

Means–end comprehension in four parrot species: explained by social complexity

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Abstract A comparative approach is required to investigate the evolutionary origins of cognitive abilities. In this paper, we compare the performance of four parrot species, spectacled parrotlets (*Forpus conspicillatus*), rainbow lorikeets (*Trichoglossus haematodus*), green-winged macaws (*Ara chloroptera*) and sulphur-crested cockatoos (*Cacatua galerita triton*) in standardized string-pulling and string-choice paradigms. We varied the spatial relationship between the strings, the presence of a reward and the physical contact between the string and the reward to test different cognitive skills requiring means–end comprehension. The species tested showed a high individual and inter-specific variation in their ability to solve the tasks. Spectacled parrotlets performed best among the four species and solved the most complex choice tasks, namely crossed-string task and broken-string task, spontaneously. In contrast, macaws and cockatoos failed to identify the correct string in these two tasks. The rainbow lorikeets were outperformed by the parrotlets, but outperformed in turn the macaws and the cockatoos. The findings can be best explained by the variation in social complexity among species, rather than in their ecology.

Keywords *Ara chloroptera* · *Cacatua galerita triton* · Comparative cognition · *Forpus conspicillatus* · Means–end relationship · *Trichoglossus haematodus*

Introduction

Biologists have long assumed that socio-ecological demands explain cognitive variation across species in both mammals and birds (Emery and Clayton 2004; Marler 1996; Seyfarth and Cheney 2002). Foraging (Harvey et al. 1980; Ratcliffe et al. 2006; Reader and MacDonald 2003) and social relationships (Dunbar 1998, 2008) have been identified as the main selective pressures shaping brain size evolution. Provided that “big brains” in birds correlate strongly with lifestyle variables such as social complexity (Burish et al. 2004) and diet (Lefebvre and Sol 2008) and assuming that domain-general cognition correlates with brain size (Sol et al. 2005), there should be demonstrable differences in performance in terms of general intelligence across species differing in their social structure and/or foraging techniques.

These technological and social brain hypotheses have increased the recent interest in problem-solving skills. Such skills, however, may not directly reflect ecological challenges (currently) faced by a species, but rather their ability to understand and to solve a novel situation. Problem-solving skills have often been tested with tasks that require some understanding of causal relationships by the subjects without needing to be solved intuitively. One such test is provided by string-pulling tasks. String-pulling requires the integration of a large number of different motions in a precise order to solve a problem. Since the problem is unlikely to have been encountered before in the animal’s life, we can test whether it can be solved without trial-and-error learning. An additional

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advantage of string-pulling experiments is their structure, which is easy to understand and to handle (Bagozkaya et al. 2010). Here the ‘proto-tool’ (the string) is connected to the reward from the beginning, enabling a direct comparison among species limited, for example, in their manipulative abilities (i.e. the majority of non-primate species).

The ability to pull a string to obtain food has been demonstrated in a variety of bird species. However, the possible mechanisms of problem-solving are different: for small song birds, for example, it has been suggested that the performance is based either on a pre-programmed behaviour or on trial-and-error learning (Altevogt 1953; Seibt and Wickler 2006; Vince 1961). So far, only corvids and parrots have been credited with showing insight into solving more complex tasks involving several strings spontaneously (Heinrich 1995; Heinrich and Bugnyar 2005; Krasheninnikova and Wanker 2010; Pepperberg 2004; Schuck-Paim et al. 2009; Werdenich and Huber 2006). Using a set of choice problems with several strings varying in their relationship to each other or to the reward allows testing whether the bird really understands the means–end relationship between string and reward and enables the analysis of various cognitive abilities involved in the problem-solving skills (Bagozkaya et al. 2010).

The aim of this study was to analyse the performance of four parrot species (two originally from Australia and two from South America) in standardized string-pulling and string-choice tasks, to test whether or not variation in cognitive skills co-varies with different degrees of social complexity or whether it could be better explained by differences in diet and feeding behaviour.

To test our hypothesis, we chose four parrot species with different social systems, spectacled parrotlets (*Forpus conspicillatus*), rainbow lorikeets (*Trichoglossus haematodus*), green-winged macaws (*Ara chloroptera*), and sulphur-crested cockatoos (*Cacatua galerita triton*). Spectacled parrotlets live in groups with a complex social dynamic where they form different social subunits, which frequently split and merge thus providing for a high number of social interactions occurring throughout the day. Furthermore, they are the only species tested that form crèches, where offspring pass through the socialization process (Wanker 2002; Wanker et al. 1996). In contrast, green-winged macaws and sulphur-crested cockatoos live in small, stable family groups centred around a single breeding pair and their offspring (Gilardi and Munn 1998; Styche 2000; Uribe et al. 1982). This social structure is also maintained when big foraging or roosting flocks of hundreds of individuals congregate (Haverschmidt 1954). Rainbow lorikeets live in fluid social groups of 10–40 individuals and congregate to large communal night roosts, but lack subunits such as crèches (Chapman 2005; Ulrich et al. 1972; Utschick and Brandl 1989; Waterhouse 1997).

In addition, the study subjects allow a variety of pairwise comparisons with regard to different ecological variables (e.g. diet and feeding mode) potentially driving the success in string-pulling tasks, since the species share some living conditions in the wild, while differing significantly in others.

Materials and methods

Subject species

The species from South America, parrotlets and macaws, are closely related, as both belong to the tribe Arini, but they differ in diet and social organization. The Australasian species, cockatoos, and lorikeets, are more distantly related (as cockatoos are in a sister relationship to all remaining psittaciforms (Psittacidae without Nestorini and Strigopini; Wright et al. 2008), and lorikeets belong to the most recent parrot tribes, but both are characteristic species of Australia preferring similar ecological habitats such as dry, open country, semi-desert, and savannah (Forshaw 2002). Furthermore, while the macaws share an arboreal feeding mode with the lorikeets, the parrotlets forage more similarly to cockatoos, searching for seeds on the ground (Koutsos et al. 2001).

Experimental predictions

Similarities in string-pulling performance between parrotlets and macaws should suggest that their close phylogenetic relationship may be responsible for similar cognitive adaptations. Similarities between parrotlets and lorikeets and between macaws and cockatoos, on the other hand, may be evidence for the influence of the species’ social organization. Any similarities in performance between macaws and lorikeets and between parrotlets and cockatoos would point at feeding mode as a potentially important factor. Furthermore, if there are no differences among the species tested, we can assume that the ability to solve various string-pulling tasks is a general trait of parrots and already occurred in the common ancestor of the psittacid lineage. Finally, a lack of any similarities in performance might also point at a possible influence of the diet on the cognitive adaptations, because the species tested feed on different types of food (parrotlets on small grass seed and fruits, macaws mainly on hard nuts, cockatoos on large seeds and bulbs, and lorikeets consume mainly nectar with a tongue especially adapted to this purpose; see Koutsos et al. 2001).

Housing conditions

All species tested were kept in semi-natural conditions, that is, in large free-flight aviaries with a variety of branches,

trunks, and perches, where visitors were able to walk into. No artificial toys, only green branches for playing and nibbling, were provided regularly. All parrots were hatched in captivity (at their institutions) and raised by their parents. All subjects were accustomed to human presence. Therefore, the living conditions in captivity were comparable across the species.

The spectacled parrotlets were obtained from the breeding stock of the Zoological Institute at the Biozentrum Grindel of the University of Hamburg. The birds were kept together in a group of 12 un-paired individuals and 5 pairs in one indoor aviary complex with an adjacent indoor aviary (6 × 3 × 2 m). They were held in two connected compartments (size of each compartment: length × width × height = 2.1 × 3.33 × 2.83 m). Nine individuals showed no interest and did not approach the string-pulling apparatus. Five individuals stopped their string-pulling behaviour after the first attempt to pull the string due to the beginning of the breeding process. Thus, the number of remaining birds tested was eight. The humidity in the area was regulated by air conditioning and varied between 40 and 60 % RH. The ambient temperature was kept between 22 and 25 °C. ‘Bird Lamp’ neon lamps were timed to simulate a day–night rhythm of 12:12 h. A large trunk with twigs was located in the centre of every compartment serving as a ‘grouptree’ (Wanker et al. 1996). Some more twigs and rotten trunks were attached, freely swinging so that the birds could perch near their nest boxes. The birds were fed three times per week (on Mondays, Wednesdays, and Fridays) with sunflower seeds, fruits, vegetables, and a seed mixture for forest birds. Once a week, pre-germinated seeds were given with a vitamin and mineral additive (‘KORVIMIN ZVT+Reptil’). Fresh water was provided ad libitum every day.

The rainbow lorikeet group contained 10 adult and three fledglings (fledglings did not participate in any test) that lived in an indoor free-flight aviary (8 × 10 × 8 m) styled as a tropical garden with an adjacent cage (4.5 × 2 × 2.5 m) in the Tierpark Hagenbeck, Hamburg. Birds were fed every day at 7 a.m. and 6 p.m. with lorikeet-porridge and fruits. The aviary was illuminated by several windows. The rainbow lorikeets were housed together with a group of ring-tailed lemurs (*Lemur catta*). The birds were tested in the adjacent cage only, to avoid any disturbance by the lemurs.

The green-winged macaws were kept together with a scarlet macaw (*Ara macao*) and the sulphur-crested cockatoos in an outdoor aviary (17.5 × 5 × 3 m) with an adjacent indoor aviary (7 × 2.5 × 3 m) at Tierpark Gettorf, Germany. The group contained four green-winged macaws, the scarlet macaw, and three sulphur-crested cockatoos. Birds were fed every day between 9 and 11 a.m. with parrot pellets and fruits. The indoor aviary was

illuminated by several windows. Water was available ad libitum and vitamins (Vita Kombex) were given twice a week. Zoo visitors could enter the outdoor aviary and feed the animals with zwieback. The macaws and the cockatoos from this aviary were not acoustically isolated, but they could not see each other during the experiment because one species (green-winged macaws or sulphur-crested cockatoos) was always tested in the indoor aviary. The scarlet macaw did not participate in any test.

All subjects of every species could be individually recognized at all times during the experimental sessions. With exception of two spectacled parrotlets, none of the subjects were familiar with object-pulling tasks prior to the experiments and did not have any experience in handling with artificial toys.

Experimental design

All strings were nailed to the underside of a horizontal perch in the aviary. Strings were made of nylon and were approximately twice as long as the body size of the species to be tested (25 cm long for spectacled parrotlets, 40 cm for the rainbow lorikeets, 90 cm for the green-winged macaws, and 80 cm for the sulphur-crested cockatoos). In the various tests, we used strings that differed in colour, length, and spatial relationships (Fig. 1). To cross the strings, we used thin wire attached to lateral walls or poles.

Testing procedure

The birds were given their regular variety of seeds on the testing days, but they were deprived of their preferred fruits and vegetables on those days. Water was available ad libitum. To keep birds motivated, we used highly favoured food rewards which were normally not available outside the experimental context: we used pieces of figs and kiwis for spectacled parrotlets, whole grapes and dates for rainbow lorikeets, and half peanuts for macaws and cockatoos. To reduce any potential neophobic reaction towards the strings, 2 days prior to the beginning of the experiments small pieces of string (<5 cm) were left hanging on the

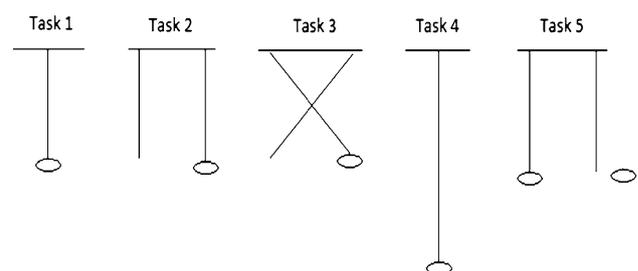


Fig. 1 Diagrams showing the single string in test 1 and 4 and the spatial relationships between the two strings in tests 2, 3ab, and 5

lateral wire walls of the aviaries. The birds had access to the string, but could not pull it or remove it from the wire.

For tests 1 and 2, all animals were tested jointly in their groups, thus a potential influence of social learning cannot be excluded. These two tasks were presented to control (1) for the ability to deal with the string and (2) to do so to obtain a food reward. In the tests 3–5 (tasks which should test whether the birds really understand the cause–effect relationship between string and reward), all birds that showed interest in the previous two tasks were tested individually in a visually isolated corner of the aviary or, in the case of the spectacled parrotlets, in a wooden box with one open side orientated towards the observer in the aviary.

We conducted two sessions per day, one in the morning (from 10 a.m.) and one in the afternoon (from 3 p.m.). In all experimental tests, subjects were presented with five sessions with five trials per session. Tests were presented in the same order for all species. To ensure that the bird's performance was not based on local enhancement, that is, choosing the string that had been manipulated last or that had moved last, we always manipulated both strings. Trials ended when a subject reached the free end of the string (regardless of whether it had the reward attached to it or not), or after a pre-determined maximum of 5 min, whichever came first.

In all choice tasks, the colours and sides associated with the reward attached to the string were alternated randomly across trials. The distance between the strings was twice the body length of the target species. The string that every bird first interacted with was scored as its choice in every trial. The choice was scored as 'correct' if the subject started with a pulling action at the rewarded string and reached the end of the string. All tests were video recorded for subsequent analysis of the birds' behaviour.

String-pulling tasks

Test 1 (single-string task)

This task tested the parrots' ability to pull up a baited reward suspended from a horizontal perch by a single string.

Test 2 (goal-directedness)

Two strings, one with the reward attached as before and one with no reward, were simultaneously presented to the birds to test whether the presence of a reward attached to the end of the string influenced the parrots' pulling behaviour. Pulling up the string with the reward more frequently would indicate that, even if string-pulling behaviour was self-rewarding, the subject could recognize the string as a means to obtain the reward.

Test 3ab (crossed-string task)

To assess whether the parrots' choice was based on the spatial or the functional relationship between string and reward, we crossed the strings. If their choice is based on the functional connection between food and string, they should pull the rewarded string. If the choice is based on the spatial relationship only, they should pull the string directly above the reward as in the trials before. We conducted five sessions with differently coloured strings (green and white; task 3a), so the birds could trace the strings from one end to the other end more easily, and 5 sessions with same-coloured strings (task 3b), where the birds did not have this support.

Test 4 (over-length-string task)

This task tested the flexibility of problem-solving in parrots as in this task the string was longer, enabling the birds to reach the reward from another perch or from the ground. To ensure that the decision to approach the string from below or above was not influenced by different starting positions of the individuals, all subjects had to start the trial from a branch above the branch to which the string had been attached.

Test 5 (broken-string task)

This task tested the ability to visually determine whether or not objects are physically connected. The birds were required to understand that the reward has to be connected to the string in order to work properly. The distance between the string and the unconnected reward placed on a wire (attached to the lateral walls of the box or to the poles) was 5 cm.

Analysis

For all individuals, we calculated the mean number of correct choices for every session. To compare among the species, we tested these individual mean values with the Kolmogorov–Smirnov procedure to test for deviation from a normal distribution. As all data were normal in distribution, we used one-way ANOVA to test whether the performance of the species in tasks 1, 2, 3a, 3b, 4, and 5 differed significantly. The Tukey test was used to identify groups that differed significantly from others. To test whether the members of a species tended to choose the correct string more often than by chance, 1-sample *t* tests were used. We also measured the relative efficiency of string-pulling behaviour for each individual and each task, expressing by how much more common effective behaviours (pulls) were than ineffective acts (drops), where relative efficiency = (frequency of effective acts—frequency of ineffective acts)/total number of acts (see also Schuck-Paim et al. 2009).

To assess quantitative differences between species, we calculated for each species the proportion of birds that solved each task on the first trial and rarely made any errors thereafter. We chose as a criterion of “rarely made any errors” achieving at least 18 correct out of a total 25 trials (one-tailed significance at the 0.05 level in a binomial test).

Due to small sample sizes for sulphur-crested cockatoos and for green-winged macaws, we present their data only to demonstrate the general tendency (the t test has only low power for small sample sizes). However, a failure to succeed in the experiment, even of a small number of individuals, but in several species tested with the same task, was interpreted as evidence for limitations in the species’ abilities. Similar results have recently been shown by Liedtke et al. (2011). The sample size was always specified as the number of individuals that participated in the tests. All tests were conducted as two-tailed and alpha was set to 0.05. Data analysis was conducted using the software programs SigmaPlot 11 and SPSS Statistics 17.0.

Results

In the following, we compare the results among species dealing with each task.

Task 1

Figure 2 shows that almost all birds of all species solved the task immediately.

There was significant differences between species in the time required for solving the task (one-way ANOVA, $F = 3.87$; $df = 3$, $P = 0.024$) as well as in the relative efficiency of the string-pulling behaviour (one-way ANOVA, $F = 11.60$, $df = 3$, $P < 0.001$). Here, the spectacled parrotlets (S.p.) were outperformed by the rainbow lorikeets (R.l.), the green-winged macaws (Gw.m.), and the sulphur-crested cockatoos (Sc.c.), that is, the spectacled parrotlets showed more ineffective acts in their performance (Tukey test, S.p. vs. R.l.: $P < 0.001$, S.p. vs. Gw.m.: $P = 0.002$, S.p. vs. Sc.c.: $P = 0.003$). Combining the results of all individuals for each species, there was a significant difference in solving time between the first and the second session for rainbow lorikeets, and for green-winged macaws between the first and the last session (Fig. 3a). There was no evidence for any session-to-session improvement in the relative efficiency of string-pulling behaviour (Fig. 3b).

Task 2

In all species, over 75 % of the birds solved the task at their first trial and rarely made any errors thereafter (Fig. 2). All

birds showed string-pulling behaviour that was clearly directed towards obtaining the reward, as the subjects clearly preferred the rewarded string (1-sample t test; S.p.: $t = 3.50$, $df = 7$, $P = 0.01$; R.l.: $t = 26.67$, $df = 9$, $P < 0.001$; Gw.m.: $t = 13.94$, $df = 3$, $P = 0.001$; Sc.c.: $t = 16.45$, $df = 2$, $P = 0.004$). All choices were made without probing the strings first. There was no significant difference in the proportion of correct choices across species (one-way ANOVA, $F = 1.14$, $df = 3$, $P = 0.36$). There was no evidence for any improvement in performance between the first and the second session or between the first and the last session (Fig. 4).

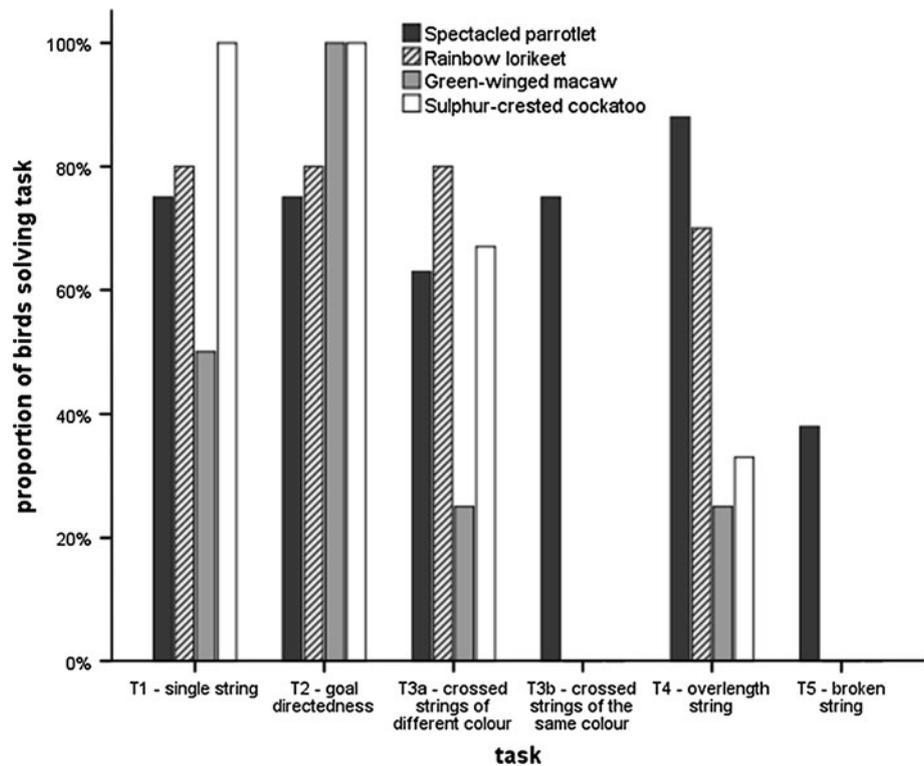
Task 3a–b

Figure 2 shows that in almost all species, over 60 % of the birds solved the task 3a right first time and rarely made any errors thereafter. However, in green-winged macaws only one individual met this criterion. Subjects of all species performed significantly better than by chance (1-sample t test; S.p.: $t = 17.83$, $df = 7$, $P < 0.001$; R.l.: $t = 14.68$, $df = 9$, $P < 0.001$; Gw.m.: $t = 17.32$, $df = 3$, $P < 0.001$; Sc.c.: $t = 9.53$, $df = 2$, $P = 0.011$). There were significant differences in the proportions of correct choices between species (one-way ANOVA, $F = 9.94$; $df = 3$, $P < 0.001$). Thus, all species could distinguish the strings of different colours and chose the correct string, but spectacled parrotlets and rainbow lorikeets did so significantly more often than the green-winged macaws and sulphur-crested cockatoos (Tukey test, S.p. vs. Gw.m.: $P = 0.002$, S.p. vs. Sc.c.: $P = 0.011$, R.l. vs. Gw.m.: $P = 0.003$, R.l. vs. Sc.c.: $P = 0.023$). Examining the results of all individuals for each species, only green-winged macaws showed differences between their first and their last session, but not between the first and the second session (Fig. 5a).

In task 3b, only members (75 %) of the spectacled parrotlets met the criterion (Fig. 2). Moreover, only the spectacled parrotlets chose the correct string at level better than chance (1-sample t test: $t = 8.85$, $df = 7$, $P < 0.001$). Green-winged macaws’ and sulphur-crested cockatoos’ probability of being correct was about chance. Interestingly, the rainbow lorikeets showed a preference for the incorrect string (1-sample t test: $t = -9.52$, $df = 9$, $P < 0.001$).

There was considerable variation in the proportion of correct choices among species (one-way ANOVA, $F = 40.89$; $df = 3$, $P < 0.001$). Spectacled parrotlets chose the correct string more often than all other species (Tukey test, S.p. vs. R.l.: $P < 0.001$, S.p. vs. Gw.m.: $P < 0.001$, S.p. vs. Sc.c.: $P = 0.003$) and the sulphur-crested cockatoos chose the correct string more often than the rainbow lorikeets (Tukey test, R.l. vs. Sc.c.: $P = 0.003$). There was no evidence for an improvement in

Fig. 2 Proportion of the birds of each species that solved the tasks at first trial and rarely made any errors thereafter. The criterion “rarely made any errors” relates to at least 18 correct choices (the number of correct choices that are 1-tailed significant at the 0.05 level with 25 trials in total)



performance, neither between the first and the second session nor between the first and the last session (Fig. 5b).

Task 4

Figure 2 shows that in task 4 several members of all species tested were able to adapt their problem-solving strategy by stopping string-pulling behaviour at their first trial and rarely changed this strategy thereafter. However, taking the group as the whole, only spectacled parrotlets and rainbow lorikeets clearly preferred the adaptive strategy (1-sample *t* test; S.p.: $t = 6.61$, $df = 7$, $P < 0.001$; R.l.: $t = 3.19$, $df = 9$, $P = 0.011$). There was significant variation among species in the proportion of strategies used (one-way ANOVA, $F = 8.65$, $df = 3$, $P = 0.001$). The spectacled parrotlets and the rainbow lorikeets obtained the reward from another perch or from the ground more frequently than the green-winged macaws and the sulphur-crested cockatoos (Tukey test, S.p. vs. Gw.m.: $P = 0.003$, S.p. vs. Sc.c.: $P = 0.002$, R.l. vs. Gw.m.: $P = 0.095$, R.l. vs. Sc.c.: $P = 0.039$). There was no evidence for any session-to-session improvement in performance (Fig. 6).

Task 5

In task 5, only members (38 %) of the spectacled parrotlets group met the criterion (Fig. 2).

The performance of these subjects was better than chance (1-sample *t* test: $t = 9.23$, $df = 7$, $P < 0.001$). In contrary, the performance of the sulphur-crested cockatoos was around chance. Interestingly, the rainbow lorikeets and the green-winged macaws preferred the incorrect string (1-sample *t* test: $t = -5.25$, $df = 9$, $P = 0.001$ and $t = -6.76$, $df = 3$, $P = 0.007$). Considerable variation in the proportion of correct choices was found among species (one-way ANOVA, $F = 36.46$; $df = 3$, $P < 0.001$). Spectacled parrotlets chose the correct string more often than all other species (Tukey test, S.p. vs. R.l.: $P < 0.001$, S.p. vs. Gw.m.: $P < 0.001$, S.p. vs. Sc.c.: $P = 0.001$), and the sulphur-crested cockatoos chose the correct string more often than the green-winged macaws (Tukey test, Sc.c. vs. Gw.m.: $P = 0.006$). No species showed evidence for changes in performance between the first and the second session or between the first and the last session (Fig. 7).

Overall, the spectacled parrotlets outperformed the green-winged macaws and the sulphur-crested cockatoos in four tasks (T3a, T3b, T4, and T5) and the rainbow lorikeets in two tasks (T3b and T5). The rainbow lorikeets outperformed the macaws and cockatoos in two tasks (T3a and T4). The sulphur-crested cockatoos in turn outperformed the rainbow lorikeets in task T3b as well as the green-winged macaws in task T5. However, here, we should differentiate between quantitative and qualitative differences. For instance, all species showed the ability to choose the rewarded string in task 2, but some species did so more

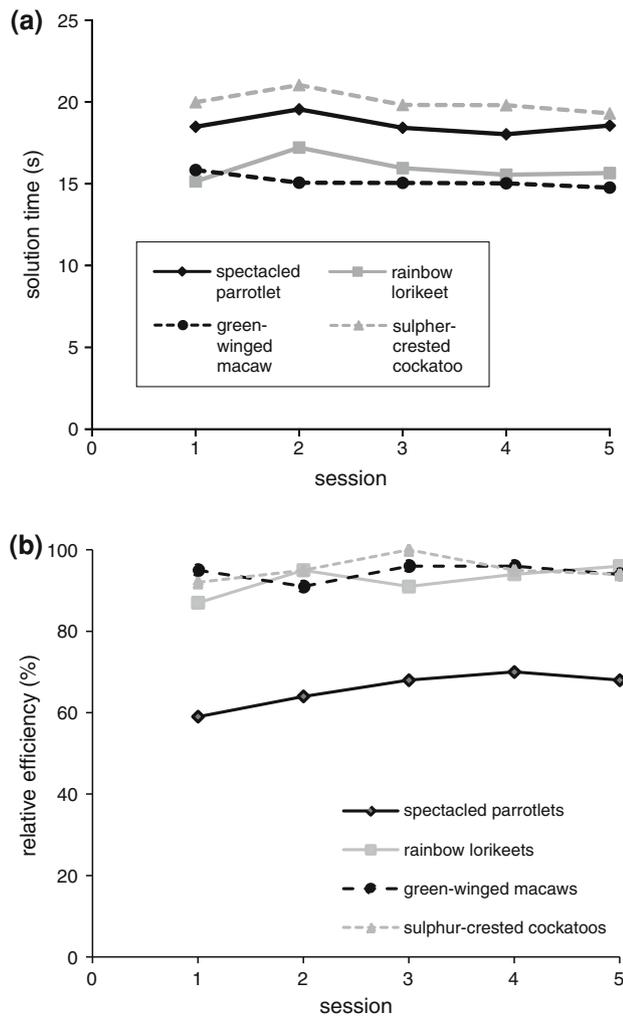


Fig. 3 **a** Performance in task 1 regarding the solution time among sessions and across species. **b** Performance in task 1 regarding the relative efficiency of string-pulling behaviour among sessions and across species

frequently than others (quantitative differences), which does not indicate a general lack of ability, however. In contrast, in task 3b and 5, only spectacled parrotlets could identify the correct string, thus outperforming the other three species (qualitative differences).

Discussion

Spontaneous string-pulling behaviour occurred in all four parrot species tested, but their performance in string-choice tasks varied. Furthermore, this study documents for the first time the ability to solve the crossed strings task spontaneously. Contrary to findings with keas (Werdenich and Huber 2006), the spectacled parrotlets performed constantly well in the task with two crossed strings of the same colour (T3b) and did not require time to adjust to the task.

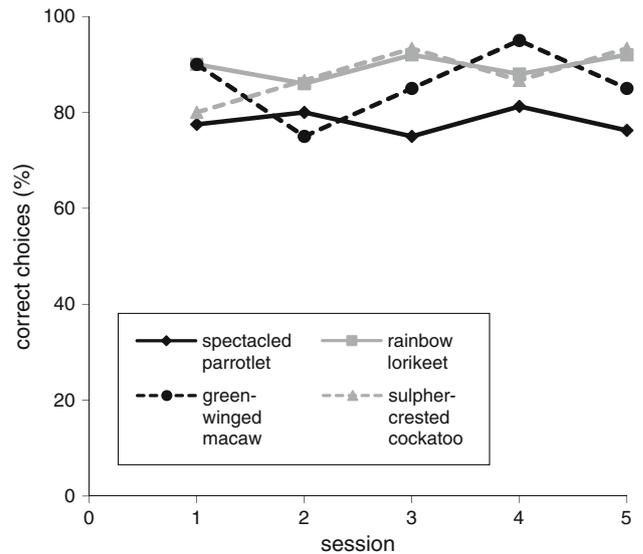


Fig. 4 Proportion of correct choices in task 2 among sessions and across species

Considering the pairwise comparisons between species, our results did not show any crucial impact of the predominant feeding mode on problem-solving skills involved in string-pulling. There were large differences among the performances of species with a similar feeding mode (lorikeets and macaws feeding mostly in the trees vs. parrotlets and cockatoos feeding mostly on the ground) as the lorikeets outperformed the macaws quantitatively in 2 tasks and parrotlets outperformed cockatoos in 4 tasks (2 qualitatively, 4 quantitatively). Furthermore, diet also did not correlate with the string-pulling performance. Contrary to the prediction that no or few similarities should occur among all species tested whether diet-influenced success in various string-pulling tasks in parrots, the performance of the lorikeets, macaws, and cockatoos was qualitatively similar. However, to test whether diet is not a variable that could potentially drive the success in string-pulling tasks comparisons involving a wider range of species are needed.

Furthermore, no evidence for phylogenetic patterns was found, as there were similarities in performance between members of superfamilies *Cacatuoidea* and *Psittacoidea* (cockatoos and macaws) while there were the strongest differences between members of the same tribe, *Arini* (parrotlets and macaws).

Therefore, the questions remain: Why did the parrotlets performed better than the other three species? And why did the lorikeets outperform (even if only quantitatively) macaws and cockatoos? One possible explanation may be that the social complexity of the tested parrot species has an influence on their general cognitive skills which facilitate solving the presented tasks. The species with complex fission–fusion organization (i.e. spectacled parrotlets)

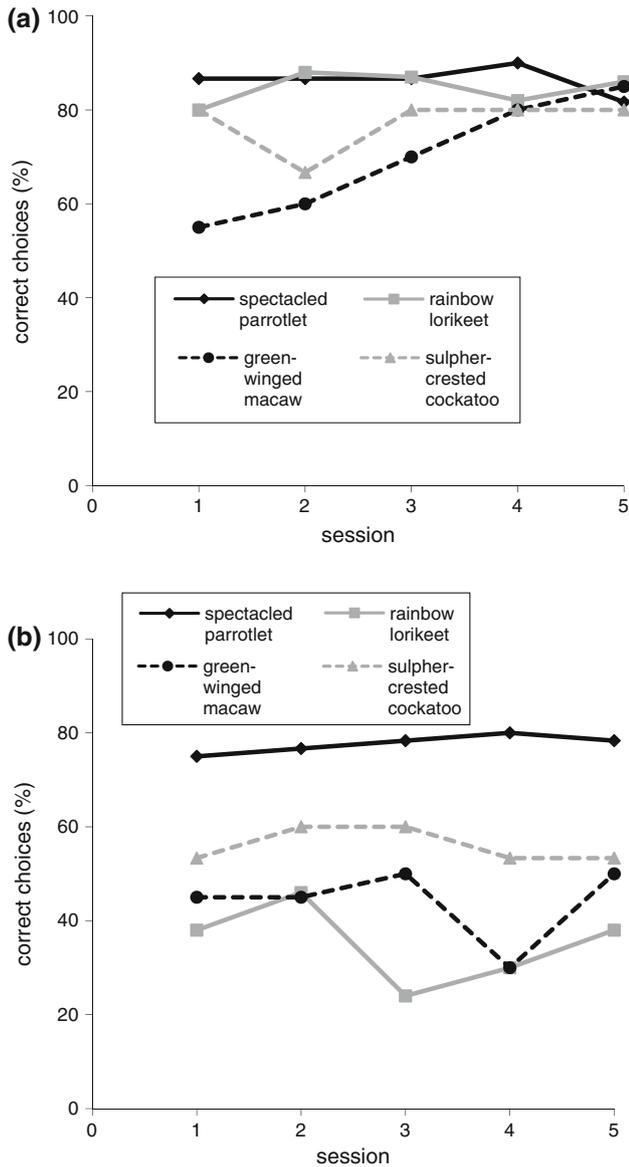


Fig. 5 **a** Proportion of correct choices in task 3a among sessions and across species. **b** Proportion of correct choices in task 3b among sessions and across species

performed best among the four species, whereas species living in fairly stable family groups (macaws and cockatoos) failed in two crucial tasks. This finding appears to be consistent with the assumption that more complex lifestyles (i.e. social structure) require more complex cognition in general (Lefebvre and Sol 2008). The performance of the rainbow lorikeets, which were outperformed by the parrotlets in two tasks, but outperformed in turn the macaws and the cockatoos, can be placed somewhere in the middle, just as their social organization can. Thus, our findings can be explained by the variation in social complexity among species, rather than by diversity in their ecology. The hypothesis that the cognitive abilities of the

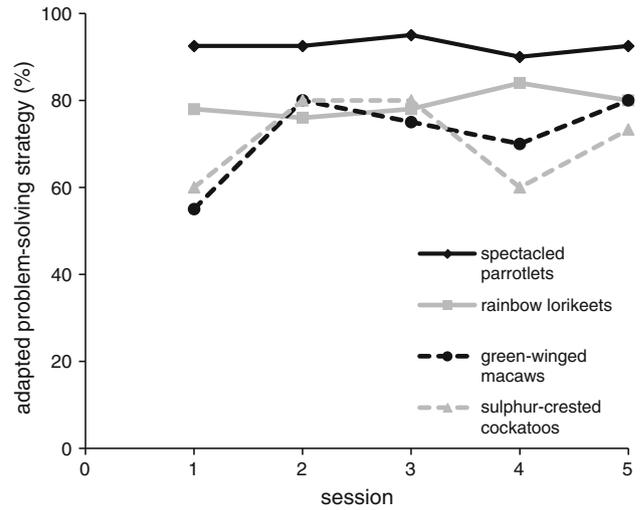


Fig. 6 Proportion of using the adapted problem-solving strategy in task 4 among sessions and across species

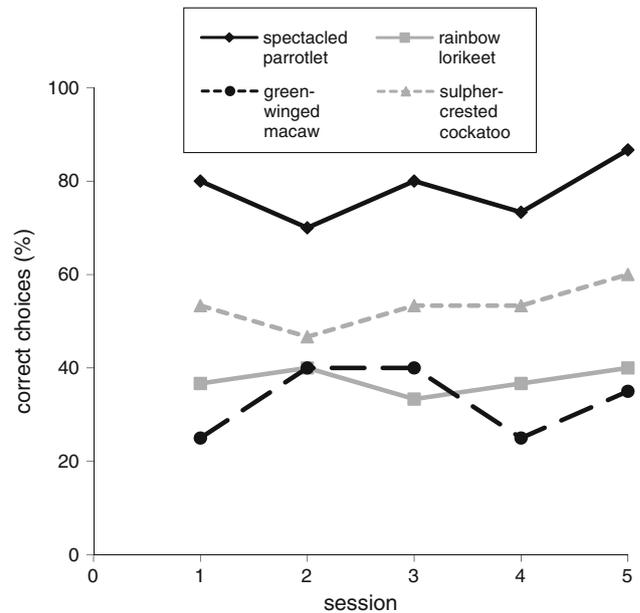


Fig. 7 Proportion of correct choices in task 5 among sessions and across species

four study species are solely determined by their social organization will need to be studied by examining the string-pulling performance of many more species, but the pattern of the present data is consistent with this possibility.

The variation in performances found could also be explained by variation in associative learning speed, so that some of the species tested may react quicker to negative outcomes than others and thus do better at some of the tasks they initially failed at. This is unlikely, however, because only the macaws improved their performance (in T3a) significantly across trials. Most of the

birds tested showed a constant performance over time. The subjects either solved the task at hand in their first attempt and continued to do so in later trials, or they failed and did not improve their performance significantly (taking the testing group as the whole) until the end of the experiment. However, different group sizes may lead to different possibilities for social learning and thus, quantitative differences between the species in task 1 and task 2 may be caused by different possibilities for social learning.

Recently Taylor et al. (2010) raised the possibility that even spontaneous string-pulling in New Caledonian Crows may be based on operant conditioning rather than on insight. In this study, we did not focus on the possibility of reinforcement of the string-pulling behaviour or on the question what are actual cognitive mechanisms underpinning spontaneous string-pulling, although the overall performance observed in this study and the manner of solving tasks argue for insight-based behaviour similar to findings in corvids and other parrots. However, even if string-pulling might be based on operant conditioning, the variation found could also be explained by differences in socio-ecological requirements faced by a species, because “birds with larger associative brain areas are able to integrate information between perceptual and motor pathways quicker than birds with smaller associative brain areas” (Taylor et al. 2010) and larger brains are linked to more complex lifestyles.

Finally, further comparative research using a variety of standardized paradigms across a wider range of species is needed to test alternative hypotheses about the origin of specific differences found and to understand how the degree of social complexity may affect the cognitive performance even in non-social contexts.

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