Serial reversal learning and cognitive flexibility in two species of Neotropical parrots (*Diopsittaca nobilis* and *Pionites melanocephala*)

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ABSTRACT Serial reversal learning of colour discriminations was assessed as an index of behavioural flexibility in two captive species of Neotropical parrots. Both species showed similar performances across serial reversals and no between species differences were observed. In a second task subjects' performances were assessed after they experienced either a low or high pre-reversal learning criterion. If reversal performances improve through processes of associative learning, a high pre-reversal criterion is expected to strengthen previously learned associations and hence impede post-reversal performances. Conversely, highly reinforced associations may facilitate the use of conditional rules that can be generalised across reversals and improve post-reversal performances. We found that high criterion subjects made fewer post-reversal errors and required fewer trials to reach criterion, than low criterion subjects. Red-shouldered macaws and black-headed caiques may therefore demonstrate capacities for solving serial reversal problems by applying conditional rules, rather than learning solely by associative processes. Such performances coincide with findings in great apes, but contrast with findings in monkeys and prosimians, which generally show impaired reversal performances when trained to a highly rigorous pre-reversal criterion. Overall, these findings suggest an evolutionary convergence of behavioural flexibility between parrots and non-human great apes.

Keywords: comparative cognition, parrots, serial reversal learning, behavioural flexibility

INTRODUCTION

The behaviours of some animals appear to be restricted by inflexible stimulus-response action patterns, whereas other animals can respond flexibly to environmental stimuli by generalising learned information across novel situations. For example, some corvids, such as blue jays (*Cynaocitta cristata*), Eurasian jays (*Garrulus glandarius*), crows (*Corvus corone*), rooks (*C. frugilegus*) and jackdaws (*C. monedula*), can extract general rules to rapidly solve a series of novel, but functionally equivalent, discrimination problems; whereas comparable studies on pigeons (*Columba livia*) reveal that they slowly learn each novel discrimination problem anew, suggesting an inability to transfer previously learned information across similar problems (Hunter & Kamil, 1971; Mackintosh, 1988; Wilson, Mackintosh, & Boakes, 1985). Pigeons fail to understand that exemplars can vary with respect to some attributes and not others, such as *same vs different* discriminations, yet they are capable of generalising *identity vs non-identity* discriminations across novel images (Blaisdell & Cook, 2005) and sounds (Cook & Brooks, 2009), and hence may show some understanding of abstract concept learning (Zentall, Wasserman, Lazareva, Thompson, & Rattermann, 2008). However, unlike capuchin (*Cebus apella*) or rhesus (*Macaca mulatta*) monkeys, pigeons generally require much more experience to do so (Katz & Wright, 2006). Primates, parrots and corvids typically outperform other animals in their capacities for analogical reasoning or solving abstract cognitive concepts. For instance, African grey parrots (*Psittacus erithacus*) can understand concepts of category and of *same-different* that are comparable to those of non-human primates (Pepperberg, 1983; 1987; 1988). Amazon parrots (*Amazona amazonica*) and hooded crows (*Corvus corone*) also spontaneously understand particular relationships between novel object pairs, demonstrating capacities for relational matching-to-sample that are on par with apes and crows (Obozova, Smirnova, Zorina, & Wasserman, 2015; Smirnova, Zorina, Obozova, & Wasserman, 2015). Capacities to generalise information across discrimination problems may therefore differ between certain species, possibly because generalising information is cognitively demanding.

Among the methods used to compare behavioural flexibility across species is serial reversal learning. Success on such tasks requires an ability to flexibly respond to a fixed set of stimuli with an alternating reward regimen (Bond, Kamil, & Balda, 2007). Serial reversal learning typically requires subjects to make a binary choice discrimination between one stimulus (i.e., a colour cue) which is repeatedly rewarded and another stimulus which is not. Subjects eventually learn to discriminate between the rewarded and non-rewarded stimuli, after which the reward contingencies are reversed (i.e. A+B– becomes A–B+). Reversed contingencies therefore require subjects to extinguish responses to previously learned associations and then re-learn each new association. Subjects initially require many trials to successfully respond to reversals, but may improve their performances with experience. However, as there are no cues to predict when the contingencies will be reversed, subjects will initially make at least one error after each reversal. Hence, an optimal performance may eventually be achieved on the second post-reversal trial. To do this, subjects must inhibit previously learned associations and adopt a *win stay–lose shift* rule: always try the response that was last rewarded, and if that is no longer rewarded, shift to the other response, otherwise stay (Levine, 1959; 1965). Animals may therefore use their previous experience to develop conditional rules that enable them to rapidly switch between contingencies; demonstrating an ability to generalise information across reversal problems (Bond et al., 2007; Day, Crews, & Wilczynski, 1999; Strang & Sherry, 2014).

Performances on reversal learning tasks have previously been used to quantify differences in learning across a wide variety of species (Bitterman, 1965). Yet distantly related species also possess dramatically different perceptual, motivational and morphological traits, which can make direct comparisons of cognitive traits difficult to interpret (Bitterman, 1960, 1965, 1975; Breland & Breland, 1961; Macphail, 1982; Pepperberg & Hartsfield, 2014; Salwiczek et al., 2012; Tomasello, Call, & Hare, 1998; Warren, 1965). One approach that attempts to alleviate such concerns is the comparative method (Harvey & Pagel, 1991). Closely related species may be expected to share similar physiological and cognitive traits as a result of common descent. Hence, by comparing closely related species that differ in certain socio-ecological aspects, any cognitive divergences can be attributed to contrasts in a species ecology or life history (Balda, Kamil, & Bednekoff, 1996; Bond, Kamil, & Balda, 2003; Bond et al., 2007; Day et al., 1999). Bond and colleagues (2003; 2007), for example, used the comparative method to reveal that increased sociality among corvids predicts aptitude on a number of cognitive tests; including serial reversal learning. An approach that has been applied specifically to serial reversal learning paradigms to reduce the confounds of interspecific differences in perception, manual dexterity and motivation, among primates, is to standardise each species' pre-reversal acquisition performances (Rumbaugh & Pate, 1984a). That is, initially training subjects to a certain level of correct choices, irrespective of the number of trials that it takes to do so, and then comparing subjects' immediate performances after the contingencies have been reversed. Thus, the structural relationships of subjects' performances are assessed, rather than making direct comparisons based on the absolute number of trials that each species requires to solve a certain problem (Bitterman, 1960, 1975; Mackintosh, 1988). The extent of pre-reversal training, however, also appears to have contrasting influences on post-reversal performances across different species. Prosimians and monkeys, for example, tend to show impaired post-reversal performances when trained to a rigorous pre-reversal criterion of 84% correct choices, but enhanced post-reversal performances when trained to a low pre-reversal criterion of 67% correct choices (Rumbaugh & Pate, 1984b). Conversely, non-human apes show enhanced performances when trained to a high pre-reversal criterion of 84% correct choices and impaired post-reversal performances when trained to a low criterion of 67% correct choices (Rumbaugh & Pate, 1984b). Hence, as the strength of the learning criterion increases, prosimians and monkeys have difficulty inhibiting their responses to previously learned associations (De Lillo & Visalberghi, 1994; Rumbaugh & Pate, 1984a, 1984b). Consequently, prosimians and monkeys are considered to solve serial reversal problems through associative processes of repeated conditioning and extinction (De Lillo & Visalberghi, 1994; Rumbaugh, 1970; Rumbaugh & Pate, 1984b). Mixed results have however been reported for rhesus macaques (*Macaca mulatta*) (Essock-Vitale, 1978; Washburn & Rumbaugh, 1991) and capuchin monkeys (*Cebus apella*) (Rumbaugh, 1970) subjected to different testing procedures; although recent studies place capuchin performances among those of other monkeys rather than apes (Beran et al., 2008; De Lillo & Visalberghi, 1994). By contrast, the improved post-reversal performances of apes at high training criterions (Essock-Vitale, 1978; Rumbaugh & Pate, 1984a, 1984b) suggest that they may understand the underlying principles of serial reversals (Shettleworth, 2010) and have been considered to reveal greater flexibility in their learning performances (Rumbaugh & Pate, 1984a, 1984b).

Such qualitative differences in learning processes among primates suggest that the ability to generalise conditional rules across reversal tasks may be cognitively demanding as it appears restricted to larger-brained species, such as apes (Rumbaugh, 1971).

Parrots and corvids possess a large cortical-like area relatively to their overall brain size (Iwaniuk, Dean, & Nelson, 2005) and high neuronal densities (Olkowicz et al., 2016), which may reflect their ability to flexibly transfer rules to novel situations (Güntürkün, Ströckens, Scarf, & Colombo, 2017). We are however unaware of any studies that have directly compared the serial reversal learning performances of species of these families at high and low pre-reversal criteria. Yet there is precedence to suggest that both families demonstrate flexibility on similar paradigms. Red-billed blue magpies (*Urocissa erythrorhyncha*) and Yellow-crowned Amazon parrots (*Amazona ochrocephala*), for instance, outperformed White Leghorn chickens (*Gallus gallus domesticus*) and Bobwhite quails (*Colinus virginianus*) on serial reversals of a spatial discrimination problem (Gossette, Gossette, & Riddell, 1966). Corvids, in particular, show rule learning across a number of different paradigms. For example, Eurasian jays (*G. glandarius*), jackdaws (*C. monedula*), rooks (*C. frugilegus*) and crows (*C. corone*), but not pigeons (*C. Zivza*), demonstrate abilities to solve problems that require the abstraction of a general rule across a change of stimuli, such as matching or oddity discriminations (Wilson et al., 1985) and learning-set problems (N. J. Mackintosh, 1988). Other corvids, such as pinion jays (*Gymnorhinus cyanocephalus*), Clark's nutcrackers (*Nucifraga columbiana*) and western scrub jays (*Aphelocoma californica*) also demonstrate capacities to positively transfer learned rules between colour and spatial serial reversal problems (Bond et al., 2007). Finally, blue jays (*Cyanocitta cristata*) transfer learned information from successive reversals to better solve learning set problems by applying a *win stay–lose shift* strategy (Kamil, Jones, Pietrewicz, & Mauldin, 1977). Although the above studies suggest that many species of corvids are capable of flexible learning, there are few studies that use comparable paradigms to investigate such flexibility in parrots. Yet there is convincing evidence to suggest flexible learning in parrots, such as an ability to understand abstract concepts of category and of *same-different* discriminations (Pepperberg, 1983; 1987; 1988), transfer physical concepts of object relations across novel problems (van Horik & Emery, 2016), and their performances on an array of complex problems show similarities to those of non-human primates and human children (Pepperberg, 2013). Together these findings suggest that parrots and corvids, along with apes, demonstrate capacities for generalised learning and flexible behaviour.

Parrots are a suitable family for investigating behavioural and cognitive flexibility as they are K-selected (Pepperberg, Gray, Lesser, & Hartsfield, 2017), and share with apes and corvids many of the socio-ecological traits that have been considered prerequisites for the evolution of cognition, such as a relatively large brain size, manual dexterity, extractive foraging, longevity and a large multi-layered social organisation (van Horik & Emery, 2011; van Horik, Clayton, & Emery, 2012). Two experiments are reported in the current study. In the first experiment, red-shouldered macaws (*Diopsittaca nobilis*) and black-headed caiques (*Pionites melanocephala*) were presented with a serial reversal learning task involving colour discriminations. The performances of each species were compared as a suggested index of their behavioural flexibility (Bond et al., 2007). To validate claims of behavioural flexibility, we first compared the reversal learning performances of two species of social parrots, black-headed caiques and red-shouldered macaws, on a serial reversal learning task. Previous findings suggest that socio-ecological differences can influence serial reversal learning performances in corvids (Bond et al., 2003, 2007). As both red-shouldered macaws and black-headed caiques possess a similar relative brain size (Iwaniuk et al., 2005) and live in complex social groups (Juniper & Parr, 2003), we may therefore expect both species to demonstrate similar responses to the alternating contingencies. However, given that red-shouldered macaws and black-headed caiques naturally inhabit contrasting environments (Juniper & Parr, 2003), any difference in their ability to respond flexibly to a serial reversal paradigm may also result from cognitive adaptations that are driven by the respective selection pressures of a given environment.

To further investigate behavioural flexibility in parrots, we also presented subjects with a second experiment. Here two alternative hypotheses are addressed: (1) that parrots' reversal learning performances improve solely through processes of associative learning, conditioning and extinction; or (2) that parrots are capable of alternative modes of learning, by generalising conditional rules across serial reversal discrimination problems. To do this, all subjects were pooled and randomly assigned to one of two conditions that required either a high or low learning criterion of successful discriminations prior to each reversal. High Criterion subjects were therefore exposed to a stricter pairing of the colour associations and hence may be confronted with greater interference during their post-reversal trials, potentially requiring a greater number of trials to extinguish and then re-learn each new contingency. By contrast, subjects exposed to a Low Criterion of learning may experience less interference during post-reversal trials. Hence, if parrots use only associative learning to solve each reversal problem, then we predict subjects in the High Criterion group to make more errors than Low Criterion subjects. Conversely, if subjects in the High Criterion group solve post-reversals with fewer errors than Low Criterion subjects, then there must be some additional generalisation of information across reversals; suggesting that their performances may be facilitated by the use of conditional rules.

GENERAL METHODS

Subjects and Housing

Four red-shouldered macaws: No.2, No.4, No.5, and No.8, and four black-headed caiques: Green, Gold, Purple, and Red, participated in this study (hereafter macaws and caiques). All subjects were male, with the exception of one female macaw (No.4). All subjects were hand-reared, approximately two years old when tested. Each species was housed in a separate indoor aviary (2m^3). None of the subjects had experience with serial reversal learning tasks, but they were experienced with a number of tasks employing object manipulation, including removing food hidden under lids or cups. Both species were raised under identical conditions and provided with equal experiences. Food and water were provided *ad libitum* and subjects' participation was voluntary.

Apparatus and Training

Two 6 cm diameter plastic lids, of different colours (depending on the experiment; see details below), were attached to a symmetrical wooden base (28 cm x 7 cm), and separated by 12 cm. Both lids were fixed to hinges and each concealed a food-well that could be baited with a reward of crushed Lafeber Nutri-Berries. More specific details of the experimental procedures are provided below. During training trials, the apparatus was presented to subjects without lids and with one food-well containing a reward. After subjects fed from the apparatus without hesitation, an orange lid was fixed to each of the baited food wells, again with only one well baited. The location of the baited well was pseudorandomised across training trials so that it did not occur on the same side over more than two consecutive trials. This procedure attempted to control for the formation of side biases and facilitate subjects' searching behaviours. To proceed to test, subjects were required to retrieve the concealed food by opening the lids at least ten times in one 10min session. Training trials were conducted *ad hoc* and no data were recorded for these sessions, as performances between birds were not comparable as some individuals required greater encouragement to interact with the apparatus through social facilitation from the experimenter.

Procedure

Subjects were not food deprived, although testing was conducted in the morning prior to their regular feeding schedule. Each subject was provided with one session of 10 trials per day. The presentation of rewarded and un-rewarded coloured lids was counterbalanced across subjects. To prevent the development of side biases, the position of the lids (i.e. left or right hand side presentation) was pseudorandomised within sessions so that the lids did not occur on the same side for more than two consecutive trials. Each subject was tested individually in a familiar enclosure (2m^3) where they were visually isolated from all other subjects. During testing days, all subjects participated in the experiment in a randomised order. Subjects were familiar with being handled by the experimenter and were transferred to the experimental cage by hand. Daily trials typically began at 08:30 and ceased around 13:00 although duration of each testing session, and the corresponding inter-trial intervals, varied depending on the subject's motivation to interact with the apparatus. The duration of a typical testing session was between 15-20 minutes per bird. During testing trials, the experimenter attempted to avoid providing subjects with any inadvertent cues to the location of the concealed reward by holding and presenting the apparatus in a symmetrical fashion and then placing his hands behind his back and looking only at the centre of the apparatus. Moreover, we consider it unlikely that experimenter cues influenced performances as similar studies have shown that African grey parrots do not readily attend to an experimenters eye-gaze direction (Giret, Miklósi, Kreutzer, & Bovet, 2009). Subjects were only allowed to upturn one lid per trial and were considered to have made a correct choice if they chose the baited lid. Hence, if subjects upturned the correct lid, they were allowed to retrieve the food reward. However, if subjects upturned the un-baited lid, then the apparatus was immediately removed. If subjects failed to upturn the baited lid on one trial, the succeeding trials followed the predetermined pseudorandomised order. The apparatus was re-baited out of view of the subject. Subjects that chose the same side over six consecutive trials in one block were considered to have developed a side bias. To correct for side biases, we presented the baited lid on the non-preferred side until the subject chose the baited side for two consecutive trials. Trials then reverted to the original pseudorandomised configuration. All trials, including side-bias-corrected and non-corrected trials were included in the subsequent analyses. We recorded all trials with a digital camcorder (JVC Everio, Model No. GZ-MG645BEK, Malaysia) and scored the number of number of trials and the number of errors to reach criterion for the initial colour association and for each subsequent reversal.

Data Analysis

Details of the number of correct trials to reach the reversal criterion, for each experiment, are described in the corresponding sections below. As any effects of extinction were expected to be most prominent in the initial post-reversal trials (Bond et al., 2007), reversal learning performances were assessed by comparing differences in errors in the first 10 post-reversal trials across subsequent reversals. We ran separate Generalised Linear Mixed-Effect Models (GLMM) with a poisson error structure for our two dependent variables (trials to criterion, and number of errors made in the first 10 post reversal trials), in R version 1.1.383 (R Development Core Team, 2014) using the lme4 package (Bates, Maechler, Bolker, & Walker, 2015). In each model (depending on the experiment) we included either species, or criterion (high or low) as fixed effects and bird identify as a random effect to control for pseudoreplication. Observational Level Random Effect (i.e. row number) were also included in each model to control for overdispersion (Harrison, 2014). In Experiment 1, we used GLMM to compare performances between species, by assessing the number of trials each species took to reach criterion in the initial colour association and first reversal discriminations. We also used GLMM to compare the number of trials each species took before reaching criterion and the number of errors they made in the first 10 post reversal trials across reversals. In Experiment 2, we used GLMM to assess performances between the High and Low Criterion groups by comparing the number of trials to reach each criteria and number of errors made in the first 10 post reversal trials for each reversal. A random subset of 46 sessions (724 trials) were coded by three naïve observers (KW and LH) for inter-observer reliability. Observers coded whether the subject made a correct or incorrect choice on a given trial. Observer congruence was 98%.

EXPERIMENT 1: Serial reversal learning performances

Methods

Apparatus

The same apparatus as in the training sessions was used but with novel coloured lids, one green and one blue.

Procedure

Subjects were presented with at least one block of 10 trials per day. If subjects reached a predetermined criterion of seven consecutive correct trials in one block of 10 trials (significant according to a binomial test with a probability of choosing either side set at 0.5), they were immediately presented with one block of 10 trials with reversed contingencies (i.e. S+ becomes S– and vice versa). To avoid satiation and encourage motivation to interact with the apparatus, subjects were presented with only one post-reversal block per day. Hence, subjects could receive a maximum of only two consecutive blocks of 10 trials per day. There were no occurrences where subjects reached criterion again during their first post-reversal block. Each subject was presented with as many blocks as required to reach eight serial reversals.

Results

Both species required fewer trials to reach criterion on the colour association discrimination than in the first reversal (GLMM: Z = 4.89 ± 0.14 SEM; P < 0.001, Figure 1). However, macaws required fewer trials than caiques to reach criterion on the initial colour association discrimination and the first reversal (GLMM: Z = -2.10 ± 0.14 SEM; P = 0.04, Figure 1). Yet, there were no overall differences in performances between caiques and macaws across the serial reversals (Figure 2a). The two species did not differ in the number of trials to reach criterion (macaws summed trials mean = 493.25 ± 67.55 SEM; caiques summed trials mean = 539.50 ± 44.23 SEM; GLMM: Z = -0.72 ± 0.10 SEM; P = 0.47) or errors made in their first 10 post reversal trials (macaws summed errors mean = 57.25 ± 2.18 SEM; caiques errors mean = 61.75 ± 1.37 SEM; GLMM: Z = -0.73 ± 0.12 SEM; P = 0.46) across the serial reversal discriminations (Figure 2). We found no difference in errors, or trials across serial reversals (Table 1).

The number of initial post-reversal blocks (i.e. the first ten trials after each reversal of the colour contingencies) where subjects developed a side bias were as follows (R1 represents the first reversal; R8 represents the last reversal): Macaws; No.2 (R1), No.4 (R7, R8), No.5 (R5), No.8 (R2, R6, R7), Caiques; Green (R2, R4, R6), Gold (R5), Purple (R5, R6, R8), Red (R3, R6).

-----------INSERT Figure 1--------------

-----------INSERT Figure 2--------------

-----------INSERT Table 1--------------

EXPERIMENT 2: High Criterion and Low Criterion Learning

Methods

Subjects, Apparatus and Training

The same subjects and general procedures as in Experiment 1 were used, however, in this experiment novel coloured lids, either pink with a green circle sticker or yellow with an orange circle sticker, were introduced. The presentation order of the rewarded colour lids was counterbalanced across subjects.

Procedure

As no between species differences were observed in Experiment 1, subjects were pooled and individuals from each species were randomly assigned into either High or Low Criterion conditions. Subjects were presented with an initial discrimination problem requiring them to learn the Colour Associations, as in Experiment 1, and then subsequent serial reversal trials. However, in this experiment, each block consisted of up to 20 trials (rather than the 10 trial blocks presented in the previous experiment).

The High Criterion group (No.4, No.5, Green & Red) were presented with reversals once they scored at least 19/20 correct choices in one 20 trial session. Conversely, the Low Criterion group (No.2, No.8, Gold & Purple) were presented with reversals once they achieved either: 15 correct choices in one 20 trial session, 7 consecutive correct choices in the first 10 trials of one session, 9/10 correct choices in either the first or last 10 trials of a 20 trial session, or 10 consecutive correct choices within one 20 trial session. The Low Criterion group included multiple pre-reversal criteria to ensure that the number of trials subjects required to reach each learned association was minimised and hence subjects were not over-trained. All criteria were significant according to a binomial test, with a probability of choosing either side set at 0.5, and alpha set at 0.05. Subjects were presented with as many trials as required to reach 11 reversals.

If subjects reached criterion within one 20 trial session, they were immediately presented with one reversal session. On two occasions, subjects (No.8 and Gold) reached criterion within their first post-reversal session (on the same day). On these occasions, we did not provide a further post-reversal session and resumed testing on the following day. Subjects therefore experienced a maximum of up to 40 trials per day. These procedures were used to maintain motivation by prohibiting subjects from becoming satiated on rewards. Side biases were corrected for, and all corrected and non-corrected trials were included in the analysis as in Experiment 1. We ceased testing individual subjects once they had participated in 11 reversals. All trials were coded live but digitally recorded for subsequent analysis if required.

Results

Low Criterion (mean = 72.75 ± 23.86 SEM) and High Criterion (mean = 75 ± 9.57 SEM) groups did not differ in the number of trials to reach criterion during the initial Colour Association discriminations (GLMM: Z = 0.92 ± 0.16 SEM; P = 0.36). There were also no differences in the number of trials to reach criterion between the Colour Association and first Reversal (GLMM: Z = 1.45 ± 0.16 SEM; P = 0.15). There were no differences in the number of trials to complete 11 serial reversals between the High and Low Criterion groups (Low summed mean = 744.75 ± 24.87 SEM; High summed mean = 695 ± 28.72 SEM; GLMM: Z = 0.85 ± 0.11 SEM; P = 0.39). However, subjects in the High Criterion group made fewer errors during the first 10 post reversal trials across successive reversals (R1-R11) than subjects in the Low Criterion group (GLMM: Z = -3.58 ± 0.09 SEM; P < 0.001; Figure 3). The number of errors, and trials to reach criterion differed across reversals (Table 3; Table 4). Subjects in the High Criterion condition showed a consistent reduction in post reversal errors from their seventh reversal onwards (Table 3), and a reduction in the number of trials to reach criterion from their third reversal (Table 4). Conversely, subjects in the Low Criterion condition showed no reduction in errors across serial reversals (Table 3), and an inconsistent reduction in trials to reach criterion on their fourth, seventh and ninth reversals (Table 4).

The number of initial blocks where subjects developed a side bias were as follows: High Criterion; No.4 (R4, R10), No.5 (R4, R5), Green (R6), Red (R1), Low Criterion; No.2 (R3), No.8 (R1, R2, R7, R10, R11), Gold (R4, R5, R9, R10, R11), Purple (R2, R3, R7, R10, R11).

-----------INSERT Figure 3--------------

-----------INSERT Table 2--------------

-----------INSERT Table 3--------------

DISCUSSION

In Experiment 1, the serial reversal learning performances of two species of parrots were investigated, as a suggested index of their behavioural flexibility (Bond et al., 2007). Macaws took fewer trials to reach criterion during the initial Colour Acquisition and first reversal. It is unlikely that these findings were due to differences in experiences, as both species had been reared, from birth, in a standardised environment with identical enrichment. It is possible that the superior performance of macaws was due to subtle differences in their overall brain-size; macaws 4.29% vs caiques 3.80% of body mass (Iwaniuk et al., 2005), yet sample sizes are low for such comparisons (macaws n = 3; caiques n = 8) and hence such interpretations remain speculative. Both species, however, showed comparable performances across subsequent serial reversals. Both species required more trials to reach criterion during the first reversal than compared to the Colour Association problem, suggesting that the previously learned contingencies initially impaired subjects' reversal performance. Hence, both species required trial and error experience of the reversed contingencies to first extinguish previously learned associations and then re-learn each following association anew. However, when trained to a pre-reversal criterion of seven consecutive correct choices in one block of 10 trials per day, we found no improvement in performances across serial reversals. Although a variety of taxa demonstrate improvements in performance across serial reversals (Bond et al., 2007; Day et al., 1999; Strang & Sherry, 2014), it remains possible that either the learning criteria in the current study was not stringent enough to facilitate improvement across reversals for caiques and macaws, or that these birds required a greater number of serial reversals before any improvement could be observed.

To determine whether the serial reversal learning performance of red-shouldered macaws and black-headed caiques were mediated solely by associatively learned processes or whether they were capable of using conditional rules to improve their performance, we randomly assigned two individuals from each species to either a High or a Low Criterion pre-reversal learning condition (Experiment 2). Although there were no differences in the number of trials to learn the Colour Association between the Low and High Criterion groups, subjects in the High Criterion group made fewer post-reversal errors than subjects in the Low Criterion group across 11 serial reversals. These findings suggest that subjects in the High Criterion group may therefore use the enhanced strength of previously learned contingencies to improve their reversal performances; in contrast to subjects in the Low Criterion group, which showed no improvement across reversals.

When presented with reversed contingencies, each previously learned association requires a number of trials before it is lost through extinction. Each new association then requires further trials to re-learn through conditioning. In the current study, the relatively poor performances of Low Criterion subjects suggests that their response to the reversals was limited to associative learning processes. Conversely, when presented with a high pre-reversal criterion, subjects made fewer post-reversal errors across successive reversals. Rather than being impaired by the enhanced strength of the conditioned associations, subjects appear to use this information to better understand the conditional principles underlying serial reversals. Such findings are consistent with the reversal performances of other large-brained species, such as non-human great apes, but contrast with those of monkeys and prosimians (Essock-Vitale, 1978; Rumbaugh & Pate, 1984a, 1984b). Although the enhanced associative strength of the contingencies may have allowed subjects to better respond to the reversed contingencies by generating a conditional rule, these findings show no evidence of a *win stay-lose shift* rule within 11 serial reversals. Support for a *win stay-lose shift* rule would only be revealed if subjects made one error after they experienced an unpredicted reversal of the previously learned contingencies. High Criterion subjects, however, made approximately three errors in their first 10 post reversal trials; although their performances may have improved with further experience. Nonetheless, results from the current study support our second hypothesis that parrots' reversal performances are not solely restricted by associative learning mechanisms, but that parrots may be capable of other cognitive modes of learning that involve an ability to generalise conditional rules across discrimination problems.

It is possible, albeit unlikely, that the High Criterion group produced fewer post reversal errors due to an Overtraining Reversal Effect (ORE). First observed by Reid (1953), the ORE is a phenomenon where overtraining on discrimination problems enhances post-reversal performances. Reid (1953) presented rats with a black-white discrimination problem in a Y maze. All of the rats were initially trained to a specific criterion, and then separated into three conditions depending on the amount of their post-criterion training. Rats exposed to increasingly rigorous training regimes made fewer post-reversal errors. Such findings are considered paradoxical as overtraining, according to classical learning theory, is predicted to increase the excitatory strength of S+ and inhibitory strength of S– and thus impede extinction when contingencies are reversed (Hull, 1943; Spence, 1956). Although ORE is commonly observed in rat studies, it is rarely reported in monkeys (Essock-Vitale, 1978; Sutherland & Mackintosh, 1971), with the exception of one account from stump-tailed macaques (Schrier, 1974). Typically, when presented with increasing numbers of acquisition trials, monkeys show impaired post reversal performances and do not improve with subsequent experience. Like monkeys, overtraining has also been reported to impair reversal performances in birds, such as myna (Gossette, 1969), chicks (Mackintosh, 1965; Warren, Brookshire, Ball, & Reynolds, 1960), pigeons and Japanese quail (Gonzalez, Berger, & Bitterman, 1966), suggesting that in these species, the ability to learn each new contingency is governed by processes of association and extinction. However, it has been suggested that post-reversal performances typical of an ORE should not only improve following overtraining, but that performances on early post-reversal trials should also be initially impaired following overtraining (Sutherland & Mackintosh, 1971; pp. 258-261). In the current study, subjects in the High Criterion condition showed a significant reduction in errors across subsequent reversals, although subjects in the Low Criterion condition did not improve their performances. If these findings were due to an ORE, we might also expect subjects in the High Criterion condition to perform significantly worse than Low Criterion subjects during initial reversals. However, performances on the first 10 post-reversal trials across the first three reversals were comparable for both Low and High Criterion subjects (see R1-R3; Figure 3), revealing that subjects were not initially impaired by differences in reversal criteria. These findings therefore suggest that subjects' performances in the High Criterion condition were unlikely to be a result of an ORE.

Parrots in the current study, like corvids (Bond et al., 2007; Hunter & Kamil, 1971; Mackintosh, 1988; Wilson et al., 1985) and non-human great apes (Essock-Vitale, 1978; Rumbaugh & Pate, 1984a, 1984b), show capacities for generalised rule learning of reversal learning discrimination problems. Rumbaugh (1995) argues that great apes, because of their ability to transfer abstract information across reversal tasks, are capable of mediating their behaviours through more cognitively demanding modes of learning than monkeys and prosimians. Such findings also correspond with species' encephalisation coefficients (Jerison, 1973; Rumbaugh & Pate, 1984b), suggesting there may be a link between relative brain size and behavioural flexibility (Emery & Clayton, 2004). Further evidence of generalised learning strategies, demonstrated by the positive transfer of information across serial reversal or learning set tasks involving disparate stimulus dimensions (i.e. space and colour), also support our findings. For example, chimpanzees and a number of species of macaques (reviewed in Macphail, 1982) and corvids (Bond et al., 2007; Gossette et al., 1966; Kamil et al., 1977; Mackintosh, 1988; Wilson et al., 1985) rapidly develop generalised learning strategies, whereas rats, cats, and pigeons do not (Durlach & Mackintosh, 1986; Mackintosh & Holgate, 1969; Mackintosh, McGonigle, Holgate, & Vanderver, 1968; Warren, 1966). More recently however, pigeons have been shown to adopt a *win stay–lose shift* rule when presented with a mid-session reversal task involving short inter-trial intervals (Rayburn-Reeves, Laude, & Zentall, 2013).

There are growing accounts of flexible behaviours in parrots and corvids (Auersperg, Szabo, Von Bayern, & Kacelnik, 2012; Auersperg, von Bayern, Gajdon, Huber, & Kacelnik, 2011; Pepperberg & Carey, 2012). The relationship between brain size and behavioural flexibility suggests that relatively large brains may afford a selective advantage when responding to unusual, novel or complex socio-ecological challenges. For instance, large brains may provide a foundation for novel or altered behaviours, which may be applied to solve an array of problems through domain general cognitive processes (Sol, 2009). Moreover, as relatively large brains are found across phylogenetically distinct species, certain cognitive traits may have also evolved independently among several vertebrate groups that share similar socio-ecological selection pressures (van Horik et al., 2012). Indeed, brain size appears to be a good proxy for the ability of species to flexibly respond to environmental change and hence fluctuations in resource abundance. As such, relative brain size correlates positively with the ability of species to accommodate habitat change (Shultz, Bradbury, Evans, Gregory, & Blackburn, 2005), climatic change (Schuck-Paim, Alonso, & Ottoni, 2008), invade novel environments (Sol, Bacher, Reader, & Lefebvre, 2008; Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005; Sol, Székely, Liker, & Lefebvre, 2007; Sol, Timmermans, & Lefebvre, 2002; Sol & Lefebvre, 2000) and generate innovative foraging behaviours (Lefebvre, Reader, & Sol, 2004; Lefebvre, Whittle, Lascaris, & Finkelstein, 1997; Reader & Laland, 2002). Hence, large brains may be particularly advantageous in complex environments or habitats that are novel or likely to change.

Given that red-shouldered macaws and black-headed caiques naturally inhabit contrasting environments (Juniper & Parr, 2003), such differences do not appear to have resulted in any obvious divergences in their abilities to respond flexibly to a serial reversal paradigm. Both macaws and caiques, however, possess a similar relative brain size (Iwaniuk et al., 2005), and share a complex social organisation characterised by long-term pair bonded relationships and fission-fusion foraging groups (Juniper & Parr, 2003). Similarities in the complexity of their social relationships, rather than habitat or foraging niche, may therefore promote behavioural flexibility in these species. Social complexity has long been considered to play an important role in the evolution of a flexible and intelligent mind (Social Intelligence Hypothesis: Humphrey 1976; Jolly, 1966), with social group size and neocortex size corresponding positively in primates (Dunbar, 1998), ungulates (Shultz & Dunbar, 2006) and cetaceans (Marino, 1996). Brain size also correlates positively in birds and mammals that form stable or pair-bonded relationships (Dunbar & Shultz, 2007; Emery, Seed, von Bayern, & Clayton, 2007; Shultz & Dunbar, 2006). Species that live in social groups, in contrast to more solitary or asocial species, may therefore develop particular cognitive adaptations to accommodate for the additional complexities that arise from maintaining relationships and flexibly interpreting others' behaviours. Hence, primates that live in groups characterised by fission-fusion social dynamics also show enhanced inhibitory control (another proposed index of behavioural flexibility), in contrast to species that live in more cohesive groups. Fission-fusion societies may therefore promote cognitive adaptations that result in greater behavioural flexibility; independent of phylogenetic relatedness or feeding ecology (Amici, Aureli, & Call, 2008). Capacities for inhibitory control have previously been demonstrated in parrots (Auersperg, Laumer, & Bugnyar, 2013; Koepke, Gray, & Pepperberg, 2015; Vick, Bovet, & Anderson, 2010) and corvids (Dufour, Wascher, Braun, Miller, & Bugnyar, 2012; Hillemann, Bugnyar, Kotrschal, & Wascher, 2014) on delayed gratification tasks. Serial reversal learning also involves inhibitory control, as it requires an ability to restrain responses to previously reinforced stimuli, and instead flexibly direct behaviours towards potentially unrewarded alternatives. Hence, it has been proposed that serial reversal learning bears resemblance to the demands of a complex social system (Bond et al., 2007). Comparative research on corvids provides support for such claims by revealing that variation in performances on serial reversal and transitive inference tasks are best explained by social complexity, rather than ecological or spatial complexity (Bond et al., 2003, 2007). The reversal learning performances in the two species of social parrots reported here may further support such claims. As such, social living may facilitate cognitive adaptations that favour an individual's ability to interpret, predict and respond flexibly to change. Behavioural flexibility may be shared among species that possess a relatively large brain size. As such, flexibility has been suggested as one of the fundamental cognitive tools that arose as a result of the evolution of complex cognition in corvids and apes (Emery & Clayton, 2004). Overall, findings from the current study provide further empirical support of an evolutionary convergence of behavioural flexibility between distantly related species that possess a relatively large brain size.

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ETHICAL STANDARDS

All research undertaken was non-invasive and therefore fell outside of the Animal (Scientific Procedures) Act, and hence did not require Home Office UK approval. Subjects were however housed in accordance with these regulations and the local ethical committee were consulted and agreed to all aspects of this research. Home Office Inspectors and veterinarians regularly visited the lab to ensure these procedures were maintained.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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Figure Legends:

Figure 1 Experiment 1. Mean number of trials (± SEM) to reach reversal criterion for the colour association (CA) and first reversal (R1) conditions, for macaws and caiques

Figure 2 Experiment 1. Mean number of errors (± SEM) for the first 10 post reversal trials across eight successive colour reversals (R1-R8) for macaws and caiques.

Figure 3 Experiment 2. Mean number of errors (± SEM) for the first 10 post reversal trials across eleven successive colour reversals (R1-R11), for Low and High Criterion conditions

Table 1 Results of GLMM of number of trials to reach criterion and errors made in the first 10 post reversal trials across serial reversals for caiques and macaws.

Table 2 Results of GLMM of number of trials to reach criterion and errors made in the first 10 post reversal trials across serial reversals for subjects trained to either a High or Low pre-reversal criterion.

Table 3 Results of GLMM of number of errors made in the first 10 post reversal trials across serial reversals for subjects trained to either a High or Low pre-reversal criterion.

Table 4 Results of GLMM of number of trials to reach criterion across serial reversals for subjects trained to either a High or Low pre-reversal criterion.

Figure 1

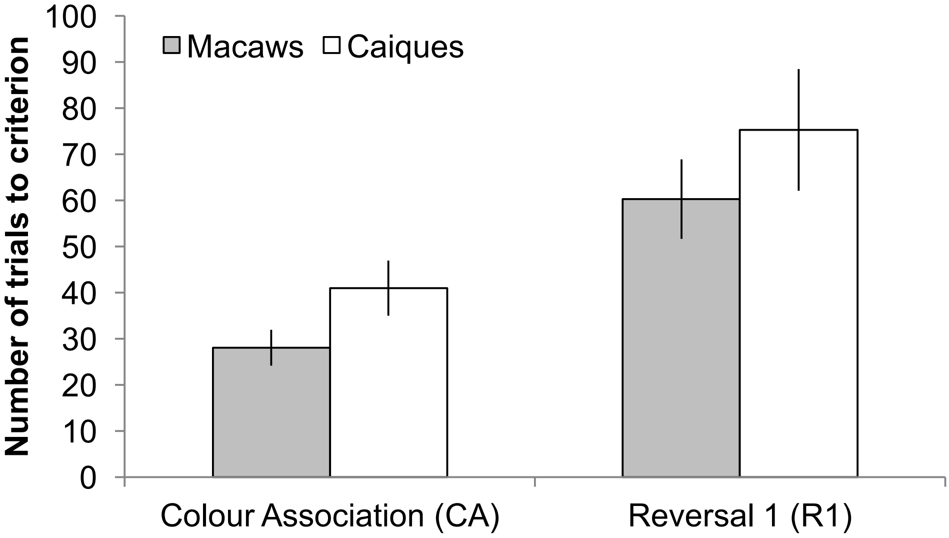
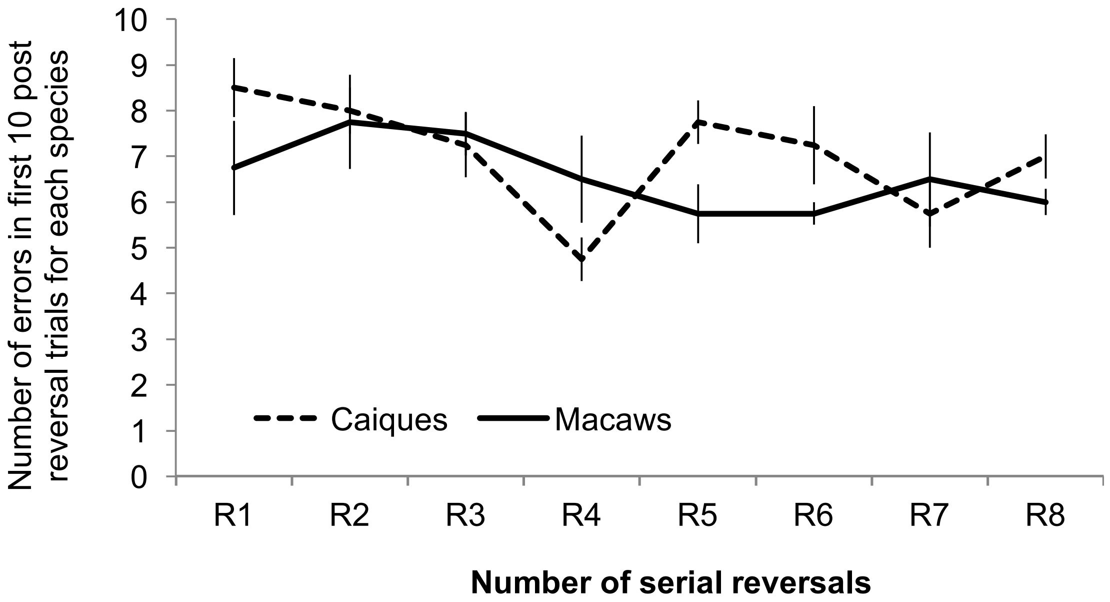

Number of trials to criterion
100
90
80
70
60
50
40
30
20
10
0
Macaws
Caiques
Colour Association (CA)
Reversal 1 (R1)

Figure 2



Number of errors in first 10 post reversal trials for each species
10
9
8
7
6
5
4
3
2
1
0
Caiques
Macaws
R1
R2
R3
R4
R5
R6
R7
R8
Number of serial reversals

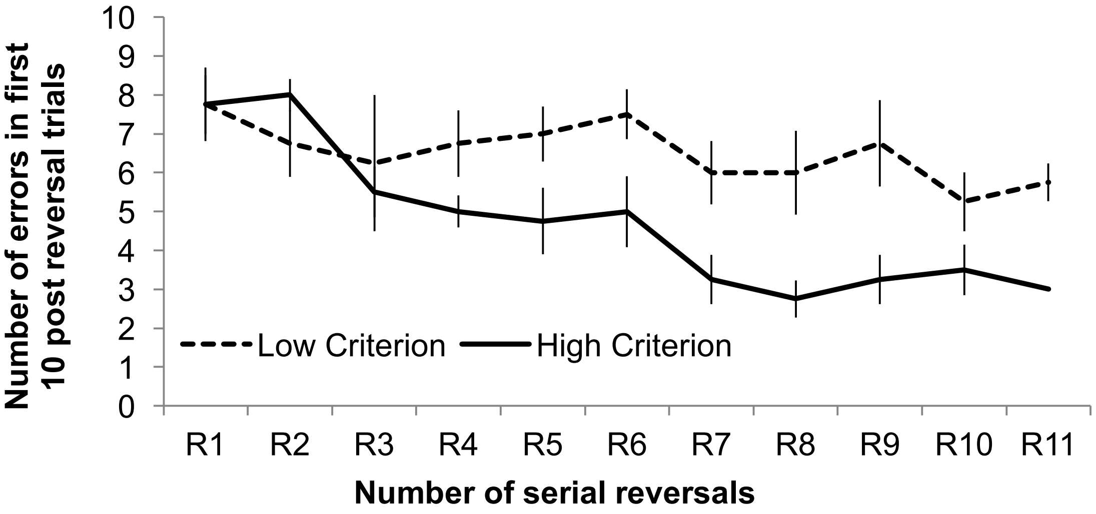

10
9
8
7
6
5
4
3
2
1
0
Number of errors in first 10 post reversal trials
Low Criterion
High Criterion
R1
R2
R3
R4
R5
R6
R7
R8
R9
R10
R11
Number of serial reversals

Figure 3

Table 1

	Errors	**Trials**
Reversal 2	Z = 0.18; 0.18 ± SEM; P = 0.86	Z = 0.59; 0.21 ± SEM; P = 0.55
Reversal 3	Z = -0.18; 0.18 ± SEM; P = 0.86	Z = -1.13; 0.21 ± SEM; P = 0.26
Reversal 4	Z = -1.55; 0.20 ± SEM; P = 0.12	Z = 0.37; 0.21 ± SEM; P = 0.71
Reversal 5	Z = -0.65; 0.19 ± SEM; P = 0.51	Z = -0.16; 0.21 ± SEM; P = 0.88
Reversal 6	Z = -0.85; 0.19 ± SEM; P = 0.40	Z = 0.60; 0.21 ± SEM; P = 0.55
Reversal 7	Z = -1.14; 0.19 ± SEM; P = 0.25	Z = -1.21; 0.21 ± SEM; P = 0.23
Reversal 8	Z = -0.85; 0.19 ± SEM; P = 0.40	n/a

Table 2

	Errors	**Trials**
Reversal 2	Z = -0.27; 0.18 ± SEM; P = 0.79	Z = -0.26; 0.15 ± SEM; P = 0.79
Reversal 3	Z = -1.43; 0.19 ± SEM; P = 0.15	Z = -2.73; 0.15 ± SEM; P < 0.01
Reversal 4	Z = -1.43; 0.19 ± SEM; P = 0.15	Z = -2.72; 0.15 ± SEM; P < 0.01
Reversal 5	Z = -1.43; 0.19 ± SEM; P = 0.15	Z = -2.91; 0.15 ± SEM; P < 0.01
Reversal 6	Z = -1.13; 0.19 ± SEM; P = 0.26	Z = -3.05; 0.15 ± SEM; P < 0.01
Reversal 7	Z = -2.49; 0.21 ± SEM; P = 0.01	Z = -3.56; 0.15 ± SEM; P < 0.01
Reversal 8	Z = -2.70; 0.21 ± SEM; P < 0.01	Z = -3.18; 0.15 ± SEM; P < 0.01
Reversal 9	Z = -2.16; 0.20 ± SEM; P = 0.03	Z = -3.96; 0.15 ± SEM; P < 0.01
Reversal 10	Z = -2.70; 0.21 ± SEM; P < 0.01	Z = -2.74; 0.15 ± SEM; P < 0.01
Reversal 11	Z = -2.70; 0.21 ± SEM; P < 0.01	n/a

Table 3

	High Criterion Errors	**Low Criterion Errors**
Reversal 2	Z = 0.13; 0.25 ± SEM; P = 0.90	Z = -0.53; 0.26 ± SEM; P = 0.60
Reversal 3	Z = -1.23; 0.28 ± SEM; P = 0.22	Z = -0.80; 0.27 ± SEM; P = 0.42
Reversal 4	Z = -1.53; 0.29 ± SEM; P = 0.13	Z = -0.53; 0.26 ± SEM; P = 0.60
Reversal 5	Z = -1.68; 0.29 ± SEM; P = 0.09	Z = -0.39; 0.26 ± SEM; P = 0.70
Reversal 6	Z = -1.53; 0.29 ± SEM; P = 0.13	Z = -0.13; 0.26 ± SEM; P = 0.90
Reversal 7	Z = -2.63; 0.33 ± SEM; P < 0.01	Z = -0.94; 0.27 ± SEM; P = 0.35
Reversal 8	Z = -2.95; 0.35 ± SEM; P < 0.01	Z = -0.94; 0.27 ± SEM; P = 0.35
Reversal 9	Z = -2.63; 0.33 ± SEM; P < 0.01	Z = -0.53; 0.26 ± SEM; P = 0.60
Reversal 10	Z = -2.47; 0.32 ± SEM; P = 0.01	Z = -1.38; 0.28 ± SEM; P = 0.17
Reversal 11	Z = -2.79; 0.34 ± SEM; P < 0.01	Z = -1.09; 0.15 ± SEM; P = 0.27

Table 4

	High Criterion Trials	Low Criterion Trials
Reversal 2	Z = -0.49; 0.11 ± SEM; P = 0.62	Z = -0.09; 0.22 ± SEM; P = 0.93
Reversal 3	Z = -5.47; 0.12 ± SEM; P < 0.01	Z = -0.78; 0.22 ± SEM; P = 0.44
Reversal 4	Z = -2.73; 0.11 ± SEM; P < 0.01	Z = -2.38; 0.23 ± SEM; P = 0.02
Reversal 5	Z = -6.24; 0.12 ± SEM; P < 0.01	Z = -0.60; 0.22 ± SEM; P = 0.55
Reversal 6	Z = -7.05; 0.12 ± SEM; P < 0.01	Z = -0.36; 0.22 ± SEM; P = 0.72
Reversal 7	Z = -4.05; 0.11 ± SEM; P < 0.01	Z = -2.74; 0.23 ± SEM; P < 0.01
Reversal 8	Z = -6.25; 0.12 ± SEM; P < 0.01	Z = -0.96; 0.22 ± SEM; P = 0.34
Reversal 9	Z = -5.47; 0.12 ± SEM; P < 0.01	Z = -2.49; 0.23 ± SEM; P = 0.01
Reversal 10	Z = -4.72; 0.11 ± SEM; P = 0.01	Z = -1.23; 0.22 ± SEM; P = 0.22