentative support for positive correlations between the males' problem-solving skills and the personality factors Dominance and Openness (to experience). No such correlations were found among the female chimpanzees' personality factors and problem-solving performance. However, supporting and expanding on an earlier study by Inoue and Matsuzawa (2011), we found tentative evidence that a female chimpanzee's estrous state influenced her success (for the more complex of the two puzzles only, see the Electronic Supplementary Materials: ESM3). In contrast to previous work with primates (e.g., Kendal et al. 2005; Reader and Laland 2001;

Massen et al. 2013), the chimpanzees' age or sex did not correlate with any of our measures of success, latency to begin interacting with the puzzle, or time spent interacting with either puzzle (the Electronic Supplementary Materials: ESM3), but these factors may be more relevant for chimpanzees when in a group setting rather than when tested individually.

From the personality traits (Table 1) associated with the personality factors Methodical and Openness (to experience), it can be seen that both these factors are comprised of traits that describe problem-solving, inquisitive or methodical chimpanzee personalities. Thus, we provide further behavioral support for these questionnaire-generated personality factors within the context of a cognitive test (in addition to those behavioral observation correlates reported by Freeman et al. 2013). However, given the traits associated with the factor Openness, it is surprising that more measures of the chimpanzees' success did not correlate with this factor. Perhaps the reason that Methodical was a more reliable correlate of their success relates to the nature of the specific novel foraging puzzles, both of which were highly organized and required specific hierarchical responses to enable success. It is possible that those chimpanzees rated highly on Openness would show greater success in more dynamic, or social, problem-solving settings (Figure 2).

Considering the traits that loaded onto Dominance, it may be not be apparent why male chimpanzees that rated highly with this factor also showed success with these puzzles (Dominance factor ratings and time spent interacting with the puzzles were significantly positively correlated for males). Although it may be that these animals were calmer and more confident when tested in an individual setting, it is also notable that human traits associated with innovation reflect chimpanzee traits associated with Dominance (e.g., 'impulsive' and 'excitable'). For example, for humans, innovation has been shown to correlate positively with traits such as 'sensation seeking' and 'risk taking' and negatively with 'dogmatism' (Goldsmith 1984; Jacoby 1971). Furthermore, in a social context, when chimpanzees had the ability to watch the methods used by their peers, a recent study found that dominant chimpanzees (here defined according to social rank rather than personality rating) were more willing, than those of low rank, to 'explore' potential methods available for solving a novel foraging task (Kendal et al. under review).

We wish to emphasize that this finding – a correlation between the males' personality factors and their success at solving the novel foraging puzzles – is not circular. Firstly, the personality rating scale was developed from staff ratings collected between 2006 and 2008 (at least three years before the present study, run in 2011), suggesting that the personality factors represent stable ratings, which are consistent and meaningful over time (Uher et al. 2008). Secondly, the factors that emerged from the rating scale (Freeman et al. 2013) were correlated against data from behavioral observations that were collected between 2004 and 2006. This is important because it provides evidence that the personality ratings were not only consistent across human raters but also correlated strongly with appropriate independent behavioral measures (Weiss et al. 2012a; Massen et al. 2013). Thirdly, and perhaps most importantly, those staff members who completed the original personality rating questionnaires were different from those who collected the observational data reported in Freeman et al. (2013), all of whom were different again from the experimenter (S.A.P.) who collected the data for this present study[1].

In addition to pinpointing particular individual factors that were predictive of chimpanzees' success with these novel foraging puzzles, this study also provides insights into chimpanzees' ability for building upon previously-gained knowledge. Of the 17 chimpanzees

[1] S.A.P. collected all the behavioral data for the present study and although other authors of this study were also co-authors for Freeman et al. (2013), none acted as raters for the generation of the chimpanzee personality traits.

that successfully solved the Pin-Release Puzzle in Phase A, by pulling out one or more of the eight trays, 14 were also able to remove one or more of the paired defenses (i.e. a pin and its associated tray) when the puzzle was re-presented in Phase B. In this way, when ‘forced’ into adding a step to their repertoire (i.e. once the pins were added), as has been shown with orangutans (Lehner et al. 2011), the chimpanzees showed some evidence for cumulative problem solving. This is notable because, instead of indicating that the chimpanzees’ responses were ‘conservative’ (e.g., Hrubesch et al. 2009; Marshall-Pescini and Whiten 2008), or ‘fixed’ (Hanus et al. 2011), the chimpanzees showed flexible learning in which they built upon their previous efforts (Manrique et al. 2013; Yamamoto et al. 2013). It had been proposed that chimpanzees’ apparent conservatism may explain their failure to exhibit cumulative culture – the accumulation of beneficial modifications to cultural traits resulting in more complex technologies than a single individual could invent in one lifetime (Lewis and Laland 2012; Marshall-Pescini and Whiten 2008) – but this, and other recent studies (e.g., Dean et al. 2012; Lehner et al. 2011; Manrique et al. 2013; Yamamoto et al. 2013), call this into question. Therefore, we welcome future studies to tease apart the impact of social influences and pressures on the cumulative problem solving of chimpanzees with respect to individual abilities and their potential for individual problem-solving (Tennie et al. 2009).

Through this study, we have identified specific personality factors (i.e. Methodical, Dominance and Openess) that are predictive of male chimpanzee foraging innovation, but not for female chimpanzees. Furthermore, we have been able to validate the chimpanzee factor Methodical, as tentatively proposed by Freeman et al. (2013). Further investigations into the importance of individual factors as predictors of innovation are vital for a detailed investigation of cumulative culture. As Ramsey et al. (2007) stated: “a complete understanding of culture requires an understanding of innovation" (p. 394). By using an individualistic approach (Herrmann and Call 2012), we have begun to identify those factors that could explain a chimpanzee's problem-solving ability and such methods may also enable us to identify those chimpanzees that are the likely innovators of novel cultural technologies. Furthermore, by considering animals at the individual-level, rather than just the group-level, researchers can investigate the potential impact of certain individuals upon their group's behavior, such as in the context of innovation (Hoffman 1959) or learning (Hopper et al. 2011).

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Figure and Table Captions

Figure 1. The two novel foraging puzzles. (**a**) The Pin-Release Puzzle (Phase B) is shown in the start position with all eight trays and their corresponding pins locked in place. In Phase A the Pin-Release Puzzle was presented to the chimpanzee in the same manner except that each of the eight pins were removed entirely. (**b**) Each pin could be removed and then the associated tray pulled out revealing a food treat placed in the tray. (**c**) The Slide-Release Puzzle in the start position with all five cups held in place by the sliding panels. (**d**) Once the sliding panels are moved to either the left or right each cup in turn could be removed revealing a food treat placed in the white cup

Figure 2. Male chimpanzee personality as a correlate of problem-solving success for which the rating was measured on a 7-point Likert scale. (a) the proportion of defenses that male chimpanzees successfully removed from the Pin-Release Puzzle (Methodical: r = 0.76, P = 0.006) and (c) Slide-Release Puzzle (Methodical: r = 0.64, P = 0.03; Openness: r = 0.64, P = 0.03; Dominance: r = 0.74, P 0.009). The length of time (seconds) that male chimpanzees spent actively interacting with the (b) Pin-Release Puzzle (Methodical: r = 0.78, P = 0.005) and (d) Slide-Release Puzzle (Methodical: r = 0.80, P = 0.003; Openness: r = 0.76, P = 0.007; Dominance: r = 0.81, P 0.003). Solid line = a significant correlation. Dotted lines = significant correlation that was non-significant after the Holm's sequential Bonferroni correction was applied.

Table 1. Each of the six chimpanzee personality (varimax-rotated) factors identified by Freeman et al. (in press) and the traits that loaded on to each. If a trait is associated with "(-)" it signifies that that trait negatively correlated with that factor e.g., the trait 'fearful' negatively correlates with the factor Dominance.

Table 2. Success shown by the chimpanzees with the Pin-Release Puzzle in Phase A and B and with the Slide-Release Puzzle. Included are the responses shown by all subjects pooled as well as just those chimpanzees which removed one or more defenses during their test session.

Table 3. The pattern of responses shown by the chimpanzees when presented with the Pin-Release Puzzle in Phase B and the proportion of the eight defense pairs removed (i.e. pin + tray). The number for each of the chimpanzee's responses relate to the number codes for each pair of associated defenses (1-8) while the letters relate to the type of defense (where $_p$ = pin and $_t$ = tray). Chimpanzees could only open a tray, in order to obtain a food reward, once that tray's associated pin had first been removed (removal of a pair of defenses). In some cases, however, chimpanzees would pull out a pin, but not release the associated tray ("Number of pins removed without tray"). For demographic information on each chimpanzee, see Table S1 in the Electronic Supplementary Material.

Figure 1
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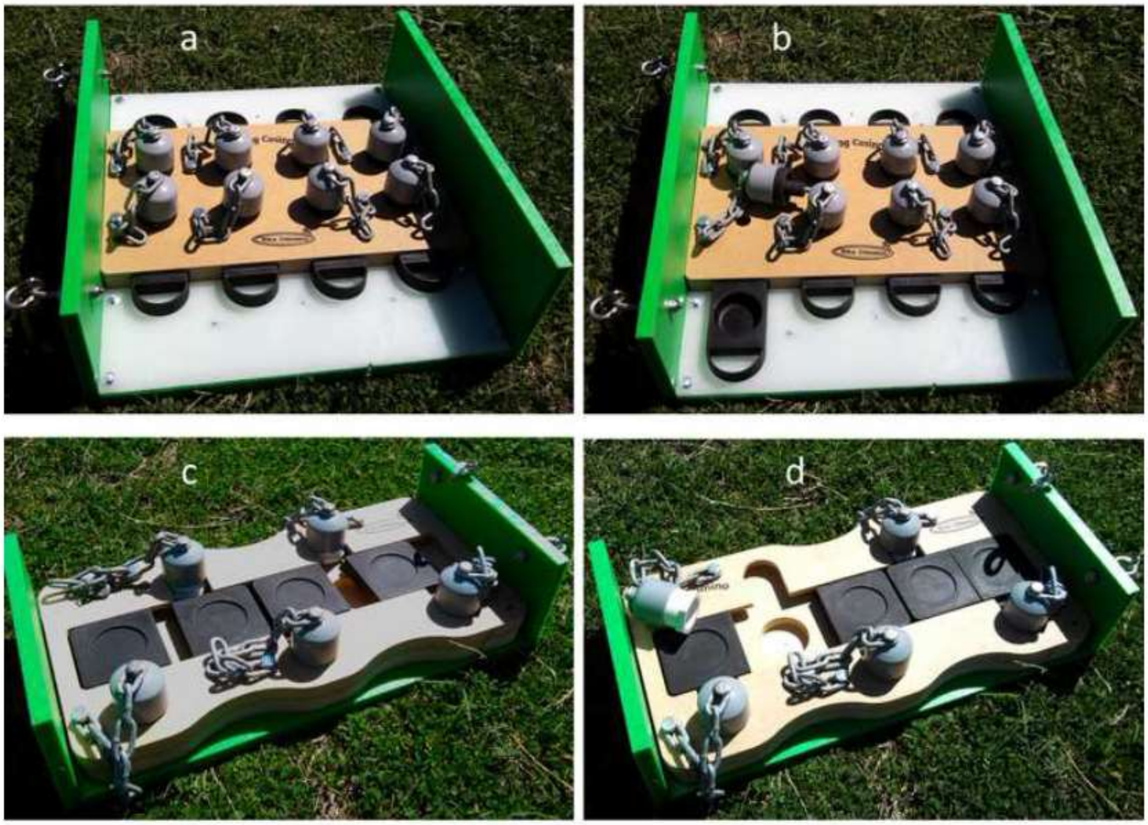

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Figure 2
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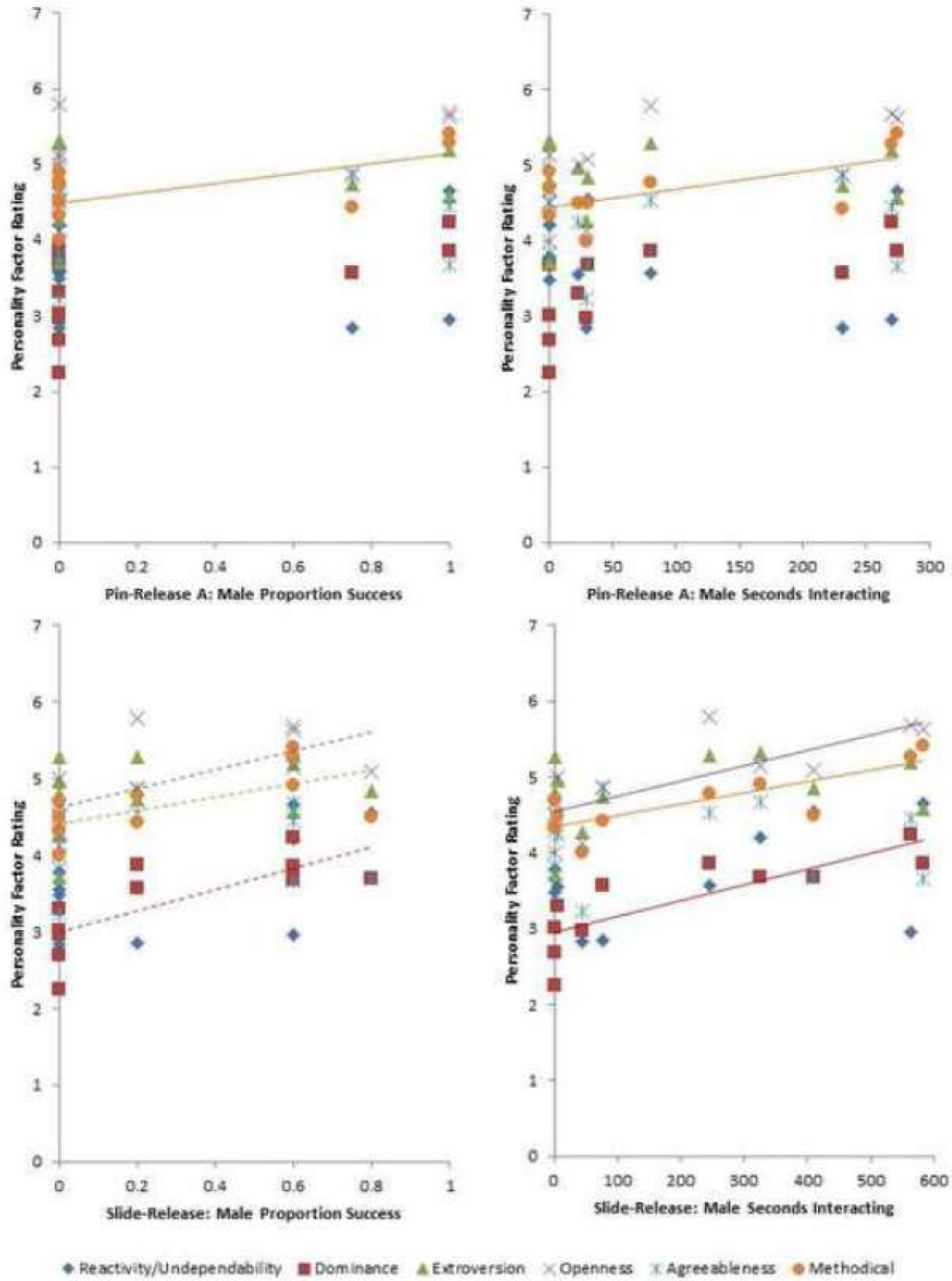

Table 1

Reactivity/ Undependability	Dominance	Extraversion	Openness	Agreeableness	Methodical
Irritable	Fearful (-)	Solitary (-)	Human oriented	Protective	Self-caring
Autistic	Timid (-)	Depressed (-)	Persistent	Considerate	Methodical
Deceptive	Cautious (-)	Active	Inventive		
Impulsive	Dominant	Playful	Intelligent		
Defiant	Dependent (-)	Sexual	Affectionate/Friendly		
Mischievous	Anxious (-)	Affiliative	Inquisitive/Curious		
Jealous	Bold				
Manipulative	Relaxed				
Stingy					
Bullying					
Aggressive					
Eccentric					
Socially-inept					
Calm (-)					
Excitable					
Temperamental/ Moody					

Table 1. Each of the six chimpanzee personality (varimax-rotated) factors identified by Freeman et al. (2013) and the traits that loaded on to each. If a trait is associated with "(-)" it signifies that that trait negatively correlated with that factor e.g., the trait 'fearful' negatively correlated with the factor Dominance.

Table 2

Personality Factor	Behavior	
	Positive Correlation	Negative Correlation
Reactivity/Undependability	**Aggressive** (intervene and sexual behavior)	**Affiliatory** (post-conflict affiliation)
Dominance	**Aggressive** (contact aggression, display, intervene, noncontact aggression, sexual behavior) **Affiliatory** (proximity)	**Submissive** (submissive)
Openness (to experience)	**Submissive** (submissive) **Affiliatory** (play)	**Affiliatory** (proximity)
Extraversion	**Aggressive** (contact aggression) **Submissive** (begging) **Affiliatory** (play)	-
Agreeableness	**Affiliatory** (affiliation)	**Aggressive** (displace)
Methodical	-	-

Table 2. The behaviors that significantly correlated (positively and negatively) with each of the six personality factors identified by Freeman et al. (2013). Each correlation provides the category of behavior followed by the specific behavioral codes in brackets. Methodical did not correlate with any of the chimpanzees' observed behaviors.

Table 3

	Personality Factor	Latency	Manipulating	Success
Pin-Release	Dominance	r = -.38, N = 12, P = 0.35	r = .68, N = 12, P = 0.02**	r = .58, N = 12, P = 0.06
	Reactivity/Undependability	r = -.30, N = 12, P = 0.01*	r = .14, N = 12, P = 0.68	r = -.10, N = 12, P = 0.76
	Extraversion	r = -.43, N = 12, P = 0.87	r = .07, N = 12, P = 0.83	r = .04, N = 12, P = 0.92
	Openness	r = -.37, N = 12, P = 0.53	r = .67, N = 12, P = 0.02**	r = .52, N = 12, P = 0.11
	Agreeableness	r = .23, N = 12, P = 0.17	r = -.04, N = 12, P = 0.92	r = .12, N = 12, P = 0.72
	Methodical	r = -.42, N = 12, P = 0.93	r = .78, N = 12, P = 0.01**	r = .67, N = 12, P = 0.02*
Slide-Release	Dominance	r = -.40, N = 12, P = 0.33	r = .81, N = 12, P = 0.00**	r = .74, N = 12, P = 0.01*
	Reactivity/Undependability	r = .02, N = 12, P = 0.10	r = .41, N = 12, P = 0.21	r = .54, N = 12, P = 0.09
	Extraversion	r = .00, N = 12, P = 0.99	r = .27, N = 12, P = 0.42	r = .32, N = 12, P = 0.34
	Openness	r = -.15, N = 12, P = 0.73	r = .76, N = 12, P = 0.01**	r = .64, N = 12, P = 0.03*
	Agreeableness	r = -.07, N = 12, P = 0.88	r = -.12, N = 12, P = 0.73	r = .95, N = 12, P = 0.10
	Methodical	r = -.29, N = 12, P = 0.49	r = .80, N = 12, P = 0.00**	r = .64, N = 12, P = 0.03*

Table 3. The correlations between the male chimpanzees' personality factor scores and success (proportion of defenses removed), latency (latency to interact), and manipulating (proportion of session actively manipulating the puzzle) when presented with the Pin-Release and the Slide-Release Puzzle (Figure 2). * denotes a correlation where $P < 0.05$ and ** denotes those correlations considered significant after the application of the false discovery rate control. Personality factor scores were originally calculated by Freeman et al. (2013).

Table 4

	Paired Defenses Removed from Pin-Release in Phase B	
Personality Factor	**Males**	**Females**
Dominance	r = .83, N = 12, P = 0.38	r = -.32, N = 24, P = 0.44
Reactivity/Undependability	r = .55, N = 12, P = 0.63	r = -.31, N = 24, P = 0.46
Extraversion	r = .27, N = 12, P = 0.83	r = .14, N = 24, P = 0.74
Openness	r = .99, N = 12, P = 0.04*	r = .44, N = 24, P = 0.28
Agreeableness	r = -.76, N = 12, P = 0.45	r = .08, N = 24, P = 0.90
Methodical	r = .99, N = 12, P = 0.08	r = .38, N = 24, P = 0.36

Table 4. The correlations between the male and female chimpanzees' personality factor scores and the number of paired defenses (i.e. a pin and tray) removed from the Pin-Release puzzle in Phase B. * denotes a correlation where $P < 0.05$ (although note that this was not considered significant after the application of the false discovery rate control). Personality factor scores were originally calculated by Freeman et al. (2013).

Table 5

	Task	Latency	Manipulating	Success
Sex	P-R A	$U = 98.0$, $N_f = 24$, $N_m = 12$, $P = 0.82$	$U = 97.5$, $N_f = 24$, $N_m = 12$, $P = 0.12$	14/24 vs 3/12, $P = 0.08$
	P-R B	$U = 22.0$, $N_f = 14$, $N_m = 3$, $P = 0.90$	$U = 27.0$, $N_f = 14$, $N_m = 3$, $P = 0.45$	14/24 vs 3/12, $P = 0.08$
	S-R	$U = 97.0$, $N_f = 24$, $N_m = 12$, $P = 0.79$	$U = 143.5$, $N_f = 24$, $N_m = 12$, $P = 0.99$	14/24 vs 7/12, $P = 1.00$
Age	P-R A	$r = -0.24$, $N = 36$, $P = 0.19$	$r = 0.18$, $N = 36$, $P = 0.25$	$r = 0.19$, $N = 36$, $P = 0.27$
	P-R B	$r = -0.39$, $N = 17$, $P = 0.13$	$r = 0.30$, $N = 17$, $P = 0.29$	$r = 0.19$, $N = 17$, $P = 0.26$
	S-R	$r = -0.22$, $N = 36$, $P = 0.23$	$r = 0.02$, $N = 36$, $P = 0.89$	$R = -0.02$, $N = 36$, $P = 0.91$

Table 5. Comparison of the chimpanzees' responses by their sex and age when presented with the Pin-Release in Phase A (P-R A), Pin-Release in Phase B (P-R B), and the Slide-Release (S-R). Between-sex comparisons were run with Mann Whitney U tests for the 'latency to interact' and 'duration manipulating' and with Fisher Exact Tests for the number of successful individuals ('success). Correlations between the chimpanzees' age and their 'latency to interact', 'duration manipulating' and 'success' were run with Pearson's correlation.